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1 **Influence of environmental conditions on the distribution of burrows of the mud crab, *Scylla***
2 ***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⁻²) 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⁻²), 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, R² = 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, R²
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, R² = 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 ± 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 ± 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⁻², 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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Figure 1

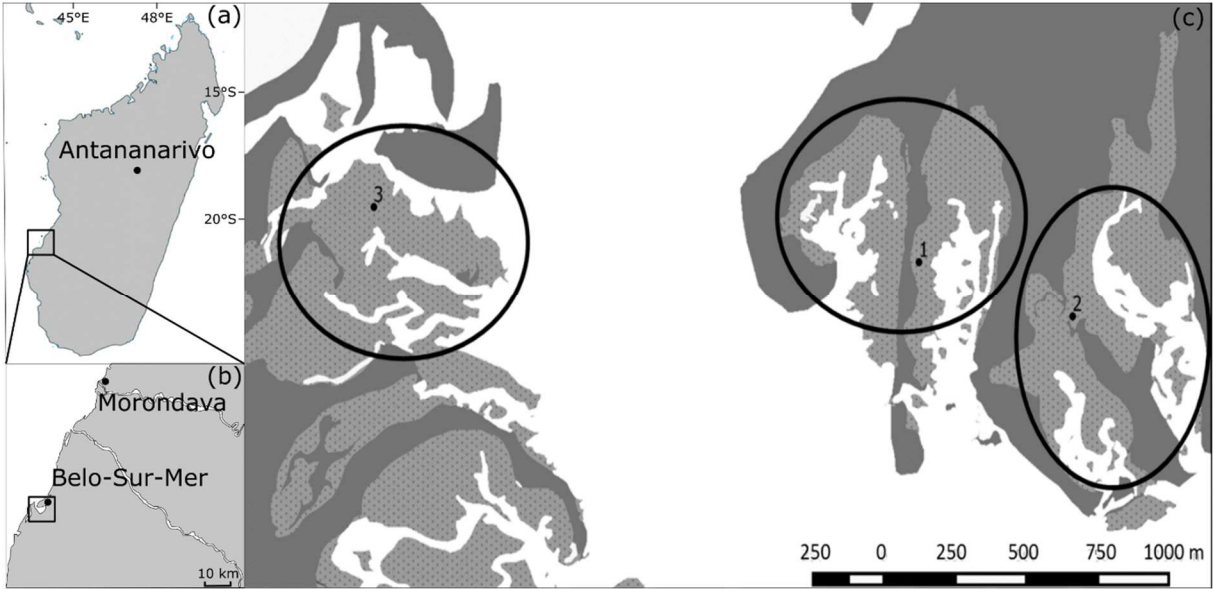


Figure 1: Location of the study area, near the village of Belo-sur-Mer (b), Southwestern Madagascar, Western Indian Ocean (a), and the three mangrove zones prospected for investigating burrow distribution of mud crab, *Scylla serrata* (c). The gray dotted shapes represent the mangrove forest areas.

Figure 2

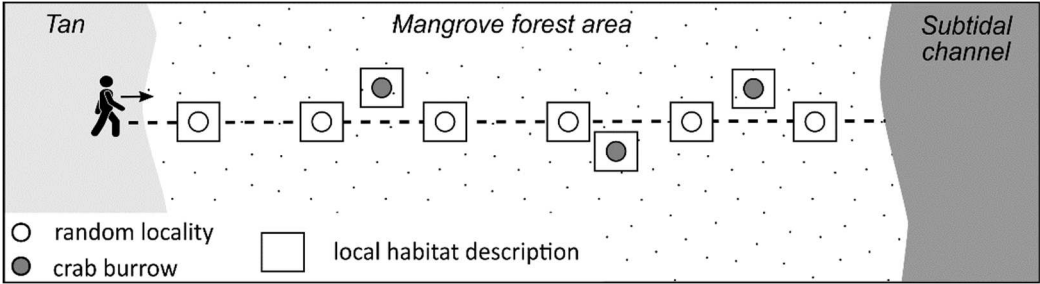


Figure 2: Conceptual view of the sampling design conducted for describing environmental conditions associated with the presence of crab burrows. The habitat conditions were described around burrows (habitat use) and at random locations along the transects to reflect the overall available conditions.

Figure 3

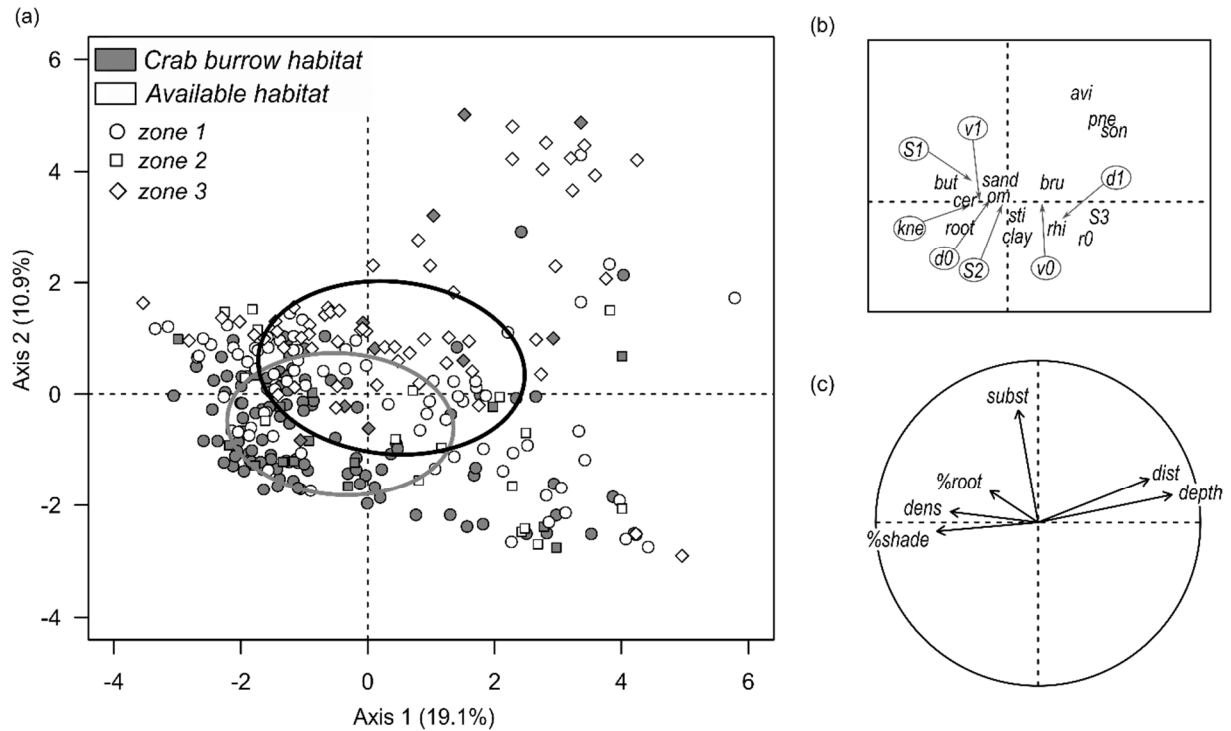


Figure 3: Projections of available (white dots) and burrows (grey dots) habitat conditions on the first factorial plan (a) of the ordination analysis performed on the 12 environmental variables (b-c). v1-v0, presence-absence vegetal material; S1-S2-S3: tree size class; d0-d1: presence-absence dead tree; 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

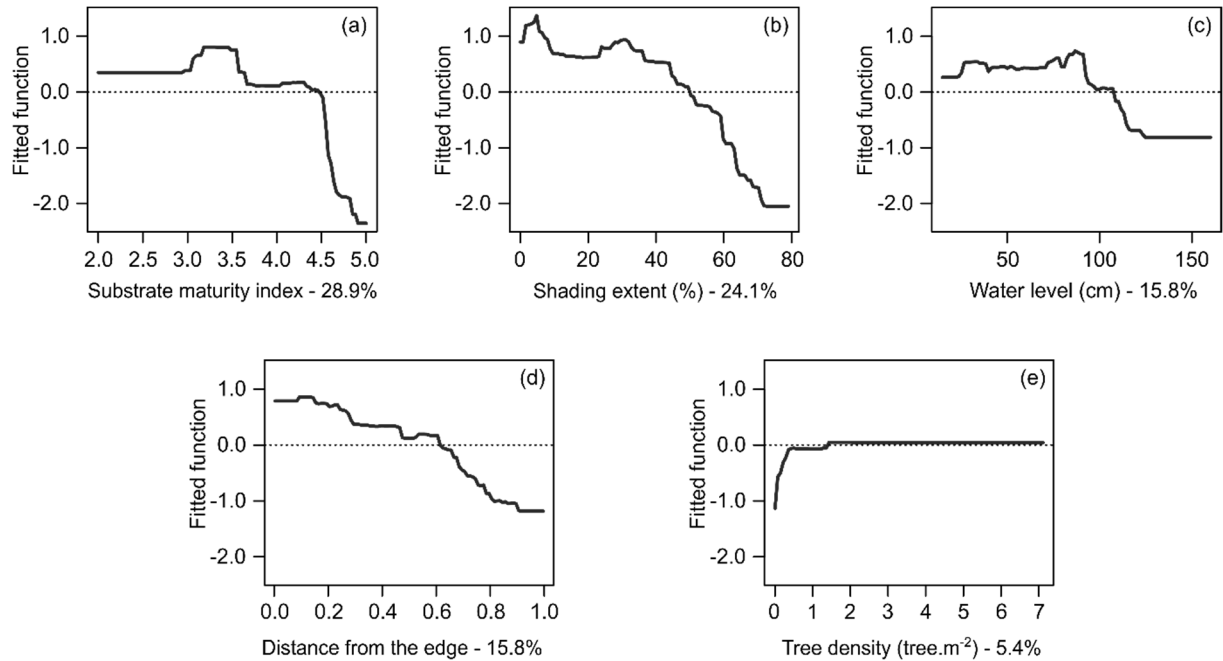


Figure 4: Partial dependence plots of the five most important variables influencing the distribution of *Scylla serrata* burrows, in the Belo-sur-mer mangrove ecosystem: (a) substrate maturity index, (b) shading extent, (c) water level at high tide, (d) distance from the edge and (e) tree density. A 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 ⁻²)	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	28.9%
Shading extent	24.1%
Relative distance from the edge	15.8%
Water level at high tide	15.8%
Tree density	5.4%
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%