

**Impact of typhoon disturbance on key ecosystem engineers in a monoculture mangrove forest plantation, Can Gio Biosphere Reserve, Vietnam**

Diele, K<sup>a,b\*</sup>, Tran Ngoc, DM<sup>c</sup>, Tran, T<sup>c</sup>, Saint-Paul, U<sup>b</sup>, Pham, QH<sup>c</sup>, Geist, S.J.<sup>b</sup>, Meyer<sup>b</sup>, F.W., Berger, U<sup>d</sup>

<sup>a</sup> Edinburgh Napier University, School of Life, Sport and Social Sciences, Edinburgh, EH11 4BN, UK

<sup>b</sup> Leibniz-Center For Tropical Marine Ecology (ZMT), Fahrenheitstr.1, 28359 Bremen, Germany

<sup>c</sup> Faculty of Biology, University of Science, Viet Nam National University, Ho Chi Minh City, 227 Nguyen Van Cu, District 5, Ho Chi Minh City, Viet Nam

<sup>d</sup> Department of Forest Biometry and Systems Analysis, Institute of Forest Growth and Forest Computer Sciences, Technische Universitaet Dresden, Postfach 1117, 01735 Tharandt, Germany

\* Corresponding author. Tel. ++44 131 455 3353; Fax ++44 131 455 2291. E-mail address: k.diele@napier.ac.uk

**Abstract**

Mangrove crabs as key ecosystem engineers may play an important role in the recovery process of storm-damaged forests. Yet, their response to storm disturbance is largely unknown. Here we compare the ground-dwelling brachyuran crab community of intact mangrove stands with that of typhoon gaps having experienced 100% tree mortality. Field work was conducted in two adjacent areas in Can Gio Biosphere

Reserve, southern Vietnam. In each area, an 18-20 yr old monoculture *R. apiculata* stand served as control and was compared with typhoon gaps where downed stems had been removed or left on-site. The gaps were 14 and 20 months old when studied in the dry and rainy season 2008, respectively. Time-based sampling of ground-dwelling crabs with hand or shovel was conducted by 4 persons inside 100m<sup>2</sup> plots during 30 min (7 replicate plots per area, treatment and month). Abiotic (sediment pH, salinity, temperature, grain size, water content, carbon and nitrogen content), and biotic measures (e.g. canopy coverage, woody debris, number of trees, leaf litter) were also taken. Despite complete canopy loss, total crab abundance has not changed significantly (in contrast to biomass) and all 12 species found in the forest were also found in the gaps, demonstrating their robustness. Another 9 gap-exclusive species were recorded and average species number and Shannon diversity were thus higher in the gaps. *Perisesarma eumolpe* was the most abundant species, both in the forest and in the gaps, and a shift from *sesarmids* (typical forest species) to *ocypodids* (more prominent in open areas) has not occurred. The persistence of litter-feeding sesarmid crabs prior to the re-establishment of a mangrove canopy is likely to depend on the availability of woody debris on the ground of the gaps, fuelling a mangrove detritus based food web, rather than one based on microphytobenthos and deposit-feeding ocypodids. The presence of burrowing crabs in the gaps suggests that important ecosystem engineering activities are still performed. However, bioturbation may be reduced as crab biomass and body size was smaller in the gaps. Follow-up assessments and field experiments are needed to understand the crabs' role in processing the woody debris, their long-term community dynamics and possible feedbacks between species shifts and gap regeneration.

**Keywords:** crabs, benthos, community, diversity, tropical storm, climate change, Perisesarma

## 1. Introduction

Tropical storms can severely damage coastal ecosystems such as coral reefs and mangrove forests and several studies suggest that their intensity might increase in the future as a result of anthropogenic climate change (Knutson and Tuleya, 2004; Trenberth, 2005; Webster et al., 2005; Mann and Emanuel, 2006). Mangrove forests are particularly vulnerable to storm disturbance due to their coastal exposure and relatively low structural diversity (i.e. monolayered versus multilayered canopies as in tropical rain forests). While post-storm surveys typically quantify tree damage and vegetation recovery (e.g. Roth, 1992; McCoy et al., 1996; Sherman et al., 2001; Milbrandt et al., 2006; Paling et al., 2008; Smith et al., 2009) no study has yet investigated the impact of large-scale storm disturbance on the invertebrate mangrove macrofauna to our best of knowledge, despite its significant impact on structure and functioning of mangrove ecosystems (for review see Cannicci et al., 2008; Lee, 2008; Kristensen, 2008; Alongi, 2009). Mangrove crabs, for example, are important ecosystem engineers (Kristensen 2008). Most species are exclusively or predominantly ground-dwelling and many construct burrows that significantly modify the topography, physicochemistry and hydrodynamics of the sediment (Warren and Underwood, 1986; Lee, 1998; Smith et al., 1991; Wolanski et al., 2001; Susilo et al., 2005; Kristensen et al., 2008). Many crabs also play a major role in nutrient cycling and energy flow within the forest by processing and retaining substantial parts of the primary production through feeding on leaf litter or microphytobenthos (e.g. Macintosh, 1988; Smith et al., 1991; Robertson et al., 1992; Koch and Wolff, 2002; Werry and Lee, 2005; Nordhaus et al., 2006). Furthermore they

can affect the structure and regeneration potential of mangrove forests by selective propagule predation (e.g. Smith, 1987; Smith et al., 1989; Dahdoud-Guebas et al., 1998; Lindquist et al., 2009). Given the ecological role of mangrove crabs, the lack of knowledge on their responses to tropical storm disturbances is surprising. Depending on their resistance or resilience, mangrove crabs may facilitate the natural re-establishment of vegetation on storm damaged areas, e.g. through continued soil oxygenation which prevents the agglomeration of toxic metabolites in the sediment. If, on the other hand, crab densities are significantly reduced or key species are temporarily lost, natural recovery may be delayed.

The present work investigates the effect of massive typhoon disturbance on the abundance and community composition of ground-dwelling mangrove crabs in Can Gio Mangrove Biosphere Reserve, South Vietnam. Typhoon Durian hit Can Gio in December 2006 and deforested a total of approx. 10 ha of 18-20 yr old *Rhizophora apiculata* plantations in the southern part of the reserve. Crabs were sampled 14 and 20 months after the typhoon event by searching the ground, the lower parts of tree trunks and underneath dead wood inside 100m<sup>2</sup> during 30 min. Given the drastic environmental changes imposed by the typhoon, it is hypothesized that species number, diversity, evenness as well as crab abundance and biomass differ significantly between intact forest and gaps. Furthermore, we predict a shift in the community of benthic crabs from a dominance of leaf litter consuming grapsoid species in the forest to a dominance of deposit-feeding ocypodoids in the gaps.

The study complements a larger Vietnamese project focussing on the recovery of mangrove vegetation in the typhoon gaps, the decomposition of woody debris and changes in sediment properties. The overall aim of the research is to describe and

understand processes and rates of floral and faunal recovery on the storm damaged sites.

## 2. Methods

### 2.1 Study area

Can Gio Mangrove Biosphere Reserve (10°22'-10°40' N, 106°46'-107°00'E) spans approx. 75.000 ha and is located 65 km south from Ho Chi Minh City in southern Vietnam (Fig. 1). The tidal regime is predominantly semi-diurnal (Van Loon et al., 2007), ranging from 2 m at mean tides to 4 m at spring tides (FAO, 1993). The climate is monsoonal with a dry season from November to April and a rainy season from mid-April to September. Average annual precipitation is approx. 1,336 mm, potential evapotranspiration amounts to 4 mm/day and mean annual relative humidity is 80% (FAO, 1993). During the Second Indochina War, more than 90% of the natural mangroves in Can Gio were destroyed (Tran et al., 2004). In 1978 replanting began, mostly with *Rhizophora apiculata*, for the production of charcoal, poles and firewood (FAO, 1993). In 2000, the area was declared an UNESCO Biosphere Reserve. Since then, harvest rotation of the monoculture mangrove plantations is no longer performed which has increased the risk of simultaneous diebacks and storm damage (see Vogt et al., in press).

*Insert Fig. 1*

*Insert Fig. 2*

In December 2006, typhoon Dorian deforested approx. 10 ha in total of 18-20 years old *R. apiculata* stands (personal communication V.N. Nam) in the southernmost part of the reserve (Fig.1), creating several large canopy gaps. We worked in gaps situated in two adjacent areas named D1 and D2, separated by a 70 m stretch of intact *Rhizophora* forest. D2 was located closer to a larger tidal channel than D1 (Dong Hoa river, Fig. 1), otherwise the environmental setting of the two areas was similar. Two types of gaps were sampled, Gcut (in D1 and D2) and Gnat (only present in D1). In Gcut gaps all downed stems had been removed by the Can Gio Forestry Department (Fig.2). Only de-rooted or broken tree stumps were left on the ground as well as large amounts of coarse woody debris (broken branches and wood chips). In Gnat all stems had been left on-site (Fig.2). The size of Gnat was approx. 23,800 m<sup>2</sup>, D1 Gcut measured 22,000 m<sup>2</sup> and D2 Gcut about 5,000 m<sup>2</sup>. In each area, the crab community of an intact *R. apiculata* forest to the north of the gaps was sampled as a control (D1 F and D2 F, Fig. 1). F, Gcut and Gnat are regarded as experimental treatment levels with F acting as control (i.e. no typhoon disturbance).

## 2.2 Crab sampling and identification

Ground-dwelling crabs were sampled in D1 and D2 in March and September 2008 and thus 14 and 20 months after the typhoon incidence, respectively (for simplicity, in the following we mostly use the term “crabs”, rather than “ground-dwelling” or “benthic” crabs). Seven independent 100m<sup>2</sup> replicate plots were sampled per treatment in each area and month (70 replicate plots in total). Plots were chosen randomly except that a minimum distance of 10 m was kept between them to avoid interactions. Furthermore mud banks near tidal creeks (swimming crabs and ocy podids abundant, but sesarmid crabs generally lacking in this open habitat) were deliberately excluded to decrease variance between replicates. To reduce potential bias caused by progressing moon

phases during subsequent field days, sampling of the seven replicate plots per treatment was distributed evenly over the time span of each field trip. Crabs were captured during daytime ebb tides, when the ground was not inundated. Preliminary observations in July 2007 and at the onset of the sampling in 2008 had shown that crabs were active on the sediment surface at all sites during this tidal phase.

The aim was to determine whether the relative abundance and species composition of ground-dwelling crabs differs between the typhoon gaps and the intact forest. Therefore we could refrain from destructive and labour-intensive methods such as excavating and sieving sediment required for an absolute quantification of the crab fauna. Instead, we employed a modified version of the semi-quantitative time-based sampling method developed by Ashton (1999; Ashton et al., 2003 a and b). Each 100m<sup>2</sup> replicate plot was sampled by a team of four people during 30 min, generating an index of abundance (sensu Ashton), rather than reflecting true crab density. This method underestimates true abundance/biomass, but the index can be used as a minimum estimate. The total catch per plot was then used for comparisons. Dense roots in the forest and deadwood in the gaps similarly hampered crab capture and we therefore applied a combination of (i) hand-catching specimens active on the sediment surface or escaping onto lower parts of tree trunks and on roots, (ii) poking cryptic specimens between roots, under deadwood or in burrows with a shovel or stick, (iii) applying gentle pressure onto the sediment to “squeeze” subsurface crabs up to the surface and (iv) paying extra attention to rarer, cryptic or fast-moving species to reduce bias in favour of the more conspicuous and catchable ones. The sampling focussed on specimens with a carapace width (CW)  $\geq$  5 mm. During the 30 min sampling intervals, the collected crabs were sedated in plastic beakers filled 1/3 with ice-chilled estuarine water to avoid stress related limb-losses. Later on, the catch was washed in ambient water and placed in bags into ice boxes. Back in the provisional field laboratory crabs were sorted to species level

using published identification keys (see below) and the total wet weight per species was taken. All crabs were frozen at -20°C and defrosted again several months later, when the CW of each crab was measured to the nearest 0.1 mm and individual wet-weights were measured to an accuracy of 0.01 g.

The species were identified using a Zeiss dissecting microscope and the following literature: Tweedie, 1949; Campbell, 1967; Serene and Soh, 1967 and 1970; Crane 1975; Dai and Yang, 1991; Davie, 1992; Yang and Sun, 1993; Tan and Humphreys, 1995; Ng, 1998; Rahayu and Ng, 2003. Nomenclature was based upon Systema Brachyurorum Part 1 (Ng et al., 2008). A reference collection containing individuals of every species is kept at the Leibniz Center for Tropical Marine Ecology, Bremen, Germany.

### 2.3 Environmental parameters

Unless otherwise stated, random triplicate sediment samples were taken in each replicate plot with a small plastic corer (50 ml) inserted 8-10 cm into the substrate. The subsamples were pooled and homogenized prior to further processing.

- *Grain size*: The homogenized sample was frozen at -20°C and analysed three times with a Laser Particle Size Distribution Analyser (HORIBA LA-300).
- *Porewater salinity*: Salinity was calculated from conductivity data, measured with a TetraCon 96 electrode (WTW Germany). Prior to measurements 5 g of each sediment sample was dissolved in 25 ml distilled water.
- *pH of the sediment*: Measurements were made with a Sensolyt SE electrode (WTW, Germany) inserted into the sediment containing porewater.



- *Sediment water content*: The homogenized sample was weighed wet, dried to constant weight at 60 °C and re-weighed. Water content was calculated from the difference between wet and dry weight.
- *Sediment organic carbon ( $C_{org}$ ) and total nitrogen (N)*: Triplicate samples were scraped off the sediment surface and frozen at -20°C until further analysis. The thawed sediment was mixed and 1 N HCL added to remove inorganic carbon. After drying at 40°C the sediment was analysed in an elemental analyser (Carlo Erba NA 1100).
- *Temperature*: Sediment temperature (at 10 cm depth) and air temperature were logged with HOBO data loggers (UA-002-08) placed in the forest (D1F) and gap (D1Gcut) over 6 days in September 2008.
- *Estimate of canopy coverage, root ground coverage and woody debris ground coverage*: visual estimation for each 100 m<sup>2</sup> replicate plot according to the following categories: 0%, 25%, 50%, 75%, 100%.
- *Trees*: Total number of live trees was counted in each 100 m<sup>2</sup> plot
- *Leaf litter and mangrove re-growth*: The number of fallen leaves, of mangrove recruits < 50 cm height and of mangrove recruits ≥ 50 cm <1m height was counted in three 1 m<sup>2</sup> quadrats inside each 100m<sup>2</sup> replicate plots.
- *Tree stumps and downed stems*: The total number of downed stems and stumps was counted for each 100m<sup>2</sup> plot.

## 2.4 Data analysis

Univariate measures used for describing the crab fauna were abundance (AB), biomass (BM) and species number (S) and, for diversity, the Shannon-Wiener Index ( $H'$ ) and Pielou's Evenness Index ( $J'$ ), both based on the mean abundances of crabs. The

programme STATISTICA (release 6) was used to detect differences between areas, treatments and months. A two or three factorial analysis of variance (ANOVA) was performed for homogeneous- (Levene's test) and normally distributed data (Shapiro test). Tukey's HSD test was applied for post hoc comparisons. Univariate data that were not normally distributed and failed homogeneity despite transformation were tested with the non-parametric Mann-Whitney U test (MW-U) or Kruskal-Wallis test (KW).

The crab community structure was analysed with non-parametric multivariate tests using the software PRIMER (release 6, Primer-E Ltd.). Similarity matrices were constructed employing the Bray Curtis similarity measure after fourth root-transforming the data to reduce the effect of the highly dominant species. The relationship between samples based on two dimensional ordination of similarity matrices calculated from mean values is presented by non-metric multidimensional scaling plots (nMDS).

Differences between areas, treatments and months were tested using a one-way or two-way- analysis of similarities permutation routine (ANOSIM). The similarity percentage routine (SIMPER) was applied to identify which species contributed most to the observed differences in the community composition.

Abiotic data were normalized ( $\log_{10}$ ) when necessary and similarity matrices constructed employing the Euclidean distance similarity measure. The routine BEST/BIOENV (Biota and/or Environment matching, using Spearman rank correlation) was used to identify the set of environmental parameters which best explained the crab community composition. To test whether significant correlations were positive or negative a Poisson-regression was performed for crab abundance data and the determining environmental parameters.

### **3. Results**

### 3.1 Crabs

#### 3.1.1 Species numbers, dominance structure, abundance/biomass and diversity

A total of 21 benthic brachyuran crab species were recorded in the 70 replicate plots sampled in *R. apiculata* forest stands (F) and the typhoon gaps Gcut and Gnat. All species except one belonged to the superfamilies Grapsoidea (n = 12) and Ocypodoidea (n = 8) (see Table 1). In March, 14 species were caught, whereas 20 were found in September (Fig. 3). In the forest plots, a total of 12 species was recorded (March and September pooled), all of which were present in the gaps also. An additional nine gap-exclusive species were found, and one, *Metaplex elegans* (# 13 in Fig. 3), was very frequent in both Gcut and Gnat (Fig. 3). Many species, particularly those first recorded in September, were only infrequently encountered (in < 25% of the plots per treatment; Fig. 3).

*Insert Fig. 3*

Altogether 8532 crab specimens were captured (F = 3557; Gcut = 3290; Gnat = 1685). The largest number caught per 30 min catching period and 100m<sup>2</sup> plot was 250 (in D2 F, September), weighing 1.2 kg in total. The rank species dominance curve for crab abundance shows a steep increase, indicating that few species contributed to the total catch (Fig. 4): 89 to 90% of the specimens captured in the forest and 72 to 75% in the typhoon gaps belonged to only two species. The species ranked as 1 was always identical (*Perisesarma eumolpe*), while the identity of the secondly ranked species differed. The rank dominance results for biomass are similar: Two species contributed 91% and 72 to 80% of the crab biomass in the forest and in the typhoon gaps, respectively.

*Insert Fig. 4*

*Insert Table 1*

*Insert Table 2*

A three-factorial ANOVA for univariate crab measures listed in Table 2 with area, treatment (only F and Gcut included due to absence of Gnat in D2) and month as factors give the following results (no interactions between factors unless stated): *Crab abundance* did not differ significantly between treatments or months, but more crabs were captured in D2 than at D1 ( $F = 21.54, P < 0.0001$ ). The interaction between area and treatment was significant ( $F = 8.36, P < 0.01$ ) as the number of crabs caught in F was higher in D2 than in D1 ( $P < 0.001$ ), more crabs were caught in D2 Gcut than in D1 F ( $P < 0.05$ ) and also in D2 F than in D1 Gcut ( $P < 0.01$ ). *Crab biomass* differed significantly for all three factors (area, treatment, month). Biomass values were higher in F than in Gcut ( $F = 110.52, P < 0.0000$ ), higher in D2 than in D1 ( $F = 43.69, P < 0.0000$ ) and higher in September than in March ( $F = 5.87, P < 0.05$ ). In contrast, *average species numbers* were significantly lower in F than in Gcut (MW-U,  $U = 145.5, P < 0.0001$ ), while differences between areas or between months (except for F D2, March lower than September: MW- U,  $U = 6.0, P < 0.05$ ) were insignificant for this parameter. The same pattern was observed for *Shannon diversity* ( $F = 8.40, P < 0.01$ ). No significant differences were observed for Pielou's *evenness* for any of the three factors (Table 2).

For D1 a separate two-factorial ANOVA was performed to account for the presence of the additional treatment category Gnat in this area. Again, *crab abundance* did not

differ between treatments or months. *Crab biomass* differed significantly between treatments (Table 2). It was higher at F than in Gcut and Gnat ( $F = 37.24$ ,  $P < 0.0000$ ), but similar for the two typhoon gaps. Biomass did not differ between months, but the interaction between treatment and month was significant ( $F = 4.43$ ,  $P < 0.05$ ): Crab biomass in the forest (both months) was higher than in Gcut in March and also higher than in Gnat in March and September. *Average species numbers* differed significantly between treatments (KW,  $H = 11.38$ ,  $P < 0.01$ ). It was lower in F than in Gcut (MW-U,  $U = 37.5$ ,  $P < 0.01$ ) and Gnat (MW-U,  $U = 34.5$ ,  $P < 0.01$ ) while Gcut and Gnat did not differ significantly. No difference in average species numbers was observed between months. *Shannon diversity* in F was significantly lower than in Gcut ( $F = 6.68$ ,  $P < 0.01$ ), while Gcut and Gnat as well as March and September had similar values. Pielou's *evenness* differed significantly between treatments in September, when it was higher in Gcut than in F (MW-U,  $U = 4.0$ ,  $P < 0.01$ ) and than in Gnat (MW-U,  $U = 8.0$ ,  $P < 0.05$ ).

The overarching pattern emerging from the above ANOVA analyses is: (i) While *total crab abundance* was similar in all treatments, *total crab biomass* in F was higher than in the typhoon gaps, (ii) *average species number* and *Shannon diversity* were generally higher in the typhoon gaps than in the forest and (iii) D2 had a higher *total crab abundance* and *biomass* than D1.

### 3.1.2 Species identities and crab community composition

From the 21 species encountered in total, only one, *Perisesarma eumolpe*, was found across all 70 plots and another one, *Clistocoeloma merguense*, was encountered in all but three plots (Table 1). Five species occurred in more than 50% of the plots (*Uca forcipata*, *Episesarma palawanense*, *Parasesarma plicatum*, *Paracleistostoma sp. 1*, *Uca flammula*) and 12 were found in  $\leq 10\%$  of the plots (Table 1). The crab species with the highest total abundance (all plots pooled together) was *P. eumolpe* ( $n = 5470$ , 64%

of the total), followed by *P. plicatum* (n = 707), *U. forcipata* (n = 659), *C. merguense* (n = 577), *Metaplex elegans* (n = 397) and *U. flammula* (n = 244) (Table 1). These six species contributed 94% of the total catch. *P. eumolpe* also presented the greatest biomass in total (15.7 kg, 67.4% of the total), followed by *P. plicatum* (2.9 kg), *U. forcipata* (1.5 kg) and *E. palawanense* (1.3 kg). Together these four species contributed 91.5 % of the total biomass (Table 1).

A total of 86 % of all specimens caught belonged to the superfamily Grapsoidea. They dominated in all areas and treatments, both in terms of abundance and biomass (Fig. 5, highlighted in green tones). Of all crabs captured in F, Gcut and Gnat, 98%, 72% and 66% were sesarmids, respectively. The superfamily Ocypodoidea contributed only 14% to the total catch (Fig. 5, highlighted in yellow). In F, 2% of all crabs were ocypodoids versus 24% in Gcut and 20% in Gnat (Fig. 5).

*Insert Fig. 5*

*Insert Fig. 6*

Figure 6 shows the nMDS ordination of fourth-root transformed crab abundance data. The biomass ordination (not plotted here) has a near-identical pattern (stress 0.18). Two main groupings are highlighted by an overlaying cluster of 60% similarity. One is dominated by the forest plots (F) and the other by the gap plots (Gcut and Gnat). The two groups are intersecting, mostly due to similarities between several F and Gnat plots in area D1. Within the forest group, D2 plots are generally less distant to each other than to plots in D1, and vice versa.

ANOSIM-results on the similarity matrix for crab abundance support the pattern shown by the nMDS: While crab communities at Gcut were similar across months, they differed significantly from those at F (two-way ANOSIM, Gnat excluded: R values 0.51 to 0.94,  $p < 0.001$ ). In area D1, average dissimilarity between Gcut and F across both months was 39.7%. The fiddler crabs *U. flammula* and *U. forcipata* contributed most to this difference. Both species were much more abundant in the gaps than in the forest (Fig. 5). *M. elegans*, the third most important discriminator, exclusively occurred in Gcut (and Gnat, see below) (Fig. 5). In area D2, average dissimilarity between Gcut and F was slightly higher with 43.0 %. Key discriminators, in decreasing importance, were *M. elegans* (absent in the forest), *U. forcipata* (more abundant in the gap), *P. plicatum* (more abundant in F) and *U. flammula* (more abundant in the gap) (Fig. 5). Crab communities at Gcut did not differ significantly between areas. In contrast, as suggested by the nMDS, differences between forest plots at D1 and D2 were significant ( $R = 0.52$ ,  $P < 0.001$ ). However, with 28.1% community dissimilarity was much smaller than between F and Gcut. The most important species discriminating D1F and D2 F were *P. plicatum* (more abundant in D2F), *U. forcipata* and *E. palawanense* (both more abundant in D1F) (Fig. 5).

For the crabs sampled in area D1, an additional one-way ANOSIM, now including the treatment Gnat was calculated. As with crab community differences between Gcut and F ( $R = 0.67$ ,  $P < 0.001$ , 40.2% dissimilarity, for discriminating species see text above), Gnat also differed from F (area D1 only, one-way ANOSIM:  $R = 0.47$ ,  $P < 0.001$ , 37.4% dissimilarity). *M. elegans* (absent in F), *Pachygrapsus sp. 1* (more abundant in Gnat), *E. palawanense* (more abundant in F) as well as *U. flammula* and *U. forcipata* (more abundant in Gnat) were the main discriminators (Fig. 5). Crab communities at Gcut and Gnat were statistically similar in March, but differed in September ( $R = 0.50$ ,  $P < 0.05$ , average dissimilarity 37.6%). *M. elegans* and *P. sp 1* were more prominent in

Gnat and the fiddler crabs *U. flammula* and *U. forcipata* more dominant in Gcut. The ANOSIM results for crab biomass data were fully concordant with the above abundance data.

The following main pattern emerges from the multivariate analysis: (i) the communities of ground-dwelling crabs in the forest differed from the ones in the gaps with *U. flammula*, *U. forcipata* and *M. elegans* as main discriminators, all three being more abundant in the gaps, (ii) communities in areas D1 and D2 differed for F (more *P. plicatum* in D2), but not for Gcut and (iii) percent dissimilarities were always lower than percent similarities, likely due to the overall dominance of *P. eumolpe*.

### 3.1.3 Total abundance and biomass and individual size and weight of *P. eumolpe*

From all crabs caught in F, Gcut and Gnat, 73%, 58% and 57% belonged to the species *P. eumolpe*, respectively. Its average abundance was significantly higher in F than in Gcut and in area D2 than in D1 (3-factorial ANOVA, Gnat excluded;  $F_{\text{treatment}} = 9.42$ ,  $P < 0.01$ ;  $F_{\text{area}} = 8.87$ ,  $P < 0.01$ ) (Table 3). Similar differences between treatments and areas also existed for biomass ( $F_{\text{treatment}} = 96.0$ ,  $P < 0.0000$ ;  $F_{\text{area}} = 16.16$ ,  $P < 0.001$ ), while across months, abundance and biomass of *P. eumolpe* was similar. When comparing the three treatments in D1, differences were only significant for biomass, which was higher in F than in the two gaps (2-factorial ANOVA,  $F = 1.87$ ,  $P < 0.0001$ ).

The largest *P. eumolpe* in F had a CW of 27.53 mm. In Gcut and Gnat maximum sizes were 24.73 mm and 24.49 mm CW, respectively. Average crab size was significantly larger in F than in Gcut, in both areas (MW-U,  $p < 0.001$ ) (Table 3). Forest crabs were also larger than those in Gnat (MW-U,  $p < 0.001$ ), while Gcut and Gnat had similar sized crabs. Area comparisons demonstrate that Gcut crabs were larger in D2 than in D1, in both months (MW-U,  $p < 0.0000$ ). Forest crabs were also larger in D2 in March (MW-U,  $p < 0.001$ ). Between-months-comparisons show that forest crabs were



smaller in March than in September (MW-U,  $p < 0.0000$ ), in both areas. Likewise, D1Gcut crabs were also smaller in March (MW-U,  $p < 0.0000$ ). Crabs from D2 Gcut as well as those from D1Gnat did not differ in size between months. The pattern for individual weight was the same as for size (Table 3).

*Insert Table 3*

### 3.2 Environmental parameters and correlation with crab distribution

Environmental parameters are shown in Table 4. Differences between the forest and gap plots regarding the measured sediment parameters were small compared to the magnitude of differences in vegetation parameters (except temperature, see below). In the gaps no live trees were left, resulting in zero canopy coverage, zero live root coverage and zero leaf litter on the ground. Mangrove recruits were almost exclusively found in the forest (Table 4). Broken tree stumps were abundant in the gaps, but largely absent in the forest. Downed stems were frequent in Gnat, while they were scarce in the forest, but also in Gcut where stems had been removed subsequent to the typhoon incidence (Table 4). Maximum air temperature in the forest was 29.9 °C (average daytime temperature  $26.40 \pm 1.65$  °C) and in the gap 40.9 °C (average daytime temperature  $29.5 \pm 3.6$  °C). In 10 cm sediment depth, maximum temperatures were 27.1 °C and 29.9 °C in the forest and gap, respectively (average daytime temperature  $25.8 \pm 0.3$  and  $28.0 \pm 0.8$  in the forest and gap).

*Insert Table 4*

*Insert Table 5*

Correlations between crab abundance and environmental variables show that the combination of canopy coverage, salinity, live root coverage, number of live trees and PHI 50 were the five factors best explaining the overall distribution pattern of the benthic crabs (Table 5; temperature data was excluded from analyses due to lacking data in March). For crab biomass fallen stems and water content were important factors. In Grapsoid crabs (*M. elegans* excluded), the correlation between live root coverage was positive for both abundance and biomass, while it was negative in Ocypodoid crabs. The distribution of *P. eumolpe* was further positively correlated with water content, canopy coverage, the number of live trees, while correlations were negative for deadwood coverage and number of fallen stems (Table 5). For the ocypodid *U. flammula* and the varunid *M. elegans* the lack of canopy coverage was important, and in the latter species, the presence of tree stumps and fallen stems were explanatory variables. For *U. forcipata* a lack of live root coverage was an important factor.

#### **4. Discussion**

Mangrove deforestation through tropical storms drastically changes the habitat for the resident benthic fauna. Areas formerly shadowed by a dense canopy suddenly experience higher temperatures and radiation compared to the previous forest microclimate (Ewel et al., 1998; Sherman et al., 2000; this study). Tree fall and uprooting alters the three-dimensionality of the former habitat with its abundant aerial and underground roots offering structural support to fauna. Due to the 100% tree mortality in the investigated typhoon gaps in Can Gio Biosphere Reserve, there was no regular leaf litter fall to the ground, a food source for many mangrove crabs (see below). Woody debris, however, was very abundant on the substrate surface of the gaps.

##### 4.1 Species number, diversity and evenness

Given the abrupt environmental change caused by typhoon Durian, we hypothesized marked differences in species numbers, diversity and evenness of the benthic crab fauna between the typhoon gaps and the adjacent intact *Rhizophora apiculata* forest. Of the 21 species found, 12 were present both in the forest and in the gaps, demonstrating their robustness to abrupt canopy disturbance, as long as woody debris is abundant (see below). Most mangrove crabs are burrowing and defend territories around their burrows. The resulting limited action radius, the large size of the typhoon gaps and the large number of burrows in the gaps suggest that the captured crabs were permanent gap inhabitants. In addition to the 12 omnipresent species, 9 were exclusively found in the gaps whereas no species occurred solely in the forest. Due to the low presence of most taxa, average species number per time based sampling (TBS) is a more meaningful parameter for comparing treatments than total species number. Maximum and minimum values ranged between  $7.71 \pm 2.75$  (D2 Gcut) and  $4.43 \pm 0.79$  (D2 F) per TBS and average species number was significantly higher in Gcut and Gnat than in the forest. The same holds true for Shannon diversity. Hence, the *R. apiculata* forest stands and the typhoon gaps differed significantly regarding these two parameters as had been expected. In contrast, Pielou's evenness was mostly similar. It was low throughout and single species dominance high as only two species contributed to 72-91% of the total crab abundance and biomass in each treatment.

Average number of crab species and Shannon diversity in the monoculture *R. apiculata* forest in Can Gio was lower than in a *R. apiculata* plantation in Klong Ngao, Thailand (average species number per TBS: max 5.71 in Can Gio versus 6.1- 6.5; diversity: 0.65- 0.88 in Can Gio versus 1.1-1.5; Macintosh et al., 2002; Ashton et al., 2003b). This could relate to the older age of the studied Can Gio forest (18-20 yrs) compared to the forest in Klong Ngao (5 yrs). Likewise in Matang, Malaysia, Sasekumar and Chong (1998) found lower macrofaunal diversity in older *Rhizophora* stands than in

intermediate aged ones (7 to 10 yrs old). Older forests have less light penetration through their canopy impeding the growth of benthic microalgae, the main food source for many deposit-feeders (e.g. Macintosh et al., 2002). Younger forests, in contrast, provide more heterogeneous food, i.e. both benthic microalgae and leaf litter from the canopy, promoting macrobenthic diversity. Furthermore they are often more diverse in their habitat structure and thus provide more niches.

#### 4.2 Crab community composition

When comparing the closed *R. apiculata* forest in the present study with the adjacent 14 to 20 months old typhoon gaps, we also hypothesized differences regarding the abundance of benthic crabs that consume leaf litter versus non-leaf-litter consuming species. Specifically, in the forest we expected a dominance of grapsid, particularly sesarmid crabs and in the gaps a dominance of ocypodids, particularly fiddler crabs. Sesarmids on the one hand are typical mangrove forest dwellers with many species consuming large amounts of leaf litter (e.g. Robertson, 1986; Steinke et al., 1993; Thongtham and Kristensen, 2005), while fiddler crabs are generally more common in open areas such as intertidal mud flats, clear-felled areas and also in young forest stands (Sasekumar and Chong, 1998; Macintosh et al., 2002; Ashton et al., 2003 a, b). Some species, however, also predominantly occur inside mature mangrove forests (e.g. *U. rapax* and *U. vocator* in North Brazil, Koch et al., 2005; Diele et al., 2010). Fiddler crabs scoop or sieve through sediment containing microalgae and microbes (e.g. Dye and Lasiak, 1986; Kathiresan and Bingham, 2001; Meziane et al., 2002; Kon et al. 2007). In Can Gio 98% of all crabs captured in the forest were indeed sesarmids. However, other than expected sesarmids still also clearly dominated in the gaps (Gcut 72%, Gnat 66%), where only 24% and 20% of the crabs were ocypodoids. A replacement of grapsids by ocypodid crabs such as observed following the formation of

smaller treefall canopy gaps (Osborne and Smith 1990) has thus not taken place. However, despite the pronounced sesarmid dominance in both habitat types, ocypodid crabs were still tenfold more abundant in the typhoon gaps than in the forest. This difference was also mirrored by the multivariate analysis that identified the fiddler crabs *Uca flammula* and *Uca forcipata* as main discriminators between the forest and gap crab communities. Their distribution was negatively correlated with parameters associated with the forest habitat, such as tree number, canopy coverage and root coverage. The increased relative abundance of fiddler crabs in the gaps may relate to enhanced growth of benthic microalgae, a major food source e.g. of *U. forcipata* (Rodelli et al., 1984; Kon et al., 2007). Algal biomass often increases in forest gaps due to increased light intensity (Granek and Ruttenberg, 2008). Diatom contents in surface sediments as well as Delta  $^{13}\text{C}$  signals of crab tissues and available food sources are subject of ongoing studies (Nguyen Thi GH, unpubl.; Tran Ngoc, unpubl.). In addition to improved food supply, fiddler crabs may also prefer more open areas over closed forests due to better visibility. Better sight facilitates their visual communication through claw waving during mate searching and antagonistic interactions (Crane, 1975; Hyatt, 1975). In the typhoon gaps, however, abundant woody debris and dead stems on the ground probably reduce the crabs' range of sight in a similar way as do aerial roots and trunks in the forest. *U. flammula*, nevertheless, is a fiddler crab that waves comparably little and may thus be less perturbed by visual obstruction than other ocypodid crabs (Nobbs, 2003). In northern Australia this species was abundant in a mangrove forest dominated by tall *Ceriops tagal* trees and absent in adjacent clearings (Nobbs, 2003). This is contrary to our study where 97% of all captured *U. flammula* specimens were gap inhabitants. A general conclusion regarding the species' preferred or typical habitat is thus not yet possible. Manipulative experiments are needed to determine the crabs' specific habitat

requirements and the effect of interspecific competition and predation on their distribution.

In addition to the two *Uca* species discriminating the crab communities in the forest and gaps, *M. elegans*, a grapsoid crab of the family Varunidae was a further key discriminator. Not a single specimen was found in the forest while the species was abundant in the gaps, particularly in Gnat. As with *U. forcipata* and *U. flammula*, its distribution was negatively correlated with canopy coverage. It was however positively correlated with fallen stems which were most abundant on the ground in Gnat. Tissue samples of Malaysian *M. elegans* indicated a  $\Delta^{13}\text{C}$  signal close to that of microalgae (Rodelli et al., 1984) suggesting that they belong to the same trophic level as the co-occurring fiddler crabs. In contrast to the exclusive gap occurrence observed in our study, in China and Thailand *M. elegans* was also found in mangrove forests, particularly in younger rehabilitated and impacted stands (Chen et al., 2007; Macintosh et al., 2002). Obviously, as for *U. flammula*, the factors ultimately determining the distribution of this species in different regions are not yet sufficiently known.

The ground-dwelling crab communities in Can Gio at the forest sites in area D1 and D2 also differed significantly from each other, but dissimilarity was lower than between forest and typhoon gaps. The most important discriminator was the sesarmid crab *Parasesarma plicatum* being 18 times more abundant in D2 F than in D1 F. *P. plicatum* was also 6 times more abundant in D2 Gcut than in D1 Gcut, but this difference was statistically insignificant. This species consumes leaf litter and animal matter (Kuroda et al., 2005; Kwok and Lee, 1995; Chen and Ye, 2008 and 2010) and also appears to feed on microphytobenthos in some areas, as indicated by respective  $\Delta^{13}\text{C}$  tissue values (Bouillon et al., 2004). *P. plicatum* was the second most abundant sesarmid crab in our study. Revealing the causes for its higher abundance of in area D2 compared to D1 was beyond the scope of this study. However, the closer vicinity of D2

to a larger tidal waterway lined with *Avicennia marina* may lead to higher inputs of estuarine or marine nutrients into this area, which may also explain the higher total crab abundance and biomass found in area D2 compared to D1.

#### 4.3 Total crab abundance, biomass and single species dominance

Irrespective of the differences between areas D1 and D2, almost equal total crab numbers were captured in the gaps and in the forest during our crab sampling (48% versus 52 % of the overall total catch in F and Gcut, respectively). The sesarmid crab *Perisesarma eumolpe*, however, was generally less abundant in the gaps than in the forest (except in D1), but it was still the dominant species in all treatments (73% to 58% of the total catch in the forest and gaps, respectively). Obviously, it does not depend on a closed canopy providing shade and leaf litter as food, although sesarmids, and in particular crabs of the genus *Perisesarma* are usually found in large numbers inside mangrove forests only. The presence of *P. eumolpe* both in the forest and the typhoon gaps demonstrates that it is a very opportunistic species. It also shows that extrapolating causality from correlations between the distribution of a crab and its environment can be misleading (Kelaher et al., 1998; Ashton et al., 2003a; Geist et al., 2012). In Thailand and Malaysia, *P. eumolpe* consumes large amounts of mangrove leaf litter and small invertebrates and green algae were also found in their stomachs (Leh and Sasekumar, 1985; Ashton, 2002). Omnivorous feeding was further observed in Singapore in a mangrove with low standing litter stock, where the crabs spent more time grazing on sediment than on leaf litter (Ya et al., 2008). During our crab sampling in Can Gio we frequently found *P. eumolpe* foraging on mangrove leaf litter. The crabs also collected sediment and debris, particularly in the typhoon gaps and the species' opportunistic feeding behaviour and food quality is now studied in more detail. Preliminary stomach content analyses suggest that in the gaps crabs consume the abundant woody debris

(Tran Ngoc, forthcoming). Dead wood is an important component of food webs and nutrient cycles in terrestrial ecosystems, despite its generally slow decay (Harmon et al., 1986; Robertson and Daniel, 1989). It contains a large proportion of cellulose which is a rich source of carbohydrate to animals, but its crystalline structure makes it difficult to digest (Linton and Greenaway, 2007). Cellulases facilitating the ingestion of cellulose have been identified in the digestive juice, gut or hepatopankreas of many crustaceans and recent findings suggest that decapod crustaceans are able to produce cellulases endogenously rather than relying upon symbiotic micro-organisms (Linton et al., 2006; Linton and Greenaway, 2007). Microbes or shipworms decomposing the downed wood may also be important for the nutrition of the crabs in the typhoon gaps, possibly more than the debris per se due to their lower CN ratio compared to macrophytic organic matter (for further discussion on adaptations of crabs to low quality mangrove-derived organic matter see e.g. Skov and Hartnoll, 2002; Bouillon et al., 2002; Linton and Greenaway, 2007). The dominance of sesarmids in the crab community of the gaps suggests that the local food web is primarily based on woody mangrove debris rather than on microphytobenthos, the main food source of many ocypodid crabs and the basis for food webs in other mangrove forest gaps (Kon et al., 2007). Larger numbers of *P. eumolpe* may only be able to persist prior to mangrove re-establishment as long as woody debris is still sufficiently available as a direct or indirect food source.

Total crab biomass as well as biomass and individual weight of *P. eumolpe* were significantly higher in the *R. apiculata* forest than in the gaps, reflecting the 15% to 29% larger size of the *P. eumolpe* crabs. The unequal crab sizes may relate to different age, or, alternatively, to dissimilar growth caused by differences in abiotic stress (e.g. reduction of feeding times and thus food intake in the gaps due to overheating) or food quality. Information on growth of *P. eumolpe* is not available from the literature, however age-at-size estimates from two other *Perisesarma* species, *P. guttatum* (Flores et al.,



2002) and *P. bidens* (Lee and Kowk, 2002) suggest that environmental factors rather than different age may explain the different body sizes of *P. eumolpe* in the forest and the gaps. Assuming a growth rate of 1.2 mm carapace width (CW) per month (as for *P. bidens* during the growing season, Lee and Kwok, 2002) implies that the largest *P. eumolpe* specimens found during the sampling in March 2008 (gaps: 24.7 mm CW; forest: 27.5mm CW) were 20 to 23 months old at a minimum and that all crabs with at least 16 mm CW onwards had already recruited before December 2006 when typhoon Durian hit the area. These age estimates are likely over-estimates as the energetically antagonistic effect of reproduction (Hartnoll, 1985) was not considered here. Hence, the smaller body size of *P. eumolpe* in the gaps probably reflect sub-optimal food and/or stressful abiotic conditions impeding the growth of this sesarmid crab. It is also possible that size-specific microhabitat preferences caused the varying abundance of large crabs. Large *P. eumolpe* were mostly found in burrows located near thick stilt roots and/or near the basis of *R. apiculata* trees. This microhabitat was rare in the gaps where most trees had been uprooted. A study on microhabitat preferences, growth rates, nutritional status and metabolism of *P. eumolpe* is now underway to understand the observed size-distribution (Tran Ngoc, forthcoming).

#### 4.4 Conclusions and outlook

The present study provides first data to fill the current gap in knowledge of the response of ground-dwelling mangrove crabs to massive tree fall caused by tropical storms. Despite 100% tree mortality and the relatively large size of the typhoon gaps in Can Gio Biosphere Reserve, total crab abundance (but not biomass) 14-20 months after the typhoon incidence was similar, and all species found in the *R. apiculata* mangrove forest were also present in the gaps. Gap-exclusive species were encountered as well, resulting in higher average species richness and diversity in the gaps, but a shift from

sesarmids (typical forest species) to ocypodids (more prominent in open areas) has not occurred. The dominant species in the forest, the sesarmid *P. eumolpe*, also dominated in the gaps, but its biomass (and in part abundance) and average body size was smaller, reducing the level of bioturbation. The fate of this opportunistic litter-feeding crab until the re-establishment of the canopy is likely to depend on the availability of woody debris on the ground of the gaps as direct or indirect food source.

Although not studied here, the continuing presence of sesarmids and the appearance of additional species may facilitate mangrove recruitment in the typhoon gaps due to the crabs' ecosystem-engineering activities (e.g. Minchinton, 2001; see Krauss et al., 2008 for review). Sesarmid crabs, on the other hand, might also delay gap regeneration through predation on propagules (e.g. Osborne and Smith, 1990). There is, however, little evidence for significant herbivory on *R. apiculata* propagules or seedlings in the planted monoculture forests in Can Gio (pers. comm. Vien Ngoc Nam), possibly due to the large size of its propagules (Clarke and Kerrigan, 2002). To fully understand the crabs' role in the process of forest recovery, follow-up assessments and manipulative experiments are needed to reveal (i) the crabs' diets and their role in the turn-over of woody debris and nutrient cycling of the gaps and (ii) their long-term community dynamics and possible feed-backs between species shifts and mangrove recruit establishment and thus gap regeneration.

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## Figure Legends

Fig. 1. Location of the study site (small rectangle) in Can Gio Biosphere Reserve, Vietnam (modified after Kautz et al. 2011); Detail view of area D1 and D2 in upper left corner: F: Intact *R. apiculata* forest used as control; Gcut: Typhoon gap with downed stems removed by the local forestry department; Gnat: Typhoon gap with downed stems left on site (absent at D2).

Fig. 2. Sampling areas. a) D1 Gcut: typhoon gap in area D1 with downed stems removed; b) D1Gnat: typhoon gap in area D1 with stems left on site; c) D2Gcut: typhoon gap in area D2 with downed stems removed; d) surrounding intact *R. apiculata* forest (F).

Fig. 3. Presence-Absence-Graph: Crab species found in intact *R. apiculata* forest and adjacent typhoon gaps in Can Gio Biosphere Reserve in March and September 2008. See Fig. 1 for abbreviations. Numbers are species identifiers; see Table 2 for species names. Species in intersections occurred in more than one site category (= treatment). Bold underlined numbers: in  $\geq 75\%$  of the replicate plots in all respective treatments; Bold numbers: In  $\geq 50\%$  of the replicate plots in all respective treatments; Italics: In  $\geq 25 < 50\%$  of the replicate plots in one or more of the respective treatments; Small underlined numbers: in  $\geq 10 < 25\%$  of the replicate plots in each respective treatment; Small numbers: in  $< 10\%$  of the replicate plots in one or more of the respective treatments.

Fig. 4. Species rank dominance curves for crab abundance in intact *R. apiculata* forest and adjacent typhoon gaps in Can Gio Biosphere Reserve in 2008 (March and September 2008 data pooled). See Fig. 1 for abbreviations.

Fig. 5. Species distribution of crabs in intact *R. apiculata* forest and adjacent typhoon gaps in Can Gio Biosphere Reserve in 2008 (March and September data pooled. 100% equals the sum of average abundance or biomass of the seven replicates of each treatment. See Fig.1 for abbreviations. Green shadings, dots or stripes: Superfamily Grapsoidea (boxes with black line: Species belonging to the family Sesarmidae); Yellow shading, dots, stripes: Superfamily Ocypodoidea.

Fig. 6. nMDS ordination for crab abundance in Can Gio Biosphere Reserve in 2008. Based on average species counts across 7 replicate plots in March (black) and 7 replicate plots in September (blue) per treatment/area of fourth-root-transformed data. Lines highlight 60% similarity. See Fig. 1 for abbreviations.

### **Table Legends**

Table1. List of species found in intact *R. apiculata* forest and adjacent typhoon gaps in Can Gio Biosphere Reserve in March and September 2008. AB and BM: Total abundance and biomass per species, respectively. Numbers in parentheses: proportion from total catch caught in the forest (values corrected for smaller total number of forest plots) NI: no identification possible due to damage of the specimen. sp: no identification to species level possible due to juvenile status or lost appendices. sp with numbers: Recognizable as distinct species but could not be identified at present time. Specimens

of all species kept at the Leibniz Center of Tropical Marine Ecology, Bremen, Germany.

a: Present in all 70 plots; b: Present in all but three replicate plots; c: Present in > 50% of the replicate plots; d: Present in  $\leq 50 > 10\%$  of the replicate plots; blank AB numbers: present in  $\leq 10\%$  of the replicate plots.

Table 2. Univariate measures of crabs captured in intact *R. apiculata* forest and adjacent typhoon gaps in Can Gio Biosphere Reserve 2008 per time based sampling (TBS, crab capture by 4 persons over 30 min in a 100 m<sup>2</sup> plot). Given are averages and standard deviations calculated for 7 replicate plots per treatment. See Fig. 1 for abbreviations.

Table 3. Average abundance (AB), biomass (BM), carapace width (CW) and individual wet weight (WW) of *Perisesarma eumolpe* in intact *R. apiculata* forest and adjacent typhoon gaps in Can Gio Biosphere Reserve in March and September 2008 per TBS. Mean  $\pm$  standard deviation. See Fig. 1 and Table 2 for abbreviations.

Table 4. Environmental parameters measured during crab sampling in intact *R. apiculata* forest and adjacent typhoon gaps in Can Gio Biosphere Reserve in March and September 2008 (data pooled). See Fig. 1 for abbreviations.

Table 5. Factors influencing the occurrence of intertidal mangrove crab in Can Gio Biosphere Reserve: BIOENV correlations based on Bray-Curtis-similarity matrices of abundance and biomass with environmental parameters. (+) and (-) indicate positive or negative correlations. All correlations were significant ( $P < 0.01$ ), except \* ( $P > 0.05$ ).

Figure 1

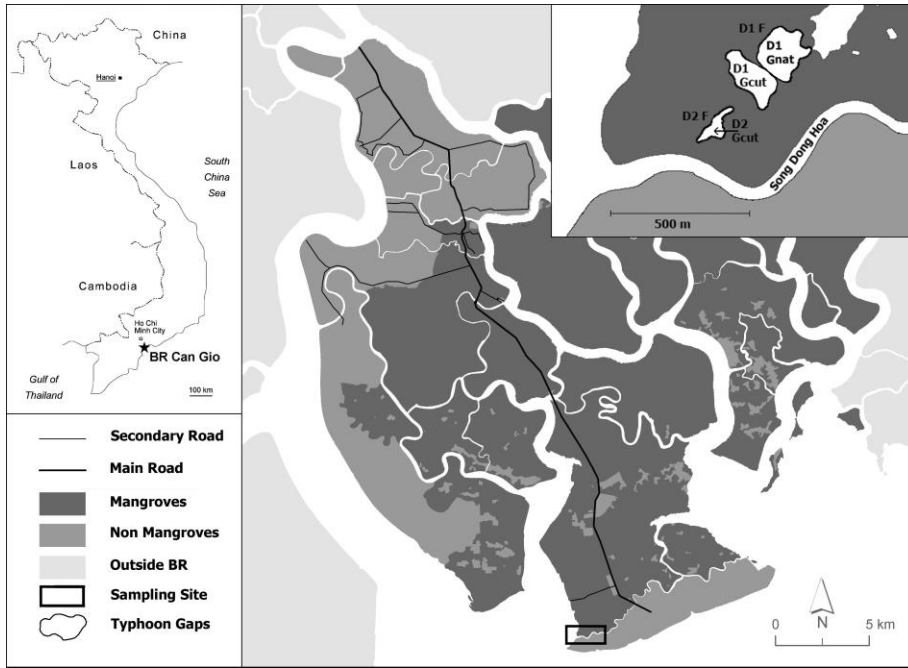


Figure 2

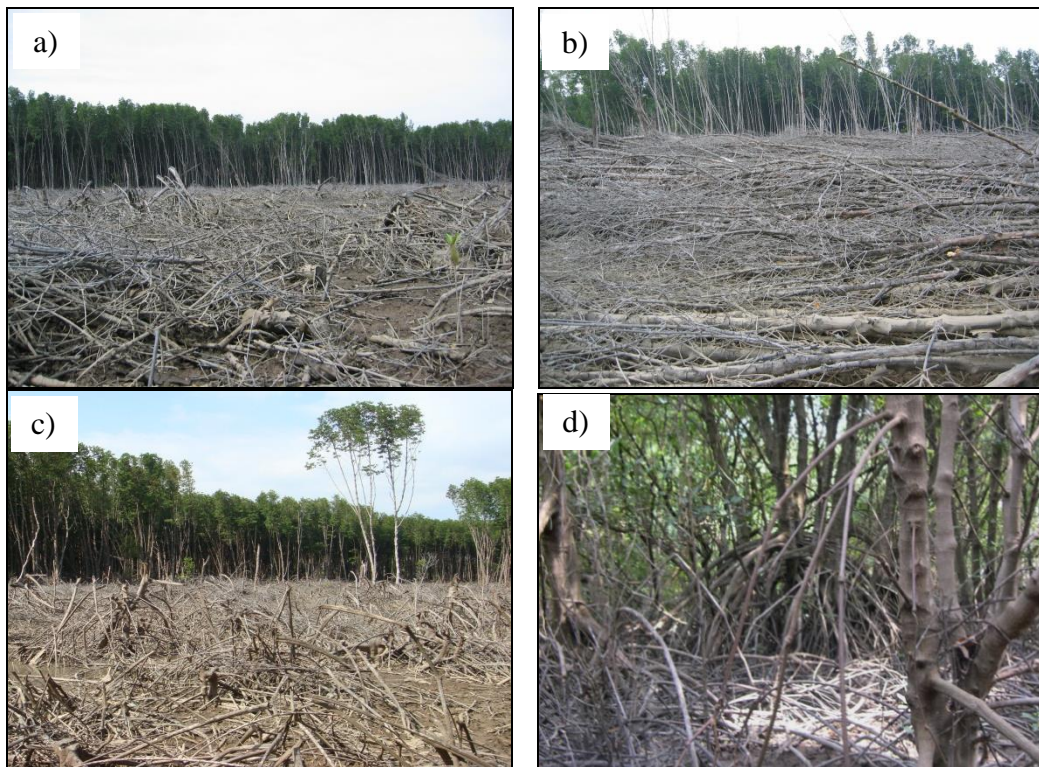


Figure 3

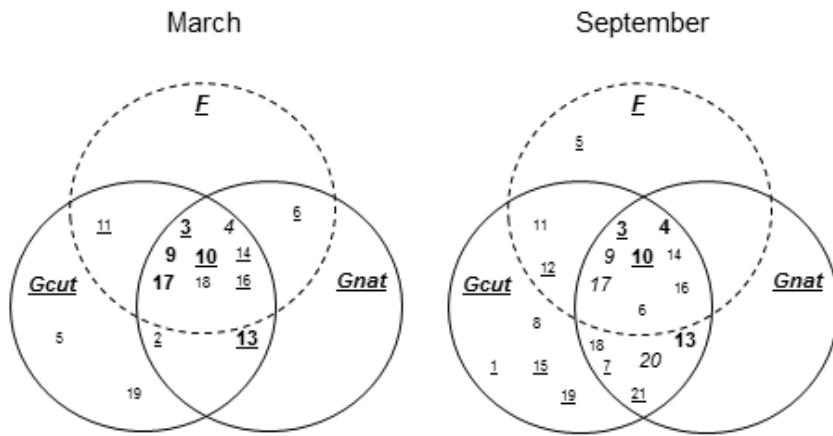


Figure 4

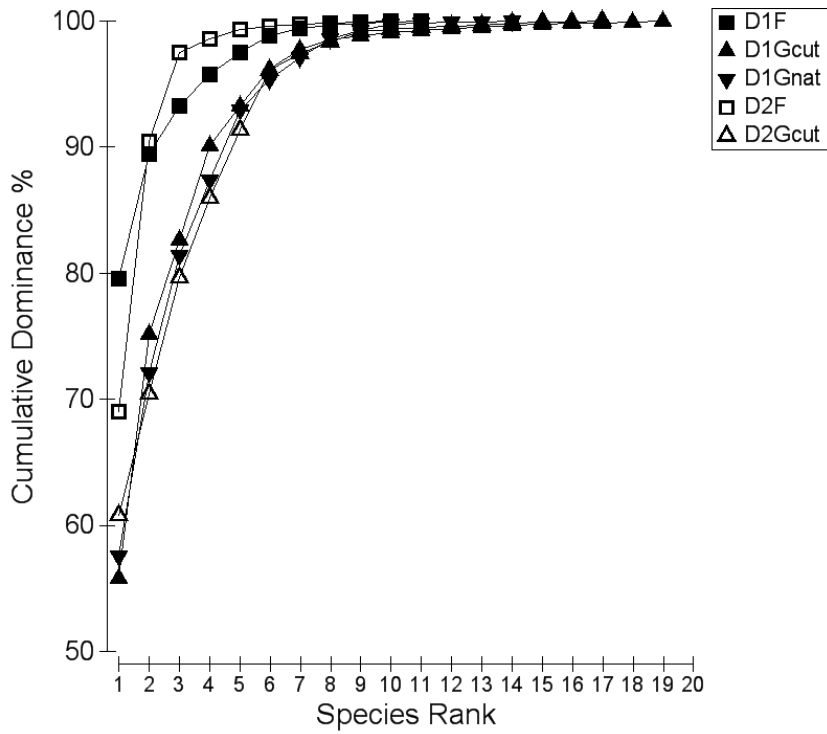


Figure 5

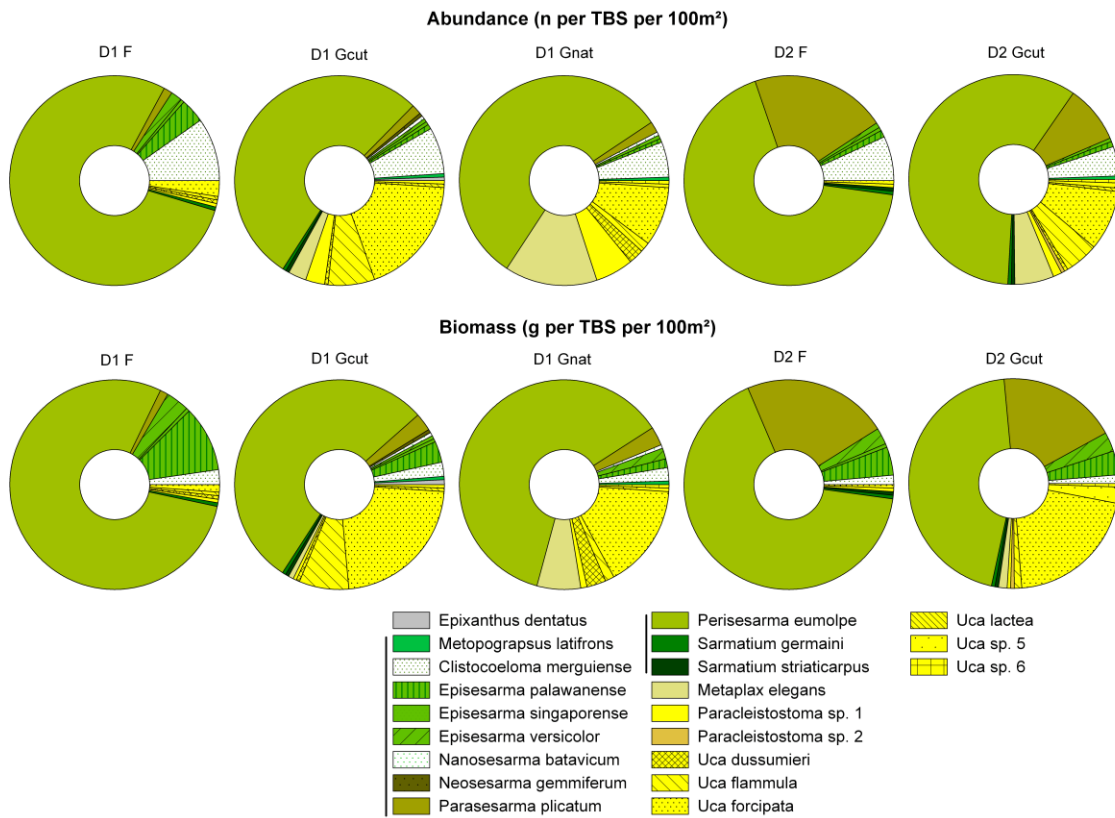


Figure 6

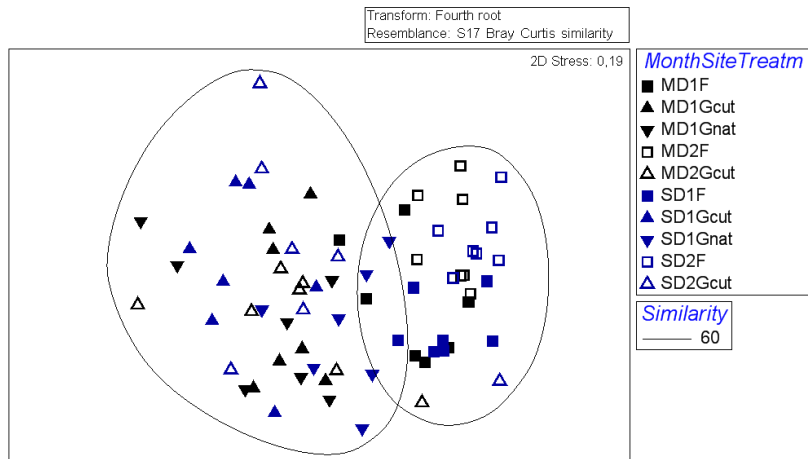




Table 1.

Superfamily	Family	ID	Species	AB (n)		BM (g)	
Eriphoidea	Oziidae	1	<i>Epixanthus dentatus</i> (White, 1848)	2	(0)	18.7	(0)
Grapsoidae	Grapsidae	2	<i>Metopograpsus latifrons</i> (White, 1847)	5	(0)	5.5	(0)
		3	<i>Clistocoeloma merguense</i> De Man, 1888	577 <sub>b</sub>	(59.8)	424.3	(70.7)
		4	<i>Episesarma palawanense</i> (Rathbun, 1914)	112 <sub>c</sub>	(75.3)	1,252.8	(83.3)
		5	<i>Episesarma singaporense</i> (Tweedie, 1936)	3	(75.0)	83.1	(89.8)
		6	<i>Episesarma versicolor</i> (Tweedie, 1940)	55 <sub>d</sub>	(83.0)	538.4	(87.0)
			<i>Episesarma</i> sp.	8	(17.7)	22.4	(91.7)
		7	<i>Nanosesarma batavicum</i> (Moreira, 1903)	6	(0)	0.9	(0)
		8	<i>Neosesarma gemmiferum</i> (Tweedie, 1936)	2	(0)	0.2	(0)
		9	<i>Parasesarma plicatum</i> (Latreille, 1806)	707 <sub>c</sub>	(77.6)	2,858.4	(84.3)
		10	<i>Perisesarma eumolpe</i> (De Man, 1895)	5470 <sub>a</sub>	(57.5)	15,658.6	(76.0)
		11	<i>Sarmatium germaini</i> (A. Milne-Edwards, 1869)	7	(66.7)	26.1	(85.2)
		12	<i>Sarmatium striaticarpus</i> Davie 1992	6	(60.0)	6.4	(85.2)
			<i>Sarmatium</i> sp. (juvenile)	4	(33.3)	0.7	(46.6)
	Varunidae	13	<i>Metaplax elegans</i> De Man, 1888	397 <sub>d</sub>	(0)	240.4	(0)
Ocypodoidea	Camptandriidae	14	<i>Paracleistostoma</i> sp. 1	180 <sub>c</sub>	(6.5)	36.7	(4.7)
		15	<i>Paracleistostoma</i> sp. 2	2	(0)	0.2	(0)
	Ocypodidae	16	<i>Uca dussumieri</i> (H. Milne Edwards, 1852)	43	(3.5)	68.2	(1.5)
		17	<i>Uca flammula</i> (Crane, 1975)	244 <sub>c</sub>	(4.2)	419.6	(3.4)
		18	<i>Uca forcipata</i> (Adams & White, 1849)	659 <sub>c</sub>	(8.2)	1,538.0	(6.2)
		19	<i>Uca lactea</i> (De Haan, 1835)	4	(0)	1.5	(0)
		20	<i>Uca</i> sp. 5	18	(0)	59.2	(0)
21	<i>Uca</i> sp. 6	4	(0)	9.0	(0)		
	<i>Uca</i> sp.	8	(0)	6.2	(0)		
NI	NI	NI		9	(65.2)	18.1	(92.6)
			Total	8,532		23,293	

Table 2.

		<b>Abundance</b>	<b>Biomass</b>	<b>Species Number</b>	<b>Shannon Diversity H'</b>	<b>Pilou's Evenness J'</b>
	<i>March</i>					
D1	F	83.14 ± 17.46	302.97 ± 93.13	5.71 ± 2.06	0.70 ± 0.22	0.41 ± 0.08
	Gcut	102.14 ± 17.52	163.10 ± 25.43	6.57 ± 1.27	1.01 ± 0.37	0.53 ± 0.15
	Gnat	123.29 ± 49.83	181.91 ± 76.07	6.86 ± 1.22	1.02 ± 0.38	0.53 ± 0.18
D2	F	146.29 ± 44.06	587.35 ± 183.22	4.43 ± 0.79	0.65 ± 0.19	0.44 ± 0.12
	Gcut	125.71 ± 24.32	275.41 ± 56.80	7.29 ± 1.80	1.05 ± 0.46	0.53 ± 0.20
	<i>September</i>					
D1	F	107.43 ± 11.62	445.14 ± 95.07	5.30 ± 0.76	0.79 ± 0.14	0.48 ± 0.08
	Gcut	119.29 ± 33.58	186.10 ± 37.91	8.71 ± 2.43	1.31 ± 0.14	0.62 ± 0.09
	Gnat	116.00 ± 20.94	132.27 ± 29.75	7.29 ± 0.95	0.94 ± 0.29	0.47 ± 0.12
D2	F	170.43 ± 50.74	764.63 ± 257.19	5.71 ± 0.76	0.88 ± 0.20	0.51 ± 0.11
	Gcut	121.57 ± 31.09	282.00 ± 128.08	7.71 ± 2.75	1.16 ± 0.54	0.58 ± 0.22

Table 3.

		<b>AB (n)</b>	<b>BM (g)</b>	<b>CW (mm)</b>	<b>WW (g)</b>
	<i>March</i>				
D1	F	68.43 ± 15.47	251.72 ± 77.45	17.45 ± 4.12	3.54 ± 2.64
	Gcut	69.50 ± 28.33	108.97 ± 38.03	13.32 ± 3.02	1.56 ± 1.32
	Gnat	57.00 ± 34.73	91.42 ± 63.14	13.52 ± 3.01	1.63 ± 1.17
D2	F	115.57 ± 29.06	452.73 ± 125.56	18.20 ± 3.68	4.49 ± 2.83
	Gcut	84.43 ± 26.06	192.51 ± 66.48	15.54 ± 3.60	2.86 ± 1.85
	<i>Sept</i>				
D1	F	83.14 ± 10.09	350.24 ± 59.04	19.17 ± 3.89	4.88 ± 3.10
	Gcut	54.00 ± 33.82	89.56 ± 54.35	14.84 ± 3.20	1.90 ± 1.47
	Gnat	80.71 ± 21.80	106.00 ± 36.81	13.63 ± 2.42	1.35 ± 0.81
D2	F	107.14 ± 43.60	463.69 ± 207.48	19.29 ± 3.51	5.20 ± 2.87
	Gcut	65.71 ± 35.08	130.12 ± 55.49	15.34 ± 3.36	2.25 ± 1.44

Table 4.

	D1			D2	
	F	Gcut	Gnat	F	Gcut
Φ50	6.30 ± 0.24	6.49 ± 0.21	6.11 ± 0.21	6.29 ± 0.23	6.33 ± 0.23
C <sub>org</sub> (%)	4.14 ± 0.49	4.48 ± 0.79	4.40 ± 0.76	3.69 ± 0.44	4.11 ± 0.62
N <sub>tot</sub> (%)	0.27 ± 0.06	0.28 ± 0.02	0.29 ± 0.05	0.22 ± 0.02	0.25 ± 0.04
C <sub>org</sub> /N <sub>tot</sub>	15.68 ± 3.10	16.33 ± 2.90	15.76 ± 3.61	17.18 ± 2.07	16.83 ± 2.55
Salinity	28.45 ± 1.91	29.01 ± 3.85	28.01 ± 4.12	28.41 ± 5.0	33.28 ± 9.52
March					
Salinity	12.90 ± 1.37	14.33 ± 2.42	14.50 ± 2.73	16.58 ± 2.86	14.15 ± 3.05
September					
pH	6.20 ± 0.43	6.46 ± 0.51	6.75 ± 0.62	6.11 ± 0.39	6.60 ± 0.30
SWC	61.17 ± 6.31	52.91 ± 4.14	57.73 ± 4.34	56.05 ± 3.59	55.45 ± 4.59
Canopy %	75.00 ± 19.61	0	0	73.21 ± 6.68	0
Live root %	48.21 ± 20.72	0	0	48.21 ± 20.72	0
Woody debris %	3.57 ± 9.08	62.50 ± 21.37	60.71 ± 12.84	0	71.43 ± 19.26
n trees in 100m <sup>2</sup>	28.71 ± 11.25	0	0	21.21 ± 9.55	0
N leaves per m <sup>2</sup>	15.83 ± 4.55	0	0	10.24 ± 3.58	0
N recruits < 50cm per m <sup>2</sup>	2.43 ± 1.39	0	0	1.79 ± 1.03	0
N recruits > 50cm per m <sup>2</sup>	0	0	0	0.05 ± 0.12	0
n stumps in 100m <sup>2</sup>	0.57 ± 1.40	11.43 ± 2.82	12.71 ± 3.67	0	13.93 ± 3.15
n downed stems in 100m <sup>2</sup>	1.29 ± 1.73	0.29 ± 0.61	24.00 ± 4.84	0.50 ± 1.09	1.07 ± 1.07

Given are means and standard deviations. Φ50: Index of surface sediment grain size distribution (median), Salinity in PSU, C<sub>org</sub>: Organic carbon content of surface sediment; N<sub>tot</sub> = Nitrogen content of surface sediment, SWC: Sediment water content.

Table 5

Crab matrix	a) BIOENV with abundance		b) BIOENV with biomass	
	Correlation ( $\rho$ )	1 <sup>st</sup> choice variables	Correlation ( $\rho$ )	1 <sup>st</sup> choice variables
All species	0.46	canopy coverage (+), salinity (-), root coverage (+), n trees (-), $\Phi$ 50 (-)	0.53	canopy coverage (+), n trees (+), root coverage (+), fallen stems (-), water content (-)
Grapsidae & Sesamidae	0.20	root coverage (+), Corg (-), $\Phi$ 50 (-), water content (+)	0.40	n trees (+), root coverage (+), Corg (-), water content (+), $\Phi$ 50 (-)
Ocypodoidea	0.42	root coverage (-)	0.44	root coverage (-)
<i>P. eumolpe</i>	0.22*	water content (+)	0.47	canopy coverage (+), deadwood coverage (-), n trees (+), fallen stems (-), water content (+)
<i>P. plicatum</i>	0.23	Ntot (-), Corg (-), water content (-), $\Phi$ 50 (+), n stumps (-)	0.23	Ntot (-), Corg (-), n stumps (-), water content (-), $\Phi$ 50 (-)
<i>M. elegans</i>	0.33	canopy coverage (-), n stumps (+), fallen stems (+)	0.37	n stumps (+)
<i>U. flammula</i>	0.33	n trees (-), canopy coverage (-), $\Phi$ 50 (+)	0.31	n trees (-), $\Phi$ 50 (+), canopy coverage (-), leaf litter (-), salinity (+)
<i>U. forcipata</i>	0.33	root coverage (-)	0.37	root coverage (-)

Variables tested in BIOENV:

Phi 50, Porewater salinity, pH, Water content (%), Corg (%), Ntot (%), Corg/Ntot, Log(Canopy coverage (%)+1), Log(average total leaf per m<sup>2</sup>+1), Log(n live trees+1) 11 Log(n stumps+1), Log(Root coverage (%)+1), Log(Deadwood coverage (%)+1), Log(n fallen stems+1), Log(average man recruit < 50cm per m<sup>2</sup>+1), Log(average man recruit > 50cm per

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