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Determining the consequences of forest degradation on mangrove epifauna in South-East Kenya

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Determining the consequences of forest degradation on mangrove epifauna in South-East Kenya

MSc by Research

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Abstract

Due to land exploitation 18% of mangrove forests in Kenya have suffered from deforestation at an average rate of 1% yr^{-1} in less than 25 years, directing attention towards the quantification of forest loss. The extent to which degraded mangrove areas occur worldwide and the consequences of mangrove degradation to ecosystem processes have not sufficiently been quantified. Here, network of fifty 10x10m sample plots in mangrove forests of Gazi Bay and Vanga Bay of southern Kenya were established, to study the effects of mangrove degradation upon changes in mangrove biogenic structure, and the provisioning of benthic epifaunal taxonomical and functional biodiversity, species abundance, community and trophic composition, as proxies for ecosystem functioning. A combination between principal component analysis (PCA) and generalized linear models (GLMM) were used to detect canopy cover as the best indicator to define forest degradation. Univariate GLMM models were also used to understand the response of benthic fauna to habitat degradation. Spatial differences in macrofauna abundance and taxonomic diversity were related to the thinning of the canopy cover. Forest degradation also revealed a reduction in crab functional diversity (FD) with high levels of FD recorded at around 50% of canopy cover, supporting the intermediate disturbance hypothesis (IDH). Habitat homogenization (reduction in biogenic structures) associated with degradation had effects on faunal community structure and composition. For instance, degraded habitats had more generalist species, such as detritivores (e.g. *Uca annulipes*), and a loss of specialists such as foli-detritivores crabs (e.g. *Chiromantess eulimene*). The results of this study showed the importance of mangrove canopy in structuring and providing a viable habitat to mangrove epifauna, thereby supporting a stable and functional ecosystem. The study shows current trends of mangrove degradation in South-East Kenya threaten faunal diversity and forest ecosystem functioning. The alteration of faunal trophic composition in mangroves could have negative feedbacks to down-stream systems, such as coral reefs, through the reduction of food source for secondary consumers such as fish and shrimp, which visit mangroves on the tide to feed on prey.

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards. ----------

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Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

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smithi, N. africanum (ex.Neosesarmatium meinerti), Chiromantess eulimene), ***Ocypodidae*** *(Uca annulipes, U. urvillei, U. chlorophtalmus, U. vocans, U. inversa, U. tetragonon),* ***Portinidae*** *(Thalamita crenata),* ***Macrophtalmidae*** *(Macrophtalmus latrelli, Macrophtalmus milloti) and* ***Grapsidae*** *(Metopograpsus oceanicus, M. thukuhar, M. messori).*

Figure 9. Functional composition of mangrove crabs in a MDS ordination, with vectors based on Pearson correlation <0.2.

Figure 10. Variation in functional diversity **(a)**, richness **(b),** redundancy (FD/H') **(c)** and evenness **(d)** of crab trophic traits along the gradient in mangrove canopy cover.

1. Introduction

Mangroves are taxonomically diverse woody plants. They are able to tolerate salt and are found in intertidal zones and estuaries, as well as fringing, sub-tropical and tropical coastlines (Primavera et al., 2019; Polidoro et al., 2010). Due to their intertidal position mangroves are associated with highly diverse biota which inhabit different niches within the forest structure (Nagelkerken et al., 2008).The links between mangroves and adjacent systems augment important ecological and economic functions, such as the dispersion of nutrients, trophic energy flow, primary productivity and habitat provision to commercial and juvenile reef species (Dorenbosch et al., 2004; Mumby et al., 2004; Primavera et al., 2019). Furthermore, mangroves show net primary productivity rates similar to those of evergreen tropical rainforests (Donato et al., 2011; Alongi et al., 2012); can sequester up to 937 tonnes of carbon per hectare and store it in their soils and biomass, contributing to 14% of global ocean carbon sequestration (Alongi et al., 2012). However, due to coastal development, over-exploitation and land-use change, mangrove forests are disappearing globally at a rate of 1–2% per annum, with larger areas being estimated to be in some state of degradation (Spalding et al., 2010; Alongi et al., 2012; Carugati et al., 2018). In the tropics alone, areas of degraded forest have been approximated to cover 500 million ha^{-1} (ITTO 2012; Putz and Romero, 2014). Despite the importance of mangroves in supporting coastal ecosystem functioning, the spatial variation in the severity of degradation, and the consequences of mangrove degradation upon ecosystem processes are largely unknown, yet are of growing concern (Ghazoul et al., 2015). This study addressed the current gaps in the literature, with the aim to inform adaptive local forest management.

1.1 Differences between forest deforestation and degradation

Although there has been an increasing effort in defining forest degradation, there have also been difficulties in disentangling research regarding deforested and degraded areas (e.g. Olander et al., 2008; Ferreira and Lacerda, 2016; Murdiyarso et al., 2009). The Food and Agriculture Organization of United Nations in 2002 (FAO) defined forest degradation as “the reduction of the capacity to provide goods and services” , while the Intergovernmental Panel on Climate Change (IPCC) defined it as “direct human-induced long-term loss of at least Y% of carbon stocks in (X) given years since time (T)” (IPCC 2003a; FAO 2011; Ghazoul et al., 2015). Some authors recognize tropical forests to be degraded once the forest has been logged (e.g. Sierra 2001), while others take this into consideration only when the forest has

been heavily burned and logged (Thompson et al., 2013). Societal and cultural perspectives largely determine what is considered degraded (Souza et al., 2005). The existence of several competing definitions has led to ambiguity and misconceptions, hindering the implementation of a clear conceptual framework to move forward (IPCC 2006; Schoene et al., 2007; Sasaki and Putz, 2009; Simula 2009; Ghazoul et al., 2015). In most cases, degradation has been considered to be a loss of some attributes, function and/or services as a response to disturbance (Murdiyarso et al., 2008; Putz and Romeo, 2014; Ghazoul et al., 2015), with disturbance being addressed as either natural or human induced. The distinction between the two latter drivers also underpin the difficulties behind determining an appropriate definition. Due to the dynamic nature of forest formations and shifting in natural compositions, ecologists are often inclined to exclude natural disturbance as a cause of degradation (Hunter 1996). Nonetheless, excluding the role of natural disturbance when assessing forest degradation rapidly became more challenging due to the global and large-scale impact humans pose upon the natural environments (Van Gemerden et al., 2003; Josefsson et al., 2009).

In this study, the following definitions will be used to clearly and consistently distinguish between degradation and deforestation:**1. Forest deforestation** according to the FAO (2015) definition is "*The conversion of forest to other land use or the permanent reduction of the tree canopy cover below the minimum 10 percent threshold*; *excluding those areas where trees have been removed due to harvesting or logging and where forest regeneration may occur naturally or with help of silviculture techniques*". **2. Forest degradation** according to Ghazoul et al., 2015 (Figure 1) *"loss of forest structures due to gradual anthropogenic activities without a change in land cover".*

1.2 *Assessing forest degradation*

In addition to the difficulties in defining forest degradation, further challenges are encountered when assessing the state of degraded mangrove forests. Most observation of degraded forests have been done with high spatial resolution satellite imagery and advance remote sensing techniques (Houghton 2012). These procedures have previously been used to assess forest loss percentages, impacts of logging on forest dynamics and provision over a period of time (see Foody and Cutler, 2003; Turner et al., 2003; Rocchini et al., 2007; Matricardi et al., 2010; Hudson et al., 2014; Perez et al., 2016; Wu et al., 2020). Nevertheless,

by using remote sensing techniques, they have not, in the main, determined how forest quality changes over time. Despite its ability to measure forest composition (e.g. tree size and species, Dalponte et al., 2018), recent studied highlighted the importance of quantifying ecosystem functioning (e.g. production, carbon sequestration and nutrient cycling) as the key in the understanding of the degradation' impact upon the forest dynamics and processes (Field et al., 2008; Ghazoul et al., 2013). Moreover, remote sensing cannot quantify changes to fauna (diversity and composition), without being coupled to ground-truthing techniques or, at best, with empirical observations on how fauna relates to forest structures. In light of this concern, there is a scarcity of studies assessing the response of fauna to forest degradation in the tropics. For this reason, ground-truthing approach was recognised as an important factor in estimating thresholds and changes in faunal diversity within selected small-scale forests (e.g. Perry et al., 2016; Perry et al., 2018). Despite some limitations (e.g. reduced scales, time and economical resources, lack of repetitive references, Cremer et al., 2019) using ground-truthing provides the opportunity to determine variations in ecological functions (e.g. habitat for organisms in different trophic level, altered community and functional compositions, Field et al., 2008), and their association with changes in forest structure parameters, information not yet accessible with the remote sensing techniques currently available. Obtaining such information may improve the capacity to deliver a promising framework by which degradation could be assessed and defined (Sasaki and Putz, 2009; Thompson et al., 2013; Ghazoul et al., 2015). This will result crucial for moving forward the capacity of practical management.

1.3 Habitat degradation and its impact on biota

Across ecosystems, habitat loss, degradation and fragmentation are typically associated with a loss of biodiversity (i.e. species diversity, richness and evenness, Primavera et al., 2019; Richardson et al., 2020). The response of biodiversity to degraded or lost habitats may include non-linear ecological responses and may be less clear-cut or not widely understood (Belshaw and Bolton, 1993; Fahrig 2003; Polidoro et al., 2010; Hanski 2011). Diverse macrofauna inhabit the mangrove forests, with crabs and gastropods as dominant epifauna, and annelids and nematodes as key infauna organisms (Fondo and Martens, 1998; Cannicci et al., 2008).

1.3.1. Crabs as key species

Some species of brachyuran crabs are leaf-litter specialists, such as members of the family *Sesarmidae*, whereas members of the family *Ocypodidae* specialise in consuming organic compounds derived from microalgal and bacterial primary production (Cannicci et al., 2008). In addition to their habitat specialisations, mangrove crabs are crucial ecosystem engineers that affect ecosystem functioning and processes (Cannicci et al., 2008). Crab bioturbation significantly decreases ammonium and sulphide concentration in the soil, boosting mangrove productivity (Cannicci et al., 2008). Crab burrows play a key role in affecting both the influx and chemistry of groundwater, preventing sediment from becoming compacted (Wolanski et al., 1992). The burrowing activity increases pore water exchange between swamp sediment and interstitial water (Ridd 1996). For these reasons, studies have been conducted on the changes of benthic macrofauna in deforested areas compared to forested sites (e.g. Tolhurst et al., 2010; Bernardino et al., 2018; Carugati et al., 2018), showing that mangrove deforestation is followed by a loss of epifaunal organisms with a shift in community composition, diversity and dominance of invertebrates (Bernardino et al., 2018; Carugati et al., 2018). Within the mangrove ecosystem, a large proportion of leaf biomass is processed by *Sesarmid* crabs. Furthermore, organic matter and energy flow pass by diverse microbial loops and are transported to the higher trophic levels through detritivores and bacterivorous populating the benthos (Nagelkerken et al., 2008; Carugati et al., 2019). Biodiversity loss in marine benthic systems, whatever the phylum considered, is typically coupled to a reduction of ecosystem functions (Carugati et al., 2019).

1.4 Determining functional variations

There is a lack of information on the structural alteration of mangrove forests through degradation, underpinning a gap in the knowledge on how this will lead to changes in faunal diversity, community composition and, consequently, food web dynamics. Studies that coupled alteration of community structures and/or loss of biodiversity with forest reduction mainly contrast only two forest states (degraded vs pristine, e.g. Bernardino et al., 2018; Carugati et al., 2018), or at best three states (degraded, restored and pristine e.g. Ferreira et al., 2015; Gorman and Turra, 2016). These studies have also highlighted that changes may occur due to the feedback mechanisms of degradation operating through reduced shading, altered biophysical parameters, changed deposition of sediments and assimilation of organic matter by benthic consumers (Demopoulos et al., 2007; Sweetman et al., 2010; Bernardino

et al., 2018; Carugati et al., 208, Figure 1). Traditionally, ecological studies which investigated mangrove-benthic community associations, focused on the changes in the taxonomic composition of macrofauna (Martens 1994; Fondo and Martens, 1998; Massou et al., 2016). Currently, there is a developing awareness towards studying species composition and variations with regard to their ecological roles and function (e.g. Richardson et al., 2017; Bernardino et al., 2018; Knoester et al., 2019; McWilliams et al., 2020; Aquilue' et al., 2020; Ford and Roberts, 2020; Freitas and Pagliosa , 2020). This arose interests in understanding how epibenthic diversity responds to anthropogenic stressors at both taxonomical and functional levels, emphasising a gap in the current literature (Lee 2008).

The principle of functional diversity, which characterise the diversity of functional traits (or functional niches) in a community, was introduced to assess ecosystem functioning (Leung 2015). Despite the abundance by which a species occur varies, different species in a community can perform similar or even the same functions (e.g. overlapping of functional niches, or functional redundancy). The reduction, loss or replacement of certain species may not automatically depict changes to the ecosystem functions overall (Petchey and Gaston, 2006; Rosenfeld 2002; Hoey and Bellwood, 2010; Leung 2015). Hence, functional redundancy is measured to evaluate the stability of ecosystem functions to species loss (Walker 1995). This understanding can be essential to comprehend the resilience of the forests, and the mangrove ecosystem as a whole.

1.5 *Research objectives and hypotheses*

The overall aim of this study was to examine the consequences of mangrove degradation on ecosystem functioning, using habitat provisioning for fauna as the focal response variable. Marine epibenthic fauna were chosen as the group for study, due to their ecological specialisation to mangroves and association with forest structure, and owing to their importance to mangrove ecosystem functioning (Nagelkerken et al., 2008; Lee 2008). The study aim was addressed through the following specific objectives: (i) establishing a degradation classification along the gradient of forest degradation (from primary forest to totally degraded, Figure 1). The degradation classification was attempted to be achieved by "a systematic arrangement of forest plots into categories according to similarity in forest structural parameters that are consistent with degradation", specifically canopy cover (%), stump density (stumps ha^{-1}), tree density (trees ha^{-1}) and above ground biomass (Mg ha^{-1}).

(ii) Measuring biophysical parameters (e.g. soil salinity, soil and air temperature, pH) to evaluate their responses to degradation; and (iii) sampling epifaunal biodiversity, community structure, and composition as proxies of ecosystem functional responses to degradation. It was hypothesised that with increase in mangrove degradation there would be: (H_1) an increase of biophysical parameter' values, which are potential stressors to fauna. This increase in stressors was expected as a response to the reduction in biogenic forest structure. (H_2) A decrease in taxonomic diversity, richness, and abundance of benthic fauna and brachyuran crabs due to a reduction in habitat complexity and availability (Bernardino et al., 2018: Freita and Pagliosa, 2020); with an increase in taxonomic evenness. (H_3) A change in the taxonomical and functional composition of brachyuran crabs (e.g. an increase in detritivores, i.e. Uca *spp.* able to thrive across different habitats) as these organisms are dependent on the forest structure for their food availability. Finally, (H_4) a decrease in the functional diversity, richness, redundancy and an increase in the evenness of brachyuran crabs, in relation to changes in taxonomic compositions and declining in efficient uses of ecological resources and niche complementarity (Richardson et al.,2017).

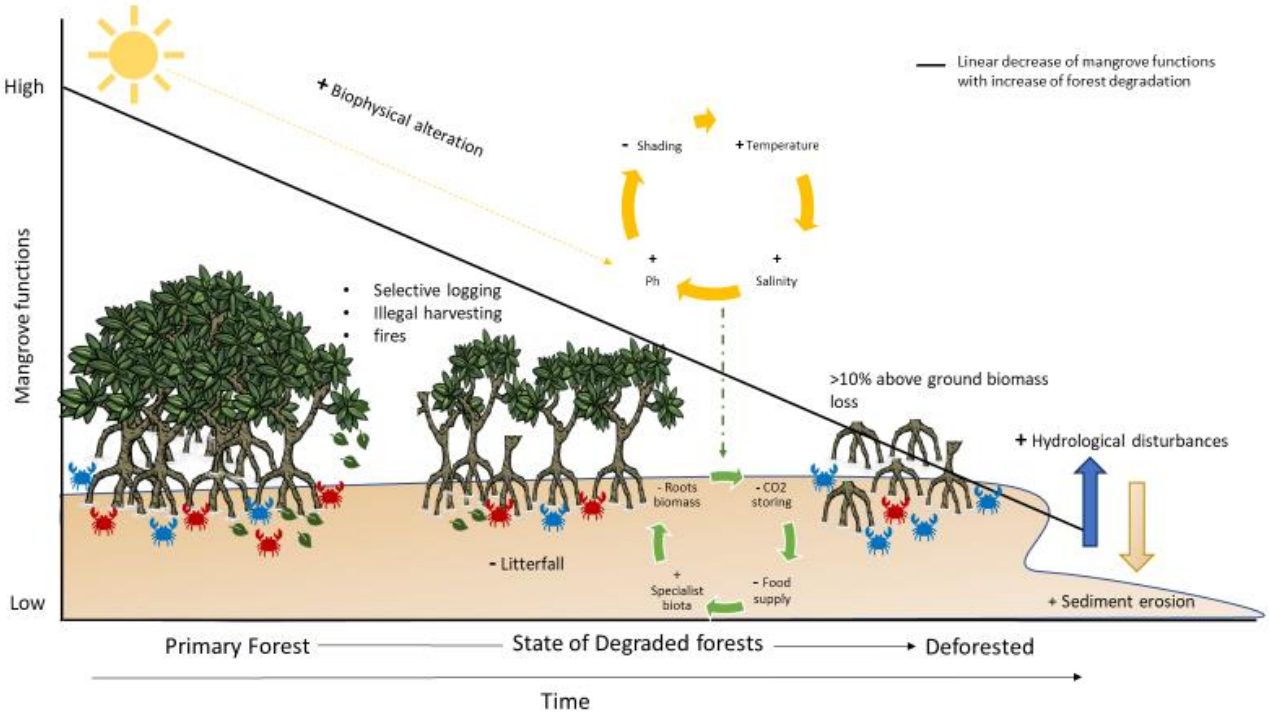


Figure 1: A hypothetical scenario of the effects of natural mangrove forest degrading due to anthropogenic disturbance over time, showing a linear decline of forest' functions. Biophysical parameters are altered by a reduction in canopy shading with positive and negative feedback mechanisms (yellow circle of arrows) causing subsequent feedback changes to biochemical

interactions in the sediment (green arrows). An increase of hydrological disturbance and sediment erosion is expected due to the removal of tree biomass. A reduction of canopy would also result in reduced litterfall, ultimately triggering a potential shift in macrofauna diversity and community composition, with specialised epifauna dominating the harshest condition.

2. Methods

2.1 Study location

The study sampled mangroves in the south of Kenya. Typically, the climate in the coastal area of Kenya is monsoonal due to the moist southeast monsoon occurring from March to September and by the dry northeast monsoon from October and March. Rains mainly occur throughout March, April and May with a shorter rainy season in October and November (Andreetta et al., 2014). The average annual precipitation varies between 1000 and 1600 mm. The average temperature oscillates between 28°C and 30°C with little seasonal variation; humidity is ~ 95%, due to the close proximity to the sea (Kitheka 1996). Mangrove forest were sampled in two bays: Gazi Bay (4° 22′ S, 39° 30′ E), which was a semi-enclosed, shallow bay, 40 km South of the city of Mombasa, and Vanga Bay at the border with Tanzania (Figure 2a). These sites are presently described.

Gazi Bay holds a 6.61 km^2 mangrove forest complex, which is up to 3.3 km across and concentrated along the northern shores of the bay (Matthijs et al., 1999). The forest display the typical vertical distribution pattern of East African mangrove forests with the seaward zone dominated by *Sonneratia-Rhizophora-Avicennia* trees whereas the intermediate zone is occupied by *Avicennia-Lumnitzera-Xylocarpus* complex with occasional dwarf *Avicennia* on the landward zone (Matthijs et al., 1999; Kairo 2001; Dahdouh-Guebas et al., 2004; Jenoh et al., 2016). Tidal amplitude ranges are 1.4 m to 4 m at neap and spring tides, respectively, generating significant flows across the bay. Salinity is influenced by freshwater influx via direct rainfall and river loss approximately 300,000 m^3 per year, of which 20 % is lost due to high evaporation, resulting in average salinity (35 up to 38 PSU max) (Kitheka 1997). Vanga is on a larger scale than Gazi Bay, with the total area of mangrove forest approximately 7 times greater than Gazi and covering 4428 ha (Figure 2b). The mangrove is spread across a series of creeks and includes stands on Sii Island, a small inhabited island 6 km from the Kenyan coast (Figure 2). Due to its greater exposure to the ocean, Vanga Bay is strongly influenced by monsoon winds, with strong and seasonal long rains occurred between April and June and short rains between October and December. The riverine influx of the Umba

river drains into the Bay via the Usambara Mountains in the North-east side of Tanzania into the Indian Ocean. In Kenya, 18% of mangrove forests have been lost at an average rate of 0.7% yr^{-1} in less than 25 years, with a difference in frequency of loss along different areas (Kirui et al., 2013; Mungai et al., 2019). One section of the forest of Gazi Bay had been protected since 2013 under the '*Mikoko Pamoja'* project; a community run and Plan Vivo associated conservation and carbon trading project that protected mangroves in the Makongeni area of Gazi Bay (Fig 2a, yellow area).

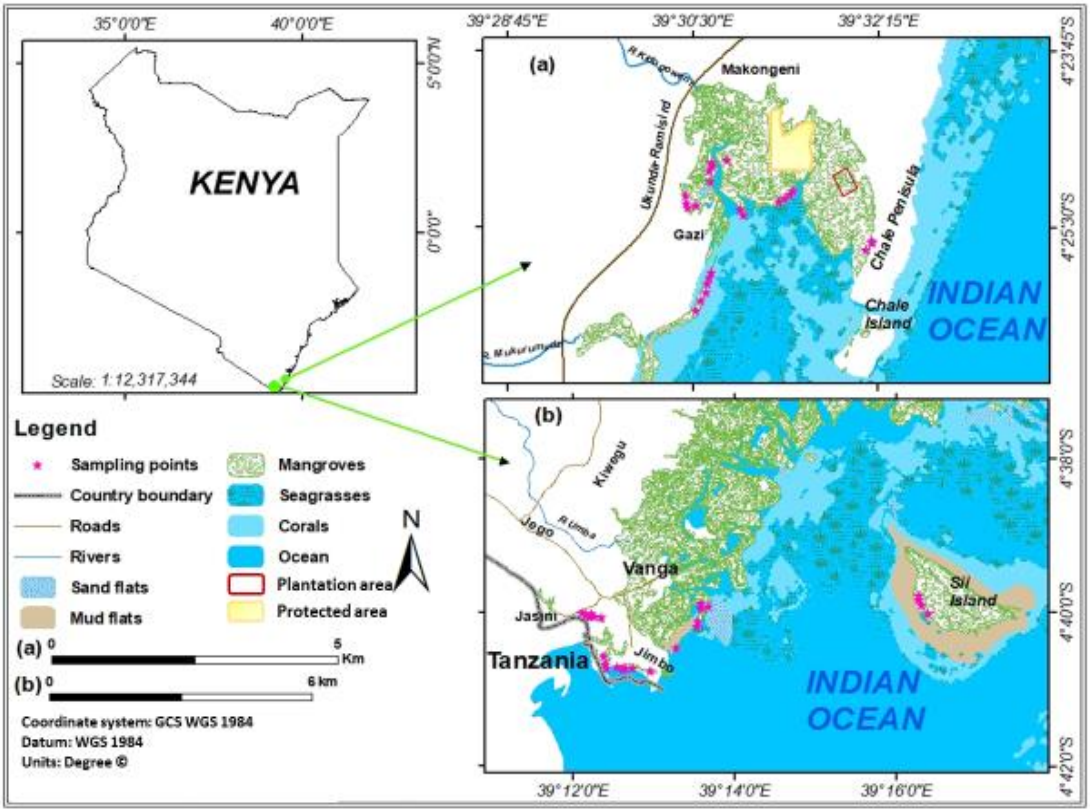


Figure 2: Map of the study area in South East Kenya, showing (a) Gazi Bay including the Mikoko Pamoja protected section (yellow) and planted areas (pink), and (b) Vanga Bay with Sii Island located 6 km off the coast.

2.2. Study design

The study design aimed to provide an impartial representation of an ordinal gradient of degradation (Figure 1) through sampling areas of varying levels of degradation, from natural forest to fully degraded. Haphazard sampling was used, in which forest areas of different levels of degradation were observed by randomly distributed observation plots (Figure 2a,b). Due to the lack of assessment of degraded areas at the observation sites, local knowledge

of the area was used to indicate which forest areas were degraded and which were not. Fifty plots of 10 x 10 m were observed in Gazi-Chale Bay (n=24), Vanga mangrove complex (n=22) and Sii Island (n=4). Plots were randomly located across the vertical (inter-tidal) gradient. Plots were kept at least 100 m away from each other, mangrove silviculture and protected areas to avoid alteration of biodiversity due to a more favourable environment. Per plot, a three-step approach was used to assess forest functioning by quantifying: 1) mangrove forest structure (Figure 3A), 2) epifaunal abundance and taxonomy (Figure 3B) and 3) biophysical parameters (Figure 3C). Sampling occurred from February until July 2019, focusing on spring tides, when mobile fauna is particularly active (Skov et al., 2002).

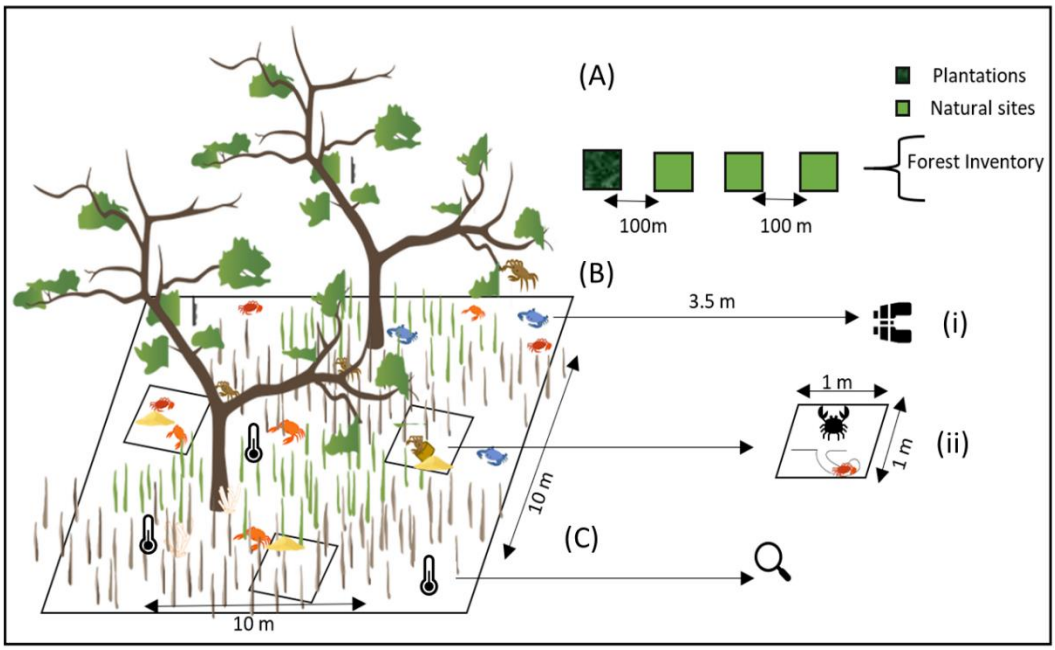
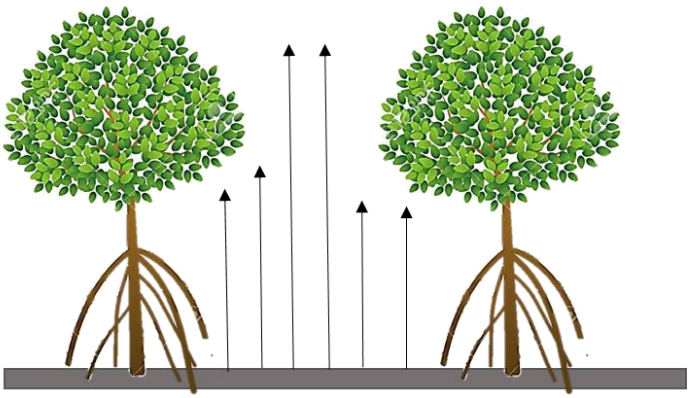


Figure 3: Overview of three-step approach per forest plot. A) Mangrove forest structure assessment using plots kept 100 m apart from each other and plantation sites, B) macrofaunal abundance and taxonomy quantification in three sub-quadrats (1x1m) used for: (i) binoculars observations of crab species and (ii) counts of crab burrows and assessment of epifaunal diversity. C) Biophysical parameters were measured at three different points within the plot.

2.3 Forest structure

Each plot area was outlined using meter tape, the GPS position was noted and all trees were identified to species. The following metrics were recorded to give data on forest structure (Figure 3A): height per tree (m), tree density (trees/ha), stem diameter per tree at breast height (DBH; at 130cm above ground level) and canopy cover (%) - defined as “the proportion of the forest floor covered by the vertical projection of the tree crowns” (Korhonen et al., 2006)

was calculated by following Korhonen et al., 2006 guidelines. It was observed at 3 points in the plot and the mean was calculated (Figure 4). Direct indicators of human disturbance were recorded as: tree stump density (stumps/ha) and number of cut branches (branches/ha). DBH measurements were taken at different positions along the stem depending on mangrove species following Kauffman and Donato (2012); e.g., for *Rhizophora mucronata* at 30cm above the highest prop root, with branches below 10 cm DBH were not measured. The height of each tree was recorded using a 4.8 m telescopic pole, which had tape markers at 25 cm intervals. When the trees exceeded 4.8 m, the pole was lifted, estimating the height of the tree as 4.8m plus the displaced height. An allometric equation specific to the study area in Kenya was used to convert DBH observations into above ground biomass of trees (AGB): $AGB\ (Mg\ ha^{-1}) = DBH(cm)*H+\rho$, where H was height (m), and ρ was wood density with



constants specific to tree species, following Cohen et al., 2013).

Figure 4: Canopy cover was quantified as the percentage of forest floor being covered by the vertical (arrows) projection of the tree crowns; figure adapted from Korhonen et al (2006).

2.4. Epifauna assessment

For each of the 10x10m plots, epibenthic fauna quantification involved two procedures (Figure $3B_{(i),(ii)}$): 1) quantification of brachyuran crabs following the two-step approach of Skov et al (2002) and 2) quantification of non-crab epifaunal abundance, including molluscs, echinoderms and crustaceans. For procedure 1) three 1x1 m^2 randomly located sub-quadrats made of pegs and strings were set out within each 10x10 m plot a day prior to observation (Skov et al., 2002). Common crabs of East African mangroves show different characteristics, with some species burrowing down in the sediment (burrowing) and others climbing the trees

or hiding among the dense roots (mobile-non burrowing). (1a) Visual counts (Skov et al., 2002) from a distance of 3.5 m in order to not disturb crabs, were used to quantify non-burrowing species. To do this, ~ one hour after the receding tide the observers stood standing still for 15 minutes to allow the less-bold species to emerge. (1b) Burrow counts were used to quantify burrowing species and categorised into four size classes: small (<4 mm), medium (4-8 mm), large (8 -20 mm) and extra-large (>35 mm). The size classification assisted with allocating crabs-burrow counts to crab families, with grapsid crabs assumed to account for the large and extra-large burrows (Skov et al., 2002) and ocypodids assumed to account for the small burrows. 2) Epifauna abundance lying within the quadrat (ind. m^{-2}) was recorded and identified at species level after the crab quantification occurred, gastropods climbing trees were excluded from estimation. To facilitate analysis of how faunal traits varied with forest structure along a degradation gradient, the following was performed for crab species only. Crabs were classified into four trophic trait-categories that cover the main feeding functions represented by mangrove crabs (Icely and Jones, 1978; Cannicci et al., 1993; Fratini et al., 2000; Gillikin et al., 2004; Cannicci et al., 2008):"foli-detritivores" i.e. feeding on mangroves propagules and fallen leaf litter, detritivores (including deposit feeders), omnivorous and predators.

2.5. Biophysical parameters

Biophysical parameters were measured as they are indicative of pressure upon fauna. All parameters were measured according to the Soil Science Methods and Application (Rowell 2014). Sampling was conducted at low tide during spring tide periods after measuring epifauna in order to reduce faunal disturbances inside the plot (Figure 3C). Soil temperature (30cm below surface) was measured at three randomly distributed points per plot and a mean calculated. As a proxy of shading, air temperature was measured from the closest point outside and inside the tree canopy using a glass thermometer. In attempt to standardised diurnal variation the following equation was used on canopy temperature extreme values: ($Temperature_{out}$ - $Temperature_{in}$). Sediment grain size was sampled by three randomly distributed soil corers at 30 cm depth per plot; the tree cores were pooled and homogenised in the laboratory and sediment grain size analysis done on a wet, ~ 5 g, sub-sample using a Mastersizer 3000 laser particle size analyser. Soil samples were analysed using a grain size distribution and statistical package with Gradistat 8 software. Soil pH, water and soil salinity were measured *in situ* with a portable Hanna HI 9812-5 Instrument multiparameter.

2.6. Statistical analysis

The analysis had two specific objectives: (1) to establish classes of mangrove forest degradation and (2) to determine the effect of degradation on the epifaunal community.

(1) Establishing classes of mangrove forests degradation

A principle component analysis (PCA) was executed on the matrix of log (x+1) converted data applied to the whole forest factors and biophysical parameters with previous normalisation of data, to identify degradation classes. The PCA aimed to reduce the number of forest and biophysical factors to cover as much inter-site variability as possible. Following Zuur et al. (2007), the results of scree plot and eigenvalues were used to retain and present a maximum number of components. A clustering algorithm (K-means) analysis was used to reduce the number of data-points and identify classes of degradation (Faber 1994). Exploratorily analyses showed that assumptions of homogeneity of variance and normality of residuals were met.

Multivariate analysis

Generalized linear mixed models (GLMMs) were used with the aim to determine how forest parameters affect canopy cover as an indicator of forest degradation and to define a comprehensive proxy involving more than one single parameter using the Akaike Information Criterion (AIC). The AIC generated for each model was compared using the ΔAICc (i) ,which indicates the differences between AIC values of the best-fit model to the other models, and the AICc weight (Wi) to estimate the probability that the tested model was the most appropriate to explain the values observed. GLMMs were preferred to ordinary linear regression models to accommodate non-stable variances and alternative exponential residual distributions (Zuur et al., 2007). GLMMs were based on the following equation, where the (Y) response variables vary according to their distribution in an exponential family (e.g. binomial, quasibinomial, Poisson and Gaussian). The mean (μ) of the distribution depends on the explanatory variables (X): $E(Y)= \mu = g\text{-}1 (X\beta)$; where E(Y) is the expected value of Y, Xβ is the linear predictor and g is the link function (Nelder and Wedderburn, 1972).

Univariate analysis

Mixed effect models were also used to test for relationships between biophysical parameters and canopy cover as proxy of degradation, following the equation: $Y= X\beta + \varepsilon$, where Y is the response vector, X is the model matrix, with typical row $x'I = (x1i, x2i, ..., xpi)$, β is the vector of regression coefficients and ε is the vector of errors (Galecki and Burxykowski, 2013). These analyses were performed using the packages qpcR, princomp, lme and stats in R studio version 3.6.

(2) Analysis of Faunal Community structure and composition

The relation of faunal structure (e.g. diversity, richness and evenness indexes) and composition (e.g. dissimilarity matrix) due to singular forest parameters were also assessed with GLMMs to understand their contribution to faunal variation. Secondly, multivariate GLMMs were used to determine whether the combination of forest variables would better predict the variation in faunal diversity than canopy cover on its own. Two models were produced: Model 1: one explanatory covariate, canopy cover as a proxy of forest degradation; and Model 2: multiple explanatory covariates, all the forest structure variables extracted from the PCA termed as "forest complexity" consisting of (canopy cover + AGB + stumps + cut branches+ basal area) with the following equation: $Y (x1i, x2i, ..., xpi)+ \mu (g-1)$. The best models were selected using the Akaike Information Criterion (AIC). The AIC model selection showed that there were other relationships within forest parameters, but models with canopy cover only stayed or were preferred as indicative of best-fit models. As it were, the analysis showed canopy cover was the most consistent forest structure parameter to explain variation in epifaunal response variables. Hence, canopy cover was used as a proxy of forest degradation in subsequent analyses to detect fauna-degradation patterns.

To evaluate the variation with forest degradation of crab community composition, biodiversity (Shannon-Wiener H'), richness and evenness, Permutational Multivariate Analyses of Variance (PERMANOVA) were used, with classes of canopy cover as the independent predictor variable and species abundance as the dependent response variables. Fourth root transformations of the data were applied prior to analyses to highlight rarer species and reduce the asymmetry of species distribution (Clarke et al., 2006). Crab community composition based on abundance and composition of trophic categories distribution along the canopy cover gradient was illustrated using Multidimensional Scaling (MDS) based on

Bray-Curtis similarities matrix. A follow-up canonical analysis of principal coordinates (CAP) was conducted to detect differences in crab community composition. The effect of canopy cover class (defined in step 1) on crab community species-composition and composition of trophic categories was evaluated using a one-way PERMANOVA. All PERMANOVA's were performed using Primer V6, PERMANOVA + add on package software. Pairwise comparisons of crab community composition were carried out at the canopy cover classes, based on unrestricted permutation of raw data, to allow for sufficient numbers of unique permutation (>500) to be analysed. To evaluate differences between canopy cover classes on the frequency of trophic groups a Similarity Percentage analysis (SIMPER) was performed on Bray–Curtis matrix dissimilarity.

Finally, the variation in the diversity of crab communities. Trophic structure was defined according to three complementary indices of functional diversity: functional richness (the number of unique trophic traits), functional evenness (the regularity of the trophic trait based on the abundance distribution) and functional redundancy (an index created as a ratio between functional and taxonomical diversity) (Villéger et al., 2008). Diversity metrics were also estimated for Shannon-Weiner diversity (H'), species richness and species evenness (species equitability), using the 'vegan', ade4' packages. GLMMs were used to estimate relationships between each diversity metric (functional richness, evenness, diversity and redundancy) with canopy cover, following the structure of model 1 above.

3. Results

3.1 Determining a classification for degradation in mangrove forests

Forest structural variables varied considerably across sites, with Sii Island and Gazi showing the least signs of degradation, and Jimbo (Vanga) and Chale (Gazi Bay) showing the highest (Table 1). A principal component analysis (PCA) performed on forest structures revealed no marked clustering of observation plots (Figure 5). Plot differentiation along PC1, which explained 39.4% of the variation among plots, was mainly driven by the higher loading of basal area (m^2) and AGB (Mg ha^{-1}) and stump density (stumps ha^{-1}). Conversely, plot differentiation along PC2 (22.8% of variation) was explained by canopy cover (%), cut branches (branches/ha); with basal area (m^2) and AGB (Mg ha^{-1}) have little influence to the PC2 (Figure 5). In effect, canopy cover (%) and stump density (stumps ha^{-1}) were negatively correlated to each other, and although they contribute to both axes, were more influenced by

PC2 and PC1 respectively. The right angle created between cut branches (branches/ha) and stump density (stumps ha^{-1}) suggested the small correlation between the two variables. Here, basal area and AGB (Mg ha^{-1}) vectors showed the strongest correlation to each other and to PC1, with the other correlations being only marginals. Overall, the PCA indicated canopy cover had a positive, although minimal association with the other observed forest factors, showing to be a fair single factor measure of forest degradation (Table 2). Canopy cover was tested against the other remaining forest factors as a proxy for forest and showed a positive regression with AGB (Mg ha^{-1}), basal area (m^2 ha^{-1}) and stump density (stumps ha^{-1}) and a negative regression with cut branch density (branches ha^{-1}, Table 2). Mixed linear models were used to test for relationships of biophysical variables (temperature, salinity, grain size, pH) with canopy cover. Comparison along the gradient in canopy cover showed that there were no significant trends for soil temperature (p =0.14), soil salinity (p =0.13) and grain size (p =0.12). Shading diminished with a reduction of canopy cover (F=37.1, d.f= 45 p = 0.001, R^2 = 0.4 , β=1.36, Figure 6a), whereas pH increased (F= 46.5, d.f= 45 p = 0.001, R^2 = 0.5 , β=0.6, Figure 6b).

Table 1: Forest structural characteristics at five sampled mangrove sites in Kenya. Sites have been ordered vertically according to perceived increase in forest degradation, with the least degraded site in the top row and the most degraded in the last row.

Degradation	Count (n)	Site	Description	Mean AGB (g)	Mean cut branches density (ind./m2)	Mean Canopy Cover(%)	Mean stumps density (ind./m2)	Mean Streightness	Mean Tree height (m)	Mean DBH
Semi pristine area	8	Sii Island, Gazi	Dense forest, high stature, well formed canopy, mature trees	230.31	2.75	80.3	0.6	3.0	2.6	9.3
Gradient of degradation ↓	11	Gazi	Dense forest, medium stature, relatively open canopies, mature well-formed canopies	346.30	13.46	55.8	4.92	2.5	2.5	7.5
	9	Gazi,Jimbo,Vanga	Moderate-high stand, harvested,	241.88	15.03	17.2	9.62	3	2.84	4.85
	9	Jimbo, Vanga	Shrub dominated, very sparse,influenced by water and	235.64	14.45	16.8	9.35	2.30	2.85	5.00
Deforested area	8	Jimbo, Chale	Waterlogged dominant, very sparse, stunted, short stands, mud-flat	44.09	35	2.5	21.625	1	0.58	1.59

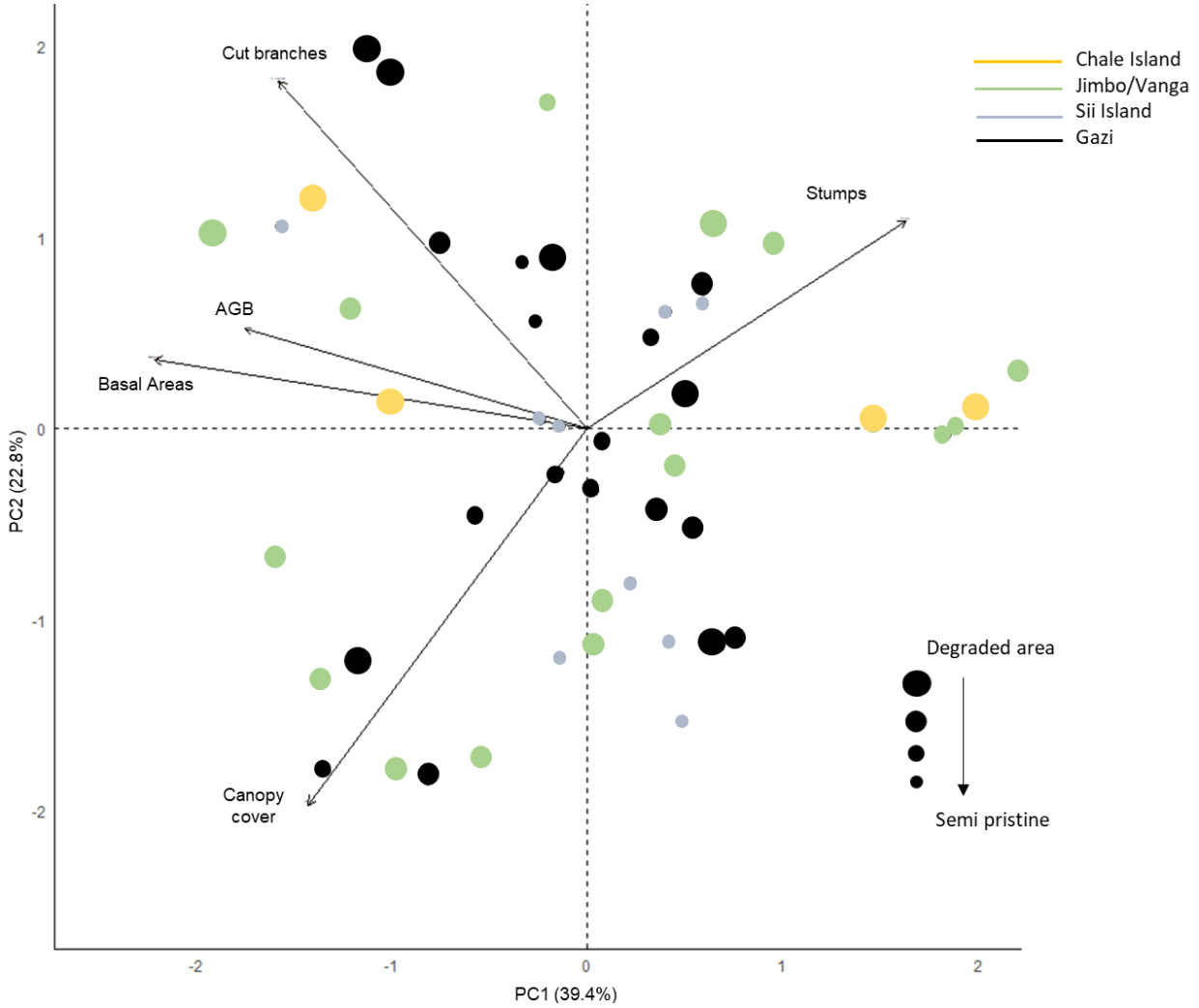


Figure 5: Principal component analysis (PCA) showing relationships among mangrove forest variables. Each dot in the PCA represents mangrove plots and was based on natural log (x+1) transformed data.

Table 2: Estimated regression parameters, standard errors, T-values, P values (**P <0.01,* P<0.05, n.s. P>0.05) for the Quasibinomial GLMM models.

Variables	Est.std	Error	T-value	P
Canopy Cover ~ AGB	0.60	0.200	3.15	**
Canopy Cover ~ Basal Area	0.00	0.000	2.04	*
Canopy Cover ~ Stumps	0.04	0.060	-2.54	*
Canopy Cover ~ Cut Branches	-0.01	0.014	-0.55	n.s.

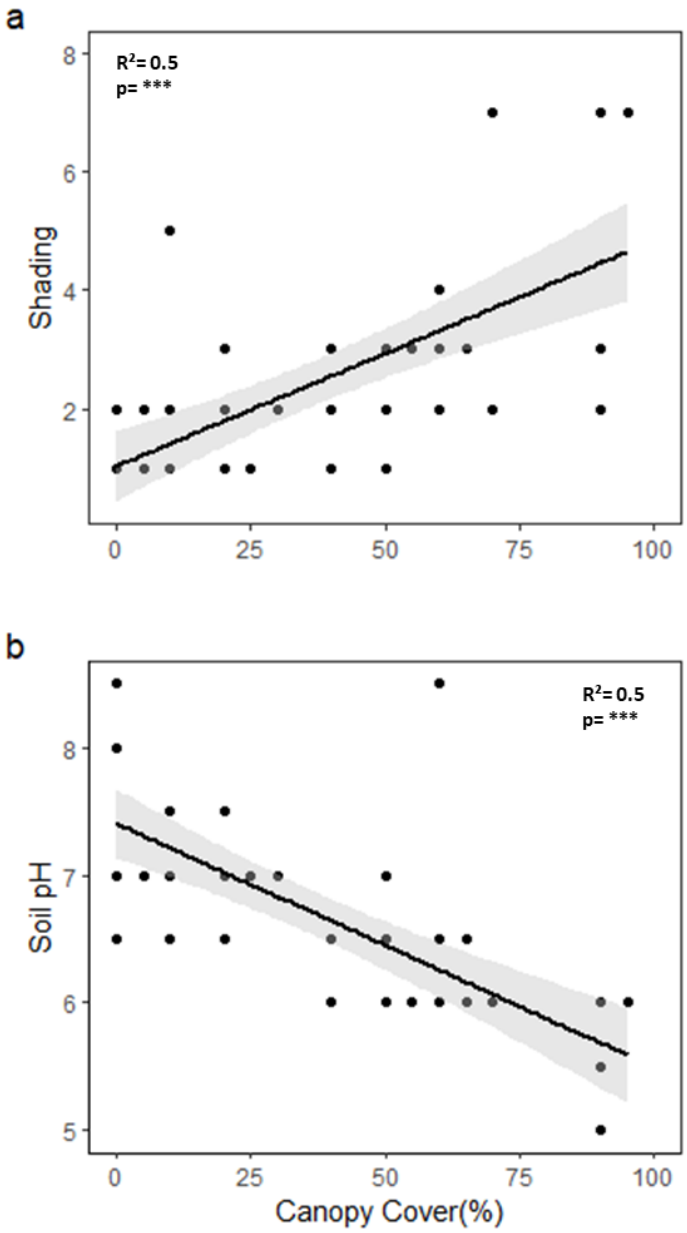


Figure 6: Relationships of **(a)** Shading (the difference between outside and inside canopy temperature) and **(b)** Soil pH with mangrove canopy cover (%).

3.2 Variation in epifaunal diversity

Across sites, 17 families, comprising 60 distinct species of epifauna including gastropods, bivalves, echinoderms and crustaceans, were identified in the mangrove forest plots. There was no clear relationship between epibenthic fauna species evenness (J) and canopy cover (Table 3), whereas abundance, richness and diversity (H') showed negative relationships

along the canopy cover (Table 3). Epibenthic faunal species richness was significantly related to all forest structure variables (GLMM forests structures: $p < 0.001$, Supplementary Table 1) while biodiversity and abundance were generally unrelated to forest structure (Supplementary Table 1). The results from the multivariate GLMMs showed that two models were within ΔAICc <1 (Supplementary Table 2). The most parsimonious models were containing only canopy cover for the majority of the taxonomic structure indexes (wAIC=1), whereas the models holding forest complexity did not provide any clearer trends. An exception was found for epifaunal species distribution, where the best model resulted to be the one having forest complexity (AICc=283.1; relative Aikake Likelihood (logLik) =1; ΔAICc=0 and wAIC =0.6).

Table 3: Akaike's information criteria (AICc), estimated regression parameters, standard errors, T-values, P values Adjusted R^2 for the binomial[a] and Gaussian distribution of GLMM univariate models testing for relationships of faunal response variables with canopy cover.

Variables	AIC_c	Est.std	Error	T-value	P
Ephibenthic Fauna					
Species abundance	283.9	0.1	0.0	4.9	***
Species richness	118.5	0.0	0.0	3.7	***
Species evenness[a]	8.05	-0.1	0.2	-0.1	n.s.
Shannon diversity	58.9	0.0	0.0	3.9	***
Crustaceans					
Species abundance	228.07	0.1	0.0	5.2	***
Species richness	71.281	0.0	0.0	3.3	**
Species evenness[a]	15.297	0.0	0.0	0.7	n.s.
Shannon diversity	40.18	0.0	0.0	3.8	***

3.4 Variation in crab diversity

Negative relationships between abundance (p =0.01), richness (p =0.01) evenness (p =0.5) and diversity (p =0.001) were shown when tested with canopy cover % (Table 3). Crab abundance distribution was the only variable which showed a consistently clear association with factors of forest degradation (Supplementary material I): when taken singularly, crab abundance was negatively related to the reduction in canopy cover (%) (R^2=0.4, F=21.9, p=0.001, d.f= 45, Figure 7a), aboveground biomass (R^2=0.3 F=4,60, p =0.001, d.f= 45, , Figure 7b) and basal area (R^2=0.3, F=4.15, p =0.001, d.f= 45, , Figure 7c), but positively related to stump density (R^2=0.1, F=-2.12, p =0.04, d.f= 45), and had no relationship with cut branch density (R^2=0.003, F=0.17, p =0.8, d.f= 45). Only two univariate models yielded < ΔAICs < 1 (Table 4). The most parsimonious model contained only canopy cover % which was more plausible (wAIC=0.6) than the next model (wAIC=0.3), which included forest structure complexity. Forest complexity did not explain clearer patters of crab abundance when modelled together (Table 4).

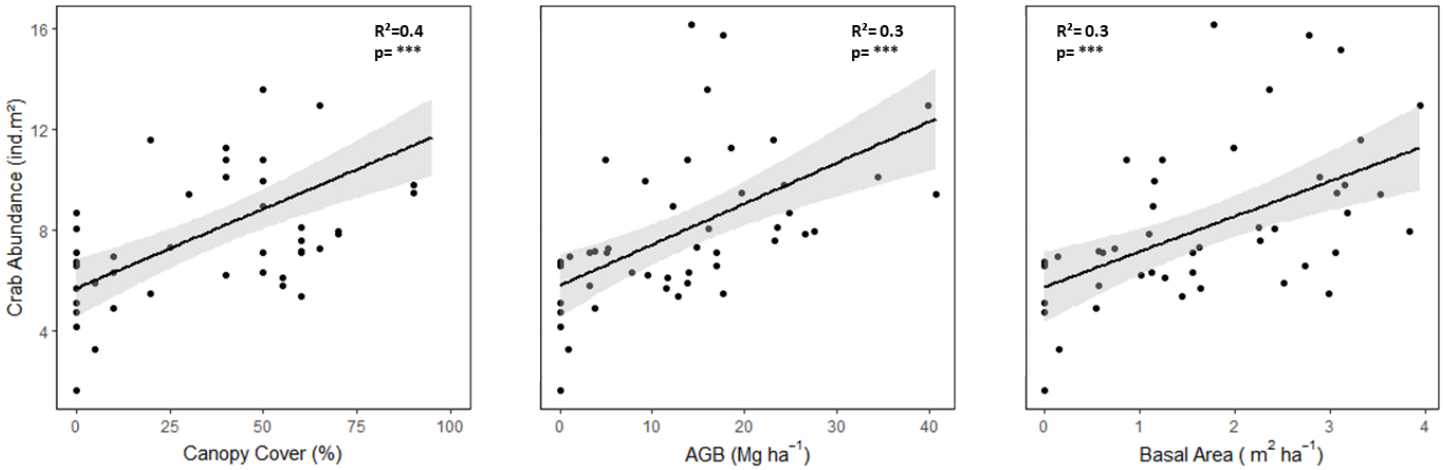


Figure 7: Relationship of crab abundance with **(a)** canopy cover, **(b)** above ground biomass (AGB) and **(c)** basal area**.**

Table 4: Model ranks for the Generalized Linear models of crabs abundance distribution with a Gaussian distribution and forest structural complexity. Models are ranked by corrected Akaike's information criteria (AICc), with all models within ΔAICc < 2 of the top ranked models. The relative likelihood and weight of evidence between each model is indicated by Akaike likelihood (logLik) and weight (wAIC) and the variables present in each model are mentioned

Model Rank	Variables	AIC_c	logLik	ΔAICc	wAIC
1	Crab abundance ~ Canopy Cover	218.98	1	0	0.6
2	Crab abundance ~ Forest complexity	223.15	0.5	1.07	0.3

3.5 Variation in the compositions of crab community and trophic categories

Crab community composition varied along the canopy cover classes (Figure 8, Table 5), with the highest dissimilarity recorded between communities inhabiting areas with canopy covers of 5 and 70 % (SIMPER pairwise test: diss%=94.36); the main species contributing to this cumulative dissimilarity were foli-detritivores, i.e. *Chiromantess eulimene* (94.84%), *Neosesarmatium smithi* (pairwise test: diss%=83.42) and omnivorous *Metopgrapsus thukuhar* (89.46%); whereas between canopy cover 5 and 60 % (pairwise test: diss%= 88.25) *Chiromantess eulimene* (pairwise test: diss%= 90.49%) and omnivorous such as: *Macrophtalamus milloti* (pairwise test: diss%= 86.94) contributed to dissimilarity (Supplementary Table 3).

Table 5: Output of the Permutational Multivariate Analysis of Variance (PERMANOVA)(Bray–Curtis similarity matrix on fourth-root transformed data) testing for effects along mangrove canopy cover classes on (i) Crab community composition and (ii) Crab trophic categories composition (df= degrees of freedom; MS=mean square; Pseudo-F= F statistic, P value *P < 0.05 and Perms=Permutation computed)

Variables	Source	df	MS	Pseudo-F	P	Perms
Crab community composition	Canopy	10	3028.10	1.42	*	998
	Redisual	36	2135.10			
Crab trophic categories composition	Canopy	10	631.04	1.73	*	999
	Redisual	36	366.87			

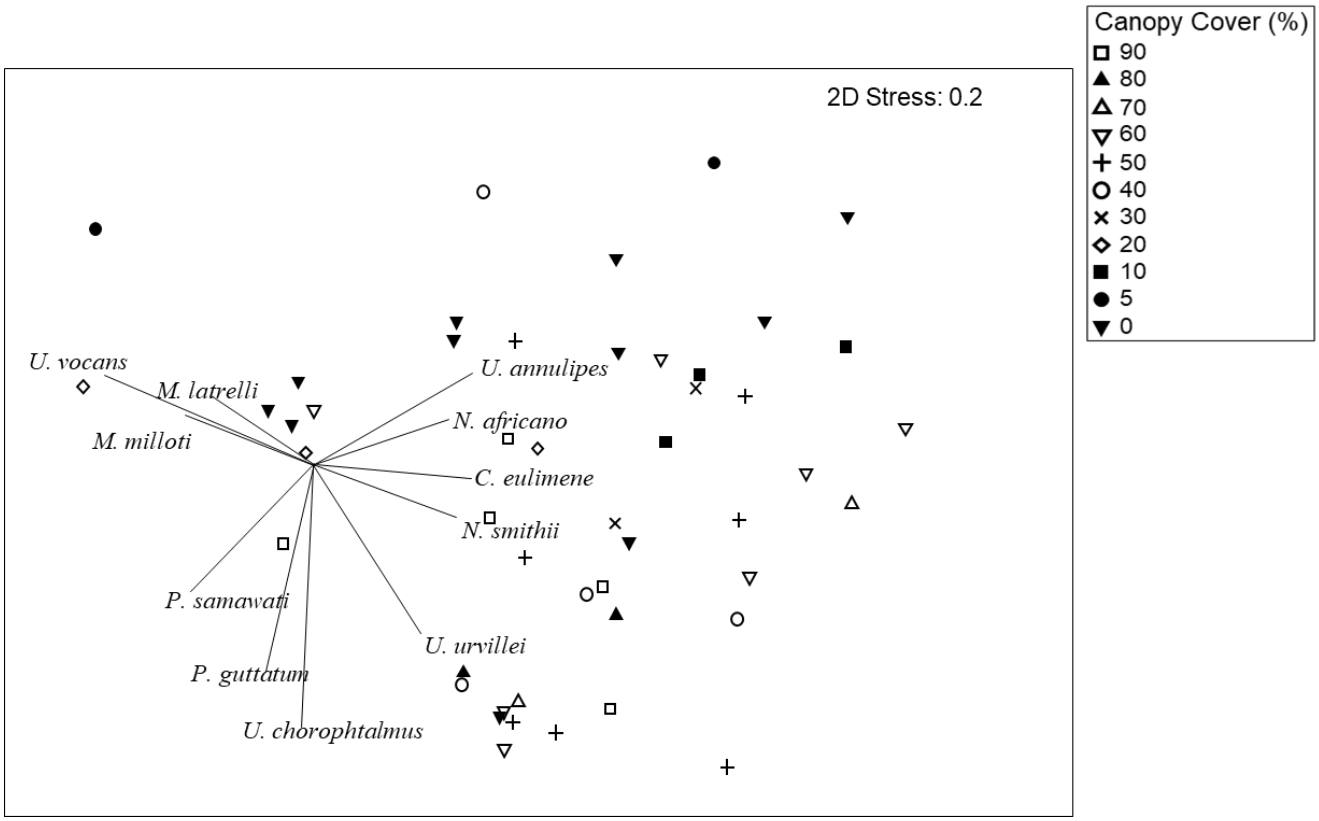


Figure 8*:* Variation in crab species composition with canopy cover classes, as described by MDS ordination, with vectors based on Pearson correlation <0.2. Crab community assemblage included species from families*:* ***Sesarmidae*** *(Perisesarma guttatum, Perisesarma samawati, Neosesarmatium smithi, N. africanum (ex.Neosesarmatium meinerti), Chiromantess eulimene),* ***Ocypodidae*** *(Uca annulipes, U. urvillei, U. chlorophtalmus, U. vocans, U. inversa, U. tetragonon),* ***Portinidae*** *(Thalamita crenata),* ***Macrophtalmidae*** *(Macrophtalmus latrelli, Macrophtalmus milloti) and* ***Grapsidae*** *(Metopograpsus oceanicus, M. thukuhar, M. messori).*

Trophic traits frequency (based on crab abundance distribution) were also related to the canopy cover classes (Table 5, Figure 9). The greatest difference in functional trait diversity was between plots with dense canopy cover and those with scarce canopy cover (%). For instance, crabs living in 5 and 90 and 0 and 90 % canopy cover resulted to be the most diverse (PERMANOVA p=0.05, p=0.03) with dissimilarity caused by the reduction in detritivores, omnivores and foli-detritivores crabs (SIMPER: cumulative diss%= 41.5, 77.06 and 92.5). The absence of predators between the 0 and 90 % canopy cover accounted for the majority of separation (SIMPER: cumulative diss %= 92.77). Similarly, communities living between 5 and 50 % canopy cover (PERMANOVA p=0.02) showed a diverse composition

due to a reduction in detritivores and foli-detritivores (SIMPER: cumulative diss%=71.7 and 100). A decrease of omnivores and detritivores was also observed in communities with low canopy cover % (0 and 5) (ANOSIM p=0.04, R^2= 0.6; SIMPER: cumulative diss% =60.04, 88.91 and 100). Yet, dissimilarity was distinguished between communities inhabiting 0 and 50 % canopy cover (PERMANOVA p=0.001) with a reduction in foli-detritivores and detritivores species (SIMPER: cumulative diss%= 83.17 and 96.45). Plots with dense canopy cover (e.g. 60 to 90%) included similar functional community composition with the major drivers of dissimilarity owing to a decrease in predators and detritivores (Supplementary Table 4).

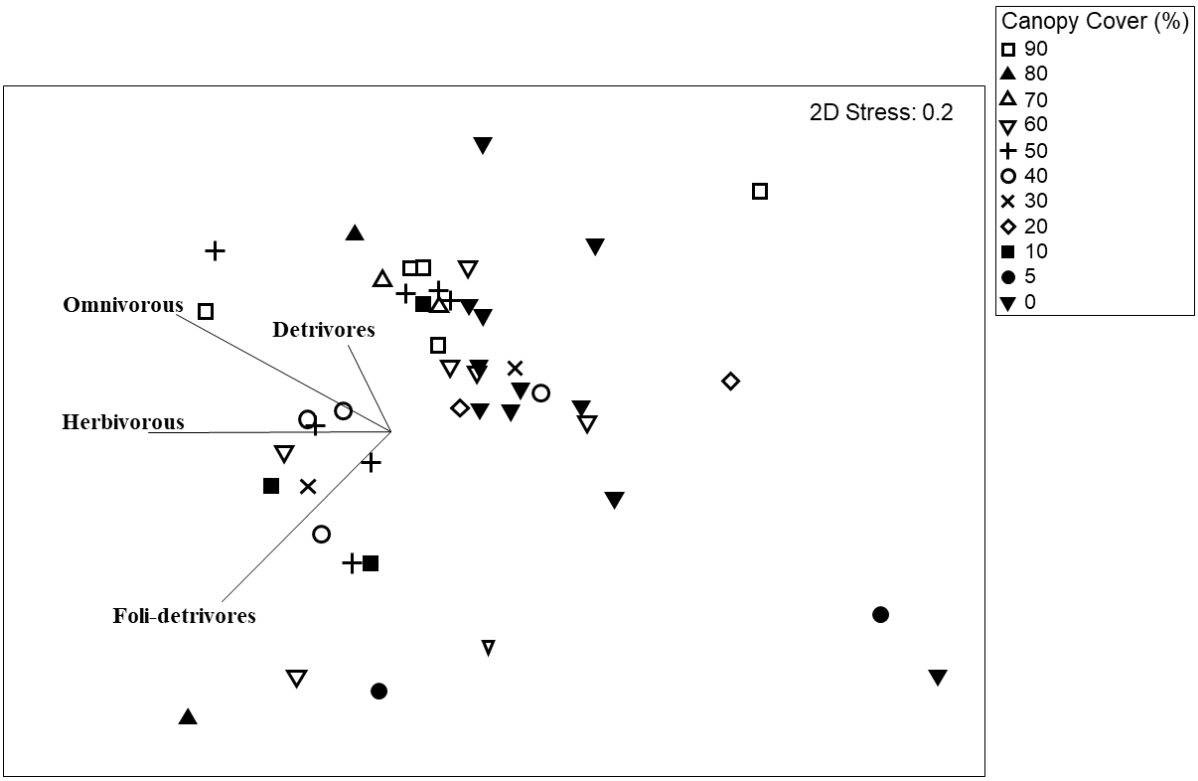


Figure 9: Functional composition of mangrove crabs in a MDS ordination, with vectors based on Pearson correlation <0.2.

3.6 Crab functional diversity and redundancy

The results from the GLMMs showed negative relationships between functional diversity and functional richness when tested against canopy cover (%) (Table 6); with functional evenness being overly-dispersed and not statistically significant (Figure 10d),and functional redundancy remained constant along the gradient in canopy cover (Figure 10d, Table 6).

Table 6: Akaike's information criterion, standard errors, T-values, P values ***P< 0.01,n.s.P>0.05 and adjusted R^2 for the Gaussian and binomial [a] GLMM distribution models.

Models	Variables	AIC_c	Est.std	Error	T-value	P
1	Functional diversity ~ Canopy Cover	45.3	0.005	0.002	2.7	*
2	Functional richness ~ Canopy Cover	74.5	0.005	0.002	2.13	*
3	Functional eveness ~ Canopy Cover	15.4	0.01	0.02	0.5	n.s.
4	Functional redundancy ~ Canopy Cover	-9.5	0	0	-0.6	n.s.

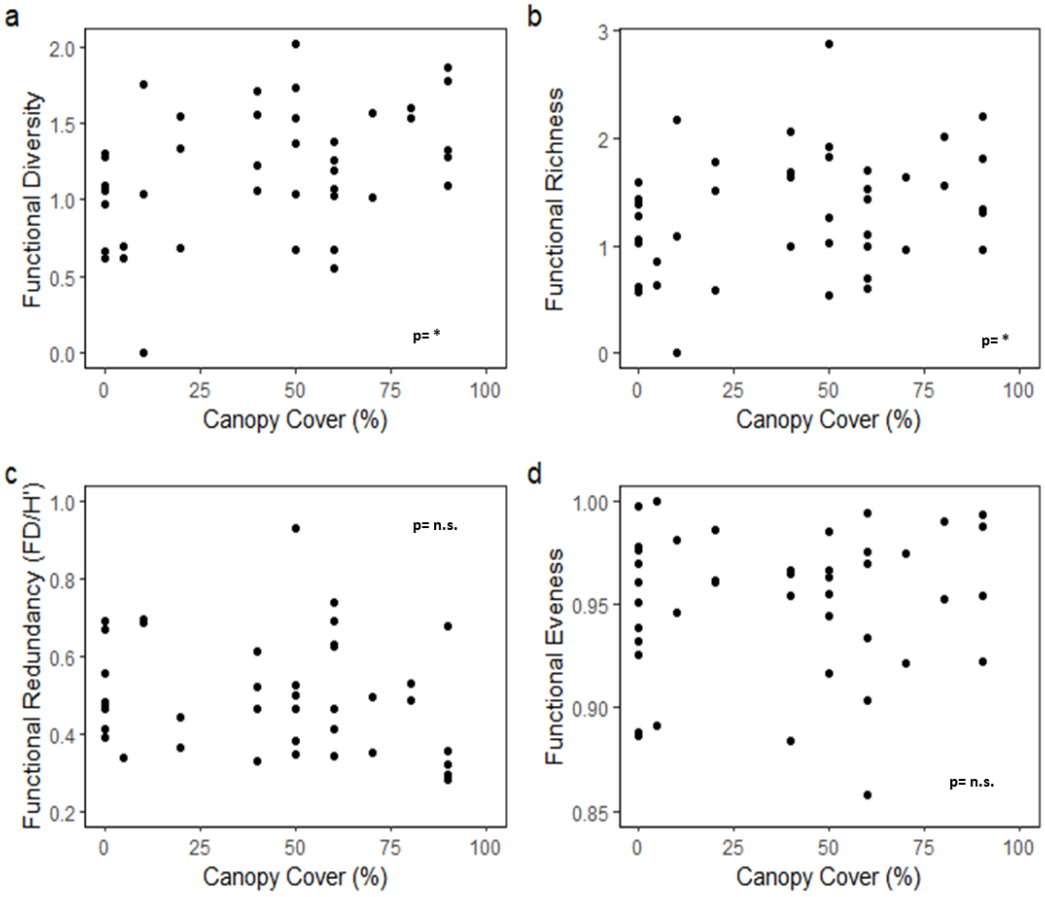


Figure 10: Variation in functional diversity **(a)**, richness **(b),** redundancy (FD/H') **(c)** and evenness **(d)** of crab trophic traits along the gradient in mangrove canopy cover.

4. Discussion:

Using in-situ observations and generalized modelling methods, this study sheds a light on the variation of macro-epifaunal abundance, taxonomical and functional structure and community composition along a degradation gradient. Canopy cover was identified as the best predictor of forest degradation and the overall epifaunal abundance, diversity and richness of fauna, but not the taxonomic evenness, diminished along the degradation gradient. A reduction in functional diversity indicated that the lower level of degradation sustained more efficient uses of resources and therefore higher productivity and niche complementarity. Generalist species were able to thrive across the degradation gradient, while drop in canopy cover saw the loss of more specialist species e.g. *Chiromantes eulimene*. Here, functional redundancy across crab communities remained similar, with some species of crabs adjusting their diet according to food availability and illustrating behavioural plasticity across trophic levels (Needham et al., 2010; Bingham et al., 2018).

4.1. Mangrove forest degradation

The results from this study showed that along a forest degradation gradient, several differences in forest structure and the associated epifaunal species composition occurred, reflecting the impact of anthropogenic disturbance on the mangrove ecosystem and its ecological processes. The effects of mangrove cutting on forest structures were clearly visible, especially in the Vanga-Jimbo mangrove complex, where features of scarce canopy cover, dense stands of only young trees and standing dead trunks were relatively abundant. With increases in degradation, differences in forest structures as a result of human degradation were evident. There was a spatial trend of variation in degradation-indicating features (e.g. stem cut density, stumps, reduction of canopy), but relationships between the forest structural parameters were not statistically consistent. In addition, predicting which variables affected the patterns of forest degradations found in the studied sites was unachievable, suggesting that other forest variables may be involved in mangrove degradation. Due to large variation in the data, it was not possible to permit statistical identification of degradation classes, despite the study intended to do so. This, could be due to mangrove forests in many places have already experienced significant changes to species composition, abundance and distribution, as a result of past cutting and other anthropogenic influences over time (Walters 2005), for which this study could not identify, due to the unavailability of historical data on site-specific mangrove exploitation and the unpredictability

of human efforts on mangrove forests. For instance, when a forest undergoes intense cutting, there are no trees where to notice cuts or cut branches (as cut trees may be fully removed). Yet the absence of stumps can mislead the representation of the forest, creating difficulties in identifying the features of the forest, such as size or length. The models used to detect relationships of reduction in canopy cover and other indicators of human disturbance (e.g. stump and cut branch densities) suggested that these relations are not always predictable. Here, the lack of consistent linear associations between forest parameters linked to degradation (e.g. cuts and stumps) and forest structure (AGB, basal area and canopy cover) meant canopy cover was used as the preferable single proxy of mangrove degradation. This choice was consistent with previous studies where canopy cover was used as an indicator of forest health and quality (Asner et al., 2004; Joshi et al., 2006; Chen et al., 2019; Wu et al., 2020). Among the several consequences of forest thinning and degradation, few studies also reported alteration of sediment characteristics from degradation (Blanco et al., 2012; Carugati et al., 2018; Perri et al., 2018; Bernardino et al., 2019). Here, only shading and soil pH varied among the biophysical parameters measured, with the greatest differences in shading found to be between forests with highly reduced (<10%) and dense (>80%) canopy cover. Soil pH showed an increase in alkalinity with degradation, which implies high pore water exchange rates (Borges et al., 2003; Call et al., 2015; Sippo et al., 2016), from two possible causes. First, it could be due to particularly high degradation of fringing mangroves, where sediment is regularly flooded and which are easier to access for loggers. Or, as this study shows, the intensification of crab burrowing creates strong perforation of soils to influence the biological turnover (Smith et al., 1991), which regulates the forest productivity and physically modifies the habitat (Stieglitz et al., 2000; Lee 2008; Noori et al., 2017). The majority of the highly degraded forests showed a great abundance of Ocypodid *crabs* (e.g. *Uca annulipes, U.vocans, U. chlorophtalmus)* which were largely responsible for the burrowing activity. Despite the variation of soil pH and shading, other soil parameters, such as salinity, temperature and grain size, showed a spatial homogeneity across the degradation gradient, supporting similar findings from another study on mangrove removal (Bernardino et al., 2018). This may be due to the constant influence of tidal cycles, that overturns and homogenises the soil and creates stabilising soil conditions across degraded habitats, even when canopy cover is fairly low; and/or it may be because belowground roots take long time to degrade after above-ground removal of trees (Bernardino et al., 2018), creating a lag in the responses of below-ground variables to degradation, and thus a mis-match between

above and below-ground indicators of degradation. Due to larger canopy gaps that occur in the degraded areas, the solar radiation penetration is greater, and the biophysical parameters may still be influenced by a functioning root structure belowground, promoting drainage, percolation and circulation of tidal flushing (McKee and Faulkner 2000; Bernardino et al., 2018). Although restricted tidal flushing due to partial or total interruption of the hydrological connectivity by disturbances are shown in large scale deforested areas, with consequently hypersaline conditions and high soil temperatures, which were not extensively looked in this study (Perez-Ceballos et al., 2020). A cause and effect relation is hard to establish due to the reciprocal effect of canopy variation on biophysical parameters, and the natural variation of biogeochemical soil components along the vertical zonation gradient. In any case, mangrove degradation resulted in a mosaic of disturbance intensities ranging from forests showing severe disturbance to forests of minimal or no disturbance. Mangrove degradation induced a reduction in environmental heterogeneity, consistent with the reduction in biogenic structures occurred after logging.

4.2 The response of biodiversity along the degradation gradient

4.2.1 Epifaunal diversity responds to habitat degradation

The taxonomic diversity, richness and abundance of mangrove epifauna all decreased with habitat degradation, with a linear decline of overall biodiversity to forest cutting. The change in epifauna with forest degradation was mainly determined by the reduction of canopy cover rather than other forest variables. Studies carried out in Mozambique also confirmed that the presence of biota in mangrove forests is strictly linked to plant cover and availability and not on the biogenic structures of the mangrove trees (Fondo and Martens, 1998). Mangrove faunal species are located according to their biophysical tolerance to environmental stressors of salinity, temperature and desiccation (Fondo and Martens, 1998). Although in this study environmental parameters (e.g. salinity and temperature) were approximately homogenous across the degradation gradient, shading, which reduced with decline in canopy cover, might have also contributed to the reduced richness and diversity. Under shade conditions, the canopy of the mangroves typically has greater amount of leaf litter, nutrients and soil moisture (Tolhurst et al., 2020). It has been previously determined how heavy shading can significantly modify processes and properties at the sediment-water interface, which may affect faunal abundance and distribution (Khon et al., 2010; Tolhurst et al., 2020). Similar patterns were also seen in Ruwa (1988), where species diversity was found to be greater under shade

conditions. Yet, as previously described in several marine communities, the response of species richness and diversity to degradation reflected a reduction of habitat availability and resources (MacNae and Kalk, 1969; Lee 2008; Carugati et al., 2019; Freita and Pagliosa, 2020). Canopy cover is also a “sensor” of a collective of forest biogenic structural variables, which on their own did not show statistically discernible relations or effects on crab abundance. Thereafter, in this study, the mechanisms associated with canopy degradation, in comparison with the biogenic structures of mangrove trees, seemed to have driven the variation in crab abundance.

The alteration of taxonomic structure may have been trigged by the diverse mechanisms involved when coping with different resource dynamics. For instance, sponges of the genus *Tedania and Halicoma sp.* feed specifically on the rich microbial community that comes from the productivity and nutrient cycling in mangroves, which promote faster growth in comparison to oligotrophic adjacent habitats such as shallow reefs (Kathiresan and Bingham, 2001); whereas other organisms like gastropods, are typically between the most copious species in mangrove forests, copying with harsh surroundings, occupying diverse trophic positions and a broad range of ecological niches (Nagelkerken et al., 2008). Here it was found that the generalists species such as the gastropod *Terebralia palustris*, became particularly abundant. Common species became rarer in areas with little degradation (e.g. *Halicloma debilis*. Supplementary Figure 1). As predicted, degradation of mangrove forests also had direct effects on the richness, diversity and composition (abundance) of decapod crabs at both the taxonomical and functional levels. Loss of crab species richness and biodiversity was particularly pronounced in highly degraded forests, although crab abundance was less affected. Changes with degradation to crab abundance were linked to alterations in forest variables, such as the frequency of tree stumps. These patterns support previous studies, where declines in crab species richness or diversity was argued to be associated with loss of specialist species (Carrete et al., 2010), the reduction in habitat complexity, the aversion to the degrading habitat conditions, or low habitat versatility (Carrete et al., 2010; Carugati et al., 2019; Bernardino et al., 2018: Freita and Pagliosa, 2020). If disturbance causes a shift in species composition, then changes in diversity before and after the occurrence might not be significantly different (Weithoff et al., 2001). Therefore, dynamic variables such as similarity indexes that provide information on compositional changes along the degradation gradient could be necessary. While species abundance of certain taxa (e.g. *Perisesarma guttatum*)

did not vary along the degradation gradient, indicating that these species have opportunistic feeding and living strategies, the abundance of other species of the family Sesarmidae (e.g. *Neosesarmatium smithi* and *N. africanum*), generally known for being specialised in foraging on mangrove leaves, declined with mangrove degradation. Species belonging to the family *Ocypoidea,* such *Uca annulipes, U. vocans* and *U. chlorophtalmus* thrived in both mud flat-open canopy forests and dense canopy forests, with some patchiness of distribution found in more selective, discriminating species, such *U. urvillei*. Such dissimilarity in community structure with habitat degradation has been suggested to result from some mangrove crabs, for instance predators, being more sensitive to degradation due to a reduction in food and shelter (Fondo and Marten, 1998). Nonetheless, several terrestrial and marine studies have proven that physical topography of structurally complex habitats can also inhibit access to food resources at fine scales (i.e. between mangrove prop roots/pneumatophores) and alter the foraging behaviour of biota (e.g Grabowski 2004; Whittingham et al., 2004; Rilov et al., 2007). Grabowski (2004) support the theory that foraging species may favour open habitats over structural complexity maybe because of the increased likeliness of spotting approaching predators. The ubiquitous nature of *Ocypodid spp.* along the degradation gradient could therefore be related to a combination of optimal foraging strategies and lower resource competition due to higher stress tolerance. Here, it was found that some species can be considered generalists and thus poor indicators of habitat degradation (e.g. *Uca annulipes*, *U. vocans*, *Perisesarma guttatum*), while others (e.g. *Chiromantess eulimene, Thalamita crenata* and *Neosermatium smithii*) were typical for more pristine habitats. Although the abundance of most species decreased with habitat degradation, the abundance of few species peaked at intermediate ~ 50 and 25 % canopy cover. Species vary in their ability to adapt to habitat degradation, depending on their biological and functional species characteristics (Carrete et al., 2010). As a consequence, degradation might drive an increase in the compositional similarity of communities due to the increase in the abundance of most winning species (generalists) and a reduction of rarer, but potentially more functionally efficient, loosing ones (McKinney and Lockwood, 1999).

4.2.2. Intermediately degraded forests yield high levels of functional diversity, species richness and complementarity

Similar to taxonomical structure results, functional richness and diversity were reduced along the degradation gradient, with the highest diversity recorded at intermediate level ~ 50 %

canopy cover. Connell (1978) stated that diversity is high when disturbances occur at an intermediate frequency or with an intermediate intensity based on the tension between strongly competitive species and those able to quickly recolonise following disturbance (Weithoff et al., 2001; Shea et al., 2004; Liu et al., 2019). In the present study, the intermediate disturbance hypothesis (IDH) could be evoked. The IDH could explain that in mildly degraded forests, sensitive species with a particular trait value persisted alongside tolerant species sustaining a high diversity within the population (Liu et al., 2019). Functional diversity was greater at low levels of degradation, where more structurally complex habitats occurred. High functional diversity is indicative of efficient use of resources and higher productivity, as the species explore different resource requirements(i.e. niche complementarity) (Petchey 2003; Petchey and Gaston, 2006). Functional diversity together with high functional richness underpin an enhancement of functional ecosystem performance and stability (Rasher et al., 2013; Richardson et al., 2017). In this study, the reduction in functional richness in highly degraded forests reflected the loss of species-rich communities, yielding less probability of containing unique single species or a combination of species with exclusive traits held by coexisting species of crabs (e.g. foli-detritivores and detritivores) (Loreau and Hector, 2001). Higher functional richness and complementarity are indicative of high productivity and functionality of the ecosystem (Sheaves and Molony, 2000; Lee 2008; Leung 2015). Hence, the loss in functional richness and ecological complementarity among species can have important and unexpected consequences for the ecosystem function of mangrove forests (Bellowood et al., 2003). For Instance, the bulk of mangrove carbon (C) is processed through Detritivores crabs, which survive on this low-quality C-rich food remains (Skov and Hartnoll, 2002). The reduction or loss of certain consumers can alter carbon sink functions (Lee et al., 2008). Crab burrow structures change functional characteristics of microbial communities inhabiting the sediment, supporting diverse characteristics of organic matter and C cycling (Gillis et al., 2019). Yet, foli-detritivores e.g. *Chiromantess eulimene*, which were previously found in the gut of fish within mangroves at high tides (Nagelkerken et al., 2008), were more abundant in low degradation, structurally heterogenous habitats. This implies that lack of heterogeneity due to habitat degradation could hinder energy flow to higher trophic levels

4.2.3. Low functional redundancy underpins behavioural plasticity

Environmental stressors and variation in habitat structure are acting as environmental filters in determining the structure of crab communities, with higher intensity of degradation acting as a major filter for unique traits within trophic structures. Although to date, studies on how mangrove degradation affects macrofaunal functional diversity and resilience are scant, these results were in line with other findings on environmental filtering shaping and diverging tropical marine communities (e.g. Ingram et al., 2009; Ford and Roberts, 2020). Functional redundancy, the presence of multiple species with similar ecological functions (Nystrom 2006), is more likely to increase in systems where environmental filtering is operating upon numerous traits (Ford and Roberts, 2020). In the mangrove systems, biogenic structures, especially dense roots already act as environmental filters for large body-size crabs, leading to trait convergence (i.e. reduction in functional niches), displaying low functional diversity and redundancy to begin with (Leung 2015). Here, although functional diversity and species richness decreased with reduction in habitat heterogeneity, functional redundancy remained similar along the mangrove degradation gradient. These patterns indicate a continuous overlap of functional niches among species, even at the most disturbed sites, and also suggest functional plasticity and functional accommodation (Needham et al., 2010; Bingham et al., 2018). Bouillon et al. (2004) emphasised how in systems where inputs from other ecosystems are considerable, juveniles of specific species, showed a high reliance on imported material and microphytobenthos. In effect, many studies on mangrove ecology have previously focused on the dietary patterns of the macrofaunal community and their opportunistic feeding behaviours (see Fratini et al., 2000; Poon et al., 2009; Giraldes et al., 2019).Giraldes et al (2019) documented the behavioural plasticity of the omnivorous *Metopograpsus messor* foraging on open mangrove ecosystems when challenging environmental conditions occurred. Yet, species of the *Sesarmidae* family were recorded to alter their diets according to some degree of seasonal, physical, climate and food availability (Poon et al., 2009). It is possible that functional replacements due to habitat degradation, lack of resources, higher enter-specific competitions and biophysical alterations may have occurred within the observed communities. The extent by which the community turnover was specifically affected by variation in diet was not possible to identity here, as disturbance dynamics are complex to examine and uncover (Nagelkerken et al., 2016). Nevertheless, it is plausible that the crab assemblage exhibits different changes in relation to forest degradation. Here, across the degradation gradient, composition of detritivores (mainly burrowing) were consistent (i.e. generalists), foli-detritivores (mobile and burrowing)

gradually reduced in abundance and predators (mobile) were only frequent in the highest canopy cover conditions. While the mechanisms of variation in trophic composition are not certain, variations in foli-detritivores and predators were most likely to occur due to changes in canopy cover of mangrove forests, which may have influenced differential foraging behaviours. With the ongoing degradation of mangrove forests, these results suggest that, key ecosystem functions of mangroves will likely change among altered habitat cases, according to the differential vulnerability of mangroves to disturbances and ecological interaction between epifauna and their environment. In the present study, macrofaunal diversity, community and trophic composition were used as main proxies of ecosystem functioning. With the reduction of epifaunal and crab communities, not only important ecosystem functions and processes of mangrove forest, such organic matter decomposition and nutrient cycling would diminish, but also, significant modification of the benthic habitat can occur. For instance, micro-epiphytic biomass can bloom due to lack of grazing (Kristensen and Alongi, 2006) causing indirect variation to the meiofaunal communities that feed on the micro-epiphytes (Carlen and Olafsoon, 2002). In addition, the connection and provision of food source for secondary consumers and food-web dynamics with adjacent fisheries may also be affected by the lack of food availability i.e. microphytes and the associated epifauna (Mumby et al., 2006; Meynecke et al., 2007; Nagelkerken et al., 2008; Sheaves 2009; Olds et al., 2013). The effects of mangrove degradation on epifauna community and functional composition need to be further investigated to assess temporal consistency and to improve the understanding of how small-scale anthropogenic disturbances interact with ecosystem functioning and services (Lee 2008; Goldenberg et al., 2018).

5. Conclusion:

The study enlightened marked changes in epifaunal composition, taxonomical and functional diversity along a mangrove degradation gradient. Changes in epifaunal abundance and diversity were less visible along the degradation gradient, but clearer at the habitat scale when contrasting semi-pristine with totally degraded sites. These patterns were likely linked to a more considerable variation in biophysical parameters and habitat heterogeneity characterised at the two ends of the degradation gradient. Crab composition was highly distinct between degraded and semi-pristine and associated with the loss of key species with defined functional traits from degraded areas. However, given the opportunistic feeding

behaviour of several key species, functional redundancy remained similar along the degradation gradient, as indicated by a consistent variation in trophic composition distribution. Overall, the study illustrated the importance of mangrove canopy to structuring and providing habitat to crabs and other epifauna, and to sustaining a stable and functional ecosystem. Canopy cover was determined as proxy of forest degradation and in many cases given the entwined mechanisms of natural ecosystems, it may not be solely representative of the dynamics occurring within the mangrove forest. Frequency of extreme weather is predicted to increase due to climate change (Dale et al., 2000). Storm damage combined with expanding coastal population, is likely to give rise to greater disturbance to mangrove forests. The lack of a distinct procedure to assess forest degradation should not be seen as a limitation, but rather a gap in the knowledge of the holistic processes taking places in this ecosystem, in the context of anthropogenic changes. By integrating ground-truthing assessments with sophisticated remote-sensing technologies it should be possible to further assess and understand the processes leading to habitat degradation, and the extent to which degradation influences mangrove capacity to provide a valuable ecosystem for biota. In this way, sustainable policies can be applied to managing mangrove forests globally.

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Supplementary Material:

Table 1: Estimated regression parameters, standard errors, T-values, P values **P <0.01,* P<0.05, n.s. P>0.05 and Adjusted R^2 for the Quasibinomial and QuasiPoisson GLMM models.

	Y	x	Est.std	Error	T-value	P
Ephibenthic fauna	**Abundance**	Canopy	0.1	0.0	4.3	**
		AGB	0.6	1.2	0.5	n.s
		Basal Area	0.0	0.0	-0.2	n.s
		TotalStumps	-0.2	0.1	-1.3	n.s
		Total Stem cuts	-0.1	0.1	-1.0	n.s
	Species Richness	Canopy	-7.5	1.6	-4.8	* **
		AGB	7.2	5.3	13.7	* **
		Basal Area	-3.3	4.7	-7.0	* **
		TotalStumps	-3.3	7.7	-4.1	* **
		Total Stem cuts	-5.1	6.2	-8.3	* **
	Shannon Diversity	Canopy	0.0	0.0	3.1	**
		AGB	0.1	0.1	0.4	n.s
		TotalStumps	0.0	0.0	0.2	n.s
		Total Stem cuts	0.0	0.0	-0.3	n.s
	Eveness	Canopy	0.0	0.3	0.0	n.s
		AGB	-0.1	1.5	0.1	n.s
		Basal Area	0.0	0.0	0.1	n.s
		TotalStumps	0.0	0.1	-0.2	n.s
		Total Stem cuts	0.0	0.1	0.2	n.s

Table 2: Model ranks for the Generalized Linear models of epifauna diversity (richness and evenness) and abundance against canopy cover and forest complexity. Models are ranked by corrected Akaike's information criteria (AICc), with all models within ΔAICc < 2 of the top ranked models. The relative likelihood and weight of evidence between each model is indicated by Akaike likelihood (logLik) and weight (wi) and the variables present in each model are mentioned.

Model Rank	Variables	AICc	logLik	ΔAICc	wi
1	Species richness ~ Canopy cover	118.5	1	0	1
2	Species richness ~ Forest complexity	123.2	0.1	4	0.1
1	Species evenness ~ Canopy cover	8.05	1	0	1
2	Species evenness ~ Forest complexity	15.92	0.01	7.8	0.01
1	Species diversity ~ Canopy cover	58.9	1	0	1
2	Species diversity ~ Forest complexity	64.32	0	5.3	0.1
1	Species abundance ~ Forest complexity	283.1	1	0	0.6
2	Species abundance ~ Canopy cover	283.9	0.6	0.8	0.4

Table3: Output of the One-Way SIMPER Pairwise test based on four root Bray Curtis dissimilarity resemblance matrix of crab species abundance distribution. Groups were categories according to their canopy cover percentages. Cut off for low contribution at 90 %.

Groups 90 & 30
Average dissimilarity = 54.59

Species	Group 90 Av.Abund	Group 30 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	2.73	1.27	10.63	1.11	19.47	19.47
U. vocans	1.51	0	7.51	1.12	13.75	33.22
U. urvillei	1.62	0	7.22	1.06	13.23	46.44
U. annulipes	2.17	3.03	6.24	1.25	11.43	57.88
P. guttatum	2.1	1.45	6.17	2.59	11.31	69.19
M. thukuhar	0.71	0.87	4.29	1.27	7.86	77.05
M. oceanicus	0.24	0.5	2.51	0.98	4.61	81.65
U. tetragon	0.57	0	2.51	0.47	4.6	86.26
T. cranata	0.44	0	2.33	0.73	4.27	90.52

Groups 0 & 90
Average dissimilarity = 65.63

Species	Group 0 Av.Abund	Group 90 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	0.55	2.73	13.64	1.45	20.78	20.78
U. vocans	1.53	1.51	8.96	1.24	13.65	34.43
U. annulipes	1.42	2.17	8.62	1.31	13.13	47.56
U. urvillei	0	1.62	7.61	1.1	11.6	59.16
P. guttatum	1.24	2.1	7.27	1.54	11.07	70.23
M. thukuhar	0.22	0.71	3.66	1.15	5.58	75.82
U. tetragon	0	0.57	2.65	0.49	4.03	79.85
T. cranata	0	0.44	2.49	0.76	3.79	83.64
M. milloti	0.3	0.28	2.42	0.65	3.69	87.33
S. elongatum	0	0.48	2.27	0.78	3.46	90.79

Groups 20 & 90
Average dissimilarity = 63.68

Species	Group 20 Av.Abund	Group 90 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	0.61	2.73	11.97	1.4	18.79	18.79
U. annulipes	1.22	2.17	9.86	1.26	15.49	34.28
U. urvillei	0	1.62	6.92	1.08	10.87	45.15
U. vocans	2.53	1.51	6.77	1.11	10.63	55.78
P. guttatum	1.29	2.1	6.52	1.2	10.23	66.01
U. tetragon	0.79	0.57	5.24	0.81	8.23	74.25
M. thukuhar	0.62	0.71	4.14	1.21	6.51	80.75
U. inversa	0.72	0	2.96	0.68	4.64	85.4
T. cranata	0	0.44	2.21	0.74	3.48	88.87
S. elongatum	0	0.48	2.06	0.76	3.24	92.11

Groups 0 & 20
Average dissimilarity = 63.78

Species	Group 0 Av.Abund	Group 20 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. vocans	1.53	2.53	14.23	1.3	22.31	22.31
U. annulipes	1.42	1.22	12.29	1.33	19.27	41.58
U. tetragon	0	0.79	7.14	0.68	11.19	52.78
P. guttatum	1.24	1.29	6.98	1.12	10.95	63.72
U.chlorophtalum	0.55	0.61	6.34	0.74	9.95	73.67
U. inversa	0.42	0.72	5.79	0.77	9.08	82.75
M. thukuhar	0.22	0.62	5.33	0.81	8.36	91.12

Groups 0 & 70
Average dissimilarity = 71.27

Species	Group 0 Av.Abund	Group 70 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	0.55	2.04	15.13	1.02	21.23	21.23
U. vocans	1.53	0	10.37	0.87	14.55	35.78
U. annulipes	1.42	0.59	9.34	1.36	13.11	48.88
N. africano	0	0.93	7.22	0.95	10.13	59.01
P. guttatum	1.24	2.05	7.17	1.06	10.06	69.08
N. smithii	0	0.71	5.49	0.95	7.7	76.78
M. thukuhar	0.22	0.71	5.25	1	7.36	84.14
C. eulimene	0	0.59	4.61	0.95	6.47	90.61

Groups 70 & 90
Average dissimilarity = 64.14

Species	Group 70 Av.Abund	Group 90 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	2.04	2.73	10.39	1.22	16.19	16.19
U. annulipes	0.59	2.17	9.14	1.39	14.25	30.45
U. vocans	0	1.51	7.22	1.13	11.26	41.71
U. urvillei	0	1.62	6.99	1.07	10.9	52.61
P. guttatum	2.05	2.1	4.96	1.17	7.73	60.34
N. africano	0.93	0	4.64	0.93	7.23	67.57
M. thukuhar	0.71	0.71	3.59	1.18	5.6	73.17
N. smithii	0.71	0	3.52	0.93	5.49	78.66
C. eulimene	0.59	0	2.96	0.93	4.62	83.28
U. tetragon	0	0.57	2.43	0.47	3.8	87.08
T. cranata	0	0.44	2.23	0.74	3.48	90.56

Groups 80 & 90
Average dissimilarity = 48.87

Species	Group 80 Av.Abund	Group 90 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.38	2.17	7.77	1.17	15.9	15.9
U. vocans	0	1.51	6.44	1.12	13.18	29.08
U. inversa	1.3	0	6.31	0.93	12.91	41.99
U. urvillei	1.09	1.62	5.95	1.05	12.17	54.16
U.chlorophtalum	3.38	2.73	5.63	1.3	11.52	65.68
P. guttatum	2.74	2.1	4.48	0.87	9.16	74.84
M. thukuhar	0.5	0.71	2.66	1.02	5.45	80.29
U. tetragon	0	0.57	2.2	0.47	4.49	84.78
T. cranata	0	0.44	1.98	0.73	4.05	88.83
S. elongatum	0	0.48	1.88	0.75	3.84	92.67

Groups 0 & 50
Average dissimilarity = 65.95

Species	Group 0 Av.Abund	Group 50 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	0.55	1.74	11.89	1.02	18.02	18.02
U. annulipes	1.42	1.6	10.17	1.21	15.42	33.44
U. vocans	1.53	0.64	10.16	1	15.41	48.85
U. urvillei	0	1.1	7.44	0.77	11.28	60.13
P. guttatum	1.24	2	6.29	0.95	9.54	69.67
U. inversa	0.42	0.47	5.05	0.62	7.65	77.32
N. africano	0	0.54	3.91	0.56	5.92	83.25
N. smithii	0	0.38	2.69	0.61	4.08	87.32
M. thukuhar	0.22	0.29	2.62	0.73	3.97	91.29

Groups 20 & 50
Average dissimilarity = 70.36

Species	Group 20 Av.Abund	Group 50 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. vocans	2.53	0.64	12.84	1.54	18.25	18.25
U. annulipes	1.22	1.6	10.07	1.12	14.32	32.57
U.chlorophtalum	0.61	1.74	10	1.03	14.21	46.78
U. urvillei	0	1.1	6.49	0.76	9.23	56
P. guttatum	1.29	2	6	0.92	8.53	64.54
U. tetragon	0.79	0	5.51	0.68	7.84	72.37
U. inversa	0.72	0.47	5.16	0.76	7.34	79.71
M. thukuhar	0.62	0.29	4.33	0.86	6.15	85.86
N. africano	0	0.54	3.39	0.56	4.81	90.67

Groups 70 & 50
Average dissimilarity = 56.12

Species	Group 70 Av.Abund	Group 50 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	2.04	1.74	12.36	1.13	22.03	22.03
U. annulipes	0.59	1.6	8.95	1.41	15.94	37.97
U. urvillei	0	1.1	6.54	0.77	11.66	49.63
N. africano	0.93	0.54	6.28	1.06	11.18	60.81
N. smithii	0.71	0.38	4.34	0.98	7.73	68.54
M. thukuhar	0.71	0.29	4.24	1.05	7.55	76.09
C. eulimene	0.59	0.2	3.86	0.99	6.87	82.96
U. vocans	0	0.64	3.29	0.59	5.86	88.82
P. guttatum	2.05	2	2.67	1.17	4.75	93.57

Groups 80 & 50
Average dissimilarity = 48.85

Species	Group 80 Av.Abund	Group 50 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	3.38	1.74	9.94	1.26	20.36	20.36
U. inversa	1.3	0.47	8.08	1.01	16.55	36.91
U. annulipes	1.38	1.6	7.84	1.02	16.06	52.97
U. urvillei	1.09	1.1	6.73	1.02	13.78	66.75
P. guttatum	2.74	2	3.98	1.81	8.14	74.89
N. africano	0	0.54	2.95	0.55	6.05	80.93
U. vocans	0	0.64	2.92	0.59	5.97	86.91
M. thukuhar	0.5	0.29	2.45	0.95	5.02	91.93

Groups 90 & 50
Average dissimilarity = 55.94

Species	Group 90 Av.Abund	Group 50 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	2.73	1.74	9.31	1.3	16.64	16.64
U. annulipes	2.17	1.6	7.77	1.21	13.89	30.53
U. urvillei	1.62	1.1	6.96	1.14	12.44	42.96
U. vocans	1.51	0.64	6.46	1.14	11.54	54.5
P. guttatum	2.1	2	4.58	1.18	8.18	62.69
M. thukuhar	0.71	0.29	2.96	1.1	5.29	67.98
N. africano	0	0.54	2.56	0.57	4.58	72.56
U. tetragon	0.57	0	2.3	0.49	4.12	76.68
T. cranata	0.44	0	2.09	0.76	3.74	80.43
U. inversa	0	0.47	2.01	0.4	3.59	84.01
S. elongatum	0.48	0	1.97	0.78	3.53	87.54
N. smithii	0	0.38	1.77	0.61	3.17	90.71

Groups 0 & 40
Average dissimilarity = 69.75

Species	Group 0 Av.Abund	Group 40 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. inversa	0.42	1.32	9.91	0.91	14.2	14.2
U.chlorophtalum	0.55	1.49	9.62	0.98	13.8	28
U. vocans	1.53	0	9.3	0.87	13.33	41.34
U. annulipes	1.42	1.11	8.89	1.17	12.74	54.08
P. guttatum	1.24	1.98	6.46	1.28	9.26	63.34
P. samawati	0	0.77	4.82	0.92	6.91	70.25
U. urvillei	0	0.82	4.82	0.57	6.91	77.15
M. thukuhar	0.22	0.75	4.74	1.4	6.8	83.95
M. oceanicus	0.15	0.6	4.41	1.01	6.32	90.27

Groups 70 & 40
Average dissimilarity = 62.84

Species	Group 70 Av.Abund	Group 40 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	2.04	1.49	11.97	1.14	19.05	19.05
U. inversa	0	1.32	8.72	0.85	13.87	32.92
U. annulipes	0.59	1.11	6.33	1.26	10.08	43
N. africano	0.93	0	5.61	0.92	8.93	51.93
U. urvillei	0	0.82	4.32	0.54	6.88	58.81
P. samawati	0	0.77	4.3	0.88	6.84	65.65
N. smithii	0.71	0.33	4.23	0.94	6.74	72.38
M. thukuhar	0.71	0.75	4.19	1.53	6.67	79.05
M. oceanicus	0	0.6	3.69	0.93	5.87	84.92
P. guttatum	2.05	1.98	3.68	1.17	5.86	90.77

Groups 80 & 40
Average dissimilarity = 48.42

Species	Group 80 Av.Abund	Group 40 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	3.38	1.49	10.01	1.13	20.68	20.68
U. inversa	1.3	1.32	7.55	1.13	15.59	36.27
U. annulipes	1.38	1.11	6.81	1.05	14.07	50.34
U. urvillei	1.09	0.82	6.46	1.01	13.34	63.68
P. guttatum	2.74	1.98	4.34	1.06	8.97	72.65
P. samawati	0	0.77	3.78	0.87	7.8	80.45
M. oceanicus	0	0.6	3.2	0.92	6.61	87.07
M. thukuhar	0.5	0.75	2.77	0.9	5.72	92.79

Groups 90 & 40
Average dissimilarity = 61.37

Species	Group 90 Av.Abund	Group 40 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	2.73	1.49	9.2	1.22	14.99	14.99
U. annulipes	2.17	1.11	8.02	1.26	13.06	28.05
U. urvillei	1.62	0.82	7	1.13	11.41	39.46
U. vocans	1.51	0	6.65	1.15	10.84	50.31
U. inversa	0	1.32	6.48	0.88	10.55	60.86
P. guttatum	2.1	1.98	4.67	1.14	7.61	68.47
U. tetragon	0.57	0.41	3.37	0.74	5.49	73.96
P. samawati	0.2	0.77	3.36	0.97	5.47	79.43
M. oceanicus	0.24	0.6	2.84	1.01	4.62	84.05
M. thukuhar	0.71	0.75	2.51	1.07	4.08	88.13
T. cranata	0.44	0	2.05	0.75	3.34	91.47

Groups 50 & 40
Average dissimilarity = 59.46

Species	Group 50 Av.Abund	Group 40 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	1.74	1.49	9.45	1.11	15.89	15.89
U. inversa	0.47	1.32	8.36	0.93	14.07	29.96
U. annulipes	1.6	1.11	8.07	1.13	13.58	43.54
U. urvillei	1.1	0.82	7.29	0.91	12.27	55.81
P. samawati	0.17	0.77	4.07	0.96	6.84	62.65
M. thukuhar	0.29	0.75	3.48	1.17	5.85	68.5
M. oceanicus	0	0.6	3.42	0.97	5.76	74.26
P. guttatum	2	1.98	3.29	1.15	5.53	79.79
N. africano	0.54	0	3.08	0.56	5.17	84.96
U. vocans	0.64	0	3.02	0.6	5.08	90.04

Groups 0 & 30
Average dissimilarity = 55.58

Species	Group 0 Av.Abund	Group 30 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.42	3.03	13.91	1.3	25.03	25.03
U. vocans	1.53	0	11.02	0.85	19.82	44.86
U.chlorophtalum	0.55	1.27	9.8	0.96	17.64	62.49
M. thukuhar	0.22	0.87	6.09	1.05	10.95	73.45
P. guttatum	1.24	1.45	4.8	0.83	8.64	82.09
M. oceanicus	0.15	0.5	3.78	0.99	6.79	88.88
U. inversa	0.42	0	3.38	0.45	6.08	94.96

Groups 20 & 30
Average dissimilarity = 70.30

Species	Group 20 Av.Abund	Group 30 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. vocans	2.53	0	18.13	2.3	25.79	25.79
U. annulipes	1.22	3.03	16.82	1.38	23.93	49.72
U.chlorophtalum	0.61	1.27	7.78	1.02	11.07	60.79
U. tetragon	0.79	0	6.46	0.63	9.19	69.97
M. thukuhar	0.62	0.87	6	0.9	8.54	78.51
P. guttatum	1.29	1.45	5.89	1.17	8.38	86.9
U. inversa	0.72	0	3.92	0.64	5.58	92.48

Groups 70 & 30
Average dissimilarity = 59.84

Species	Group 70 Av.Abund	Group 30 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	0.59	3.03	17.18	2.44	28.71	28.71
U.chlorophtalum	2.04	1.27	14	1.04	23.4	52.11
N. africano	0.93	0	6.63	0.85	11.08	63.19
M. thukuhar	0.71	0.87	5.82	1.02	9.72	72.91
N. smithii	0.71	0	5.04	0.85	8.42	81.32
C. eulimene	0.59	0	4.24	0.85	7.08	88.4
P. guttatum	2.05	1.45	4	1.21	6.68	95.09

Groups 80 & 30
Average dissimilarity = 53.57

Species	Group 80 Av.Abund	Group 30 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	3.38	1.27	13.23	1.24	24.69	24.69
U. annulipes	1.38	3.03	11.42	0.95	21.32	46.01
U. inversa	1.3	0	8.91	0.85	16.63	62.64
P. guttatum	2.74	1.45	7.18	3.11	13.4	76.04
U. urvillei	1.09	0	5.53	0.86	10.32	86.36
M. thukuhar	0.5	0.87	4.74	1.12	8.84	95.2

Groups 50 & 30
Average dissimilarity = 54.25

Species	Group 50 Av.Abund	Group 30 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.6	3.03	10.8	1	19.91	19.91
U.chlorophtalum	1.74	1.27	10.76	1.08	19.82	39.74
U. urvillei	1.1	0	6.89	0.75	12.7	52.43
M. thukuhar	0.29	0.87	4.95	1.11	9.12	61.56
P. guttatum	2	1.45	3.62	1.27	6.68	68.23
N. africano	0.54	0	3.6	0.55	6.64	74.87
U. vocans	0.64	0	3.43	0.59	6.32	81.19
M. oceanicus	0	0.5	2.74	0.95	5.05	86.24
U. inversa	0.47	0	2.7	0.39	4.97	91.21

Groups 40 & 30
Average dissimilarity = 57.80

Species	Group 40 Av.Abund	Group 30 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.11	3.03	12.87	1.26	22.27	22.27
U. inversa	1.32	0	9.25	0.83	16	38.27
U.chlorophtalum	1.49	1.27	8.98	1.03	15.53	53.8
M. thukuhar	0.75	0.87	5.32	1.79	9.21	63.01
U. urvillei	0.82	0	4.51	0.53	7.8	70.81
P. guttatum	1.98	1.45	4.5	4.02	7.78	78.6
P. samawati	0.77	0	4.5	0.87	7.78	86.37
M. oceanicus	0.6	0.5	3.74	0.98	6.48	92.85

Groups 0 & 60
Average dissimilarity = 67.72

Species	Group 0 Av.Abund	Group 60 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.42	1.72	12.91	1.33	19.07	19.07
U. vocans	1.53	0.55	12.15	0.92	17.94	37.01
U.chlorophtalum	0.55	1.28	11.18	0.88	16.51	53.52
P. guttatum	1.24	1.43	8.16	1.18	12.05	65.56
N. smithii	0	0.65	5.2	0.84	7.68	73.24
M. thukuhar	0.22	0.34	3.46	0.75	5.1	78.35
U. inversa	0.42	0	3.33	0.47	4.91	83.26
C. eulimene	0	0.34	2.83	0.61	4.18	87.44
M. oceanicus	0.15	0.29	2.79	0.7	4.12	91.56

Groups 20 & 60
Average dissimilarity = 74.64

Species	Group 20 Av.Abund	Group 60 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. vocans	2.53	0.55	16.56	2.32	22.19	22.19
U. annulipes	1.22	1.72	12.28	1.12	16.46	38.65
U.chlorophtalum	0.61	1.28	9.32	0.95	12.49	51.14
P. guttatum	1.29	1.43	7.54	1.13	10.11	61.25
U. tetragon	0.79	0	6.36	0.69	8.52	69.77
M. thukuhar	0.62	0.34	5.06	0.88	6.78	76.55
N. smithii	0	0.65	4.45	0.83	5.96	82.5
U. inversa	0.72	0	3.91	0.69	5.24	87.74
C. eulimene	0	0.34	2.41	0.6	3.22	90.96

Groups 70 & 60
Average dissimilarity = 59.27

Species	Group 70 Av.Abund	Group 60 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	2.04	1.28	13.94	1.17	23.52	23.52
U. annulipes	0.59	1.72	10.92	1.25	18.42	41.94
P. guttatum	2.05	1.43	6.6	1.26	11.14	53.08
N. africano	0.93	0.14	6.54	1.03	11.03	64.11
N. smithii	0.71	0.65	5.16	1.01	8.71	72.82
M. thukuhar	0.71	0.34	4.8	1.02	8.1	80.93
C. eulimene	0.59	0.34	4.13	0.96	6.97	87.9
U. vocans	0	0.55	3.71	0.39	6.26	94.16

Groups 80 & 60
Average dissimilarity = 60.32

Species	Group 80 Av.Abund	Group 60 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	3.38	1.28	12.33	1.41	20.44	20.44
U. annulipes	1.38	1.72	9.96	1.13	16.52	36.96
U. inversa	1.3	0	8.83	0.96	14.64	51.6
P. guttatum	2.74	1.43	7.71	1.37	12.79	64.39
U. urvillei	1.09	0	5.51	0.96	9.13	73.52
N. smithii	0	0.65	3.83	0.82	6.36	79.88
U. vocans	0	0.55	3.19	0.39	5.29	85.17
M. thukuhar	0.5	0.34	3.06	0.99	5.08	90.25

Groups 90 & 60
Average dissimilarity = 63.89

Species	Group 90 Av.Abund	Group 60 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	2.73	1.28	10.74	1.33	16.81	16.81
U. annulipes	2.17	1.72	9.17	1.35	14.36	31.16
U. vocans	1.51	0.55	8.11	1.22	12.69	43.86
U. urvillei	1.62	0	7.21	1.11	11.28	55.14
P. guttatum	2.1	1.43	6.55	1.28	10.25	65.39
M. thukuhar	0.71	0.34	3.43	1.15	5.36	70.75
N. smithii	0	0.65	3.29	0.84	5.16	75.91
U. tetragon	0.57	0	2.51	0.49	3.93	79.84
T. cranata	0.44	0	2.32	0.76	3.63	83.47
S. elongatum	0.48	0	2.15	0.78	3.36	86.83
M. oceanicus	0.24	0.29	1.98	0.78	3.09	89.92
P. samawati	0.2	0.24	1.81	0.6	2.83	92.75

Groups 50 & 60
Average dissimilarity = 61.34

Species	Group 50 Av.Abund	Group 60 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	1.74	1.28	11.01	1.13	17.95	17.95
U. annulipes	1.6	1.72	10.93	1.2	17.82	35.77
U. urvillei	1.1	0	6.83	0.78	11.14	46.91
P. guttatum	2	1.43	5.99	1.22	9.77	56.68
U. vocans	0.64	0.55	5.88	0.68	9.58	66.26
N. smithii	0.38	0.65	4.47	0.97	7.28	73.54
N. africano	0.54	0.14	3.94	0.66	6.43	79.97
C. eulimene	0.2	0.34	2.84	0.73	4.62	84.59
M. thukuhar	0.29	0.34	2.79	0.83	4.54	89.14
U. inversa	0.47	0	2.68	0.4	4.37	93.51

Groups 40 & 60
Average dissimilarity = 64.88

Species	Group 40 Av.Abund	Group 60 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.11	1.72	10.04	1.15	15.48	15.48
U.chlorophtalum	1.49	1.28	9.45	1.02	14.56	30.04
U. inversa	1.32	0	9.15	0.89	14.11	44.15
P. guttatum	1.98	1.43	6.12	1.31	9.43	53.58
P. samawati	0.77	0.24	4.75	0.98	7.32	60.91
U. urvillei	0.82	0	4.49	0.57	6.92	67.83
N. smithii	0.33	0.65	4.26	0.93	6.56	74.39
M. thukuhar	0.75	0.34	4.2	1.36	6.48	80.87
M. oceanicus	0.6	0.29	3.75	1.03	5.78	86.65
U. vocans	0	0.55	3.33	0.4	5.13	91.78

Groups 30 & 60
Average dissimilarity = 53.40

Species	Group 30 Av.Abund	Group 60 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	3.03	1.72	13.75	1.36	25.74	25.74
U.chlorophtalum	1.27	1.28	10.57	0.99	19.79	45.53
P. guttatum	1.45	1.43	6.06	1.46	11.34	56.88
M. thukuhar	0.87	0.34	5.67	1.1	10.61	67.49
N. smithii	0	0.65	4.76	0.82	8.91	76.4
U. vocans	0	0.55	3.94	0.39	7.38	83.78
M. oceanicus	0.5	0.29	3.37	0.95	6.32	90.1

Groups 0 & 10
Average dissimilarity = 59.38

Species	Group 0 Av.Abund	Group 10 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.42	2.65	13.31	1.3	22.41	22.41
U. vocans	1.53	0	12.77	0.88	21.51	43.92
P. guttatum	1.24	1.31	10.14	1.22	17.07	60.99
N. africano	0	0.58	5.54	0.67	9.34	70.33
U.chlorophtalum	0.55	0	5.17	0.46	8.71	79.04
M. thukuhar	0.22	0.33	4.14	0.79	6.97	86.01
U. inversa	0.42	0	3.98	0.46	6.7	92.71

Groups 20 & 10
Average dissimilarity = 77.19

Species	Group 20 Av.Abund	Group 10 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. vocans	2.53	0	21.04	2.53	27.25	27.25
U. annulipes	1.22	2.65	17.89	1.85	23.17	50.43
P. guttatum	1.29	1.31	9.27	1.22	12.01	62.44
U. tetragon	0.79	0	7.61	0.67	9.86	72.3
M. thukuhar	0.62	0.33	5.94	0.92	7.69	80
N. africano	0	0.58	4.6	0.65	5.96	85.96
U. inversa	0.72	0	4.4	0.67	5.7	91.66

Groups 70 & 10
Average dissimilarity = 65.08

Species	Group 70 Av.Abund	Group 10 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	0.59	2.65	16.39	2.75	25.18	25.18
U.chlorophtalum	2.04	0	15.92	0.91	24.47	49.65
P. guttatum	2.05	1.31	8.92	1.33	13.71	63.35
N. africano	0.93	0.58	7.54	0.95	11.59	74.94
N. smithii	0.71	0	5.82	0.91	8.95	83.89
M. thukuhar	0.71	0.33	5.59	1.08	8.59	92.47

Groups 80 & 10
Average dissimilarity = 67.29

Species	Group 80 Av.Abund	Group 10 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. chlorophtalmi	3.38	0	22.34	14.38	33.2	33.2
U. annulipes	1.38	2.65	11.35	1.05	16.87	50.06
U. inversa	1.3	0	10.25	0.91	15.24	65.3
P. guttatum	2.74	1.31	10.14	1.51	15.07	80.37
U. urvillei	1.09	0	6.15	0.91	9.13	89.5
N. africano	0	0.58	3.88	0.63	5.77	95.27

Groups 90 & 10
Average dissimilarity = 65.93

Species	Group 90 Av.Abund	Group 10 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	2.73	0	15.92	1.62	24.15	24.15
U. vocans	1.51	0	8.35	1.15	12.67	36.82
P. guttatum	2.1	1.31	7.95	1.37	12.06	48.88
U. urvillei	1.62	0	7.94	1.09	12.04	60.92
U. annulipes	2.17	2.65	6.68	1.61	10.13	71.05
M. thukuhar	0.71	0.33	3.57	1.09	5.41	76.46
N. africano	0	0.58	3.28	0.67	4.97	81.43
U. tetragon	0.57	0	2.76	0.48	4.19	85.62
T. cranata	0.44	0	2.61	0.74	3.96	89.58
S. elongatum	0.48	0	2.37	0.76	3.59	93.17

Groups 50 & 10
Average dissimilarity = 61.06

Species	Group 50 Av.Abund	Group 10 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	1.74	0	12.47	0.98	20.42	20.42
U. annulipes	1.6	2.65	11.07	1.11	18.13	38.55
P. guttatum	2	1.31	8.15	1.34	13.34	51.89
U. urvillei	1.1	0	7.86	0.77	12.87	64.76
N. africano	0.54	0.58	6.17	0.86	10.1	74.85
U. vocans	0.64	0	3.83	0.6	6.28	81.13
M. thukuhar	0.29	0.33	3.04	0.83	4.98	86.12
U. inversa	0.47	0	3.03	0.4	4.97	91.08

	Group 40	Group 10				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.11	2.65	12.37	1.27	18.11	18.11
U. inversa	1.32	0	10.7	0.86	15.67	33.78
U.chlorophtalum	1.49	0	9.71	0.96	14.22	48
P. guttatum	1.98	1.31	7.99	1.48	11.7	59.7
P. samawati	0.77	0	5.07	0.9	7.43	67.13
U. urvillei	0.82	0	5.06	0.55	7.41	74.55
M. oceanicus	0.6	0	4.46	0.96	6.53	81.08
M. thukuhar	0.75	0.33	4.2	1.1	6.14	87.22
N. africano	0	0.58	4.08	0.66	5.98	93.2

Groups 30 & 10
Average dissimilarity = 36.50

	Group 30	Group 10				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	1.27	0	8.88	0.91	24.33	24.33
P. guttatum	1.45	1.31	7.85	1.4	21.52	45.85
M. thukuhar	0.87	0.33	6.62	1.15	18.14	63.99
N. africano	0	0.58	4.98	0.63	13.65	77.65
U. annulipes	3.03	2.65	4.65	1.11	12.74	90.39

Groups 60 & 10
Average dissimilarity = 62.14

	Group 60	Group 10				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.72	2.65	14.55	1.62	23.41	23.41
U.chlorophtalum	1.28	0	11.06	0.83	17.8	41.21
P. guttatum	1.43	1.31	9.87	1.31	15.88	57.09
N. smithii	0.65	0	5.53	0.84	8.9	65.99
N. africano	0.14	0.58	5.3	0.79	8.52	74.51
U. vocans	0.55	0	4.57	0.4	7.35	81.86
M. thukuhar	0.34	0.33	4.03	0.88	6.49	88.35
C. eulimene	0.34	0	3.01	0.62	4.85	93.2

Groups 0 & 5
Average dissimilarity = 74.19

	Group 0	Group 5				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. vocans	1.53	1.25	15.44	1.11	20.81	20.81
U. annulipes	1.42	0.81	11.74	1.31	15.83	36.64
P. guttatum	1.24	0	11.54	1.69	15.56	52.2
U. inversa	0.42	0.81	10.19	1.02	13.74	65.93
M. latrelli	0	1.04	9.11	0.94	12.27	78.21
M. milloti	0.3	0.66	6.58	0.99	8.87	87.08
U.chlorophtalum	0.55	0	5.4	0.45	7.28	94.36

Groups 20 & 5
Average dissimilarity = 75.57

Species	Group 20 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. vocans	2.53	1.25	13.95	1.02	18.46	18.46
U. annulipes	1.22	0.81	11.45	1.24	15.16	33.61
P. guttatum	1.29	0	9.4	1.26	12.44	46.05
U. inversa	0.72	0.81	8.35	1.02	11.05	57.1
U. tetragon	0.79	0	7.96	0.64	10.54	67.64
M. latrelli	0	1.04	7.69	0.89	10.17	77.81
M. thukuhar	0.62	0	5.29	0.64	7	84.81
M. milloti	0	0.66	4.85	0.89	6.41	91.23

Groups 70 & 5
Average dissimilarity = 94.36

Species	Group 70 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P. guttatum	2.05	0	16.89	4.15	17.9	17.9
U.chlorophtalum	2.04	0	16.46	0.86	17.45	35.35
U. vocans	0	1.25	9.24	0.87	9.8	45.14
N. africano	0.93	0	7.95	0.86	8.42	53.57
M. latrelli	0	1.04	7.72	0.87	8.19	61.75
U. inversa	0	0.81	7.49	0.87	7.93	69.68
U. annulipes	0.59	0.81	6.92	1.11	7.33	77.02
N. smithii	0.71	0	6.04	0.86	6.4	83.42
M. thukuhar	0.71	0	5.7	0.86	6.04	89.46
C. eulimene	0.59	0	5.08	0.86	5.38	94.84

Groups 80 & 5
Average dissimilarity = 87.65

Species	Group 80 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U.chlorophtalum	3.38	0	22.98	7.6	26.21	26.21
P. guttatum	2.74	0	18.44	9.32	21.04	47.25
U. inversa	1.3	0.81	9.45	1.22	10.78	58.03
U. annulipes	1.38	0.81	9.07	1.29	10.35	68.38
U. vocans	0	1.25	7.86	0.85	8.97	77.35
M. latrelli	0	1.04	6.57	0.85	7.49	84.84
U. urvillei	1.09	0	6.28	0.86	7.17	92.01

Groups 50 & 5
Average dissimilarity = 87.77

Species	Group 50 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P. guttatum	2	0	15.37	2.98	17.51	17.51
U.chlorophtalm	1.74	0	12.87	0.95	14.66	32.17
U. annulipes	1.6	0.81	11.02	1.42	12.55	44.73
U. vocans	0.64	1.25	8.84	0.98	10.07	54.8
U. inversa	0.47	0.81	8.24	1.06	9.39	64.19
U. urvillei	1.1	0	8.11	0.75	9.24	73.43
M. latrelli	0	1.04	7.1	0.94	8.09	81.51
M. milloti	0	0.66	4.47	0.94	5.1	86.61
N. africano	0.54	0	4.28	0.55	4.87	91.48

Groups 40 & 5
Average dissimilarity = 86.94

Species	Group 40 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P. guttatum	1.98	0	13.75	4.44	15.82	15.82
U. inversa	1.32	0.81	10.27	1.14	11.82	27.64
U.chlorophtalm	1.49	0	9.97	0.93	11.47	39.1
U. vocans	0	1.25	8.23	0.92	9.47	48.57
U. annulipes	1.11	0.81	8.05	1.13	9.26	57.83
M. latrelli	0	1.04	6.88	0.92	7.91	65.75
M. thukuhar	0.75	0	5.67	1.5	6.52	72.26
P. samawati	0.77	0	5.21	0.88	6	78.26
U. urvillei	0.82	0	5.19	0.54	5.97	84.23
M. oceanicus	0.6	0	4.61	0.92	5.3	89.53
M. milloti	0	0.66	4.34	0.92	4.99	94.52

Groups 30 & 5
Average dissimilarity = 83.52

Species	Group 30 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	3.03	0.81	19.69	2.11	23.57	23.57
P. guttatum	1.45	0	13.2	3.31	15.81	39.38
U. vocans	0	1.25	9.9	0.84	11.85	51.23
U.chlorophtalm	1.27	0	9.14	0.86	10.95	62.18
M. latrelli	0	1.04	8.27	0.84	9.9	72.08
U. inversa	0	0.81	8.24	0.83	9.86	81.94
M. thukuhar	0.87	0	6.26	0.86	7.49	89.43
M. milloti	0	0.66	5.21	0.84	6.24	95.67

Groups 60 & 5
Average dissimilarity = 88.29

Species	Group 60 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	1.72	0.81	13.6	1.3	15.41	15.41
P. guttatum	1.43	0	12.83	1.34	14.54	29.94
U. vocans	0.55	1.25	11.76	0.99	13.31	43.26
U.chlorophtalm	1.28	0	11.5	0.8	13.03	56.28
M. latrelli	0	1.04	8.16	0.96	9.24	65.52
U. inversa	0	0.81	8.03	0.95	9.09	74.61

Groups 20 & 5
Average dissimilarity = 75.57

Species	Group 20 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. vocans	2.53	1.25	13.95	1.02	18.46	18.46
U. annulipes	1.22	0.81	11.45	1.24	15.16	33.61
P. guttatum	1.29	0	9.4	1.26	12.44	46.05
U. inversa	0.72	0.81	8.35	1.02	11.05	57.1
U. tetragon	0.79	0	7.96	0.64	10.54	67.64
M. latrelli	0	1.04	7.69	0.89	10.17	77.81
M. thukuhar	0.62	0	5.29	0.64	7	84.81
M. milloti	0	0.66	4.85	0.89	6.41	91.23

Groups 70 & 5
Average dissimilarity = 94.36

Species	Group 70 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P. guttatum	2.05	0	16.89	4.15	17.9	17.9
U.chlorophtalum	2.04	0	16.46	0.86	17.45	35.35
U. vocans	0	1.25	9.24	0.87	9.8	45.14
N. africano	0.93	0	7.95	0.86	8.42	53.57
M. latrelli	0	1.04	7.72	0.87	8.19	61.75
U. inversa	0	0.81	7.49	0.87	7.93	69.68
U. annulipes	0.59	0.81	6.92	1.11	7.33	77.02
N. smithii	0.71	0	6.04	0.86	6.4	83.42
M. thukuhar	0.71	0	5.7	0.86	6.04	89.46
C. eulimene	0.59	0	5.08	0.86	5.38	94.84

Groups 10 & 5
Average dissimilarity = 79.93

Species	Group 10 Av.Abund	Group 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
U. annulipes	2.65	0.81	18.7	2.27	23.39	23.39
P. guttatum	1.31	0	13.97	1.13	17.48	40.87
U. vocans	0	1.25	11.61	0.91	14.53	55.4
U. inversa	0	0.81	10.03	0.91	12.55	67.95
M. latrelli	0	1.04	9.7	0.91	12.14	80.09
N. africano	0.58	0	6.21	0.64	7.77	87.86
M. milloti	0	0.66	6.12	0.91	7.65	95.51

Table 4: Output of the One-Way SIMPER Pairwise test based on four root Euclidean distance resemblance matrix of crab trophic categories. Groups were categories according to their canopy cover percentages. Cut off for low contribution at 90 %.

Groups 0 & 20

Average squared distance = 5.93

	Group 0	Group 20				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	1.43	0.73	1.86	1.29	31.28	90.98

Groups 0 & 70

Average squared distance = 2.94

	Group 0	Group 70				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	1.43	2.31	1.12	0.73	38.15	81.80
Detritivores	0.3	0	0.535	0.40	18.20	100.00

Groups 20 & 70

Average squared distance = 9.59

	Group 20	Group 70				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	0.73	2.31	3.61	1.25	37.62	100.00

Groups 0 & 80

Average squared distance = 7.30

	Group 0	Group 80				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	3.04	2.64	2.65	1.17	36.28	36.28
Foli-detritivores	0	1.03	2.12	0.98	29.06	65.35
Omnivorous	1.43	2.44	1.99	0.79	27.32	92.67

Groups 20 & 80

Average squared distance = 11.38

	Group 20	Group 80				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	0.73	2.44	4.67	0.99	41.05	41.05
Detritivores	2	2.64	4.59	0.75	40.31	81.35
Foli-detritivores	0	1.03	2.12	0.91	18.65	100.00

Groups 70 & 80

Average squared distance = 6.75

	Group 70	Group 80				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	3.97	2.64	3.9	0.87	57.70	57.70
Foli-detritivores	0	1.03	2.12	0.87	31.42	89.12
Omnivorous	2.31	2.44	0.734	1.49	10.88	100.00

Groups 0 & 90

Average squared distance = 4.35

	Group 0	Group 90				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	1.43	1.91	1.53	0.90	35.20	35.20
Detritivores	0.3	0.283	0.765	0.59	17.61	84.29
Foli-detritivores	0	0.283	0.4	0.50	9.20	93.49

Groups 20 & 90

Average squared distance = 10.59

	Group 20	Group 90				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2	3.96	6.04	0.82	57.05	57.05
Omnivorous	0.73	1.91	3.46	1.11	32.72	89.77
Detritivores	0	0.283	0.4	0.48	3.78	93.55

Groups 70 & 90

Average squared distance = 2.42

	Group 70	Group 90				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	2.31	1.91	1.2	0.53	49.64	49.64
Detritivores	0	0.283	0.4	0.47	16.55	66.19
Foli-detritivores	0	0.283	0.4	0.47	16.55	82.74
Predator	0	0.238	0.283	0.47	11.71	94.45

Groups 80 & 90

Average squared distance = 8.53

	Group 80	Group 90				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	2.44	1.91	1.94	0.62	22.76	69.28

Foli-detritivores	1.03	0.283	1.94	0.94	22.72	92.00

Groups 0 & 50

Average squared distance = 4.03

	Group 0	Group 50				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	1.43	2.25	1.24	0.67	30.68	30.68
Foli-detritivores	0	0.755	1.04	0.95	25.93	83.17
Detritivores	0.3	0	0.535	0.41	13.29	96.45

Groups 20 & 50

Average squared distance = 9.87

	Group 20	Group 50				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2	3.63	5.05	0.76	51.16	51.16
Omnivorous	0.73	2.25	3.64	1.12	36.82	87.98
Foli-detritivores	0	0.755	1.04	0.93	10.57	98.55

Groups 70 & 50

Average squared distance = 1.97

	Group 70	Group 50				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0	0.755	1.04	0.92	53.02	53.02
Detritivores	3.97	3.63	0.461	0.80	23.43	76.45
Omnivorous	2.31	2.25	0.321	0.80	16.29	92.75

Groups 80 & 50

Average squared distance = 6.13

	Group 80	Group 50				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2.64	3.63	3.41	0.94	55.52	55.52
Foli-detritivores	1.03	0.755	1.61	0.97	26.26	81.79
Omnivorous	2.44	2.25	0.974	0.99	15.88	97.67

Groups 90 & 50

Average squared distance = 3.71

	Group 90	Group 50				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	1.91	2.25	1.37	0.58	37.02	37.02
Foli-detritivores	0.283	0.755	1.02	0.94	27.41	64.43

Detritivores	3.96	3.63	0.562	0.81	15.15	79.58

Groups 0 & 40

Average squared distance = 4.09

	Group 0	Group 40				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0	1.24	2.29	1.01	55.95	55.95
Omnivorous	1.43	1.92	0.776	0.60	18.98	74.93
Detritivores	0.3	0	0.535	0.40	13.09	88.02

Groups 20 & 40

Average squared distance = 8.85

	Group 20	Group 40				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2	3.33	3.85	0.72	43.49	43.49
Omnivorous	0.73	1.92	2.72	1.12	30.68	74.16
Foli-detritivores	0	1.24	2.29	0.98	25.84	100.00

Groups 70 & 40

Average squared distance = 3.17

	Group 70	Group 40				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0	1.24	2.29	0.95	72.10	72.10
Detritivores	3.97	3.33	0.446	2.03	14.07	86.16
Omnivorous	2.31	1.92	0.439	0.87	13.84	100.00

Groups 80 & 40

Average squared distance = 5.62

	Group 80	Group 40				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2.64	3.33	2.59	1.19	45.99	45.99
Foli-detritivores	1.03	1.24	1.86	0.86	33.02	79.01
Omnivorous	2.44	1.92	1.18	0.87	20.99	100.00

Groups 90 & 40

Average squared distance = 4.44

	Group 90	Group 40				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0.283	1.24	1.99	0.91	44.73	44.73
Omnivorous	1.91	1.92	1.23	0.70	27.75	72.48
Detritivores	0.283	0	0.4	0.49	9.01	93.63

Groups 50 & 40

Average squared distance = 2.65

	Group 50	Group 40				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0.755	1.24	1.46	0.81	55.12	55.12
Omnivorous	2.25	1.92	0.613	0.70	23.14	78.26
Detritivores	3.63	3.33	0.433	1.01	16.35	94.61

Groups 0 & 30

Average squared distance = 3.44

	Group 0	Group 30				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0	0.949	1.8	0.98	52.38	52.38
Omnivorous	1.43	1.89	0.663	0.57	19.26	71.64
Detritivores	3.04	3.2	0.441	0.60	12.81	100.00

Groups 20 & 30

Average squared distance = 7.90

	Group 20	Group 30				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2	3.2	3.54	0.67	44.77	44.77
Omnivorous	0.73	1.89	2.56	1.15	32.40	77.17
Foli-detritivores	0	0.949	1.8	0.91	22.83	100.00

Groups 70 & 30

Average squared distance = 2.82

	Group 70	Group 30				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0	0.949	1.8	0.87	63.91	63.91
Detritivores	3.97	3.2	0.637	1.88	22.60	86.51
Omnivorous	2.31	1.89	0.381	0.79	13.49	100.00

Groups 80 & 30

Average squared distance = 5.53

	Group 80	Group 30				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2.64	3.2	2.44	1.25	44.01	44.01
Foli-detritivores	1.03	0.949	1.97	0.87	35.57	79.58
Omnivorous	2.44	1.89	1.13	0.82	20.42	100.00

Groups 90 & 30

Average squared distance = 4.22

Variable	Group 90 Av.Value	Group 30 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0.283	0.949	1.67	0.94	39.43	39.43
Omnivorous	1.91	1.89	1.15	0.70	27.21	66.64
Detritivores	0.283	0	0.4	0.47	9.47	93.30

Groups 50 & 30

Average squared distance = 2.64

Variable	Group 50 Av.Value	Group 30 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0.755	0.949	1.41	0.96	53.48	53.48
Omnivorous	2.25	1.89	0.551	0.66	20.85	74.32
Detritivores	3.63	3.2	0.536	0.93	20.27	94.60

Groups 40 & 30

Average squared distance = 2.18

Variable	Group 40 Av.Value	Group 30 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	1.24	0.949	1.74	0.83	79.59	79.59
Omnivorous	1.92	1.89	0.392	0.87	17.95	97.55

Groups 0 & 60

Average squared distance = 3.62

Variable	Group 0 Av.Value	Group 60 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0	0.704	1.16	0.86	32.00	32.00
Omnivorous	1.43	1.57	0.977	0.72	26.99	58.99
Detritivores	0.3	0	0.535	0.41	14.79	100.00

Groups 20 & 60

Average squared distance = 7.53

Variable	Group 20 Av.Value	Group 60 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2	3.15	3.94	0.72	52.35	52.35
Omnivorous	0.73	1.57	2.43	1.04	32.27	84.62
Foli-detritivores	0	0.704	1.16	0.84	15.38	100.00

Groups 70 & 60

Average squared distance = 3.64

	Group 70	Group 60				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	2.31	1.57	1.25	0.66	34.30	34.30
Detritivores	3.97	3.15	1.24	0.71	33.93	68.23
Foli-detritivores	0	0.704	1.16	0.83	31.77	100.00

Groups 80 & 60

Average squared distance = 6.82

	Group 80	Group 60				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2.64	3.15	2.9	1.01	42.60	42.60
Omnivorous	2.44	1.57	2.08	0.73	30.57	73.18
Foli-detritivores	1.03	0.704	1.83	0.96	26.82	100.00

Groups 90 & 60

Average squared distance = 4.94

	Group 90	Group 60				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	1.91	1.57	1.77	0.79	35.85	35.85
Detritivores	3.96	3.15	1.32	0.73	26.82	62.67
Foli-detritivores	0.283	0.704	1.16	0.90	23.49	86.17

Groups 50 & 60

Average squared distance = 3.76

	Group 50	Group 60				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	2.25	1.57	1.38	0.65	36.70	36.70
Foli-detritivores	0.755	0.704	1.14	0.96	30.26	66.96
Detritivores	3.63	3.15	1.1	0.68	29.25	96.21

Groups 40 & 60

Average squared distance = 3.30

	Group 40	Group 60				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	1.24	0.704	1.7	0.86	51.46	51.46
Omnivorous	1.92	1.57	1.01	0.66	30.70	82.16
Detritivores	3.33	3.15	0.59	0.60	17.84	100.00

Groups 30 & 60

Average squared distance = 3.10

	Group 30	Group 60				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0.949	0.704	1.62	0.96	52.31	52.31
Omnivorous	1.89	1.57	0.91	0.64	29.33	81.64
Detritivores	3.2	3.15	0.57	0.62	18.36	100.00

Groups 0 & 10

Average squared distance = 4.33

	Group 0	Group 10				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0	1.19	2.13	1.33	49.21	49.21
Omnivorous	1.43	2.08	1.03	0.69	23.75	72.96
Detritivores	0.3	0	0.535	0.40	12.37	100.00

Groups 20 & 10

Average squared distance = 9.06

	Group 20	Group 10				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2	3.2	3.74	0.69	41.27	41.27
Omnivorous	0.73	2.08	3.19	1.12	35.22	76.50
Foli-detritivores	0	1.19	2.13	1.28	23.50	100.00

Groups 70 & 10

Average squared distance = 3.36

	Group 70	Group 10				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0	1.19	2.13	1.24	63.34	63.34
Detritivores	3.97	3.2	0.823	1.12	24.47	87.81
Omnivorous	2.31	2.08	0.41	0.72	12.19	100.00

Groups 80 & 10

Average squared distance = 5.55

	Group 80	Group 10				
Variable	Av.Value	Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2.64	3.2	2.63	1.09	47.47	47.47
Foli-detritivores	1.03	1.19	1.81	0.91	32.55	80.02
Omnivorous	2.44	2.08	1.11	0.82	19.98	100.00

Groups 90 & 10

Average squared distance = 4.78

Variable	Group 90 Av.Value	Group 10 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0.283	1.19	1.86	1.15	38.85	38.85
Omnivorous	1.91	2.08	1.33	0.64	27.80	66.65
Detritivores	0.283	0	0.4	0.48	8.37	94.08

Groups 50 & 10

Average squared distance = 2.85

Variable	Group 50 Av.Value	Group 10 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0.755	1.19	1.38	0.97	48.43	48.43
Detritivores	3.63	3.2	0.724	0.88	25.39	73.82
Omnivorous	2.25	2.08	0.604	0.71	21.17	94.99

Groups 40 & 10

Average squared distance = 2.29

Variable	Group 40 Av.Value	Group 10 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	1.24	1.19	1.48	0.81	64.43	64.43
Omnivorous	1.92	2.08	0.57	0.92	24.89	89.32
Detritivores	3.33	3.2	0.245	1.35	10.68	100.00

Groups 30 & 10

Average squared distance = 2.41

Variable	Group 30 Av.Value	Group 10 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0.949	1.19	1.68	0.91	69.51	69.51
Omnivorous	1.89	2.08	0.497	0.94	20.61	90.11

Groups 60 & 10

Average squared distance = 3.60

Variable	Group 60 Av.Value	Group 10 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0.704	1.19	1.62	1.01	44.89	44.89
Omnivorous	1.57	2.08	1.22	0.68	33.92	78.81
Detritivores	3.15	3.2	0.763	0.66	21.19	100.00

Groups 0 & 5

Average squared distance = 4.83

Variable	Group 0 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Foli-detritivores	0	0.866	1.5	0.98	31.08	31.08
Omnivorous	1.43	0.5	1.41	1.08	29.32	60.40
Detritivores	0.3	0	0.535	0.40	11.09	100.00

Groups 20 & 5

Average squared distance = 4.96

Variable	Group 20 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	2	2.05	2.1	1.18	42.22	42.22
Foli-detritivores	0	0.866	1.5	0.91	30.21	72.43
Omnivorous	0.73	0.5	1.37	0.77	27.57	100.00

Groups 70 & 5

Average squared distance = 8.80

Variable	Group 70 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	3.97	2.05	3.73	5.26	42.35	42.35
Omnivorous	2.31	0.5	3.57	1.55	40.60	82.95
Foli-detritivores	0	0.866	1.5	0.87	17.05	100.00

Groups 80 & 5

Average squared distance = 8.99

Variable	Group 80 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	2.44	0.5	4.69	1.07	52.22	52.22
Detritivores	2.64	2.05	2.46	1.22	27.35	79.56
Foli-detritivores	1.03	0.866	1.84	0.87	20.44	100.00

Groups 90 & 5

Average squared distance = 9.12

Variable	Group 90 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Detritivores	3.96	2.05	3.78	2.70	41.47	41.47
Omnivorous	1.91	0.5	3.25	1.24	35.59	77.06
Foli-detritivores	0.283	0.866	1.41	0.94	15.46	92.52

Groups 50 & 5

Average squared distance = 7.78

Variable	Group 50 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	2.25	0.5	3.57	1.26	45.91	45.91
Detritivores	3.63	2.05	2.83	1.51	36.36	82.26
Foli-detritivores	0.755	0.866	1.24	0.95	15.90	98.16

Groups 40 & 5

Average squared distance = 5.79

Variable	Group 40 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	1.92	0.5	2.5	1.13	43.13	43.13
Detritivores	3.33	2.05	1.65	3.61	28.55	71.68
Foli-detritivores	1.24	0.866	1.64	0.81	28.32	100.00

Groups 30 & 5

Average squared distance = 5.34

Variable	Group 30 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	1.89	0.5	2.33	1.12	43.60	43.60
Foli-detritivores	0.949	0.866	1.66	0.87	31.05	74.65
Detritivores	3.2	2.05	1.35	2.66	25.35	100.00

Groups 60 & 5

Average squared distance = 5.26

Variable	Group 60 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	1.57	0.5	2.05	0.98	39.07	39.07
Detritivores	3.15	2.05	1.77	1.04	33.58	72.65
Foli-detritivores	0.704	0.866	1.44	0.96	27.35	100.00

Groups 10 & 5

Average squared distance = 6.18

Variable	Group 10 Av.Value	Group 5 Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Omnivorous	2.08	0.5	3.05	1.21	49.34	49.34
Foli-detritivores	1.19	0.866	1.57	0.90	25.47	74.80
Detritivores	3.2	2.05	1.56	1.19	25.20	100.00

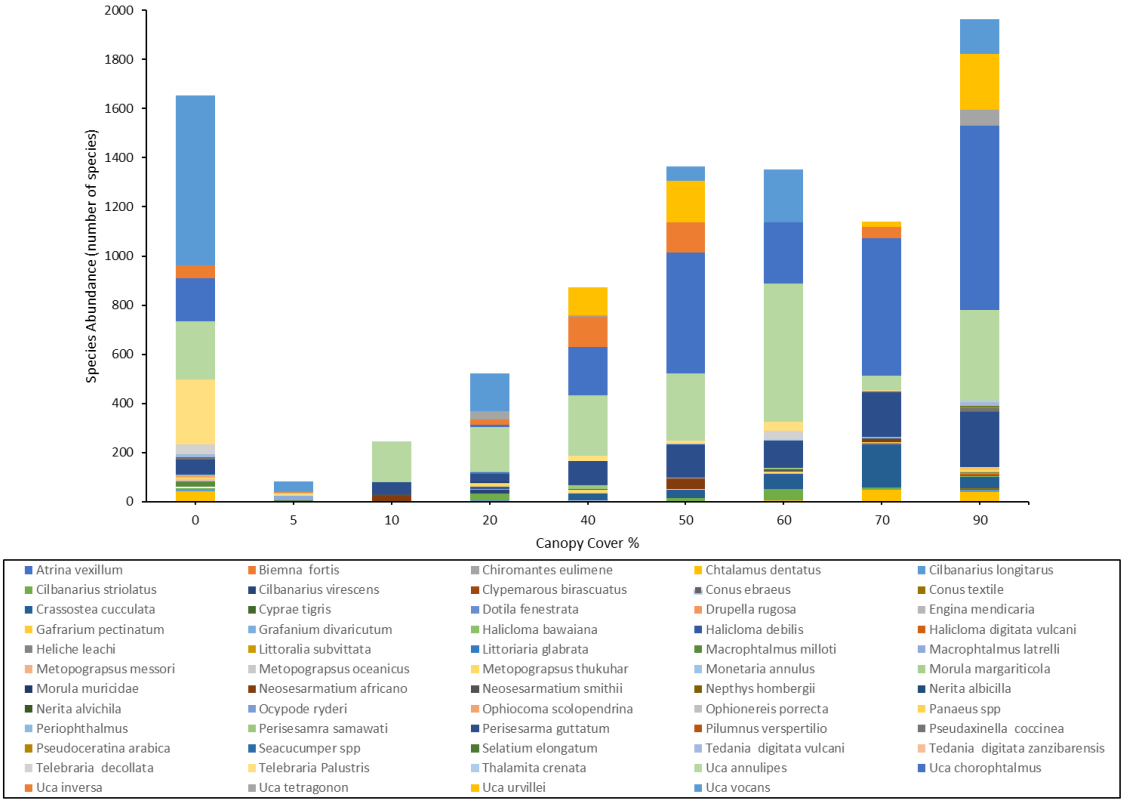

Figure 1: The overall epifaunal abundance distribution along the gradient of canopy cover.