Impacts of Disturbances on Species Specific Interactions between Crabs and Plants in Mangrove Ecosystems

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Chapter 2

Disturbance Strongly Alters Crab-Vegetation Interactions in Mangrove Ecosystems

Abstract

The vegetation dynamics and biogeochemistry of mangrove ecosystems intimately relates to the density and activity of crabs. These ecosystems are often subject to human disturbances, but relatively little is known about the functioning of disturbed mangrove ecosystems in general and the ecological consequences of disturbance in mangrove ecosystems, particularly with respect to mangrove crab-vegetation interactions. We therefore aimed to determine the interrelationships between crab and plant species in disturbed mangrove ecosystems compared to the undisturbed mangrove ecosystems on six islets of the Segara Anakan mangrove forest in Java, Indonesia. The cover of mangrove trees in the disturbed sites was 67% lower compared to the undisturbed sites, while the cover of understory species and unvegetated areas in the disturbed sites was69 % and 15% higher, respectively. We found a 28% lower crab species richness and a 32% lower crab biomass in the disturbed sites. Redundancy Analysis (RDA) on crab species abundances constrained by plant species composition explained 53% of the total variance and vice versa RDA on mangrove vegetation constrained by crab species abundances explained 64% of the total variance. Meanwhile, a RDA on mangrove vegetation constrained by environmental parameters explained 57 % of the total variances. Our results suggest that species-specific crab-plant interactions in the disturbed sites differ dramatically from those in the undisturbed sites, which may amplify the decrease in plant diversity and crab abundance and could destabilize the whole ecosystem, pushing it away from the undisturbed state.

Keywords: mangrove functioning, disturbance, coverage, species richness, abundance, species specific crab-vegetation interaction, Segara Anakan mangrove

1. Introduction

The ecological importance and the functioning of mangrove ecosystems is generally well known and thoroughly studied (Boto and Bunt 1981, Twilley et al. 1986, Daniel and Robertson 1990, Bouillon et al. 2002, Nordhaus et al. 2006, Alongi 2008). Prior to the 1980s, the structure and functioning of mangrove ecosystems was understood as being primarily the result of abiotic processes such as the duration and frequency of tidal flooding (Lugo and Snedaker 1974, Christensen 1978), the salinity regimes (Edward 1978), the properties of mangrove sediment such as its soil texture (Icely and Jones 1978), and nutrient availability (Christensen and Andersen 1977). In line with this paradigm, it was stated that tidal current removed and transported mangrove litter to adjacent ecosystems (Warbuton 1978, Boto and Bunt 1981). In the early 1980s, a shift in paradigm took place (Cannicci et al. 2008) when a number of studies demonstrated that biotic factors (Smith III 1987, Smith III et al. 1991), especially crabs (Robertson 1986, Sousa and Mitchell 1999, Smith et al. 2009), played an important role in both structuring mangrove vegetation and in the functioning of this ecosystem (Smith III et al. 1991, Emmerson and McGwynne 1992, Casariego et al. 2011).

Particularly sesarmid crabs play a significant role in structuring mangrove vegetation by consuming seeds and propagules (Smith III 1987, McKee 1995, Sousa and Mitchell 1999, Bosire et al. 2005), thereby strongly constraining the establishment of new individuals. In addition, several experimental studies demonstrated that crab burrowing activities (Warren and Underwood 1986, Otani et al. 2010) had significant effects on soil chemistry resulting in enhanced mangrove productivity (Smith III et al. 1991, Kristensen 2008, Smith et al. 2009). Finally, and maybe most importantly, a large number of studies on the feeding ecology of crabs (e.g. Asthon, 2002; Imgraben, 2008; Nordhaus, 2011) revealed their critical role in the energy and mass balance of mangrove ecosystems (Robertson,1986; Casariego 2011) by recycling plant biomass and nutrients and by retaining them within the system (Nordhaus, 2006; Chen 2008). Removal and consumption of litter by sesarmid crabs equaled 33% to 80% of the total mangrove primary production (Ashton 2002, Chen et al. 2008, Thongtham et al. 2008). Altogether, this information points to the importance of crab-vegetation interactions, on top of abiotic drivers, in determining mangrove ecosystem dynamics at undisturbed conditions.

However, mangrove ecosystems in many part of the world are increasingly disturbed (Burbridge 1982, Valiela et al. 2001, Alongi 2002). Most apparent are anthropogenic disturbances in the form of tree cutting (Ellison 1996, Sakho et al. 2011). The functioning of disturbed mangrove ecosystem in general and the ecological consequences of disturbance in mangrove ecosystems are less studied and therefore less understood (Field 1998). A few studies evaluated the impact of disturbances on mangrove forest structure and regeneration (Walter 2005), on meiobenthos community (Gheskiere et al. 2005, Dye 2006) and on bacterial diversity (Granek and Ruttenberg 2008). However, there has been no study that examined the coupling of crab-vegetation in disturbed mangrove ecosystems, despite the established importance of crab-vegetation interactions for this ecosystem.

In this study, we therefore aimed to determine the interrelationships between crab species and vegetation in disturbed mangrove ecosystems in comparison to crab-vegetation interrelationships in undisturbed mangrove systems. Specifically we asked whether i) disturbance increases or decreases mangrove tree abundances, understory cover and plant species richness, ii) environmental parameters change with disturbance ,iii) species richness of crabs, their abundance and biomass decrease in the disturbed mangrove, and iv) crab and plant species have species specific co-occurrences. We hypothesized that i) disturbed mangrove system will have lower plant species richness, lower tree cover and higher understory cover, ii) mud depth, salinity, PO_4 and SO_4 will be higher while the silt percentage, clay percentage, organic C content, and concentrations of nitrate and ammonium in mangrove soil will be lower with disturbance, iii) disturbed mangrove ecosystem will have a lower crab diversity, abundance and average biomass compared to the undisturbed mangrove and iv) that while environmental conditions will change upon disturbance, the shifts in plant species composition will be more strongly related to crab species composition than to environmental drivers. To test these hypotheses, we measured and compared the species identities and cover of vegetation and the distribution, abundances and biomass of crabs and environmental parameters in six paired disturbed and undisturbed sites of the Segara Anakan mangrove forest in Java, Indonesia.

2. Methods

2.1. Study area: Segara Anakan mangrove forest

The Segara Anakan forest is a mangrove area located in the Segara Anakan Lagoon, in the South Western part of Central Java, Indonesia. The Segara Anakan Lagoon is an enclosed estuary (Bird 1982) connected to the open sea through two points, one in Cilacap strait in the eastern part of the lagoon and is around 17 km long and one in Selok Jero strait which directly connects the western part of the lagoon to the Indian Sea. Many major rivers-Cibereum, Cikujang, Cikande, Penikel, Dangal, Ujung Alang, Citanduy, Kembang Kuning- and their tributaries carry a lot of sediment from the watershed areas and deposit them in this estuary (Sutomo 1982). These sediments, which largely originate from deforested areas, formed new-land areas which slowly became islets within the lagoon. Mangrove forest grows in these newly-formed lands. In the early 1990s there had at least been 6 main islets which together covered almost halve of the lagoon areas and which all have been occupied by mangrove vegetation. Djohan (2007) reported that in 1997 individuals of the mangrove tree species *Avicennia alba*, *Sonneratia alba*, *Sonneratia caseolaris*, *Rhizophora apiculata*, *Aegiceras corniculatum*, *Xylocarpus granataum* and *Nypha fruticans*, *Rhizophora apiculata* and two understory species comprised of *Acanthus ilicifolius* and *Derris trifoliata* occupied these islets. Recent studies in 2006 found 10 mangrove species in the Segara Anakan Lagoon and 21 mangrove tree species in the eastern part of Segara Anakan area (Hinrichs et al. 2009). Hinrichs (2009) concluded that the Segara Anakan Lagoon mangrove ecosystems have relatively high species richness.

During the last 30 years, most of the Segara Anakan mangrove suffered from continuous and intensive anthropogenic disturbances of tree logging. Since the early 1980s, the Segara Anakan Lagoon mangrove areas have decreased by 50%(Ardli and Wolff 2008). The cutting of *Bruguiera, Rhizophora, Sonneratia* and even *Aegiceras* promoted the understory of *Derris trifoliata* and *Acanthus ilicifolius* to grow and as a result they now occupy large parts of the disturbed areas. Hinrichs (2009) reported that the coverage of *Derris trifoliata* in the Centre of the lagoon reached 45% while in the eastern part of Segara Anakan area *Derris trifoliata* covers 15% of the total area. Another study conducted in 2006 in this area reported that despite the heavy disturbances the Segara Anakan Lagoon the mangrove forests are surprisingly rich in crab species with densities of (28 ± 23) ind. m^{-2} for adult and (18 ± 25) ind. m^{-2} for juvenile crabs (Geist et al. 2012). The co-occurrence of disturbed and undisturbed mangrove systems in close proximity and on individual islets make the Segara Anakan Lagoon ideal to test our hypotheses on the crab-vegetation interrelationships of disturbed vs. undisturbed mangrove ecosystems.

2.2. Study sites

We selected six main islets in the Segara Anakan Lagoon which had already been occupied by mangrove trees for at least 15 years (Figure 1.1). In each of these islets we selected a disturbed and an undisturbed site. Disturbed sites were characterized by the left-overs of cut mangrove trees or dead tree trunks. We excluded newly disturbed areas to avoid temporal bias. Undisturbed sites were characterized by at least 75% mangrove tree cover. To avoid edge effect sand to ensure independence, the distances between the disturbed sites and their respective undisturbed sites was at least 100 meters. All sites were sampled twice. The first measurement was done in September 2010 (dry season) and the second measurement was done in February 2011 (wet season).

2.3. Measurement of plant cover

Four permanent plots of 50 m x 50 m were established in each of the disturbed and undisturbed sites. All together we measured 48 plots. We measured the coverage of each individual tree present within the plots and of all shrubs/lianas of *Derris trifoliata*, *Acanthus illicifolius* and the fern *Acrosticum speciosum*. When *Acanthus illicifolius* and *Derris trifoliata* occurred within a permanent plot, we established 10 subplots of 1m x 1m, put them randomly in the permanent plots, counted the number of individual shoots of *Acanthus illicifolius* and *Derris trifoliata* within each subplot and measured the length of 10 to 12 leaves of *Derris trifoliata* and *Acanthus illicifolius* from each sub plot to reliably estimate their actual coverage.

2.4. Crab collection

A modified enclosure-removal method was used to collect crabs. Two sub-plots of 50cm x 50 cm were established randomly within each of the 48 permanent plots. Due to the relatively small size of the crabs, this plot size was large enough to collect a representative sample. Four acrylic glass plates (50 cm x 25 cm each) were positioned in the sediment of each replicate sub-plot to prevent crabs from escaping. We then collected all crabs present within the subplots. First we collected all crabs outside their burrows. We then cleaned the area from roots or shrubs and dug each burrow up to the depth of 0.75 meter to collect the remaining crabs. All crabs found were kept in collection boxes, and were transferred alive to the laboratory for further measurements.

2.5. Measurement of environmental parameters

We determined a range of environmental parameters within each permanent plot. This included salinity of pore water, using an Atago Master-S 10 M Refractometer and pH of the pore water using the pH tester Hanna HI-98107. Maximum tidal regimes were measured from sediment surface to the highest point of the last tidal water marked on trunks found in the plot. Mud consistency was determined by measuring how deep the researcher (65 kg) sunk into the sediment. The temperature of the mud on the surface, at the depth of 20 cm from the sediment surface and the air temperature below the canopy were measured using a glass mercury thermometer. Soil samples were also collected from each permanent plot using a soil core of 7 cm in diameter to a depth of 20 cm for further physical and chemical analysis.

2.6. Characterization of the crabs

We washed the crabs with fresh water to clean them from the mud and stored them in a refrigerator. We then weighed each individual crab for fresh weight, measured the width and length of the carapace, identified its sex and when it was female we checked whether it was bearing eggs or not. We kept each individual in an envelope and dried them at 60^{o}C for 96 hours. After drying, we measured the dry weights of each individual crab and identified each of them to species according to Campbell (1967), Crane (1975), Davie (1992), Rahayu and Davie (2002), Davie (2003), Kitaura (2006), and Ng et al. (2008).

2.7. Soil sample analysis

The pipette method (Gee and Bauder 1986) was applied to determine the proportion of sand, silt and clay in the sediment. Soil N was determined colorimetrically by a modified method described by Felker (Felker 1977) after a standard Kjeldahl digestion of 2 g of air-dried soil (Bremner and Mulvaney 1982). Extractable P was determined using the colorimetric method of Olsen & Sommers (Olsen and Sommers 1982). Soil ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were determined using the Nessler method. A turbidimetric method was used to determine soil sulphate concentrations (Banwart and Bremner 1976).

2.8. Data analysis

Repeated measurement (RM-)ANOVA was performed in R project with (Ez) library to examine differences in tree cover, shrub cover, and the proportion of open area across the disturbed and undisturbed sites. Within this analysis, disturbance (absence-presence) and sampling period (September-February) were both treated as within-subject factors. All data were analyzed at the plot level, using averages as obtained through the subplot measurements, thus avoiding pseudo replication. A similar analysis was applied to examine differences in crab species richness, total crab abundances, total crab dry weight biomass and the proportion of ovigerous females across the sites and across the two sampling periods. We also analyzed the differences for all individual crab species using the same set-up.

Additionally, Principal Component Analyses (PCA) and Redundancy Analyses (RDA) were performed in R (R Development Core Team 2009), package vegan (Oksanen et al. 2008). First, we submitted the data on plant species composition collected during the two sampling periods from the six undisturbed sites and six disturbed sites all together to a principal component analysis (PCA) to analyze species coexistence patterns and changes therein between the seasons. The same was done for the crab species composition. Subsequently, using the redundancy analysis (RDA), we constrained the patterns of crab abundance and crab biomass by the coverage of the individual plant species from the six disturbed sites and six undisturbed sites. In a second set of RDAs, we constrained the patterns of crab abundance and crab biomass by the environmental parameters collected. We also run a RDA constraining plant species abundance by crab abundance, given that the vegetation-crab interactions are not one-directional. Finally, we also run an RDA on the data set of the undisturbed sites separately from the data set of the disturbed sites to better understand the mangrove crabs-vegetation links as well as to compare the tightness of the constraints between the disturbed and the undisturbed mangrove ecosystems.

3. Results

3.1. Plant species richness and coverage as affected by disturbance

No significant difference was found ($P > 0.05$) in plant species richness between the disturbed and the undisturbed sites and between two sampling periods. However, a significant difference ($P < 0.001$) was found in trees cover with 67% higher coverage in the undisturbed sites compared to the disturbed sites. There was no significant difference between the first and second sampling periods (P = 0.19) nor any interaction between sampling period and disturbance (P = 0.28). Also the RM-ANOVA on the coverage of understory species *Acanthus ilicifolius, Derris trifoliata* and *Acrosticum speciosum* showed significant difference (P < 0.003) with 69% higher understory cover in the disturbed areas. However, again, there was no significant difference between the first and second sampling periods (P = 0.761) and no interaction between sampling period and disturbance (P = 0.309). When taken together, the RM-ANOVA did not show a significant difference (P = 0.66) between the disturbed sites and the undisturbed sites nor between the first and the second sampling periods (P = 0.19) in total plant cover. This result shows that the significant differences between the undisturbed sites and the disturbed sites do not rest in the total cover of plants, but on the replacement of e trees by understory species (Table 2.1; Figure 2.1).

Table 2.1. Average coverage (m^2 ha^{-1}) of mangrove shrubs, mangrove trees and unvegetated areas in the undisturbed areas and the disturbed areas of the six study isletsduring the first (September, dry season) and second sampling period (February, wet season) with Standard Error of the Means.

Mangrove plant species	First sampling period		Second sampling period	
	Undisturbed	Disturbed	Undisturbed	Disturbed
Acanthus ilicifolius L.	463± 146	2058 ± 229	464 ± 146	2038 ± 293
Acrostichumspeciosum Wild.	105 ± 105	0	102± 102	0
Derris trifoliate Lour	221 ± 146	4848 ± 997	214 ± 148	4868 ± 1001
Aegicerascorniculatum (L.) Blanco	1051± 399	45 ± 44	1027± 393	45 ± 44
Avicennia alba Blume	2839± 968	855± 820	2848± 969	856± 820
Bruguieragymnorhiza (L.) Lamk.	38± 38	10±10	0	5 ± 5
Bruguieraparviflora (Roxb) W.& A. ex Griff	1475 ± 1475	0	1483 ± 1483	0
Bruguierasexangula (Lour.) Poir.	41± 41	0	78 ± 78	0
Nyphafruticans Wurmb.	364 ± 225	131 ± 50	367± 228	112 ± 50
Rhizophoraapiculata Bl.	2782± 569	98 ± 78	2584 + 623	95 + 78
Sonneratia alba J. Smith	255 ± 127	58± 23	249± 129	59± 23
Xylocarpusmoluccensis (Lamk.) M. Roem.	38± 38	7± 4	41± 41	7 ±5
Unvegetated/Open area	384± 105	1890 ± 183	534 ± 195	1912 ± 170

3.2. Disturbance altered soil chemical environment parameters

No significant difference (P > 0.05) was found in the maximum tidal regimes, salinity regimes, mud depth, temperature regimes and the proportion of sand and clay between the undisturbed and the disturbed sites (Table 2.2). Significant difference was found only for silt, being higher in the disturbed areas. Differences were found between the two sampling periods with significantly lower mud depth, lower salinity regimes and a lower proportion of silt and a significantly higher proportion of clay for the second sampling period. There was no interaction between disturbance and time. No significant difference was found in the concentration of soil organic C, soil NO_3^-, and soil NH_4^+ between the disturbed and the undisturbed sites. However, significantly lower NH_4^+concentrations were found in the second sampling periods with a significant interaction between time and disturbance. Significant differences were also found for the concentrations of soil $SO_4^{2-}$and soil PO_4^{3-}both between sampling periods and disturbance regime with higherPO_4^{3-}concentrations in the disturbed and first sampling periods and higherSO_4^{2-} concentrations in the undisturbed sites and for the second sampling period, without any significant interaction between disturbances and times.

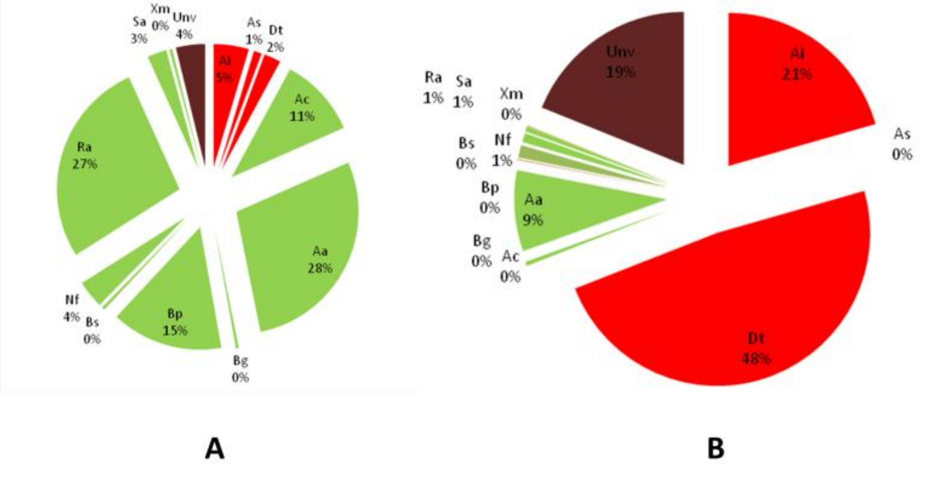


Figure 2.1. The proportion (%) of total coverage of mangrove trees and unvegetated areas (Unv) (brown color) in the undisturbed sites **(A)** and the disturbed sites **(B)** of Segara Anakan mangrove forest, Cilacap, Central Java, Indonesia. Aa: *Avicennia alba*, Ac: *Aegiceras corniculatum*, Bg: *Bruguiera gymnorhiza*, Bp: *Bruguiera parviflora*, Bs: *Bruguiera sexangula*, Nf: *Nypha fruticans*, Ra: *Rizhophora apiculata*, Sa: *Sonneratia alba*, Xm: *Xylocarpus molucensis* (green color), mangrove shrubs Dt: *Derris trifoliata*, Ai: *Acanthus illicifolius*, As: *Acrosticumspeciosum* (red color).

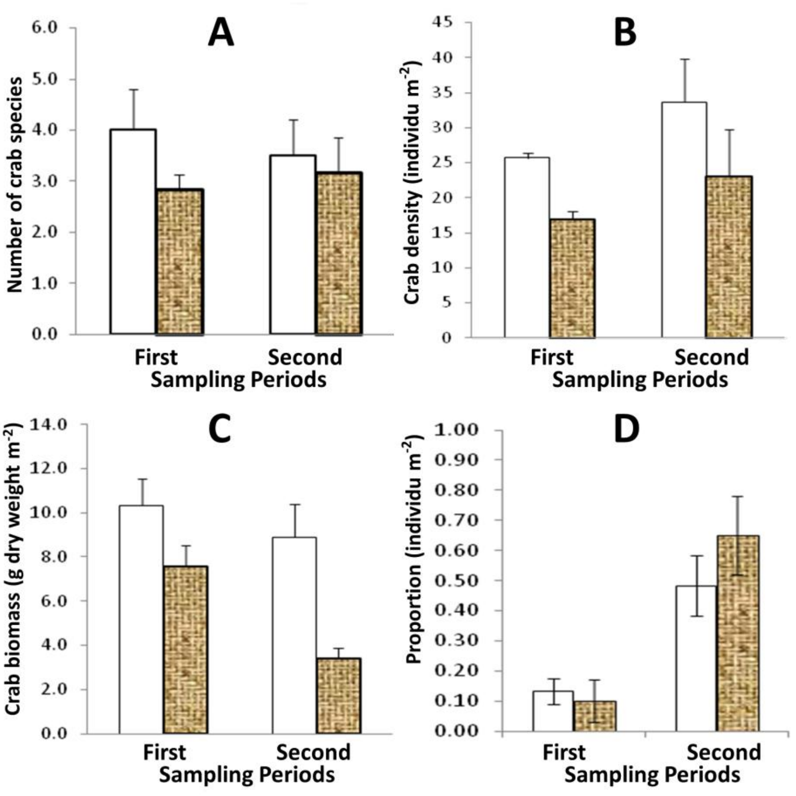


Figure 2.2. Characteristics of crab prevalence as affected by disturbance and season, for a) species richness, b) mangrove crab abundance (indv. m^{-2}), c) mangrove crab biomass (g dry weight m^{-2}) and d) the proportion of ovigerous females in the six undisturbed sites (open) and the six disturbed sites (shaded) during the first and second sampling periods. (Error bars = SEM).

Table 2.2. P values of two-way ANOVAs (with disturbance and time as factors) of the environment parameters measured in the six pairs of the disturbed and the undisturbed areas during the first and second sampling periods. (The asterisk symbol of *= significant to 0.01; ** = significant to 0.001 and *** significant to 0.0001)

Environment Parameters	Disturbance	Time	Time* Disturbance
Mud depth	0.20	0.01 *	0.84
Maximum Tides	0.66	0.08	0.96
Surface soil temperature	0.09	0.51	0.96
Soil temperature at10 cm depth	0.29	0.56	0.82
Ambient temperature	0.45	0.43	0.64
Salinity Regimes	0.98	0.19	0.98
Pore-water pH	0.75	0.25	0.60
Percentage of Sand	0.97	0.45	0.80
Percentage of Silt	0.04 *	0.001 **	0.52
Percentage of Clay	0.06	0.001 **	0.50
Soil Organic Carbon content	0.09	0.60	0.78
Soil Nitrate content	0.58	0.16	0.27
Soil Ammonium content	0.19	0.0002 ***	0.0003 ***
Soil Phosphate content	0.02 *	0.001 **	0.49
Soil Sulphate content	0.004 **	0.001 **	0.68

Table 2.3. The abundance of mangrove crab species (indv. m-2) in the disturbed and undisturbed sites of SegaraAnakan Mangrove forest during the first (September, dry season) and second (February, wet season) sampling period with Standard Error of the Means.

Mangrove crab species	**First Sampling Period**		**Second Sampling Period**	
	Undisturbed sites	**Disturbed sites**	**Undisturbed sites**	**Disturbed sites**
Perisesarma indiarum	18.00 ± 2.54	10.33 ± 2.68	22.66 ± 3.63	12.50 ± 1.33
Paracleistostoma laciniatum	1.67 ± 0.76	0.17 ± 0.17	8.33 ± 3.08	6.50 ± 4.46
Perisesarma semperi	0	3.00 ± 1.24	0.33 ± 0.33	0.66 ± 0.33
Uca coarctata	2.33 ± 0.17	0	0.17 ± 0.17	0.67 ± 0.67
Metaplax elegans	1.50 ± 1.31	1.66 ± 1.66	0	0
Sarmatium crassum	0.67 ± 0.49	0.67 ± 0.42	0.17 ± 0.17	0.66 ± 0.49
Ilyoplax strigicarpus	0.17 ± 0.17	0	0	1.50 ± 1.50
Episesarma singaporense	0.33 ± 0.21	0.83 ± 0.65	0.17 ± 0.17	0.17 ± 0.17
Episesarma versicolor	0	0.17 ± 0.17	1.16 ± 0.60	0.17 ± 0.17
Perisesarma darwinense	0.67 ± 0.49	0	0.17 ± 0.17	0.17 ± 0.17
Grapsus tenuicrustatus	0.17 ± 0.17	0	0.17 ± 0.17	0
Episesarma chengtongense	0	0	0.17 ± 0.17	0
Episesarma mederi	0	0	0.17 ± 0.17	0
Perisesarma bidens	0.17 ± 0.17	0	0	0

3.3. Mangrove crab species richness, abundance and biomass as affected by disturbance

Ten crab species were found in both disturbed and undisturbed sites and four crab species were found only in the undisturbed sites during the two sampling periods (Table 2.3). When analyzing all species together, the RM-ANOVA showed no significant difference (P = 0.45) in the number of crab species present in the disturbed sites and the undisturbed sites nor between the first and second sampling periods (P = 0.87) (Figure 2.2A). In contrast, disturbance significantly (P = 0.02) affected the total abundance of crab species, with the abundance in the disturbed sites being lower (32%) by about 7 individual crab m^{-2} than in the undisturbed sites (Figure 2.2B). There was no significant difference in the abundance of crabs between the first and second sampling periods. This indicates that the differences in crab abundances are not driven by seasonal differences but by disturbance. When analyzing the abundance of each individual crab species, most of the crab species were not affected by disturbance or by season of sampling. Only the abundances of *Perisesarma indiarum* and *Perisesarma semperi* were significantly decreased and increased, respectively, by disturbance (P = 0.005 and P = 0.032, respectively). The strong differences in abundance of sympatric species was confirmed in the PCA analysis (Figure 2.3A), showing that conspecific species within the genera of Perisesarma and Episesarma responded strongly differently to disturbance.

Also for the average crab dry weight biomass there was a trend (P = 0.052) for lower biomass at the disturbed sites compared to the undisturbed sites (Figure 2.2C). Yet, in contrast to crab abundance, there was a significant difference between the first sampling periods and the second sampling periods (P = 0.015), with the first sampling period showing higher crab biomass. We found no significant difference in the proportion of ovigerous crabs between the disturbed and the undisturbed sites (Figure 2.2D), however a significant difference (P = 0.012) was found between the first and the second sampling periods. Yet, there was no interaction between sampling periods and disturbances (P = 0.33) indicated the differences in the proportion of ovigerous crabs were driven by seasonal differences and not by disturbance.

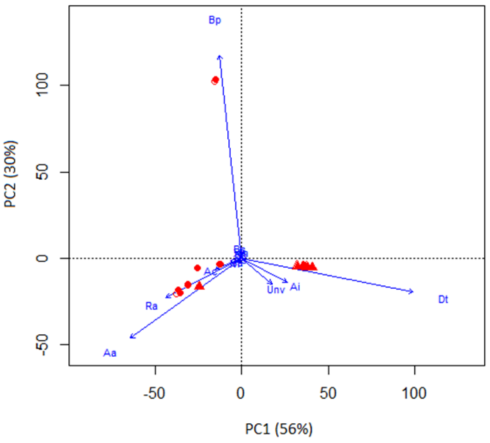
3.4. Species-specific crab-vegetation interactions upon disturbance

The first two axes of the PCA on the coverage of individual plant species across all sites and for both sampling periods, including the coverage of unvegetated areas, (Figure 2.3B) explained 86% of the variance in vegetation distribution. The first PCA axis (57%) shows that the disturbed sites (at the right hand side of Figure 2.3B) are separated from the undisturbed sites (at the left hand side of Figure 2.3B).The disturbed sites are mainly driven by the cover of the understory species *Derris trifoliata*, with secondary influence by *Acanthus ilicifolius* and unvegetated area. The undisturbed sites, in contrast, are most strongly determined by the trees *Avicennia alba, Rhizophora apiculata* and *Aegiceras corniculatum*. One undisturbed site (Site 2) deviated from this pattern and was strongly dominated by trees of *Bruguiera parviflora* and *Bruguiera sexangula*.

The Redundancy Analysis (RDA) on crab species composition as constrained by vegetation explained 53% of the total variance (Figure 2.4A). Vice versa, the RDA on vegetation constrained by crab species composition explained 64% of total variances (Figure 2.4B). These RDAs consistently showed species-specific crabs-vegetation interrelationships within both the disturbed and the undisturbed sites. The disturbed sites with dominance of *Derris trifoliata* and *Acanthus ilicifolius* was linked to *Perisesarma semperi, Episesarma singaporense*, and *Metaplax elegans*. In the undisturbed sites crabs *Paracleistostoma laciniatus, Ilyoplax strygicarpus* and *Metaplax elegans* linked to *Avicennia alba* while *Perisesarma indiarum* always linked to *Bruguiera parviflora* and *Sonneratia alba* (Figures 2.4A and 2.4B). On the other hand, the RDA on the species composition of crabs and vegetation by environmental parameter explained 77% and 74% of the total variance, respectively. When we analyzed the dataset of the disturbed sites separately from that of the undisturbed sites, the RDA on the crab abundances as constrained by vegetation explained 66% of thetotal variance in the undisturbed sites, while in the disturbed sites the RDA explained 56%. This difference was even stronger when constraining vegetation distribution by crab abundance, which allowed explaining 98% of the total variance in the disturbed sites and 84% in the undisturbed sites. These RDA results emphasize the importance of species specific crab-vegetation links in mangrove ecosystems.

4. Discussion

The previously commonly accepted view on the superiority of a-biotic factors in structuring and functioning of mangrove ecosystem has been increasingly challenged by studies showing the strong links between crabs and plant species. Despite the resulting clear shift in paradigm, there has never been any study examining and analyzing to what extent biotic or abiotic factors relate to mangrove vegetation composition. Nor have there been any study related to the impacts of disturbance on the relative importance of these drivers. Through our study design with paired and replicated disturbed and undisturbed plots, we were able to differentiate among these factors. Our RDA results on the interplay between crabs, vegetation and abiotic factors demonstrate their similarly important roles, but at different scales. Environmental drivers differentiate among crab abundances among individual site-sampling period combinations. Mangrove vegetation composition, however, clearly separated crab community composition as affected by disturbance. While crab community composition was strongly affected by disturbance, plant species richness nor richness of the crab community were significantly altered by disturbance. The coinciding drastic changes in plant and crab species composition point to important and species-specific altered links between crabs and vegetation upon disturbance. Moreover, disturbance increased the tightness of crab-vegetation interrelationships with potentially crucial ecological impacts on the functioning of the disturbed system, drifting away from its initial undisturbed state.



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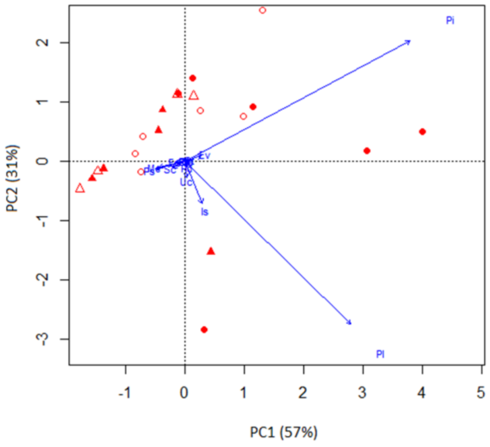

B

Figure 2.3. Principal Component Analysis of **(A)** the cover of individual mangrove plant species and the unvegetated areas, and **(B)** the crab species composition in the disturbed sites (circle) and undisturbed sites (triangle) during the first (open) and second (closed) sampling periods. *Ec = Episesarma chengtongense, Em = Episesarma mederi, Es = Episesarma singaporense, Ev = Episesarma versicolor, Gt = Grapsus tenuicrustatus, Is = Ilyoplax strigicarpus, Me = Metaplax elegans,Pl = Paraclesitostoma laciniatum, Pb = Perisesarma bidens, Pd = Perisesarma darwinense, Pi = Perisesarma indiarum, Ps = Perisesarma semperi, Sc = Sarmatium crassum, Uc = Uca coarctata;* Aa = *Avicennia alba*, Ac = *Aegiceras corniculatum*, Bg = *Bruguiera gymnorhiza*, Bp = *Bruguiera parviflora*, Bs = *Bruguiera sexangula*, Nf = *Nypha fruticans*, Ra = *Rhizophora apiculata*, Sa = *Sonneratia alba*, Xm = *Xylocarpus molucensis* , mangrove shrubs Dt = *Derris trifoliata*, Ai = *Acanthus illicifolius*, As = *Acrosticum speciosum.* Open circle = Undisturbed sites of the first sampling period, open triangle = disturbed sites of the first sampling period, closed circle = undisturbed sites of the second sampling periods, closed triangle = disturbed sites of the second sampling period. Percentages indicate variance explained by each PC axis.

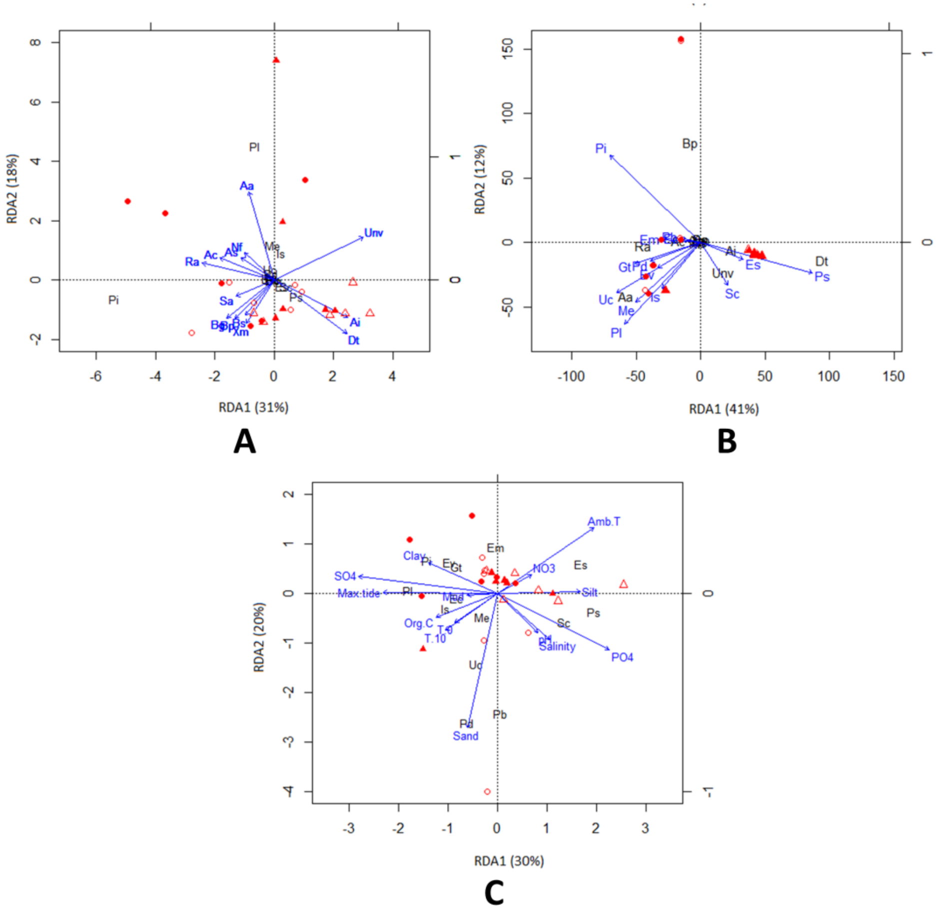

Figure 2.4. RDAs of **(A)** mangrove crabs species abundance constrained by mangrove vegetation coverage, **(B)** mangrove vegetation constrained by mangrove crab abundances, and **(C)** mangrove crab abundance constrained by environmental parameters. Percentages indicate variance explained by each RDA Axis). *Ec = Episesarma chengtongense, Em = Episesarma mederi, Es = Episesarma singaporense, Ev = Episesarma versicolor, Is =Ilyoplax strigicarpus, Me = Meta plaxelegans, Pl = Paraclesitostoma laciniatus, Pb = Perisesarma bidens, Pd = Perisesarma darwinense, Pi = Perisesarma indiarum, Ps = Perisesarma semperi, Sc = Sarmatium crassum, Uc = Uca coarctata;* Aa = *Avicennia alba*, Ac = *Aegiceras corniculatum* Ai = *Acanthus illicifolius*, As = *Acrosticum speciosum,* Bg = *Bruguiera gymnorhiza*, Bp = *Bruguiera parviflora*, Bs = *Bruguiera sexangula*, Dt = *Derris trifoliata*, Nf = *Nypha fruticans*, Ra = *Rhizophora apiculata*, Sa = *Sonneratia alba*, Xm = *Xylocarpus molucensis*, Unv = unvegetated areas. Max. tide = Maximum tidal regimes, Mud = mud depth, T0 = surface soil temperature, T10 = soil temperature in the depth of 10 cm below surface, Amb T = Ambient temperature under the mangrove canopy, Salinity = salinity regimes, Org C = soil organic carbon, NO3 = soil Nitrate, PO4 = Soil phosphate, SO4 = Soil sulphate, pH = pore water pH, Sand = percentage of sand, Silt = percentage of silt, clay = percentage of clay. Open circle = Undisturbed sites of the first sampling period, open triangle = disturbed sites of the first sampling period, closed circle = undisturbed sites of the second sampling periods, closed triangle = disturbed sites of the second sampling period.

4.1. Disturbance did not significantly alter environmental parameters, mangrove plant species richness or crab species richness

Disturbance significantly altered the mangrove vegetation structure by decreasing trees cover and increasing understory cover and open areas in the disturbed sites. In contrast to our hypothesis, disturbance did not significantly alter environmental parameters except for a reduction in the concentrations of soil $SO_4^{2-}$and increasing PO_4^{3-}in the disturbed sites. Most of the environmental parameters being measured varied, however, between two sampling periods indicating their promptness to seasonal dynamics rather than to disturbance (Table 2.3). No significant difference between the disturbed and the undisturbed sites was found for plant species richness and crab species richness despite an actual lower number of plant species (23%) and crab species (28%) in the disturbed sites. The covariates crab and plant species richness are in accordance to the commonly accepted hypothesis that increasing plant diversity provides an increasing number of microhabitats for crabs (Ashton et al. 2003). However, in contrast to that view, the direct impact of environmental factors on biodiversity seems limited given that species richness did not differ between the seasons, whereas environmental variables varied most at the temporal scale.

4.2. Mangrove disturbance significantly decreased crab abundance

In contrast to the crab species richness, crab abundances significantly decreased (32%), coinciding with the decreasing tree cover (67%) and the increasing of understory cover (69%) in the disturbed sites, despite the insignificant difference in the total cover of plants between the disturbed and the undisturbed sites. Little is known about the drivers of crab abundance. So far, results on crab abundance as affected by disturbance are idiosyncratic. We found a decrease in abundance upon disturbance, while Kelaher et al. (1998) and Skilleter (2000) found the increasing number of Ocypodid and Grapsid crabs abundances in disturbed sites compared to undisturbed control sites in Australia and Diele (2012) found no difference in crab abundance upon disturbance in Vietnam.

The decreasing crab abundance upon disturbance in our study (while no effect of season on crab abundances was found), in contrast to those of previous studies, seems mainly due to decreases in the abundance of the most abundant species, *Perisesarma indiarum*, by almost one third compared to its abundance in the undisturbed sites. This result may mirror the direct impact of decreasing *Rizhophora apiculata* and *Sonneratia* *alba* in the disturbed sites, two mangrove plant species with strong links to *Perisesarma indiarum* occurrences in the undisturbed sites.

The decreasing crab abundance upon disturbance may reduce the proportion of mangrove litter being processed (Robertson 1986, Lee 1989, Emmerson and McGwynne 1992) and decrease the available food sources for other taxa such as the bacterial community, deposit feeders, filter feeders as they rely on shredded leaves and feces provided by mangrove crab community (Lee 1997). In the end, the decreasing crab abundance could potentially generate a negative feed-back to the mangrove productivity (Smith III et al. 1991). Last but not least, the decreasing crab abundance will certainly seriously impact the structure of sediments which in turn will not only affect the belowground faunal community, but more importantly could negatively affect the growth and sustainability of tree vegetation (Kristensen and Alongi 2006).

4.3. Mangrove disturbances tighten crab-vegetation species specific links

Our RDAs show that the two most abundant crab species, i.e. the Sesarmid crab *Perisesarma indiarum* and the Ocypodid crab *Paracleistostoma laciniatum* are linked to different vegetation components. *Perisesarma indiarum* is linked to *Rhizophora apiculata* and *Sonneratia alba* while *Paracleistostoma laciniatum* seems associated to *Avicennia alba* (Figure 2.5A). Probably the association of the tiny *Paracleistostoma laciniatum* to *Avicennia alba* is primarily a matter of safety, providing a safe haven within the pneumatophores root system of *Avicennia alba*. Food availability seems of lesser importance given that the distribution of algal biomass does not seem to be correlated to the prevalence of *Avicennia alba* (Beanland and Woelkerling 1983). On the other hand, our finding that *Perisesarma indiarum* was related to the occurrence of *Rhizophora apiculata* coincides with results byYa (2008) who showed that *Perisesarma indiarum* consumed the leaves of *Rhizophora apiculata* more than its sympatric *Perisesarma eumolpe*. Furthermore, this RDA also reveals that even within a genus there are strong differences: the sympatric perisesarmid crabs *Perisesarma indiarum* and *Perisesarma semperi* show differential responses to disturbance as separated by RDA Axis 1 (Figure 2.5A).The *Perisesarma indiarum* was mainly associated to the undisturbed sites, and its conspecific *Perisesarma semperi* more with the disturbed sites. Our study also found that the sympatric Episesarmid crabs *Episesarma singaporense* and *Episesarma versicolor*, while overall equally abundant (Table 2.2), were also separated along opposite directions of the disturbed and the undisturbed sites (Figure 2.5B). Interestingly, while these episesarmid crabs are twice to triple the size of the perisesarmid crabs, they were often found sharing communal burrows with *Perisesarma semperi* in areas dominated by the understory species *Derris trifoliata* or *Acanthus ilicifolius*.

When we analyzed the dataset of the disturbed sites separately from that of the undisturbed sites, it was clear that the expression of mangrove crabs-vegetation links strongly depended on disturbance. Crab species composition was explained better(67%)by vegetation composition at undisturbed sites than at disturbed sites (56%), while on the other hand, vegetation composition was better explained by crab species composition at disturbed (98%) than at undisturbed sites (84%). This difference is probably due to the relatively similar plant species composition upon disturbance, consistently dominated by *Derris trifoliata* and *Acanthus ilicifolius*, which may be relatively easy to constrain. On the other hand, despite similar species richness for individual plots, the beta plant diversity was higher at undisturbed sites. This higher beta diversity might provide better means to constrain crab species composition. Altogether, this implies that crab-species interactions are of a different nature at disturbed and undisturbed mangrove ecosystems. Moreover, these results suggest that the understory species *Derris trifoliata* and *Acanthus ilicifolius* play a decisive role in changing these interactions.

4.4. Implications for the functioning of disturbed mangrove ecosystems and our ability to restore mangrove ecosystems

Mangrove crab-vegetation interactions are highly important, in the undisturbed but even more compelling in the disturbed mangrove systems. While previous studies showed significant correlations between individual mangrove crab species and mangrove vegetation through observations (Dahdouh-Guebas et al. 2002, Lee and Kwok 2002)or feeding experiments in the laboratory or in the field(Ashton 2002, Nordhaus et al. 2006), the interpretation of many of these studies was hampered by unexplained environmental factors. Our results show mangrove crab-vegetation interrelationship as affected by disturbance are independent of environmental variation given that environment factors were mostly unrelated to disturbance but more susceptible to seasonal dynamics. Even more crucial is that mangrove crab-vegetation interactions are highly species-specific: disturbed mangrove ecosystems, with its inherently different vegetation composition, are also characterized by a different crab community. The dominant abundance of *Perisesarma indiarum* (18.00 to 22.66 ind. m^{-2}) -associated with the tree species

Rhizophora apiculata and *Sonneratia alba*-in the undisturbed sites could be the most important ecosystem engineer to retain mangrove primary production within the system. In contrast to this, the species-specific crab-vegetation interactions in disturbed mangrove ecosystems, deviating from those in undisturbed ecosystems, may amplify the direction of change and could destabilize mangrove ecosystems, pushing it away from the undisturbed state for both tree and crab species prevailing at undisturbed conditions. The dominance of *Derris trifoliata* and *Acanthus ilicifolius* in the disturbed sites was linked to the presence of *Perisesarma semperi* and *Episesarma singaporense*. This reflects a strong species turnover within the crab community between conspecific species and contrasts to the commonly accepted yet unproven view that mangrove ecosystem used to have great resilience and easy to recover over disturbances. Instead, our study shows that disturbance on mangrove vegetation significantly alters crab-vegetation links which in turn potentially generate different vegetation composition and therefore a potentially a different ecosystem functioning compared to the existing undisturbed one. These findings are in line with the proposition of Field (1998) that the intrinsic structure and function of disturbed and undisturbed mangrove ecosystems alike could be crucial to understand the complete picture of mangrove ecosystems.

While we did not find a significant impact on total crab species richness, it is likely given the highly species-specific nature of the interactions and on the different nature of those interactions in the disturbed sites, that in the long run the elimination of tree species will cause the local extinction of particular crab species. Our findings that four crab species were absent in the disturbed sites but still present in the undisturbed sites, and that crab abundances decreased in the disturbed sites, support these expectations. This has major implications for efforts that promote and implement ecological restoration of disturbed mangrove ecosystems (Michener 1997, Ellison 2000). Given the species-specific interactions, mangrove restoration may not be the relatively ‘simple’ case of removing the stressors that caused the removal of trees to bring the ecosystem back into, as nearly as possible, its original condition (Field et al. 1998, Bosire et al. 2008). Instead, restoration of the habitat conditions that allow these species-specific interrelationships to prosper may be needed to replace the structural or functional characteristics of an undisturbed mangrove ecosystem. Further study needs to be done to examine how those interrelationships can be best promoted and whether the disturbed mangrove system have the opportunity and potential to recover as closely as possible to its initial undisturbed state.

5. Conclusions

Disturbance did not change crab species richness but significantly decreased crab species composition and altered the nature of mangrove crabs-vegetation links. The species-specific crab-vegetation interactions in the disturbed sites are of a different nature than those in the undisturbed sites. Together, this may amplify the direction of the change and could destabilize the whole ecosystem, pushing it away from the undisturbed state and hampering restoration.

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