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# Contrasted resistance and resilience of two mangrove forests after exposure to long-term and short-term anthropic disturbances

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## 1 Abstract

2 Mangroves, coastal forests under the influence of tides, are known to be very resilient when  
3 they face natural disturbances such as storms or tsunamis. While they provide several ecological  
4 services, they are threatened by many anthropic pressures. The aim of this study was to assess  
5 and to compare the stability of two mangrove fringes defined by contrasted set of natural  
6 constraints and exposed to pretreated domestic wastewaters discharges. The *in situ*  
7 experimental system set up in Mayotte Island (Indian Ocean) allowed us to determine both the  
8 short-term (2 years) and the long-term (9 years) resistance and the resilience. We focused on  
9 vegetation and crabs, an essential component of mangroves fauna. Wastewater discharges  
10 induced increases in tree coverage, leaves productivity and pigment content, and a decrease in  
11 crab diversity and density. Within 2 years after the release of the disturbance, several parameters  
12 reach back control values indicating fast resilience. Our results notably emphasized the high  
13 stability of the mangrove fringe dominated by *Rhizophora mucronata* trees, which was both  
14 more resistant and more resilient. This makes this fringe more suitable for application purposes,  
15 such as outfall for domestic wastewaters treatment plants.

16

17

18 **Key words:** anthropic disturbance, crabs, ecosystem resistance, ecosystem resilience,  
19 mangrove trees.

20

## 21 **1. Introduction**

22 Mangroves are ecotone ecosystems influenced by tides in tropical and subtropical latitudes  
23 (Blasco, 1991). They are established in coastal shallow areas, sheltered from the wave energy  
24 (Thom, 1984). These overall nutrient-poor forests (Boto and Wellington, 1984) have a high  
25 litter productivity and they are part of the main sources of organic matter for the coastal marine  
26 food webs (Komiyama et al., 2000; Mohamed et al., 2016). Mangrove forests provide many  
27 ecosystem services for human society and marine communities such as providing varied food  
28 and material resources (Lee et al., 2014). Thanks to the tree roots, they participate to the  
29 sediment stability (Blasco, 1991) and the protection of coasts from erosion, wind, tsunamis and  
30 cyclones (Alongi, 2008). They are essential for the local fauna providing habitats for fishes,  
31 prawns and crabs (Aburto-Oropeza et al., 2008), as well as for birds, mammals and reptiles  
32 (Alongi, 2002). Mangroves actively participate to the nutrient trapping and remineralization of  
33 organic matter from leaching of soils (Ewel et al., 1998; Wang et al., 2010). Finally, they have  
34 also a high potential of carbon sequestration and storage due to rapid rates of net primary  
35 production and sedimentation (Alongi, 2012; Donato et al., 2011; Komiyama et al., 2008).

36 In 2014, global mangroves were estimated to cover 81,484 km<sup>2</sup> of the earth's surface (119 278  
37 km<sup>2</sup> for the 1980s), namely around 0.7% of tropical forest surface (Hamilton and Casey, 2016),  
38 over 110 countries and territories (Giri et al., 2011). But mangroves are threatened  
39 environments. In addition to being continuously submitted to environmental pressures (salinity  
40 gradients, tidal cycle, soil instability, temperature) (Feller et al., 2010), mangroves are also  
41 affected by anthropic pressures caused by the proximity with urban centers and aquatic farms  
42 (Prasad, 2012; Zhang et al., 2014). Since the 1980s, 32% of mangroves have disappeared  
43 because of anthropic activities (Giri et al., 2011; Hamilton and Casey, 2016): overexploitation  
44 of wood (Alongi, 2002), deforestation to develop aquaculture, agriculture, tourism and urban  
45 development (Giri et al., 2011). Mangrove trees and sediment biocenosis are directly exposed  
46 to the pollutants that accumulate in sediments such as heavy metals or organic contaminants  
47 like pesticides (Lewis et al., 2011; Zhang et al., 2014), oil spills (Duke, 2016), domestic or  
48 industrial wastewaters (Bartolini et al., 2011; Molnar et al., 2013).

49 The stability of mangroves exposed to anthropogenic disturbances is defined by their properties  
50 of resistance and resilience (Pimm, 1984). The resistance is the degree to which a variable  
51 remains unmodified during the exposure to a disturbance while the resilience is defined as the  
52 rate of return to the initial state after the end of a disturbance (Pimm, 1984). The high resilience  
53 capacities of mangroves were revealed after strong natural events (*e.g.* hurricane, intensive

54 winds and drought events) by the recovery of parameters as the normalized difference  
55 vegetation index (NDVI) (Galeano et al., 2017) and the net primary productivity (Danielson et  
56 al., 2017). In contrast, there is a lack of knowledge about the resilience capacities of mangrove  
57 following their exposure to pollutants such as wastewaters, oil spills etc. The stability of  
58 mangrove ecosystem strongly depends on forest structure stability, but also on the stability of  
59 the fauna, particularly the crabs, engineer species of this environment (Jones et al., 1994; Lee,  
60 1998). Indeed, crabs, by their habitat and their bioturbation activity, play a crucial ecological  
61 role in the structural and functional stability of mangrove ecosystems (Cannicci et al., 2008).  
62 They physically modify the structure of sediments (Kristensen, 2008), favor their oxygenation  
63 (Smith et al., 1991) and their enrichment in organic matter, shredding and burying leaves and  
64 propagules into their burrows. They improve as well the circulation of water and organic matter  
65 (Botto et al., 2006; Camilleri, 1992; Gutierrez et al., 2006).

66 Mangroves species are spatially organized along environmental gradients of salinity, nutrient  
67 availability, and temperature, according to the sediment characteristics and the length of  
68 immersion by tides (Ball, 1998; Robertson and Alongi, 1992). In such spatially and temporally  
69 heterogeneous zonation, the response of biocenosis to anthropic pressures is hard to predict.  
70 One critical question is to understand how the stability of mangroves varies among the different  
71 zones of vegetation. This would indeed influence the conservation strategies for these  
72 threatened environments. Our main hypothesis is that the mangrove **fringe** where the  
73 disturbance induces effects similar to those associated with the local natural constraints should  
74 be the most stable.

75 To test this hypothesis, we focused on two contrasted mangrove **fringes**, one flooded at each  
76 tide, dominated by *Rhizophora mucronata* trees, and the other one less exposed to tides and  
77 more submitted to aridity and salinity, dominated by *Ceriops tagal* trees (Tomlinson, 2016). In  
78 these mangrove zones, trees and other organisms are exposed to different set of constraints. In  
79 the *Rhizophora*-dominated zone the conditions are more constant, buffered by the tides but the  
80 longer immersion duration leads to longer anoxia of the sediment. In the *Ceriops*-dominated  
81 zone, the influence of tides is less important, the anoxia periods being therefore shorter, and the  
82 organisms are exposed to much stronger variations of the salinity and humidity. To compare  
83 the stability of these two mangrove zones, we used an *in situ* pilot project set up since 2008 in  
84 a mangrove of Mayotte Island in order to assess the ability of mangroves to be used as a  
85 receptacle for pretreated domestic wastewaters (PW) (Herteman et al., 2011). As the anthropic  
86 disturbance, PW discharges bring freshwater and nutrients, especially nitrogen, which should  
87 notably increase sediment anoxia through an increase of microbial activity in the sediments

88 (Capdeville, 2018). Previous results obtained with this pilot study showed a moderate long-  
89 term (6 years) impact of PW on the ecosystem without dysfunction of the ecosystem, which  
90 helped to highlight long-term resistance properties of the mangrove. The discharges induced  
91 even so a stronger growth of mangrove trees in both zones and a modification of the crab and  
92 meiofauna community structure. At long-term, the *R. mucronata* mangrove zone appeared more  
93 resistant than the *C. tagal* mangrove zone (Capdeville et al., 2018). This supports our main  
94 hypothesis, since this zone is naturally more exposed to anoxia. The remaining question is what  
95 would be the short-term resistance and the resilience capacities of these systems. To answer  
96 this, the experimental system was modified and the response of vegetation and crab  
97 communities were monitored during 2 years. Our hypotheses are that (i) as for what was  
98 observed at long-term, the short-term impact of anthropic disturbance will be higher in the *C.*  
99 *tagal* mangrove zone and (ii) the mangrove compartments of the two zones have fast resilience  
100 capacities.

101

## 102 **2. Material and methods**

### 103 **2.1. Study site**

104 In April 2008, an *in situ* experimental system has been set in the mangrove of Chirongui Bay,  
105 South-West of Mayotte Island, a French department located in the Mozambique Channel,  
106 South-West of Indian Ocean (12°55'S, 45°09'E), as described by Herteman et al. (2011). Since,  
107 this study site has continuously collected domestic wastewaters from Malamani village (250  
108 inhabitants-equivalent). The wastewaters are pretreated in a horizontal primary settlement tank  
109 with integrated sludge digester. Then, they are carried through a pipe network to the mangrove  
110 areas. PW are characterized by nitrogen and phosphorous inputs as described by Capdeville et  
111 al. (2018). From April 2008 to October 2015, PW have been discharged once per 24 h, during  
112 a low tide, for one hour (10 m<sup>3</sup>) onto mangrove areas (around 675 m<sup>2</sup>, 15 m x 45 m) dominated  
113 by the mangrove trees *Ceriops tagal* (Perr.) C.B. Robinson and *Rhizophora mucronata* Lam  
114 respectively (Figure 1). The hydraulic loading rate has been 14.8 L.m<sup>-2</sup>.d<sup>-1</sup>, which is equivalent  
115 to a daily rainfall event of 14.8 mm. Close to these two “impacted” areas, two other areas not  
116 subjected to PW discharges were used as “control” areas (Figure 1).

117 The beginning of our study (T0) corresponds to October 2015. Indeed, at this date the  
118 experimental setting described above was changed to assess the resilience and the short-term  
119 resistance capacities of the mangrove ecosystem. In each mangrove zones, four new different  
120 areas were designed (225 m<sup>2</sup>, 15 m x 15 m). On the one hand, one part of the initial impacted  
121 areas was kept impacted in the new discharge network (R-II or C-II meaning *Rhizophora* or

122 *Ceriops* Impacted-Impacted) while another one was disconnected and no more subjected to PW  
123 discharges (R-IC or C-IC meaning *Rhizophora* or *Ceriops* Impacted-Control). On the other  
124 hand, one part of the initial control area was kept un-impacted (R-CC or C-CC meaning  
125 Control-Control) while another one was connected to the network to receive PW discharges (R-  
126 CI or C-CI meaning Control-Impacted) (Figure 1). The impacted areas received the same PW  
127 discharge than before 2015, a volume of 10 m<sup>3</sup> each day (Figure 1).

128  
129 The *R. mucronata*-dominated experimental areas are closer the lagoon (about 400 m) than the  
130 ones dominated by *C. tagal* (about 500 m), and are submerged in mean 4.33 hr/day against 0.88  
131 hr/day for the other zone. The insular mangrove trees of the two mangrove zones have a weak  
132 development compared to continental mangroves. The height average of mangrove trees are  
133 1.92 m and 2.92 m for *C. tagal* mangrove trees in control and impacted area, respectively, and  
134 6.49 m and 8.85 m for *R. mucronata* mangrove trees in control and impacted areas, respectively.  
135 Besides, the *C. tagal* mangrove zone is a shrubby mangrove, characterized by a marked foliage  
136 yellowing (personal observations).

137  
138 The PW were mainly composed of organic matter, nitrogen (mainly ammonia form) and  
139 phosphorus nutrients, discharged in the mangrove areas with surface loading rates (for dry  
140 season, in g.m<sup>-2</sup>.d<sup>-1</sup>) of 6.1 for chemical oxygen demand, 2.0 for biological oxygen demand after  
141 5 days, 2.13 for suspended solids, 0.99 for total nitrogen and 0.111 for total phosphorus (data  
142 obtained from 2015 to 2017 from SIEAM – Syndicat Intercommunal d'Eau et d'Assainissement  
143 de Mayotte, France). The crab community and litter production were monitored throughout the  
144 experiment (Figure 2). Leaf analyses (size and pigment content) were performed after 12 and  
145 19 months and the analysis of the canopy by NDVI index was performed shortly before T0 and  
146 after 23 months.

147

## 148 **2.2. Water analyses**

149 The salinity and temperature of water were measured directly in the field in residual pools  
150 (surface water) and in piezometers (porewater, approximately 1 m depth) at low tide and  
151 samples were taken and stored at 4°C for later determination of nutrient (NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup> and  
152 PO<sub>4</sub><sup>3-</sup>) concentrations. Analyses were performed by the HydrôRéunion Laboratory (La  
153 Réunion, France) using classic colorimetric methods according to standard methods (APHA et  
154 al., 1992). Mean values were obtained from two-day measurements under similar hydrological  
155 conditions, in the upper and lower parts of the areas (total of 4 measures) just before the

156 modification of the experimental set-up (October 2015), and from two-day measurements in  
157 one part of each area in October 2017.

158

## 159 **2.3. Measurements of canopy pigmentation by NDVI**

160

### **2.3.1. Satellite imagery**

161 We used Pléiades satellite images acquired over the study site during dry seasons 2015 and  
162 2017 (Table 1). Images were provided by AIRBUS D&S and are available at  
163 <http://www.intelligence-airbusds.com/fr/4952-geostore>. The pixel size resolution was 2 meters  
164 in multispectral mode. Spectral channels available are blue (0.430 – 0.550  $\mu\text{m}$ ), green (0.500 –  
165 0.620  $\mu\text{m}$ ), red (0.590 – 0.710  $\mu\text{m}$ ) and near infra-red (0.740 – 0.940  $\mu\text{m}$ ). The provider  
166 corrected geometrically and radiometrically images from ground and sensor distortion and  
167 systematic effects of the atmosphere (molecular or ‘Rayleigh’ diffusion). Four ground control  
168 points were manually added in order to correctly align 2015 and 2017 images. BD ORTHO  
169 2016 was chosen as the target image to align other scenes. BD ORTHO 2016 was provided by  
170 the French Institute for Geographic and Forest Information and is available at  
171 <http://professionnels.ign.fr/donnees>.

172

173

### **2.3.2. Remote sensing vegetation index**

174 Based on observations made over the field area by aerial survey, high greenness of the  
175 mangrove canopy was assumed to correspond to wastewater impacted vegetation. In order to  
176 determine the density of green at top of canopy on satellite images, the Normalized Difference  
177 Vegetation Index was used (NDVI; Tucker, 1979). NDVI values were extracted inside each  
178 experimental 15 m x 15 m areas (64 values per area) and for each satellite image (2015, 2017).  
179 In order to compare values between satellite scenes (different sun angle, canopy shadows), a  
180  $\Delta\text{NDVI}$  was calculated by subtracting to each NDVI value the average NDVI values for the  
181 corresponding control area (same vegetation and same date). Statistical analyses were  
182 performed on the percent of NDVI increase compared to the average of corresponding control  
183 area for each mangrove zone.

184

185

## **2.4. Leaf measurements**

186 On each of the 8 areas, 50 mature leaves of dominant mangrove tree species were randomly  
187 collected 12 months (October 2016, end of dry season), and 19 months (May 2017, end of rainy  
188 season) after T0. Dry weights of leaves were obtained after desiccation in an air oven at 60°C  
189 during 3 days. Leaf areas were estimated from digital pictures of leaves by color adjustment,

190 scaling and binarization using Image J software (version 1.48h3). The specific leaf area (SLA),  
191 *i.e.* the ratio between the leaf area and the leaf dry weight was then calculated.

192

## 193 **2.5. Photosynthetic pigment analyses**

194 On each of the 8 areas, 12 and 19 months after T0, 12 mature leaves of the dominant mangrove  
195 tree species were randomly collected, kept in a cooler box during transport, and stored at -20°C  
196 until storage at -80°C at the laboratory. Pigments were extracted from one disk (Ø 16 mm) per  
197 leaf. Disks were cut, crushed with 50 mg of Fontainebleau sand, and rinsed with 20 mL of  
198 methanol (Sigma-Aldrich, France). Around 20 mL of sample were transferred into a tube and  
199 placed in an ultrasound cold bath for 5 min. Mixtures were then placed at -20°C for 15 min and  
200 centrifuged at 4°C, 1700 g (High Conic Rotor, Thermo Scientific) for 5 min. One mL of  
201 supernatant was filtered on 0.2 µm PTFE membrane syringe filter (Ø 13 mm, VWR  
202 International, USA) and placed in a 2 mL-vial (Agilent Technologies). To prevent degradation  
203 of pigments, extractions were performed under dark conditions and samples stored on ice during  
204 handling. The extracts were stored a few days at -80°C before High Performance Liquid  
205 Chromatography (HPLC) analysis with a 100 µL-loop auto-sampler and a quaternary solvent  
206 delivery system coupled to a diode array spectrophotometer (LC1200 series, Agilent  
207 technologies, USA). The mobile phase was prepared (solvent A: 70:30 (v/v) methanol: 1M  
208 ammonium acetate and solvent B: 100% methanol) and programmed (minutes; % solvent A; %  
209 solvent B): (0; 75; 25), (1; 50; 50), (20; 30; 70), (25; 0; 100), (32; 0; 100) according to the  
210 analytical gradient protocol described by Barlow et al. (1997). The column was then  
211 reconditioned to original conditions over a further 12 min. Pigment separation was performed  
212 through a C8, 3 µm-column (MOS-2 HYPERSIL, Thermo Scientific, USA). The diode array  
213 detector was set at 440 nm to detect carotenoids, at 665 nm for chlorophylls and pheopigments.  
214 Pigments were identified by comparing their retention time and absorption spectra with those  
215 of pure standard pigments (DHI LAB products, Denmark). Each pigment concentration was  
216 calculated by relating the peak area of its chromatogram with the corresponding area of  
217 calibrated standard using ChemStation software (version A.10.02, Agilent technologies). **The**  
218 **standards used for calibration were pheophorbide a, fucoxanthin, violoaxanthin, astaxanthin,**  
219 **diadinoxanthin, alloxanthin, myxoxanthophyll, zeaxanthin, lutein, chlorophyll a, chlorophyll b,**  
220 **phaeophytin a, β-carotene. The detection threshold was 0.1 ng.** In parallel with extraction, one  
221 disk per leaf was dried and weighted in order to express the pigment concentration per dry  
222 weight unit.

223



## 2.6. Productivity of mangrove trees

In order to collect leaves, flowers and fruits from mangrove trees, 3 nets (1 m<sup>2</sup>) were randomly positioned in each mangrove area, 1.7 m above soil to avoid contact with high tides. Net contents were sampled every two weeks, sorted according to plant parts and tree species and weighted after desiccation in an air oven (60°C, 48 h). The analyses focused on the leaf litter. For each net, the mean number of leaves (both *C. tagal* and *R. mucronata* species) per week and per m<sup>2</sup> was calculated for each of the 4 successive seasons of the experiment (wet season 1 from November 2015 to May 2016, wet season 2 from November 2016 to May 2017, dry season 1 from June to October 2016, and dry season 2 from June to October 2017).

## 2.7. Monitoring of crabs

Once a month between November 2015 and November 2017, the total number of crabs and crab holes were counted within the same 4 plots (1 m<sup>2</sup>) on each of the 8 areas to calculate crab and hole densities, the Shannon diversity index and the relative abundance of crab species. The specific compositions of crab communities from each area were compared with the Bray Curtis similarity index.

## 2.8. Statistical analyses

Statistical analyses were performed using the PAST software (PAleontological STatistics, versions 2.17 and 3.06) (Hammer *et al.*, 2001). The normality was checked on each dataset with the Shapiro-Wilk test and data were transformed if needed. When data were normally distributed, two-way ANOVAs were used to test the effects of mangrove zone (*C. tagal* vs *R. mucronata*) and treatment (control vs impacted areas) per date, followed by a Fisher post-hoc test. The non-parametric Kruskal-Wallis test was used with Mann-Whitney test for pairwise comparisons of non-parametric data. Data given in the text are means  $\pm$  SE. For all statistical analyses, significance was inferred at  $p < 0.05$ .

# 3. Results

## 3.1. Water composition

The temperature, conductivity, salinity and nutrient composition of water before T0 and at the end of the experiment are given in Table 2. Given the low level of replication of these data (n=4 for 2015 data except for some missing data in the *C. tagal* area, and n = 2 for 2017 data), statistical analyses could not be performed. However clear tendencies could be observed. At

257 long-term, in surface water, the PW discharges induced a decrease in salinity and an increase  
258 in  $\text{NH}_4^+$  and  $\text{NO}_2^-$  concentrations in both mangrove zones. Depending on meteorological  
259 conditions, water temperature decreased in impacted areas. This was associated with an increase  
260 in  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  in the *R. mucronata* mangrove zone. In porewater, PW discharges induced  
261 an increase in salinity, along with increases in  $\text{PO}_4^{3-}$  and  $\text{NH}_4^+$  concentrations in both mangrove  
262 zones. At short-term, the concentrations of nutrients were intermediate between those of CC  
263 and those of II respective areas, except for water surface in *C. tagal* mangrove zone. In that  
264 area,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{NO}_2^-$  concentrations were higher than in the C-II area. Two years after the  
265 PW discharges were stopped, the nutrient concentrations in surface water were close from those  
266 of the control area, except for  $\text{NH}_4^+$  concentration in R-IC area, which was still high. In  
267 porewater,  $\text{PO}_4^{3-}$  concentrations remained high in both mangrove zones.

268

### 269 **3.2. Vegetation compartment**

#### 270 **3.2.1. Measurements of canopy pigmentation by NDVI**

271 The increase of NDVI in each area of *C. tagal* and *R. mucronata* mangrove zones compared to  
272 the respective control areas was measured just before T0 (August 2015) and after 23 months  
273 (September 2017) (Figure 3). At T0, the NDVI was significantly higher in CI areas compared  
274 to CC areas, especially in the *R. mucronata* zone. This observation was unexpected, and may  
275 be explained by small-scale variations of the natural slope of the field, leading to small  
276 contamination of a part of the control areas. At both dates, the values of NDVI were higher in  
277 impacted areas of *C. tagal* (C-II) and *R. mucronata* (R-II) mangrove zones than in the  
278 corresponding control (CC) areas, with in mean 21.6 and 9.6% of increase, respectively. This  
279 long-term effect of PW discharges was almost stable during the 2 years of the study. Twenty-  
280 three months after the PW discharge were stopped, the increase percentage of NDVI in C-IC  
281 and R-IC areas decreased towards the values of control areas, though they remained higher,  
282 with 8.7 and 5.3%, respectively. The effect of PW on the NDVI decreased during this period  
283 by 60% in the *C. tagal* mangrove zone and by 45% in the *R. mucronata* zone, indicating a  
284 partial resilience. At T23, the increase percentages of NDVI in C-CI and R-CI areas had reached  
285 the values of C-II and R-II areas, respectively.

286

#### 287 **3.2.2. Leaf responses**

288 The figure 4 presents the measures of specific leaf area (SLA) made 12 and 19 months after T0.  
289 As expected from the previous results of Capdeville et al. (2018), the SLA in control areas of  
290 both mangrove zones were significantly lower than the SLA in impacted areas. The increase

291 induced by PW discharges was in mean 43% in C-II area, and 22% in R-II area. The SLA in IC  
292 areas was significantly higher than in II areas after 12 months without PW but after 19 months,  
293 it significantly decreased toward the SLA of respective control areas. However, in C-IC area  
294 the SLA value was still higher than in the control while in R-IC area the SLA was lower than  
295 in the control. The SLA in C-CI and R-CI areas significantly increased over time, by 39% and  
296 16%, respectively, at 19 months. In C-CI area the values of C-II area were reached but in R-CI  
297 area the valued remained lower than those of R-II areas.

298

299

### 3.2.3. Photosynthetic pigment analysis

300 The dynamics of mature leaves pigment contents was studied 12 and 19 months after T0 (Figure  
301 5). The pigments of leaves from *C. tagal* and *R. mucronata* mangrove zones were in mean  
302 mainly composed by 56% of chlorophyll *a*, 26% of chlorophyll *b*, 7% of xanthophyll, 6% of  $\beta$ -  
303 carotene, 3% of neoxanthin and 1% of phaeophytin *a*. We focused on the first four major  
304 pigments: chlorophyll *a*, chlorophyll *b*, xanthophyll, and  $\beta$ -carotene. For these pigments, over  
305 time, the concentrations were significantly higher in leaves from impacted area than in control  
306 area in the *C. tagal* mangrove zone (Figure 5). In *C. tagal* mangrove zone, the chlorophyll *a*  
307 and the xanthophyll concentrations decreased in leaves from the IC area compared to the II area  
308 after 19 months. The concentrations of chlorophyll *b* and the  $\beta$ -carotene, remained similar in  
309 C-IC and in C-II areas, showing no resilience. In parallel, a significant increase of the pigment  
310 concentrations (except for the  $\beta$ -carotene) in CI area was already observed at 12 months,  
311 indicating a fast response. Regarding the *R. mucronata* mangrove zone, the differences between  
312 pigment concentrations in CC and II areas were less marked, with only non-significant  
313 tendencies. The PW discharges induced a significant increase of chlorophyll *a* and chlorophyll  
314 *b* concentrations in the CI area after 12 months.

315 Several ratios have been used to estimate the pigment degradation and the response of mangrove  
316 trees to environmental changes. The chlorophyll *a*: carotenoids and chlorophyll *a*: phaeophytin  
317 *a* ratios are negatively correlated to chlorophyll *a* degradation. No significant decrease of these  
318 ratios was observed in any areas of *C. tagal* and *R. mucronata* mangrove zones compared to  
319 the control areas, except for the R-CI area (with chlorophyll *a*: phaeophytin *a* ratio,  $p < 0.001$   
320 with Tuckey pairwise test). An increase of chlorophyll *b*: xanthophyll ratio is an indication of  
321 nutrient oversupply in the environment (MacFarlane and Burchett, 2001), and a decrease of the  
322 chlorophyll *a*: chlorophyll *b* ratio shows a tree adaptation to environmental changes due to an  
323 excess of nitrogen (Kitajima and Hogan, 2003). No significant modification of the chlorophyll  
324 *a*: chlorophyll *b* ratio was observed in any area. In contrast, a significant increase of the

325 chlorophyll *b*: xanthophyll ratio was observed only in C-CI and R-CI areas compared to  
326 respective control areas after 12 months ( $p < 0.001$  for *C. tagal* mangrove zone and  $p = 0.046$   
327 for *R. mucronata* mangrove zone, with Tuckey pairwise test).

328

#### 329 **3.2.4. Vegetation productivity**

330 Results of vegetation productivity were focused on the total number of leaves calculated per  
331 season from November 2015 to October 2017 (Figure 6). Since the production of leaves was  
332 season-dependent for the *R. mucronata* mangrove zone, with a lower production during dry  
333 season, and since it was highly variable from one month to another, it was chosen to represent  
334 the mean production during each season of the experiment. During the first wet season (from  
335 November 2015 to May 2016), the total production of leaves was equivalent between CC and  
336 CI areas and was significantly lower in these areas than in the II and IC areas. During the other  
337 seasons, no significant differences could be observed, especially during the dry seasons.  
338 However, there was a clear tendency for the productivity to increase in C-CI and R-CI areas  
339 and to decrease in R-IC area during the second wet season.

340

### 341 **3.3. Crab community**

342 The temporal dynamics of crab communities has been examined with linear regression over  
343 time for each plot individually. The Table 3 gives the comparisons of these slopes between the  
344 different mangrove areas.

345

#### 346 **3.3.1. Density of crabs and crab holes**

347 At T0, though the differences were not significant, the crab densities in impacted areas ( $8.62 \pm$   
348  $0.99 \text{ ind.m}^{-2}$  for C-II and  $10.37 \pm 2.04 \text{ ind.m}^{-2}$  for R-II) tended to be lower than in the control  
349 areas ( $12.75 \pm 2.33 \text{ ind.m}^{-2}$  for C-CC and  $13.37 \pm 1.11 \text{ ind.m}^{-2}$  for R-CC) (Figure 7A).  
350 Concerning crab holes, their density was significantly higher in C-CC area ( $28.25 \pm 2.83$   
351  $\text{holes.m}^{-2}$ ) than in C-II area ( $16.37 \pm 3.55 \text{ holes.m}^{-2}$ ), and higher in R-CC ( $28.5 \pm 4.24 \text{ holes.m}^{-2}$ )  
352 compared to R-II ( $21 \pm 4.37 \text{ holes.m}^{-2}$ ).

353 In the *C. tagal* mangrove zone, the dynamics of crab density showed contrasted tendencies on  
354 the different areas (Figure Supplementary Material 1). While this density was rather stable in  
355 C-CC and C-II areas, as indicated by similar low slopes (Table 3), it tended to decrease ( $p <$   
356  $0.0001$  for the regression) in C-CI area as a consequence of the short-term impact of PW  
357 discharges. On the contrary, the density increased during the studied period in the C-IC area ( $p$   
358  $= 0.035$  for the regression), suggesting a resilience. At the last sampling date, the crab density

359 reached higher values ( $p = 0.032$ ) in the C-IC area ( $19.5 \pm 1.8$ ) than in the C-CC area ( $12.8 \pm$   
360  $1.1$ ). The short-term impact in C-CI area was almost stronger than the long-term impact in C-II  
361 area, since the crab density tended to be lower in C-CI area at the last sampling date ( $4 \pm 1.2$   
362 compared to  $7.5 \pm 0.8$ ,  $p = 0.071$ ).

363 No significant differences in the dynamics of crab density was observed in *R. mucronata*  
364 mangrove zone (Table 3).

365 Regarding the density of crab hole, the hole number also decreased over the months in C-CI  
366 area ( $p = 0.0304$  between T0 and T24 with Mann-Whitney pairwise test). The same trend was  
367 observed for *R. mucronata* mangrove zone but the PW effect was lower than in *C. tagal*  
368 mangrove zone.

369

### 370 **3.3.2. Crab diversity**

371 The dynamics of the  $\alpha$ -diversity of crab communities, based on the Shannon diversity index, is  
372 given in the figure SM2. In control areas, the Shannon index was in mean higher in the *C. tagal*  
373 mangrove zone than in the *R. mucronata* mangrove zone (t-test,  $p = 0.024$ ). As for the density  
374 of crabs, significant differences between areas were found only in the *C. tagal* mangrove zone  
375 (Figure 7B). At the beginning of the experiment, the Shannon index was significantly lower in  
376 C-II area than in C-CC area. A similar trend was observable in the *R. mucronata* mangrove  
377 zone

378 On the *C. tagal* mangrove zone, the Shannon diversity index tended to decrease slightly during  
379 the studied period in the CC area, but slower than in the II are (Figure SM2, Table 3). This  
380 decrease of  $\alpha$ -diversity was stopped by the end of PW discharges in the IC area, and was  
381 accelerated by PW discharges in CI area. This indicates the beginning of resilience and a strong  
382 short-term impact. After 24 months, the Shannon diversity indexes were not significantly  
383 different in C-CC and C-IC areas (data not shown).

384

### 385 **3.3.3. Crab specific dominance**

386 The composition of crab species living in Malamani mangrove was described by Capdeville *et*  
387 *al.* (2018). Nine species were observed: *Perisesarma guttatum*, *Neosarmatium smithii*,  
388 *Neosarmatium meinerti*, *Parasesarma leptosoma*, *Tabuca urvillei*, *Cranuca inversa*, *Austruca*  
389 *annulipes*, *Paraleptuca chlorophthalmus* and *Gelasimus vocans*. The crabs belonged to two  
390 groups: the Sesarmidae, feeding on leaves and the Ocypodidae, detritivores.

391 During the 2 years of the experiment, the Sesarmidae group was largely dominant representing  
392 in average  $62.1 \pm 6.2\%$  and  $76.7 \pm 9.9\%$  of individuals in C-CC and R-CC areas, respectively.

393 This proportion was significantly higher in C-II area and equivalent in R-II area, with  $92.8 \pm$   
394  $3.2\%$  (Student test,  $p = 0.004$ ) and  $88.1 \pm 3.1\%$  of individuals (Student test,  $p = 0.31$ ),  
395 respectively. No resilience was observed in C-IC after 24 months without PW discharge. The  
396 short-term impact of PW discharge induced a significant increase of Sesarmidae proportion  
397 from 12 months only in C-CI area, no significant effect of PW being observed in R-CI area  
398 (data not shown).

399 The dominant crab species in Malamani mangrove areas is the Sesarmidae *Perisesarma*  
400 *guttatum* (Milne-Edwards, 1869). In contrast, as for the proportion of Sesarmidae, the  
401 proportion of *P. guttatum* was significantly higher in C-II area ( $69.3 \pm 1.5\%$  of individuals) than  
402 in C-CC area ( $33.9 \pm 6.8\%$  of individuals) (Student test,  $p = 0.002$ ) (Figure 7C). During the  
403 experiment, this proportion was quite stable in the C-CC area, while it kept increasing in the C-  
404 II area (Figure SM3, Table 3). This increase was quite similar to the one observed on the C-CI  
405 area, indicating comparable rhythms for the short-term and long-term impacts. The negative  
406 slope of the regression in the C-IC area suggests the beginning of resilience.

407 No significant effect of PW discharges on *P. guttatum* proportion was observed in the *R.*  
408 *mucronata* mangrove zone (Figure 7C)

409  
410 The specific compositions of crab communities were compared overtime between all areas with  
411 the Bray-Curtis similarity index (Figure 8). The similarity between the control and impacted  
412 areas was low throughout the study from T0 to T24. From T0 to T18, the similarity between C-  
413 IC and C-CC areas was similar to the one between C-II and C-CC areas, but after 24 months it  
414 was significantly higher (Figure 8A). In parallel, the similarity between C-IC and C-II areas  
415 progressively decreased. This highlights a resilience of the specific composition of crab  
416 community in *C. tagal* mangrove zone. In the *R. mucronata* mangrove zone, no resilience was  
417 observed (Figure 8B). After 6 months of PW discharges, the similarity between C-CI and C-  
418 CC areas decreased overtime, so that at 12 months it was equivalent to the similarity between  
419 C-II and C-CC (Figure 8C). Conversely, the similarity between C-CI and C-II areas increased  
420 overtime, and started to be significantly higher to the similarity between C-CC and C-II at 18  
421 months. For the *R. mucronata* mangrove zone, no clear tendency could be observed, the  
422 similarities between all the areas being rather low (Figure 8D).

423

#### 424 **4. Discussion**

425 After a first study comparing the resistance of *C. tagal* and *R. mucronata* mangrove zones after  
426 4 to 6 years of disturbance (Capdeville et al., 2018), the present study assessed the resistance

427 after a shorter (0-2 years) and longer (7-9 years) disturbance, and the resilience of both zones.  
428 To our knowledge, this is the first study allowing the *in situ* assessment in natural conditions of  
429 a whole ecosystem after several years of controlled disturbance.

430

#### 431 **4.1. Short-term resistance**

432 Short term effects of PW discharges were studied on CI areas. The macroscopic observation of  
433 mangroves through satellite photographs showed an increase of the NDVI in these areas after  
434 23 months of PW discharge (Figure 3). The NDVI index allows to characterize the plant cover  
435 which is correlated with the productivity of mangrove tree, the leaf area index and with the  
436 photosynthetically active biomass of canopy (Tucker, 1979). This short-term impact of PW  
437 discharges was quite similar in both mangrove zones. Nevertheless, because of the micro-relief  
438 of the field and the relative position of control and impacted areas, the control area in the *R.*  
439 *mucronata* mangrove zone may have been received a small part of the PW flow which would  
440 have lowered the contrast with the impacted area. In this study, the discharges had a positive  
441 effect on NDVI, unlike what can be observed with other stresses such as intensive winds and  
442 droughts which induce a mangrove tree defoliation and consequently a decrease of NDVI  
443 (Galeano et al., 2017). This increase of NDVI can be explained by the increases of SLA and  
444 pigment contents observed for the leaves collected in C-CI and R-CI areas (Figure 4 and 5).  
445 The short-term impact significantly appeared after 19 months of exposure for the SLA and after  
446 12 months for the pigment contents. It was associated with modifications of the chlorophyll *b*:  
447 xanthophyll ratio, caused by an excess of nutrients in C-CI and R-CI areas (Macfarlane and  
448 Burchett, 2001). The effect of PW was visible after more time in these areas than similar effects  
449 which were observed after only 12 months in the same mangrove areas by (Herteman et al.,  
450 2011). Except for the NDVI, these effects were much more marked for the *C. tagal* mangrove  
451 zone, suggesting a higher resistance of the vegetation in the *R. mucronata* mangrove zone. This  
452 is consistent with our hypothesis. It may be notably explained by the initially lower  
453 concentrations of nitrate and ammonium in the *C. tagal* zone (Capdeville et al., 2018), leading  
454 to a stronger response of vegetation when it is increased by the nutrient inputs associated with  
455 PW discharges.

456 The resistance capacity of crab community was assessed quantitatively (density of crabs) and  
457 qualitatively (specific composition) but also through their bioturbation activity (density of  
458 holes). For most of the studied parameters, the effects of PW discharges were more marked in  
459 the *C. tagal* mangrove zone. Therefore, as for the vegetation compartment, the crab community  
460 seemed more resistant in the *R. mucronata* mangrove zone. The effect of PW discharges on

461 crab density tended to be stronger at short term than at long-term effect (Figure SM1), which  
462 suggests an adaptation of crabs after several years of discharges, at least in terms of density.  
463 The decrease of crab diversity observed in *C. tagal* mangrove zones may be explained by the  
464 increase of *P. guttatum* proportion overtime. All results were in accordance with the decrease  
465 of the similarity between the C-CI and C-CC areas and the increase of the similarity between  
466 the C-CI and C-II areas.

467 The crabs play an essential role on the functioning of mangrove (Kristensen, 2008). They are  
468 influenced by modifications of environmental conditions like temperature, mangrove tree  
469 species, food availability, grain size and porosity of sediments and salinity gradient (Frusher et  
470 al., 1994; Steinke et al., 1993). Modifications of crab community may be dramatic for mangrove  
471 functioning (Cannicci et al., 2008; Lee, 2008). The various effects observed in this study,  
472 though significant, remain limited. Contrasted results have been reported for mangrove crabs  
473 exposed to anthropic disturbances. For instance, Lee (1995) observed an increase of the density  
474 of Ocypodidae crabs exposed to organic pollution from human facilities and Cannicci et al.  
475 (2008) noticed an enhanced diversity of Ocypodidae and Sesarmidae crabs exposed to  
476 wastewaters in peri-urban mangroves. In contrast, Penha-Lopes et al. (2009) reported a decrease  
477 of survival for crabs in a sewage-exposed mangrove mesocosm. In the present study, despite  
478 the negative effects on the density of crabs, no mortality was observed.

479 The response of crabs may be directly linked to the presence of PW (decrease of salinity, input  
480 of micropollutants), or linked to the associated modifications of the environment (oxygen  
481 concentration in sediments, light, temperature, modifications of food sources). Indeed,  
482 modifications of SLA and NDVI may indicate a higher canopy cover and less light at the  
483 sediment surface. The increase of leaves production may have been beneficial for the  
484 Sesarmidae, as they are feeding on leaves. The decrease of Ocypodidae proportion may be  
485 explained by the preference of these species for open areas (Nobbs and McGuinness, 1999),  
486 where they prefer to dig their hole, near to their food source (particular matter or algal biofilm)  
487 (Litulo, 2005). In contrast, *Perisesarma guttatum*, whose proportion significantly increased in  
488 C-CI area prefers shaded areas (Lee, 1998).

489

#### 490 **4.2. Long-term resistance**

491 Long term effects of PW discharges were observed on the II areas, which have been exposed  
492 to PW discharges during 9.5 years, at the end of the experiment. As for the short-term response  
493 to the disturbance, the *R. mucronata* mangrove zone was more resistant than the *C. tagal*  
494 mangrove zone. In a previous study, we have shown that after 6.5 years of discharges, PW



495 induced an increase of vegetation growth, pigment content, leaf productivity, canopy closure, a  
496 modification of crab communities and a decrease of crab density and diversity (Capdeville et  
497 al., 2018). After 3 more years of discharges, some parameters kept on increasing or decreasing,  
498 which indicates a worsening of the impact of PW discharges. This was the case for the SLA  
499 and for several pigment of leaves, compared to the values measured after 6.5 years, or for the  
500 density of crab holes, the crab diversity and the proportion of *P. guttatum*, compared to T0  
501 values. For the last parameter, the rate of increase was even identical at long term than at short  
502 term. This suggests that the vegetation is still responding to the anthropic disturbance, while  
503 the crab community is more affected.

504

#### 505 **4.2. Resilience capacity of the 2 mangrove zones**

506 The resilience depends on the duration, the frequency, the intensity and the spatial extent of the  
507 disturbance (Alongi, 2008). These parameters drive the recovery regulators like the nutrient  
508 availability and the species composition (Danielson et al., 2017). The ability of a community to  
509 recover relies on individual-, population- or community-level properties (Shade et al., 2012). It  
510 will notably depend on the resistance of individuals, on their tolerance, on their plasticity, on  
511 the diversity of the community or on the possibilities of immigration. Species richness and  
512 evenness were shown to significantly contribute to the stability of communities (Wittebolle et  
513 al., 2009). The mangrove ecosystems have demonstrated considerable resilience capacities that  
514 can be explained by a chronic exposition to natural disturbances like the fluctuations of the sea  
515 level, the temperature, the freshwater and salt exposure and the variation of the anoxia (Alongi,  
516 2008). These disturbances contribute to the selection of resistant and tolerant species.  
517 Therefore, mangroves would have a strong potential of resilience after strong punctual  
518 disturbances such as storms, hurricanes (Danielson et al., 2017), tsunamis (Alongi, 2008),  
519 intensive drought, and strong winds (Galeano et al., 2017). Except for the study of Smith et al.  
520 (2016) who considered the resilience of mangroves after 32 years of wastewaters exposure, the  
521 resilience of mangrove submitted to anthropic pollution is poorly studied so far, most studies  
522 focusing on the response during the disturbance rather than when the disturbance is released.  
523 The resilience of the two mangrove zones was monitored on the IC areas. Except for phosphate  
524 concentration in porewater, nutrient concentration in residual water in these areas were close  
525 from those measured in the control. After 23 months without discharge, a partial recovery was  
526 visible on the NDVI values measured in both areas (Figure 3). These results were consistent  
527 with leaf area measurements, for which the resilience was complete since no more difference  
528 could be observed with control areas after 19 months without discharge (Figure 4). This

529 resilience was more marked in *R. mucronata* mangrove zone than in *C. tagal* mangrove zone.  
530 The importance of tides in the process of resilience was emphasized by Smith et al. (2016), who  
531 studied an intermittently closed/open lake/lagoon (ICOLL) mangrove previously impacted by  
532 wastewaters discharges. They showed that the rate of recovery of this mangrove was much  
533 lower than those of mangroves in more open systems, where the influence of tides is higher.  
534 The fact that the *R. mucronata* mangrove zone is more often flooded than the other zone may  
535 contribute to its faster resilience, notably through the leaching of sediments.

536 Surprisingly, the resilience was less marked in terms of pigment concentration. In the *C. tagal*  
537 mangrove zone, it was only observed for the chlorophyll *a* and the xanthophyll concentrations  
538 (Figure 5). Similarly, the resilience was not very clear for the leaf productivity in this zone after  
539 24 months without PW discharge (Figure 6). This indicates a delay in the response of these  
540 parameters, which may simply be linked to the tree physiology. In the present case, satellite  
541 imaging and NDVI measurement seem to be the most sensitive way to assess fast vegetation  
542 resilience.

543 The resilience capacities of the mangroves were also evaluated for crab communities. The crab  
544 density in C-IC area reached a higher density than in control area (see Figure SM1). Such a  
545 rebound when a disturbance is released has been observed in very variable systems. For  
546 instance, after a desiccation period, the density and activity of microalgae can quickly reach  
547 higher values than before the desiccation (Barthes et al., 2015). A similar phenomenon was  
548 observed for the SLA, in the R-IC area (Figure 4). A longer monitoring of the study site could  
549 have shown a return to the same values than in the control areas. This emphasizes the difficulty  
550 of studying the resilience of natural ecosystems: the long time required to observe full recovery.

551 Except for the proportion of *P. guttatum*, for which only a stabilization was observed, a  
552 resilience, at least partial, was observable for the parameters describing crab communities. This  
553 fast resilience cannot be explained by a modification of food sources because the leaf  
554 productivity did not change in C-IC area. In contrast, it may be linked to the decrease of NDVI  
555 and to an opening of the canopy. Surprisingly, the resilience was efficient on crab diversity in  
556 C-IC area of *C. tagal* mangrove zone but no resilience was observed on the Sesarmidae and  
557 Ocypodidae proportions. The Sesarmidae group remained the dominant crab group. But the  
558 proportion of the dominant crab species, belonging at the Sesarmidae group, *P. guttatum*,  
559 reached back its initial value. All these results were confirmed with the increase of the similarity  
560 between the C-IC area and the control area indicating the resilience of the specific composition  
561 after 24 months in *C. tagal* mangrove zone. On the other hand, in this analysis, no resilience  
562 was observed in *R. mucronata* mangrove zone. Such contrasted results depending on the

563 considered descriptor highlight the importance of considering multiple parameters to assess the  
564 resilience of a community, and even more for the resilience of an ecosystem.

565

## 566 **5. Conclusion**

567 The results of this field study confirm our two hypotheses: (i) as for what was observed at long-  
568 term, the short-term effects of the anthropic disturbance are more pronounced in the *C. tagal*  
569 mangrove zone, and (ii) the 2 mangrove zones showed rather fast resilience, some parameters  
570 fully recovering within 19 months. The higher stability of the *R. mucronata* zone makes it much  
571 more suitable for exploitation purposes, notably for its use as a receptacle for pretreated  
572 wastewaters. It should be however noted that the effects PW discharges observed on the *C.*  
573 *tagal* areas may be considered as positive, since the growth and productivity of the mangrove  
574 forest were enhanced. The disturbance acted like addition of fertilizer in a nutrient-limited  
575 ecosystem, indicating some positive consequences of anthropogenic disturbance.

576 The use of mangroves for sewage treatment purpose has been suggested very early (Nedwell,  
577 1975) and has been tested in several microcosms experiments (e.g. Su et al., 2011; Tam, 1998)  
578 or in constructed mangroves (e.g. Tam et al., 2009; Wu et al., 2008). However, to our  
579 knowledge, the experimental system of Malamani was the first one to be set up in a natural  
580 mangrove, at an operational scale since it helped to manage wastewaters from all a housing  
581 estate, and at long-term. Moreover, the study of mangrove resilience after such a controlled  
582 disturbance at these spatial and temporal scales seems to be unique in the literature.

583 The stability of mangrove, as a result of both resistance and resilience, observed in the present  
584 study, should be considered in the context of a small-medium disturbance. In the case of a  
585 stronger disturbance, like an oil slick, the time scale could have been quite longer (Thompson  
586 et al., 2009). Ecosystem resilience is often considered as favored by biodiversity (Gunderson,  
587 2000). In the present case, tree diversity was equivalent in both zones (Capdeville et al., 2018),  
588 while crab diversity was significantly higher in the less stable zone. This seems contradictory,  
589 but it may be linked to the fact that the diversity index used does not consider the respective  
590 roles of species in the ecosystem (Yan et al., 2011). Our study, performed *in situ* and in  
591 controlled conditions highlights another level of mangrove forest heterogeneity through the  
592 stability of the ecosystem facing anthropic disturbance. Though additional studies are required  
593 to build a map of mangrove stability, this should be taken into account for the preservation of  
594 these threatened ecosystems.

595

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602

## 603 7. References

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**Table 1.** Characteristics of the Pléiades images used in this study. Tide level was estimated using the tide model of the French National Hydrographic and Oceanographic Administration (SHOM).

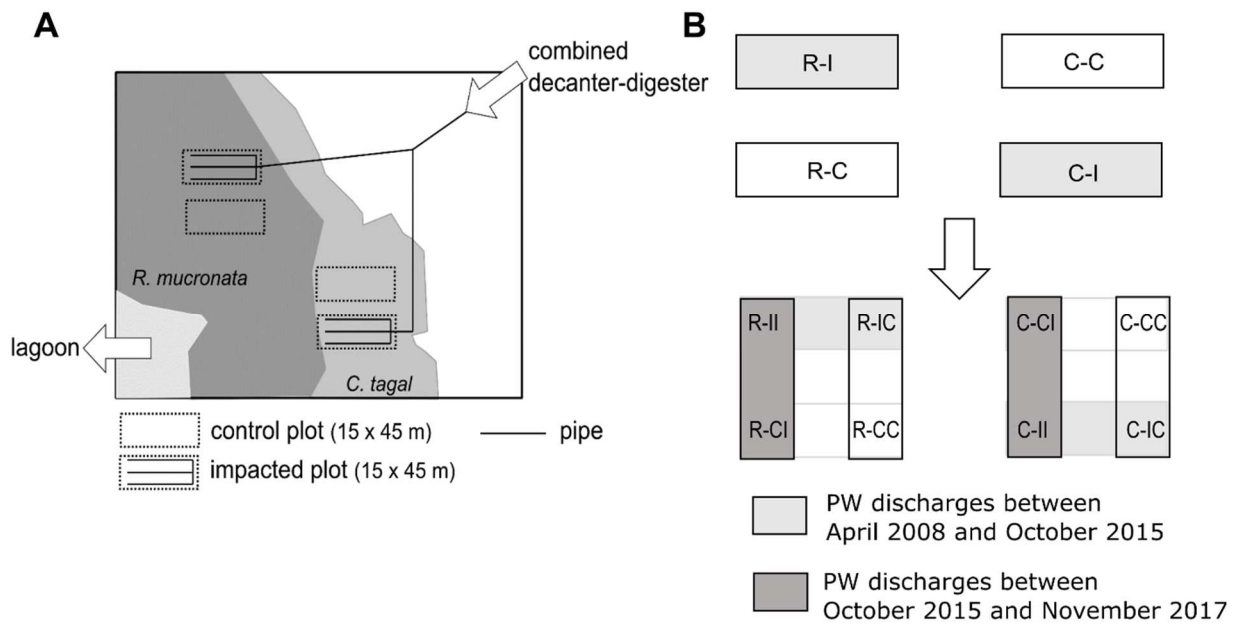
Satellite platform	Acquisition date	Time (UTC 0)	Tide level (m)
PHR 1A	2015-08-11	07:28	1.76 (rising)
PHR 1B	2017-09-11	07:17	2.13 (falling)

**Table 2.** Physical-chemistry of surface water and sediment porewater assessed at T0 and after 24 months (mean  $\pm$  SE, n=4 for *R. mucronata*, n=2-4 for *C. tagal*). C: control area, I: impacted area, CI: areas set-up to study short-term impact, IC: areas set up to study the resilience.

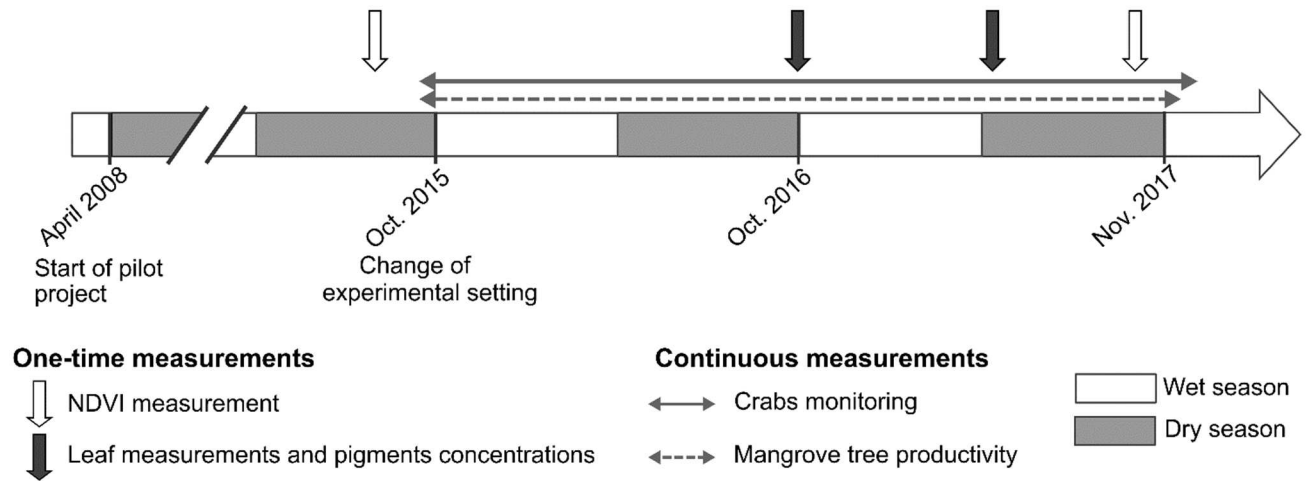
				Temperature (°C)	Conductivity (mS cm <sup>-1</sup> )	Salinity (psu)	PO <sub>4</sub> <sup>3-</sup> (μM)	NH <sub>4</sub> <sup>+</sup> (μM)	NO <sub>3</sub> <sup>-</sup> (μM)	NO <sub>2</sub> <sup>-</sup> (μM)
Surface water	<i>C. tagal</i>	October 2015	C	23.2 $\pm$ 1.2	61.3 $\pm$ 1.6	41.1 $\pm$ 1.3	0.83 $\pm$ 0.01	37.97 $\pm$ 20.28	1.05 $\pm$ 0.21	0.61 $\pm$ 0.11
			I	22.8 $\pm$ 0.2	53.6 $\pm$ 2.7	35.3 $\pm$ 2.0	0.37 $\pm$ 0.15	293.78 $\pm$ 147.20	1.28 $\pm$ 0.64	4.20 $\pm$ 0.08
		October 2017	CC	30.1 $\pm$ 1.8	67.0 $\pm$ 3.45	45.9 $\pm$ 2.75	0.99 $\pm$ 0	0.31 $\pm$ 0.26	0.06 $\pm$ 0.055	0.1 $\pm$ 0.05
			CI	29.3 $\pm$ 2.45	61.9 $\pm$ 1.7	42.4 $\pm$ 1.65	0.40 $\pm$ 0.30	97.06 $\pm$ 75.96	0.58 $\pm$ 0.15	0.70 $\pm$ 0.38
			IC	26.5 $\pm$ 0.05	63.9 $\pm$ 0.45	43.4 $\pm$ 0.35	1.02 $\pm$ 4.56	0.46 $\pm$ 0.05	0.21 $\pm$ 0.77	0.06 $\pm$ 0.01
	<i>R. mucronata</i>	October 2015	C	24.4 $\pm$ 0.1	57.8 $\pm$ 0.5	38.6 $\pm$ 0.3	0.75 $\pm$ 0.28	4.16 $\pm$ 3.78	0.18 $\pm$ 0.10	0.07 $\pm$ 0.01
			I	24.8 $\pm$ 0.4	51.7 $\pm$ 2.5	34.0 $\pm$ 1.8	13.2 $\pm$ 11.17	671.10 $\pm$ 423.06	0.51 $\pm$ 0.10	0.50 $\pm$ 0.12
		October 2017	CC	27.3 $\pm$ 0.10	56.2 $\pm$ 0.10	37.5 $\pm$ 0.05	0.83 $\pm$ 0.03	0.45 $\pm$ 0.12	0.08 $\pm$ 0.08	0.10 $\pm$ 0.01
			CI	26.7 $\pm$ 0.20	55.3 $\pm$ 0.25	36.6 $\pm$ 0.20	0.67 $\pm$ 0.08	10.80 $\pm$ 2.44	0.25 $\pm$ 0.04	0.08 $\pm$ 0.02
			IC	26.8 $\pm$ 0.10	56.3 $\pm$ 0.45	37.4 $\pm$ 0.40	0.42 $\pm$ 0.07	31.26 $\pm$ 0.09	0.99 $\pm$ 0.12	0.42 $\pm$ 0.03
II	26.7 $\pm$ 0.20	54.3 $\pm$ 0.45	35.8 $\pm$ 0.30	5.63 $\pm$ 1.80	141.30 $\pm$ 42.39	0.82 $\pm$ 0.63	0.55 $\pm$ 0.12			
Porewater	<i>C. tagal</i>	October 2015	C	24.8 $\pm$ 0.2	59.1 $\pm$ 2.3	39.5 $\pm$ 1.7	5.93 $\pm$ 1.28	0.38 $\pm$ 0.23	0.35 $\pm$ 0.20	0.06 $\pm$ 0.01
			I	25.0 $\pm$ 0.0	67.3 $\pm$ 0.3	45.8 $\pm$ 0.2	10.79 $\pm$ 2.10	0.14 $\pm$ 0.09	0.39 $\pm$ 0.22	0.07 $\pm$ 0.00
		October 2017	CC	25.6 $\pm$ 0.05	64.7 $\pm$ 0.65	43.9 $\pm$ 0.55	4.02 $\pm$ 1.58	0.08 $\pm$ 0.08	0.15 $\pm$ 0.15	0.10 $\pm$ 0.01
			CI	25.4 $\pm$ 0.20	40.3 $\pm$ 0.65	25.8 $\pm$ 0.45	1.17 $\pm$ 0.26	23.18 $\pm$ 2.77	0.42 $\pm$ 0.31	0.22 $\pm$ 0.10
			IC	25.4 $\pm$ 0.05	69.2 $\pm$ 0.45	47.4 $\pm$ 0.35	24.96 $\pm$ 4.56	0.05 $\pm$ 0.05	0.77 $\pm$ 0.77	0.08 $\pm$ 0.01
	II	25.6 $\pm$ 0.05	67.4 $\pm$ 0.10	46.0 $\pm$ 0.05	37.40 $\pm$ 4.39	476.19 $\pm$ 36.02	0.06 $\pm$ 0.06	0.07 $\pm$ 0.01		
	<i>R. mucronata</i>	October 2015	C	24.8 $\pm$ 0.3	56.0 $\pm$ 0.9	36.5 $\pm$ 0.5	4.56 $\pm$ 2.12	0.20 $\pm$ 0.07	0.24 $\pm$ 0.03	0.08 $\pm$ 0.02
			I	24.8 $\pm$ 0.0	61.8 $\pm$ 2.0	41.6 $\pm$ 1.5	11.79 $\pm$ 2.04	1.31 $\pm$ 0.41	0.16 $\pm$ 0.04	0.06 $\pm$ 0.00
		October 2017	CC	25.5 $\pm$ 0	55.0 $\pm$ 0.10	36.5 $\pm$ 0.05	1.83 $\pm$ 0.05	0.41 $\pm$ 0.34	0.28 $\pm$ 0.11	0.07 $\pm$ 0.01
			CI	25.7 $\pm$ 0.05	53.1 $\pm$ 0	35.1 $\pm$ 0	3.94 $\pm$ 0.34	1.90 $\pm$ 0.54	0.10 $\pm$ 0.10	0.02 $\pm$ 0.02
			IC	25.3 $\pm$ 0.10	65.7 $\pm$ 0	44.6 $\pm$ 0	24.98 $\pm$ 1.2	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	0.09 $\pm$ 0.05
			II	25.4 $\pm$ 0	56.5 $\pm$ 0	37.6 $\pm$ 0	9.57 $\pm$ 0.05	10.68 $\pm$ 0.96	0.10 $\pm$ 0.10	0.06 $\pm$ 0.02

**Table 3.** Mean slopes of the regressions over time for the crab density, Shannon diversity index and proportion of *Perisesarma guttatum* measured on the 4 plots of the different mangrove areas. The letters indicate statistically homogeneous groups (Fisher post-hoc test after ANOVA). (n=4). (CC: control – still control, CI: control – then impacted, IC: impacted – then control, II: impacted - still impacted, NS: non significant).

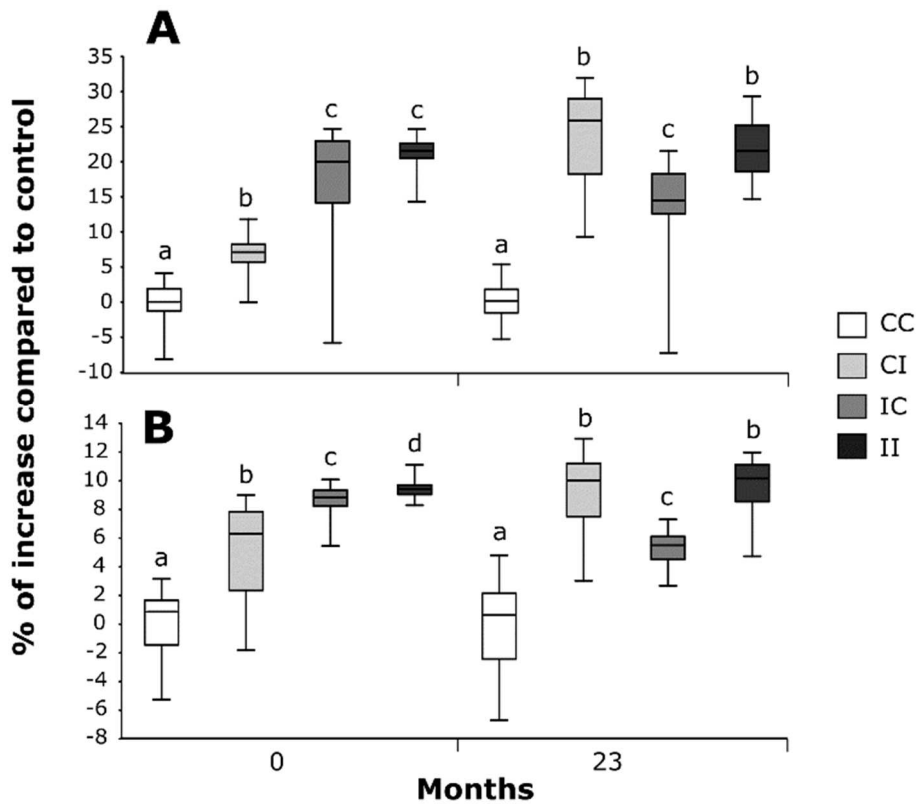
	Crab density		Shannon diversity index		% <i>P. guttatum</i>	
	<i>C. tagal</i>	<i>R. mucronata</i>	<i>C. tagal</i>	<i>R. mucronata</i>	<i>C. tagal</i>	<i>R. mucronata</i>
CC	-0,092 <sup>a</sup>	-0,259	-0,0106 <sup>a</sup>	-0,0136 <sup>a</sup>	-0,002 <sup>a</sup>	0,845
CI	-0,600 <sup>b</sup>	-0,262	-0,0555 <sup>b</sup>	-0,0355 <sup>b</sup>	1,950 <sup>b</sup>	2,032
IC	0,189 <sup>c</sup>	-0,129	0,0018 <sup>a</sup>	-0,0208 <sup>ab</sup>	-0,478 <sup>a</sup>	1,179
II	-0,188 <sup>a</sup>	-0,218	-0,0350 <sup>c</sup>	-0,0217 <sup>ab</sup>	1,892 <sup>b</sup>	1,099
ANOVA	***	NS	***	*	**	NS



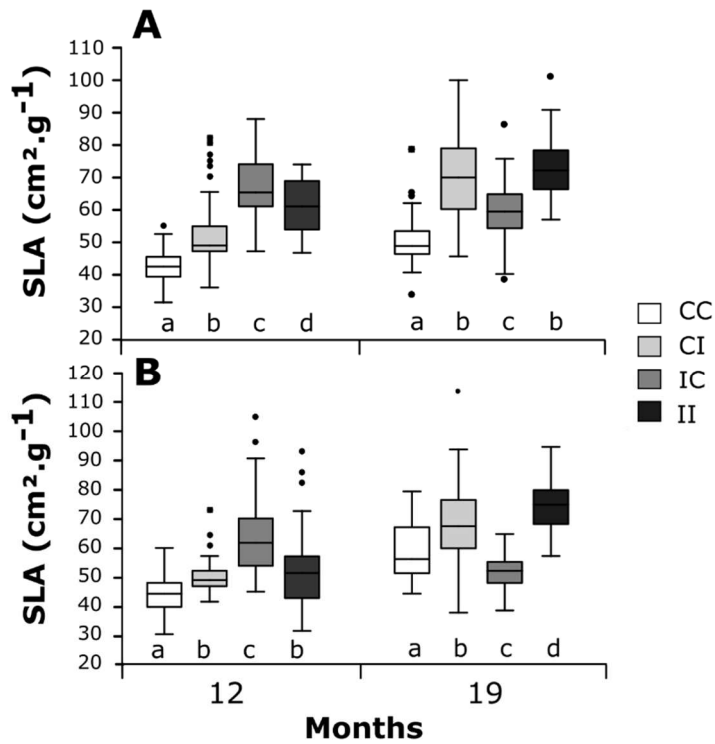
**Figure 1.** Schematic representation of the study site, with the impacted and control areas in the *Rhizophora mucronata* and *Ceriops tagal* mangrove zones and the pipe network (A). Modifications of the areas (I: impacted, C: control, II: impacted - still impacted, CC: control – still control, CI: control – then impacted, IC: impacted – then control) in the *R. mucronata* zone (R-XX) and in the *C. tagal* zone (C-XX) (B).



**Figure 2.** Organization of sampling during the study period from October 2015 (T0) to November 2017.

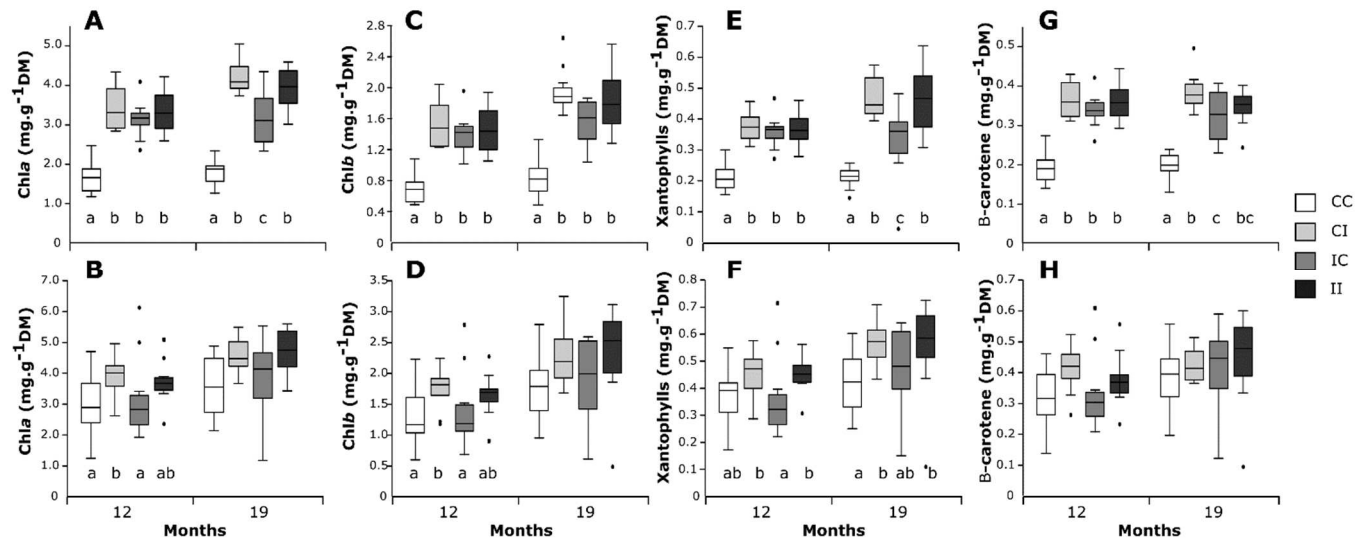


**Figure 3.** Increase percentage of NDVI in all areas compared to the respective control areas (CC), for *C. tagal* (A) and *R. mucronata* (B) mangrove zones, at T0 and after 23 months. The letters indicate statistically homogeneous groups, determined independently for each date (Fisher post-hoc test after ANOVA or Kruskal-Wallis) (CC: control – still control, CI: control – then impacted, IC: impacted – then control, II: impacted - still impacted).

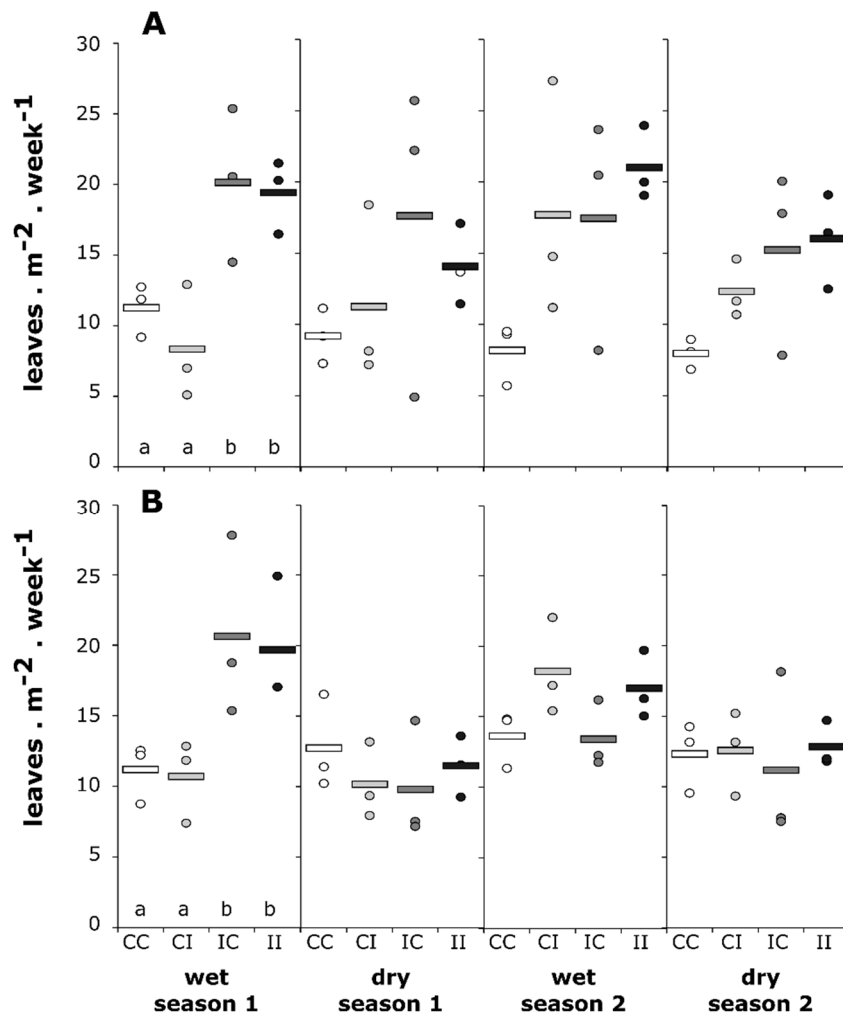


**Figure 4.** Specific leaf area (SLA) of each area for *C. tagal* (A) and *R. mucronata* (B) mangrove zones, measured 12 and 19 months after T0. The letters indicate statistically homogeneous groups, determined independently for each date (Fisher post-hoc test after ANOVA) (CC: control – still control, CI: control – then impacted, IC: impacted – then control, II: impacted - still impacted). (n = 50).

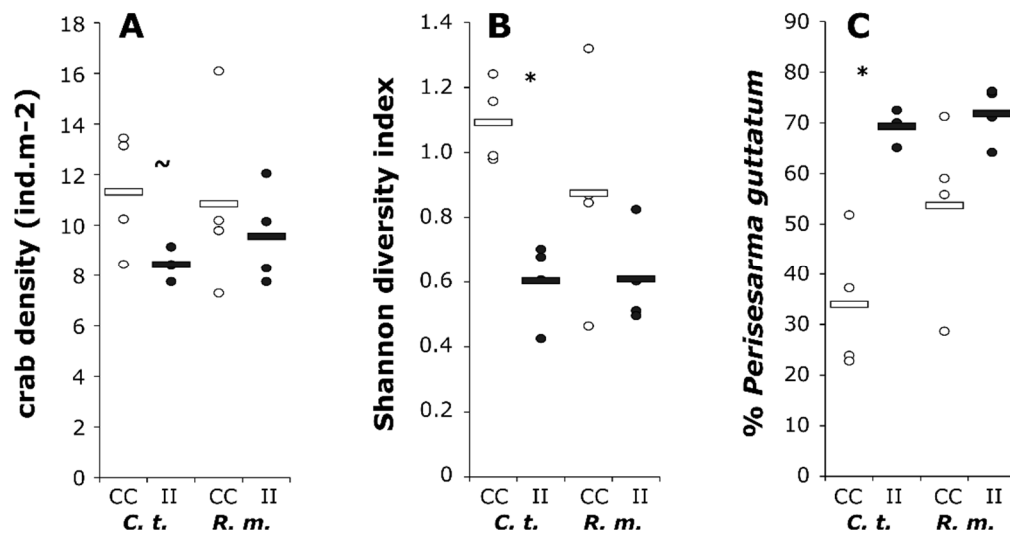




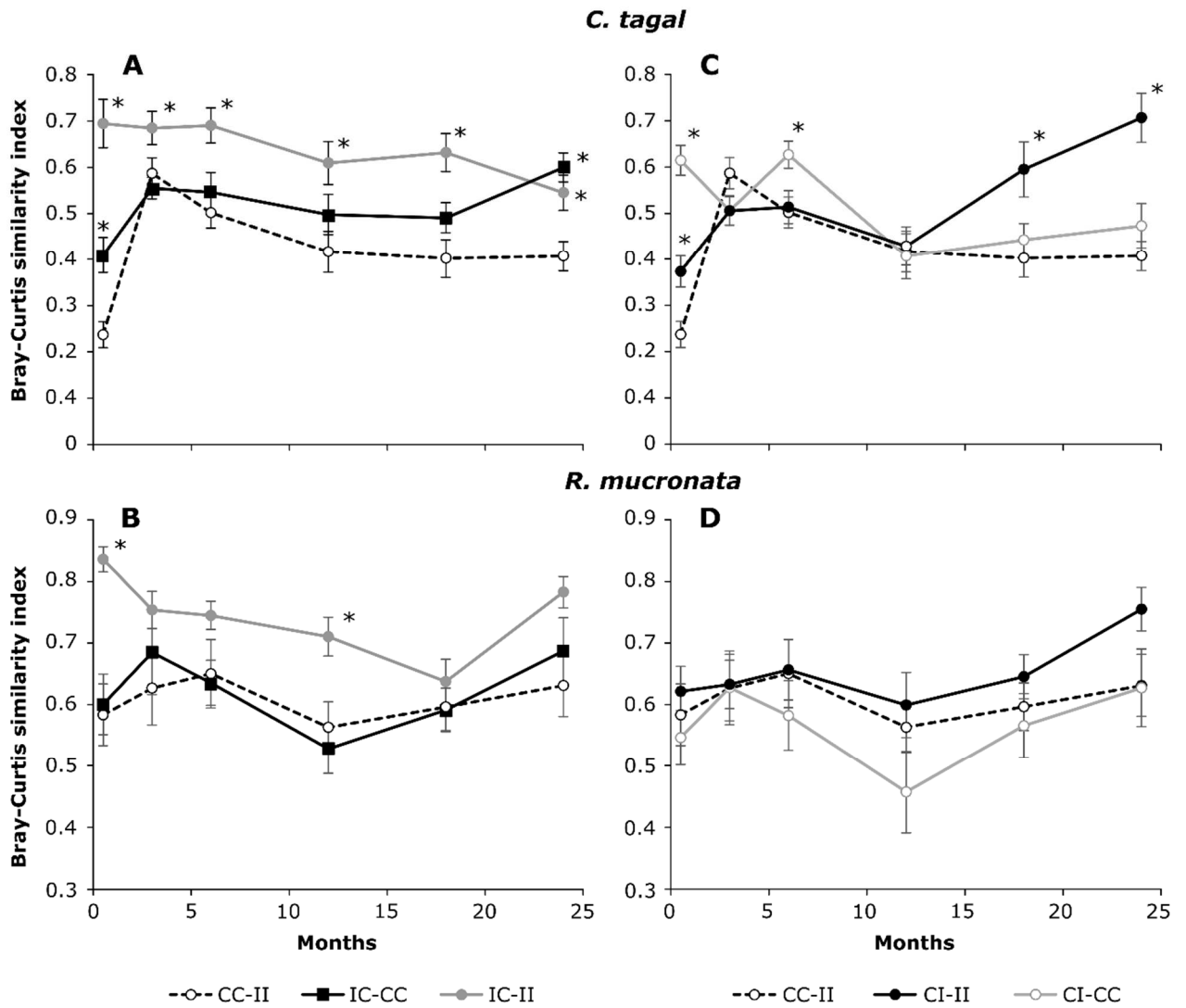
**Figure 5.** Pigment concentrations in all areas of *C. tagal* (A, C, E, G) and *R. mucronata* (B, D, F, H), 12 and 19 months after T0. The letters indicate statistically homogeneous groups, determined independently for each date (Fisher post-hoc test) (CC: control – still control, CI: control – then impacted, IC: impacted – then control, II: impacted - still impacted). No letters for non-significant ANOVA (n = 12).



**Figure 6.** Scatter plot of the leaf productivity of mangrove areas in the *C. tagal* (A) and *R. mucronata* (B) mangrove zones. The mean numbers of leaves per m<sup>2</sup> and per week were calculated during each season of the experimentation period (from October 2015 to October 2017). The letters indicate statistically homogeneous groups, determined independently for each date (Fisher post-hoc test after ANOVA) (CC: control – still control, CI: control – then impacted, IC: impacted – then control, II: impacted - still impacted). No letters for non-significant ANOVA. (the bars represent the means, n = 3).



**Figure 7.** Crab density (A), Shannon diversity index (B) and *P. guttatum* proportion (C) in CC (control – still control) and II (impacted - still impacted) areas in the *C. tagal* (*C. t.*) and *R. mucronata* (*R. m.*) mangrove zones. The points represent the mean of all the measurements made on a plot between November 2015 and November 2017, the bars represent the means of the 4 plots. Asterisks indicate significant differences between CC and II areas. ~ :  $p = 0.057$ .



**Figure 8.** Dynamics of Bray-Curtis similarity index determined after crab community composition between areas in *C. tagal* (A, C) and *R. mucronata* (B, D) mangrove zones. (A, B) highlight of the resilience and (C, D) highlight of the short-term impact. Asterisks indicate significant differences with the similarity index calculated between CC and II areas. (mean  $\pm$  SE, n = 16).