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# Influence of environmental conditions on the distribution of burrows of the mud crab, *Scylla serrata*, in a fringing mangrove ecosystem

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20 **Abstract**

21 Mud crab, *Scylla serrata*, is a common mangrove species in the Indian Ocean. Over the last  
22 decades, fishing pressure has greatly increased especially in Madagascar. Therefore,  
23 improving the knowledge of mud crab biology and ecology is crucial to guide conservation  
24 and restoration plans. This study aimed at describing the distribution of burrows of the mud  
25 crab in a mangrove in southwestern Madagascar. Burrows fulfill an essential functional role  
26 by limiting the exposure of crab to environmental stress, such as desiccation during low tide,  
27 and predation. A total of 140 burrows were observed and available conditions were described  
28 at 168 random sampling points at low tide in three different mangrove zones, during the dry  
29 season (July 2014). Twelve environmental factors were recorded to reflect the position within  
30 the mangrove, the substrate composition and the surrounding floristic structure. A  
31 multivariate ordination analysis highlighted an overall association between burrows and  
32 specific habitat conditions. Boosted regression trees then indicated that the burrows  
33 distribution was predominantly explained by the avoidance of hard substrates. The  
34 occurrence of burrows was positively related to the upper intertidal zone of the mangrove  
35 where the water level was below 100 cm. Although the tree density had a positive effect, the  
36 occurrence of burrows was higher for low percentage of shade (<40%). These results provide  
37 insight for identifying mangrove areas that have an essential functional role for the  
38 conservation of mud crab populations.

39 Key words: mangrove crab, crustacean, habitat conditions, substratum composition, floristic  
40 structure

41

## 42 **1. Introduction**

43 Crabs populations are widespread throughout the mangroves and intertidal zones in tropical  
44 and subtropical regions (Brown, 1993). Over the last decades, the growing interest for some  
45 species of this resource has led to the development of commercial fisheries (e.g. Bonine et al.,  
46 2008 ; Dumas et al., 2012) and farms (Mirera et al., 2014) throughout the Indo-Pacific region.  
47 In addition, crabs play a key role in the food chain (Wolff et al., 2000), the plant cycle  
48 (Schories et al., 2003), and in the bioturbation of sediment (Smith et al., 1991; Kristensen,  
49 2008). However, the combined effect of overfishing and expanding degradation of mangrove  
50 ecosystem can affect the sustainability of local crab populations (Le Vay et al., 2008; Cheung  
51 et al., 2010; Mirera et al., 2013). Recently, the environmental authorities of the West-Indian  
52 Ocean have developed conservation programs focused on the restoration of mangrove  
53 ecosystems and regulation of crabs' fisheries to ensure the resource sustainability (e.g. Mirera  
54 et al. 2017a). In this context, improving knowledge of crabs' ecology is essential to better  
55 understand population dynamics and, in turn, to efficiently guide restoration and  
56 preservation plans.

57 Burrows play a pivotal role in ecology and population dynamic of many crabs. Burrowing into  
58 the mud reduces the risk of predation during critical stages of their life cycle such as resting,  
59 molting and mating (e.g. Warren, 1990; Chan et al., 2006; Mirera 2017b). Burrows are also  
60 used to store food and water at low tide (Dittmann, 1996). This crucial role suggests that  
61 burrows are not randomly distributed in different mangrove habitats. For instance, the crabs  
62 need to return periodically to their burrows, which probably limits the distance crabs can  
63 move for foraging activity. Therefore, food availability should play an important role in  
64 selecting the burrowing location (Hill, 1978). Several studies demonstrated that the

65 distribution of crab and burrows is influenced by environmental factors, operating at various  
66 spatio-temporal scales (Icely and Jones, 1978; Jones and Simons, 1981; Piou et al., 2009). For  
67 example, different studies have associated burrow locations to sediment composition  
68 (Frusher et al., 1994; Ribeiro et al., 2005; Pandya and Vachhrajani, 2010), soil complexity  
69 (Ringold, 1979; Capehart and Hackney, 1989; Wang et al., 2014), and mangrove vegetation  
70 structure (Koch et al., 2005; Li et al., 2015).

71 The mud crab, *Scylla serrata*, is a widespread species in estuarine and mangrove habitats in  
72 the Indo-Pacific region (Le Vay, 2001). *Scylla serrata* juveniles and adults are observed in a  
73 wide range of environmental conditions (Hill, 1978; Hyland et al., 1984). Hill et al. (1982)  
74 demonstrated that juveniles (2.0-9.9 cm in carapace width) of *S. serrata* are resident in  
75 mangrove forests, whereas sub-adults (10.0–14.9 cm) and adults (>15.0 cm) mostly move  
76 with the tide between the intertidal and subtidal mud flats fringing the mangrove forest.  
77 However, sub-adults and adults also commonly occupy permanent burrows in intertidal areas  
78 of the mangrove forests (Le Reste et al. 1976; Brown 1993; Ewel et al. 2009). While it is still  
79 unclear why distinct behaviors (i.e. moving with the tide or burrowing) are reported in mud  
80 crab (Alberts-Hubatsch et al., 2016), the use of burrow can contribute to improve survival  
81 during vulnerable periods of environmental stress (e.g. low tide period) by providing water  
82 reserve and refuge from predators (Warren, 1990; Thongtham and Kristensen, 2003). In  
83 Madagascar, *S. serrata* is an important economic resource for local communities (Lebigre,  
84 1987) who traditionally catch them in their burrows during low tide, consequently they have  
85 been under increasing fishing pressure for the last decades (Fondo et al., 2010). While the  
86 biology and ecology of mud crabs have already been well studied (Alberts-Hubatsch et al.,  
87 2016), little is known about the factors influencing the distribution of populations along  
88 environmental gradients (Dumas et al., 2012).

89 The present study aimed at describing the environmental factors influencing the burrows  
90 distribution of *S. serrata* in a mangrove ecosystem in southwestern Madagascar, on the basis  
91 of a set of 12 environmental variables, reflecting the local conditions, floristic structure and  
92 sediment composition.

## 93 **2. Materials and Methods**

### 94 *2.1. Study site*

95 The studied mangrove ecosystem was close to the village of Belo-sur-Mer, southwestern  
96 Madagascar (Fig. 1a-b). The fringing mangrove forest extends over 2400 hectares and is  
97 predominantly subjected to marine influence (Chartier and Henry, 1997). Crabs, mainly *S.*  
98 *serrata*, are heavily fished in this ecosystem, especially in the closest zone to the village of  
99 Belo-Sur-Mer. The study was conducted during the dry season (July 2014) in three different  
100 zones of approximately 19 ha each (Fig. 1c). They were selected to cover a wide range of  
101 habitat conditions: zones #1 and #2 are small bays protected from the waves and wind with a  
102 dominant clay-sand substrate, whereas zone #3 is more expose to wind and waves with a  
103 dominant sand substrate.

### 104 *2.2. Sampling procedure*

105 Habitat conditions were described at low tide along transects across mangrove zones from  
106 the 24 of July 2014 to the 31 of July 2014. Transects extended from the main channel to the  
107 mangrove forest edge (upper tidal limit), or from the forest edge to the channel. The distance  
108 between two successive transects was approximately 100 m (mean = 115 m, SD= 75 m) and  
109 was chosen to capture a large range of available habitat conditions. The transect lengths

110 ranged between 75 and 300 m, depending on the distances separating the channel from the  
111 mangrove forest edge.

112 Two complementary sampling procedures were conducted to compare the available  
113 environmental conditions in the mangrove with those used by *S. serrata* for burrowing (Fig.  
114 2). In this approach, a difference between the two sets of conditions indicates that burrows  
115 were not uniformly distributed in mangrove because of species preference for environmental  
116 factors. For each sampling procedure, a total of eleven, three, and five transects were  
117 prospected in zones #1, #2 and #3 respectively. The first sampling procedure involved a  
118 systematic description of the diversity of habitats (available habitat) in the studied zones. The  
119 habitat conditions were described at 20 meters intervals along each transect. The distance  
120 between two successive points was estimated using a hip chain. The distance of the first point  
121 from transect origin was randomly selected from 1 to 20 m based on random number tables.  
122 In the second sampling procedure, the habitat conditions in proximity of burrows were  
123 described to reflect the habitat used for burrowing. In this procedure, an experienced crab  
124 fisherman followed the transects to detect the presence of *S. serrata* burrows. When he  
125 spotted a burrow, habitat conditions around the burrow were described and the distance  
126 separating the burrow from the transect was recorded. This measure aimed at evaluating the  
127 potential bias in burrow detection by fisherman due to tree cover. When a crab was present  
128 in the burrow, the fisherman tried to catch it during 10 minutes maximum to limit the time  
129 spent at each burrow. The geographic coordinates (latitude and longitude) of each point of  
130 available habitat and each burrow were recorded using a portable GPS (GPSMAP 64s).

### 131 *2.3. Habitat description*

132 Twelve environmental variables were recorded at each point of available habitat and near  
133 each burrow (less than one meter) to provide an accurate description of substratum  
134 composition, hydrological conditions and floristic structure.

### 135 *2.3.1. Substratum composition*

136 Two synthetic variables were used to describe substratum composition: the dominant  
137 substrate class and a maturity index. A minimum 20 cm of substrate was cored less than 1m  
138 from each sampling points. Cores were split in layers of homogenous type and consistency.  
139 The substrate class of each layer was visually classified by an experienced operator, according  
140 to five categories (i.e. clay, silt, organic matter, sand, roots). The dominant substrate class was  
141 defined as the one having the greatest thickness in the first 20 cm of substrate. The maturity  
142 index was estimated according to the soil classification proposed by Pons and Zonneveld  
143 (1965), conventionally used for thiosoils and sulfatosoils. Maturity classes were assigned to  
144 the core layers according to the degree of maturation of the soil: 1- not mature (fluid, soft,  
145 cannot be contained in the hand), 2- little mature (no consistency, very plastic, passes  
146 between fingers), 3- semi-mature (very malleable, plastic, stick to the hand but escapes  
147 between fingers), 4- almost mature (malleable, little plastic, stick to the hand, requires force  
148 to passes between fingers), 5- mature (very consistent, resists to the pressure of the hand).  
149 The maturity index was then estimated by averaging all the maturity classes of the first 20 cm  
150 of substrate weighted by their thickness.

### 151 *2.3.2. Hydrological conditions*

152 The local hydrological conditions were described using two variables reflecting the extent of  
153 flooding conditions at the sampling point. The first one was the mean water level at high tide  
154 (m), which was estimated based on the maximum height where oysters and barnacles were

155 present on the closest tree from the sampling point. The second variable was the relative  
156 distance from the mangrove forest edge. This parameter was calculated by projecting the  
157 geographical coordinates of the sampling points on aerial photography (WGS 84), using GIS  
158 (Quantum GIS Brighton 2014). The relative distance from the edge of the mangrove forest  
159 ( $D_{edgeR}$ ) was then estimated following equation (1):

$$160 \quad (1) \quad D_{edgeR} = \frac{D_{transect}}{D_{tot}}$$

161 where  $D_{transect}$  is the distance (m) between the sampling point and the edge, and  $D_{tot}$  the  
162 distance (m) between the edge and main channel at low tide. The mangrove forest edge (i.e.  
163 tan part usually naked or little vegetated) and channel were detected visually on aerial  
164 photography. The main channel was defined as a continuous zone from the bay where the  
165 substrate was visible (i.e. absence or low vegetal cover). In large areas without vegetation, or  
166 in areas where the channel was not visible from aerial photographs, the limit of the channel  
167 was confirmed during field work.

### 168 *2.3.3. Floristic structure*

169 The floristic variables around the sampling points were described using the Quarter Point  
170 Method (Mitchell, 2010). Space was divided into four quadrants centered on the sampling  
171 point. The first axis of the quadrants was positioned parallel to the transect and the second  
172 axis perpendicularly to the first. In each quadrant, the closest tree from the sampling point  
173 was spotted and five parameters were recorded: distance from the sampling point (m), tree  
174 species, size class (i.e. <2 m, 2 to 5 m, >5 m), radius of basal area (m) and state (i.e. dead or  
175 alive). Distances and radius were measured using a laser meter (Leica DISTO D5). The radius  
176 of the basal area was defined as the distance from the trunk to the edge of its leaves. Trees  
177 were considered dead when no leave was observed. Finally, four synthetic variables reflecting

178 the floristic structure of each point were described: the dominants tree species and size class,  
179 the presence of dead trees among the four trees and the average density of tree. The  
180 dominant species was defined as the most abundant tree species among the four sampled  
181 trees. In case of co-dominance, the dominant species retained was the one showing the  
182 greatest radius of the basal area. The dominant size class was selected following the same  
183 procedure. The mean density of trees ( $D_{tree}$  tree.m<sup>-2</sup>) was estimated using the following  
184 equation adapted from Mitchell (2010) (2):

$$185 \quad (2) \quad D_{tree} = \frac{1}{(\overline{Dist})^2}$$

186 where  $\overline{Dist}$  is the mean distance between the four closest trees and the sampling point.

187 Complementary variables reflecting the local ground structure were also collected. These  
188 variables were recorded within a quadrat of one square meter centered on the sampling  
189 point. The presence of vegetal material (tree and non-woody plant) was recorded. The  
190 percentage of roots (%) was visually estimated by an experienced operator. The dominant  
191 root class was classified according to four categories, i.e. knee, pneumatophore, stilt, buttress  
192 (Tomlinson, 1986). Finally, the shading extent (%) was estimated from photographs taken  
193 toward the sky from the sampling point using a camera (GoPro White Edition). Each picture  
194 was transformed into a binary image (i.e. black and white), the black percentage was  
195 calculated using Image J (Rasband, 2015). This percentage reflects the proportion of space  
196 occupied by vegetal materials (trunk, leafs, roots) between the camera and the sky, and was  
197 thus considered as a proxy of the shade extent.

#### 198 *2.4. Statistical analyses*

199 In a first step, an ordination analysis using the environmental variables was performed to  
200 highlight the overall distribution of burrows within the available habitat conditions. Hill and  
201 Smith (1976) ordination method was preferred to a normed Principal Component Analysis  
202 because of the possibility to consider simultaneously continuous and categorical variables.  
203 The continuous variables were normed and scaled, and then the 12 environmental variables  
204 were simultaneously included in the ordination analysis because of their low degree of  
205 pairwise correlation (Kendall correlation coefficient ranging from 0.03 and 0.48). The  
206 sampling points with missing values were removed from the ordination analysis because the  
207 method could not handle missing data. Then, a permutational multivariate analysis of  
208 variance (permanova; Anderson, 2001) based on 999 permutations was conducted to test  
209 difference in habitat conditions between zones and sampling procedure (available habitat vs.  
210 burrow habitat). A significant difference suggests a non-random distribution of burrows  
211 across the set of environmental factors. Moreover, the interaction between zones and  
212 sampling procedure was also tested to investigate if the habitat conditions used by mud crabs  
213 for building burrows differed between zones.

214 Finally, a Boosted Regression Tree (BRT) analysis was performed to investigate the relative  
215 importance of variables and their partial effects on the distribution of burrows. BRT provides  
216 a flexible approach to model a response variable according to mixed types of predictors:  
217 continuous and categorical. This method is suited to identify relevant predictors from a large  
218 set of candidate variables, does not require previous data transformation, and handles  
219 missing data (Elith et al., 2008). In the present study, a BRT model was fitted with a logit link  
220 function to model the presence of burrows (binary response) using the 12 environmental  
221 variables as independent predictors. The sampling zone was also added as additional  
222 explanatory variable to investigate whether the habitat conditions used by crabs differed

223 between zones. The sampling points describing the available habitat conditions were used to  
224 generate pseudo-absence data (Pearce and Boyce, 2006) that are assumed to represent true  
225 absence ( $p = 0$ ) in the model, whereas the data collected in proximity to the burrows  
226 represented habitat used by crab for burrowing ( $p = 1$ ). A first BRT model was fitted following  
227 the standard procedure proposed by Elith et al. (2008). The learning rate was fixed at 0.005  
228 and the tree complexity (i.e. number of nodes for each tree) was fixed at three as advised for  
229 small size samples (250-500 lines) to combine a minimum of 1 000 trees in the final model.  
230 The optimal number of trees was determined on the basis of AUC criteria (i.e. area under the  
231 ROC curve) following a 10-fold cross-validation procedure (Elith et al., 2008). The relative  
232 importance of environmental variables was evaluated using the measure proposed by  
233 Friedman and Meulman (2003), implemented in the *gbm* package. This measure reflects the  
234 relative influence of each predictor on the response variable. Finally, a simplified model was  
235 built, keeping the variables with relative contribution above 5% only. For these most  
236 influential variables (contribution >5%), partial dependence plots were provided to describe  
237 the effects of environmental variables on the burrow occurrences. This procedure provides a  
238 visualization of the fitted functions in the BRT, by showing the effect of a variable after  
239 accounting for the average effects of all others (Elith et al., 2008). In such plots, a deviation of  
240 fitted function values from 0 indicates a positive effect on occurrence probability (positive  
241 deviation) or avoidance (negative deviation) for the given environmental variable.

242 Statistical analyses were conducted using the R v. 3.3.1 software (R Core Team, 2016)  
243 implemented with the '*ade4*' package (Chessel et al., 2004) for ordination analysis and the  
244 '*gbm*' (Ridgeway and al. 2013) and '*Dismo*' packages (Hijmans and van Etten, 2014) for BRT  
245 analyses.

### 246 3. Results

247 A total of 168 sampling points distributed along the 19 transects were described to reflect the  
248 available habitat conditions (Table 1). No crab burrow was observed within a few meters of  
249 these points. The experienced fisherman observed 140 burrows of *S. serrata* and the habitat  
250 conditions were systematically described in proximity to the burrows (i.e. used habitat). The  
251 rate of burrow occupancy was 55.7%, as suggested by the presence of crab prints reported by  
252 the professional fisherman. However, only 22 crabs were captured because the fisherman  
253 failed to extract several crabs from the burrows. All of them were *S. serrata*, which confirms  
254 that the fisherman correctly identified the burrows and prints of the target species. The  
255 carapace widths ranged between 6.5 and 13.3 cm (mean  $\pm$  sd : 9.5  $\pm$  1.5 cm), indicating that  
256 most of individuals were sub-adults. The 140 burrows were spotted at a distance from the  
257 transect ranging from 0.1 to 11 m. This detection distance was not significantly correlated  
258 with the tree density (Pearson correlation test, cor = -0.05,  $t$  = -0.69,  $n$  = 140, p-value = 0.48),  
259 suggesting that the fisherman's ability to detect burrows was not biased by the density of the  
260 surrounding vegetation. Consequently, all the 140 burrows were considered to characterize  
261 the environmental conditions associated with crab burrows.

#### 262 3.1. Multivariate ordination

263 The multivariate analysis on the set of 12 environmental variables was performed using 287  
264 sampling points (i.e. 152 points of available habitat, and 132 points of burrow habitat) as 21  
265 were removed due to missing data. The two first axes expressed respectively 19.1% and  
266 10.9% of the total inertia (Fig. 3a). The first axis mainly reflected association between floristic  
267 structure and hydrologic variables (Fig. 3b-c). The relative distance from mangrove forest  
268 edge and the water level at high tide were positively correlated to the first axis, whereas the

269 shading extend, tree density, and dominant tree size were negatively related to this axis. The  
270 second axis largely discriminated a gradient of substratum composition, as suggested by the  
271 correlation of this axis with substrate maturity index and dominant substrate class (Fig. 3c).  
272 Overall, the zones #1 and #3 were associated to harder substrate consistency because of the  
273 presence of sand, whereas the zone #2 was featured by clay substrate (Table 1). The zone #3  
274 was associated to presence of *Avicennia* sp., *Sonneratia* sp. and pneumatophores roots, which  
275 were less common in other sites (Fig. 3). A gradient in average tree density was observed  
276 between zones (from 0.37 to 0.70 tree.m<sup>-2</sup>), but the percentage of shade remained  
277 comparable (from 40 to 47% in average, Table 1).

278 The three zones were significantly segregated in the first factorial plan (permanova, n = 287, F  
279 = 13.5, R<sup>2</sup> = 0.08, p-value < 0.001), which confirmed that these areas are featured by different  
280 environmental conditions. Similarly, the habitat conditions used by crab for digging burrows  
281 were significantly segregated from the available conditions (permanova, n = 287, F = 21.7, R<sup>2</sup>  
282 = 0.07, p-value < 0.001). In contrast, the interaction between the zones and the sampling  
283 procedures (available habitat or burrow habitat) was not significant (permanova, n = 287, F =  
284 1.1, R<sup>2</sup> = 0.006, p-value = 0.359), which suggested that the conditions used by crabs for  
285 burrowing did not differed between zones. The projections of available habitat conditions  
286 were widely dispersed in the plan, whereas burrow-habitat conditions were more  
287 concentrated, and often associated with negative values on the first axis and second axis (Fig.  
288 3a). This factorial distribution suggested that burrows were usually detected in shallow areas  
289 near to the mangrove forest edge, where the floristic structure is relatively dense and the  
290 substrate is malleable. The presence of plant materials and roots, especially knee and buttress  
291 roots, within the quadrat was also often associated with burrow-habitat conditions, as well as  
292 small size of tree, and *Ceriops tagal* as the dominant tree species.

293 3.2. BRT analyses

294 The complete model integrating the 12 environmental variables as predictors was fitted with  
295 an optimal number of 1 400 trees and explained 66.4 % of the mean total deviance, as  
296 evaluated by cross-validation. The model showed high capacity of discrimination with an AUC  
297 value of  $0.915 \pm 0.016$ . Five environmental variables showed a relative importance above 5 %.  
298 Substrate maturity index was the most influential factor on burrows distribution (Table 2).  
299 The shading extent, the relative distance from the edge and the water level also contributed  
300 to explain burrows distribution in the mangrove with a relative contribution above 10 %. As  
301 previously suggested by the ordination analysis, the burrows distribution was poorly  
302 influenced by the sampling zone (relative importance  $< 0.01\%$ ; Table 2), which indicated that  
303 the habitat conditions used for burrowing did not differed between zones.

304 The simplified model, including only the most influential variables (contribution above 5 %,  
305 see Table 2), remained well adjusted and showed high discrimination capacities (explained  
306 deviance = 61.7%; AUC =  $0.914 \pm 0.018$ ). The partial response for the substrate maturity index  
307 indicated a clear avoidance of hard substratum for building burrows (Fig. 4a). The values of  
308 fitted function were maximum for a substrate maturity index ranging between 3.0 and 3.7,  
309 and dropped when maturity index was higher than 4.4. The partial response of shading extent  
310 was higher for the lower percentage of shade ( $< 40\%$ ) and gradually decreased with higher  
311 percentage (Fig. 4b). The low water levels ( $< 100$  cm at high tide) positively influenced the  
312 occurrence of burrows, whereas deeper areas did not appear suitable for burrowing (Fig. 4c).  
313 The partial response for the relative distance from the edge gradually decreased from the  
314 mangrove forest edge to the channel (Fig. 4d). Finally, the maximum values of fitted function

315 were observed for a density of tree over 0.5 tree.m<sup>-2</sup>, which indicated an avoidance of non-  
316 treed areas (Fig. 4e).

#### 317 **4. Discussion**

318 Burrows play a determinant role in mud crab ecology by providing refuges from predators  
319 during critical stages such as molting, mating and periods of environmental stress (Warren,  
320 1990; Thongtham and Kristensen, 2003; Mirera 2017b). Habitat conditions around burrows  
321 should thus provide advantageous set of environmental parameters to ensure these  
322 ecological functions, resulting in a non-random distribution of burrows in the mangrove  
323 ecosystem. Our results confirmed this assumption showing that the distribution of *S. serrata*  
324 burrows was significantly influenced by environmental conditions. In this study, the crabs  
325 collected in the intertidal mangrove were essentially sub-adults, because the local size-at-  
326 maturity is 13.8 cm for females and 11.3 for males (Rasoanirina et al. 2015). For these  
327 individuals, the most influential factor was the substratum composition, but hydrologic  
328 conditions and floristic structure also appeared to influence the distribution of burrows.

329 For most benthic species, such as crabs, soil sediment proprieties are determinant in habitat  
330 choice (e.g. Ewa-Oboho, 1993; Mokhtari et al., 2015; Checon and Costa, 2017). The  
331 substratum composition can affect the density of crabs' burrows (Li et al. 2015) because soil  
332 consistency impacts the ability of crabs to dig and maintain the structure of burrows (Frusher  
333 et al., 1994; Ribeiro et al., 2005; Mokhtari et al., 2015). Our results demonstrated that  
334 substrate consistency (i.e. maturity index) was the most influential parameter for explaining  
335 the spatial distribution of *S. serrata* burrows. The occurrence of burrows was maximum for  
336 intermediate levels of substrate consistency but showed a sharp decrease for higher levels of  
337 consistency (i.e. maturity index > 4.4), reflecting a clear avoidance of hard substrate for

338 burrowing. Similarly, Bertness and Miller (1984) showed that hard substratum can limit the  
339 burrowing ability of *Uca pugnax* in salt marshes along the coast of North America. However,  
340 the presence of hard structural elements is required to ensure the stability of burrows, when  
341 flooded during high tide, and to limit the maintenance costs. In another mangrove ecosystem  
342 in Madagascar, Le Reste et al. (1976) only observed *S. serrata* burrows where the mud was  
343 sufficiently compact. Our results also support this observation because the occurrence of  
344 burrows decreased in areas with low substratum consistency (i.e. maturity index < 3.0). While  
345 a soft substratum makes burrowing easier for crabs, an overly fluid consistency is unlikely to  
346 protect the burrows from collapsing with tidal currents.

347 In mangrove forests, the shade produced by the vegetation may limit the evaporation rate  
348 and regulate the temperature regime, which in turn can influence the habitat conditions for  
349 crabs (Nobbs, 2003). In the upper intertidal areas that are only immersed during limited  
350 periods of time, the canopy cover can play an important role in the regulation of soil  
351 temperature (Nobbs and Blamires, 2015). Surprisingly, our results revealed positive influence  
352 from low to middle shading rates with a threshold occurring at about 40%. This result is in  
353 accordance with findings of Trivedi et al. (2012) who reported a more widespread distribution  
354 of *S. serrata* in open mudflat habitats compared to others brachyuran crab species. High  
355 levels of canopy cover has also been demonstrated to be associated with lower density of  
356 several crab species burrows in Luoyangjiang Estuary (China) and was explained by change in  
357 light intensity and availability of shade, which may control the activity pattern of crabs  
358 (Nobbs, 2003; Li et al., 2015). Therefore, despite a positive influence of tree density, low  
359 levels of canopy cover appeared more suitable for the mud crabs. In contrast, the floristic  
360 composition was not identified as a major factor influencing the distribution of burrows. The  
361 tree species and their size, as well as the kind of roots, did not affected the occurrence of

362 burrow in the studied area, underlining the poor selectivity of mud crabs for these  
363 parameters. Nevertheless, the tree assemblages can influence the soil structure and  
364 consistency (e.g. Krauss et al. 2014), which are keys components for burrowing.

365 At low tide, intertidal areas are commonly occupied by juveniles and sub-adults that are  
366 found under mangrove leaves or in shallow burrows (Mirera 2017b), whereas larger crabs  
367 tend to live in sub-tidal and offshore areas (Walton et al. 2006). The burrows depicted in the  
368 present study were essentially those of sub-adults (carapace widths between 6.5 and 13.3  
369 cm), which can use the intertidal-flat boundary-zone for molting (Mirera 2017b). Our results  
370 demonstrated that the occurrence of burrows was higher in shallow areas located close to  
371 the mangrove forest edge. The suitability of the shallow upper intertidal areas may be  
372 explained by the reduced hydraulics forces in these areas. Indeed, Kabashi and Mazda (2005)  
373 and Mullarney et al. (2017) demonstrated that the water velocities observed in mangrove  
374 forests during tides flows decreased when the distance from the main channel increased. As  
375 high flow velocities are more likely to damage the burrows structures, their positions in areas  
376 with low flow velocities (i.e. closer to the mangrove forest edge) may help limiting the  
377 damage caused by tidal flow.

## 378 **5. Conclusion**

379 In summary, our results indicated that the distribution of *S. serrata* burrows in the mangrove  
380 was more related to substratum and shade extend than to the vegetation composition. Such a  
381 result confirms the importance of mudflats and other soft substratum areas located in the  
382 upper mangrove areas for the mud crab settlement. Conservation plans to mitigate the  
383 depletion and fragmentation of mangrove forest due to human activities (e.g. coastline  
384 reshaping, dikes and dam construction) or the alteration of environmental quality (e.g.

385 pollution) should thus primary focus on these critical habitats for mud crabs populations.  
386 Nevertheless, physicochemical conditions, such as salinity, were not considered in this study,  
387 but may significantly influence the inter-seasonal variability in mud crab burrows' distribution.  
388 As our study was conducted during the dry season, further studies investigating how the  
389 influence of environmental factors on mud crabs burrows distribution varies among season  
390 are needed to complement our findings.

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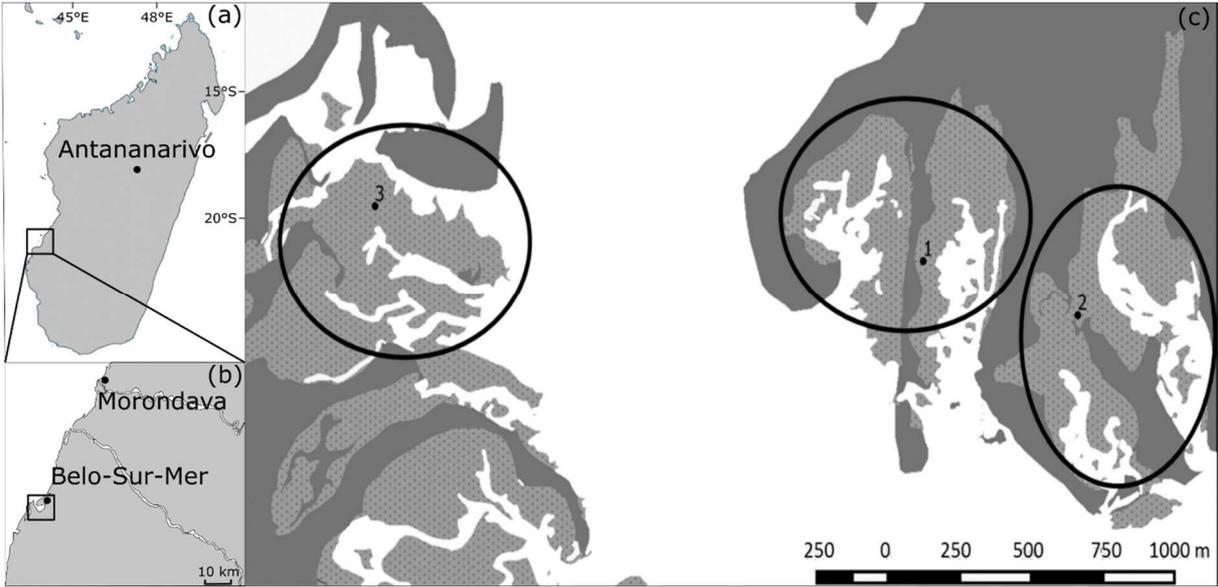
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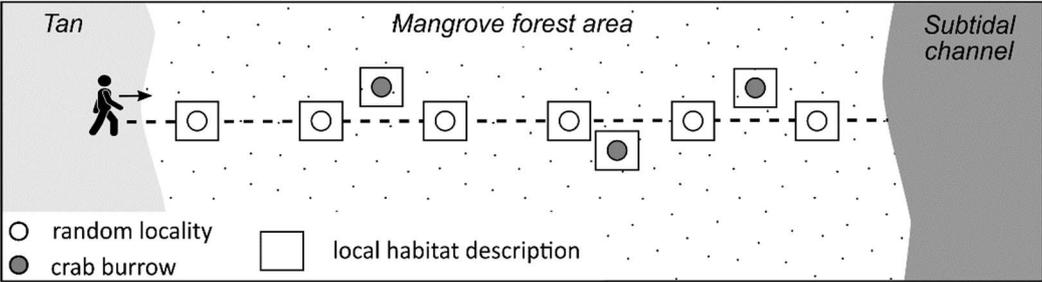
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Figure 1



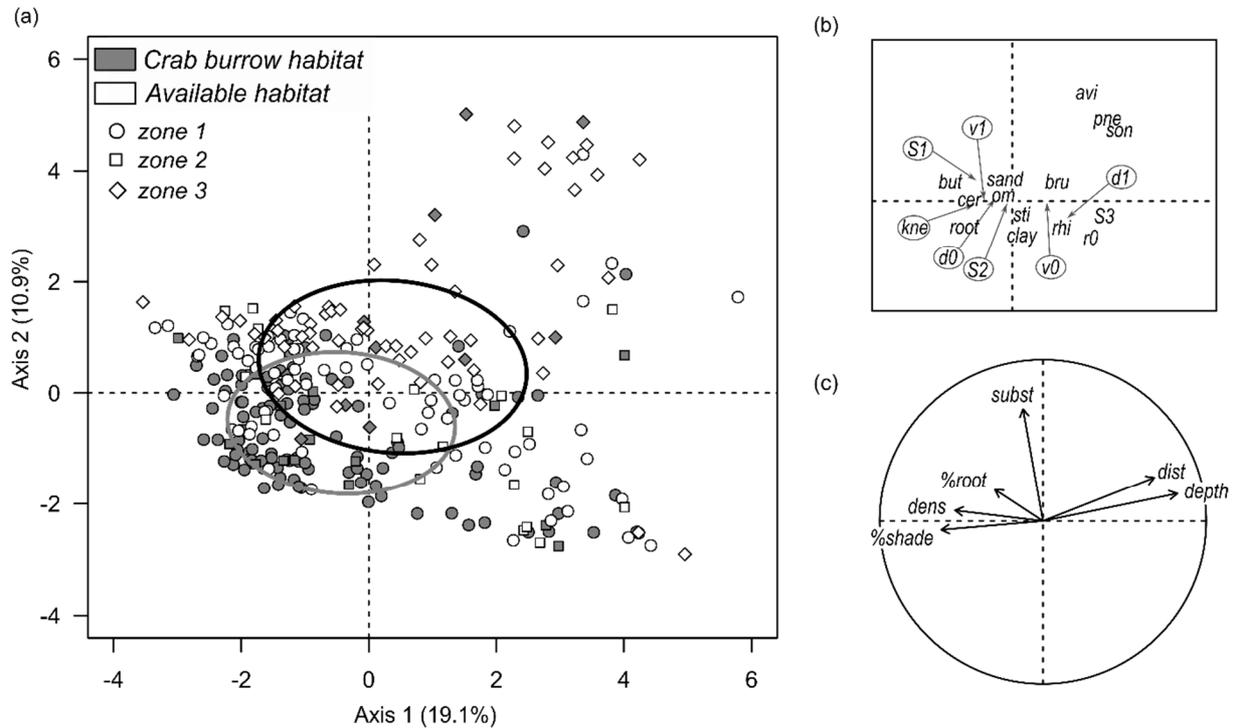
**Figure 1:** Location of the study area, near the village of Belo-sur-Mer (b), Southwestern Madagascar, Western Indian Ocean (a), and the three mangrove zones prospected for investigating burrow distribution of mud crab, *Scylla serrata* (c). The gray dotted shapes represent the mangrove forest areas.

Figure 2



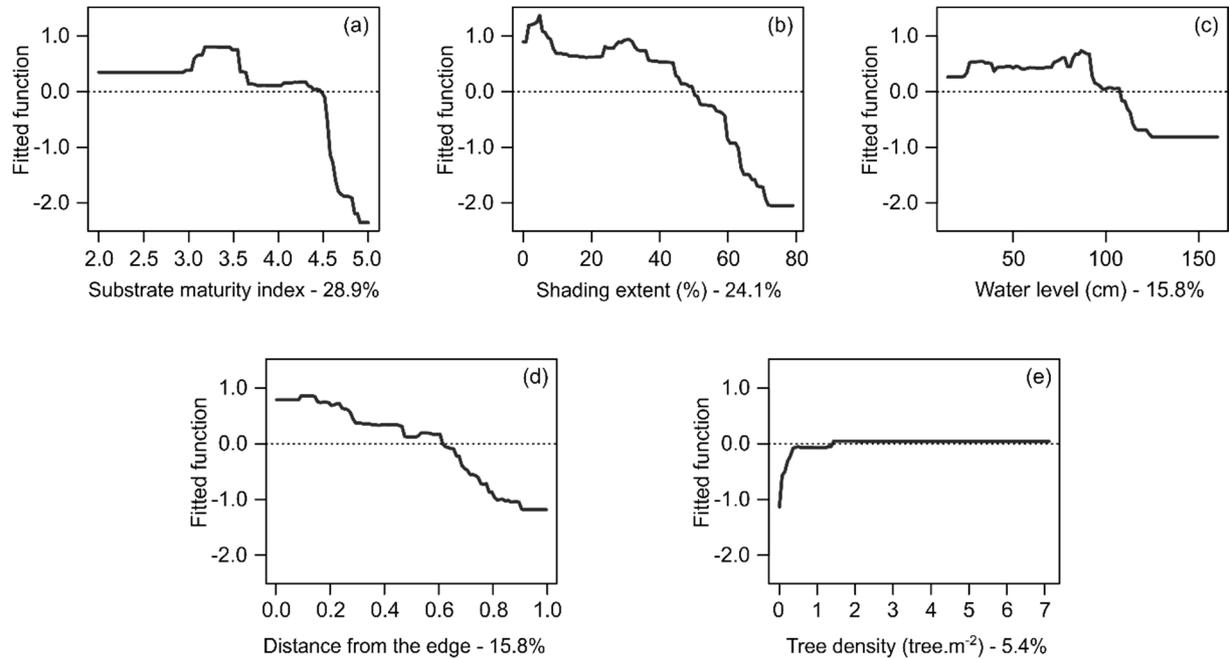
**Figure 2:** Conceptual view of the sampling design conducted for describing environmental conditions associated with the presence of crab burrows. The habitat conditions were described around burrows (habitat use) and at random locations along the transects to reflect the overall available conditions.

Figure 3



**Figure 3:** Projections of available (white dots) and burrows (grey dots) habitat conditions on the first factorial plan (a) of the ordination analysis performed on the 12 environmental variables (b-c). v1-v0, presence-absence vegetal material; S1-S2-S3: tree size class; d0-d1: presence-absence dead tree; r0-r1: presence-absence of roots; dominant roots class: kne: knee roots, pne: pneumatophores, sti: stilt roots, but: buttress roots; dominant tree species cer: *Ceriops tagal*, rhi: *Rhizophora* sp., son: *Sonneratia* sp., avi: *Avicennia* sp., bru: *Bruguiera* sp.; dominant substrate class: om: organic matter, clay, sand; %shade: shading extent, dens: tree density, %roots: percentage of roots, subst: substrate maturity index, dist: relative distance to the edge, depth: water height at high tide.

Figure 4



**Figure 4:** Partial dependence plots of the five most important variables influencing the distribution of *Scylla serrata* burrows, in the Belo-sur-mer mangrove ecosystem: (a) substrate maturity index, (b) shading extent, (c) water level at high tide, (d) distance from the edge and (e) tree density. A positive deviation from zero (dashed lines) of fitted function indicates a positive influence, whereas a negative deviation indicates an avoidance for the value of the environmental variable. Low values of maturity index indicate fluid mud consistency whereas larger values reflect hard substrate.

**Table 1:** Summary of environmental variables used to describe the influence of environmental conditions on *Scylla serrata's* burrows occurrences. The mean (or mode for categorical variables, \*) are indicated for each environmental variable measured at 20-meters intervals along transect (available conditions) and in proximity to the burrows (burrows conditions). The mean carapace width of mud crabs was indicated for each zone.

Habitat variable	Available conditions			Burrow conditions		
	Zone 1	Zone 2	Zone 3	Zone 1	Zone 2	Zone 3
Dominant substrate class	sand*	clay*	sand*	clay*	clay*	sand*
Substrate maturity index	4.35	3.74	4.85	3.76	3.53	4.43
Water level at high tide (cm)	72.40	73.83	76.42	51.27	49.74	66.14
Relative distance from the edge	0.43	0.76	0.79	0.33	0.54	0.67
Dominant tree species	ceriops*	ceriops*	ceriops*	ceriops*	ceriops*	ceriops*
Dominant tree size class (m)	2 to 5*	2 to 5*	2 to 5*	2 to 5*	2 to 5*	2 to 5*
Presence of dead tree	absence*	absence*	absence*	absence*	absence*	absence*
Tree density (tree.m <sup>-2</sup> )	0.58	0.37	0.70	0.71	0.47	0.74
Presence of vegetal material	absence*	absence*	presence*	presence*	presence*	absence*
Percentage of roots (%)	17.35	24.21	13.32	15.95	20.68	24.57
Dominant root class	knee*	stilt*	knee*	knee*	knee*	knee*
Shading extent (%)	47.66	44.53	40.75	43.51	39.94	22.86
Mean carapace width (cm)	/	/	/	9.51	8.20	8.50

**Table 2:** Relative importance of the 12 environmental variables for explaining the occurrences of *Scylla serrata*'s burrows, as inferred from the BRT model. The zone of sampling was added as additional explanatory variable. The bold values identified the threshold level (5 % of relative importance) used to simplify the model.

Habitat variable	Relative importance
Substrate maturity index	<b>28.9%</b>
Shading extent	<b>24.1%</b>
Relative distance from the edge	<b>15.8%</b>
Water level at high tide	<b>15.8%</b>
Tree density	<b>5.4%</b>
Presence of dead tree	2.4%
Presence of vegetal material	1.8%
Dominant root class	1.5%
Percentage of roots	1.4%
Dominant substrate class	1.4%
Dominant tree species	0.8%
Dominant tree size class	0.7%
Sampling zone	0.1%