

# Functional responses of mangrove fauna to forest degradation

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## ABSTRACT

Structural degradation of mangroves through the partial removal of trees is globally pervasive and likely to affect ecological functioning, including habitat provisioning for biodiversity. Biodiversity responses will depend on the severity of degradation, yet few studies have contrasted and quantified several degradation states. Addressing this knowledge gap, we sampled faunal diversity across a range of mangrove forests in southern Kenya. Canopy cover was the strongest predictor of faunal responses among forest structural variables. Faunal abundance, species richness and biodiversity all decreased with reduction in canopy cover, and taxonomic and functional composition changed. The trophic diversity of crabs peaked at intermediate canopy cover, with degraded habitats having more generalist species and fewer specialists. Functional redundancy was unaffected by canopy thinning. The decline in functional diversity and richness of brachyuran crabs with canopy cover implies that resource-use efficiency weakens with increasing degradation. Our results are indicative of significant alterations to forest functioning with degradation, because epibenthic fauna are important regulators of mangrove ecosystem processes, including nutrient cycling and carbon.

**Keywords:** biodiversity, faunal response, forest quality, functional plasticity, functional redundancy, habitat provisioning, species composition, tropical forests.

## Introduction

Mangrove forests are disappearing globally at a rate of 0.2–0.7% per annum because of coastal development, over-exploitation and land-use change, with larger areas being estimated to be in some state of degradation (Bryan-Brown *et al.* 2020). In the tropics alone, degraded forest cover  $5 \times 10^8$  ha (International Tropical Timber Council & International Tropical Timber Organization 2012; Putz and Romero 2014). The effect of degradation is of growing concern, because mangroves support multiple coastal processes and ecosystem services (Ghazoul *et al.* 2015). Although there has been an increasing effort in defining forest degradation, there have also been difficulties in disentangling degradation from deforestation (Murdiyarto *et al.* 2009; Ferreira and Lacerda 2016). Some authors recognise tropical forests to be degraded once the forest has been logged (Sierra 2001), whereas others take this into consideration only when the forest has been heavily burned or logged (Thompson *et al.* 2013). The existence of several competing definitions of degradation has led to ambiguity and misconceptions, hindering the implementation of a clear conceptual framework for moving forward (Pipatti *et al.* 2006; Schoene *et al.* 2007; Sasaki and Putz 2009; Ghazoul *et al.* 2015). In most cases, degradation is considered in terms of a loss of some attributes, function or services in response to disturbance (Fig. 1; Murdiyarto *et al.* 2009; Putz and Romero 2014; Ghazoul *et al.* 2015) with societal and cultural perspectives largely determining what is considered ‘degraded’ (Souza *et al.* 2005).

In addition to the difficulties in defining degradation, further challenges are encountered when assessing degraded forests. Recent studies have highlighted the importance of quantifying responses to ecosystem functioning (e.g. productivity, carbon sequestration and nutrient cycling) as key to understanding the impact of degradation to forest

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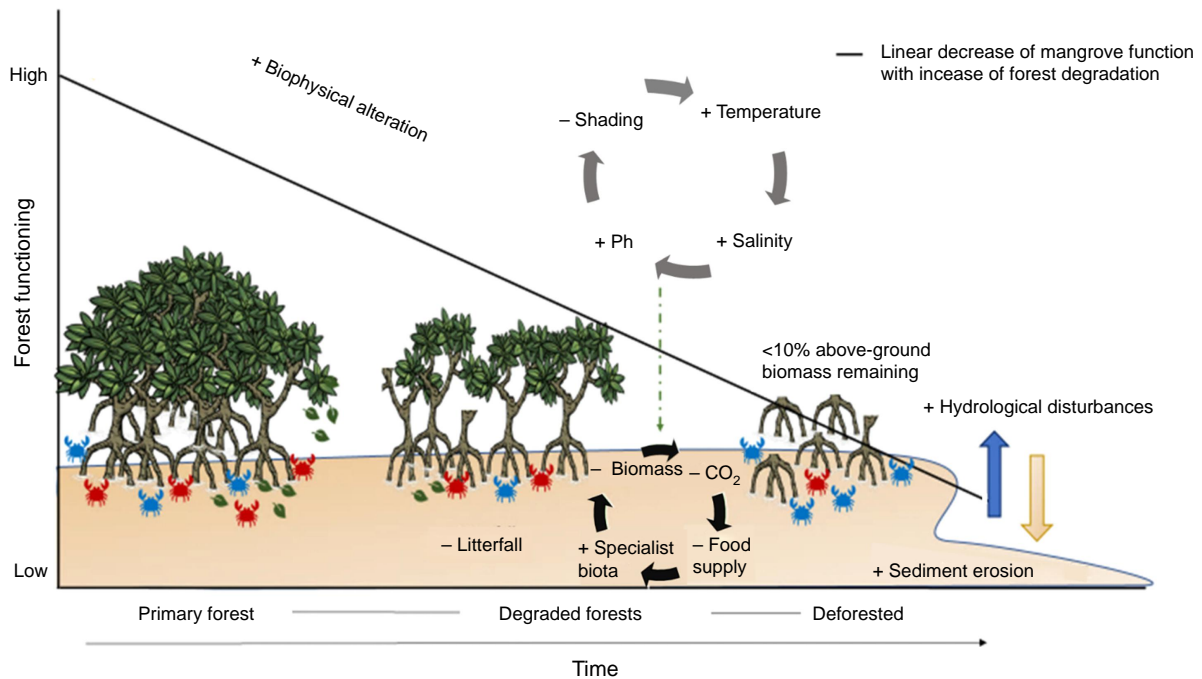
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**Fig. 1.** Functional implications of degrading mangroves from primary forest to fully deforested (<10% above-ground biomass remaining: Food and Agriculture Organization of the United Nations 2011). We depict a linear decline in function with degradation, although responses could be non-linear, invariant, or positive, depending on the functional process considered. Stressors to trees and fauna (e.g. desiccation risk, salinity, hydrological forcing) are predicted to increase with reduction in biomass and canopy cover through feedback-loop change to biophysical properties. We expect canopy loss to diminish litterfall food for fauna and to alter faunal composition and diversity.

dynamics and processes (Field *et al.* 2008; Ghazoul *et al.* 2015). Although remote-sensing is widely used to detect changes in forest cover, it cannot assess the breadth of changes to forest quality or faunal assemblage (diversity, richness, evenness) and composition (community structure) from degradation, without coupling to ground-based observations (Dalponte *et al.* 2018). Yet, there is a relative scarcity of ground-based studies that quantify structural degradation directly (tree stumps, branches removed, tree density and size compositional change, etc.) and there are even fewer studies that combine observations of structural degradation with measures of functional processes, despite ground-based observations being essential for estimating threshold responses of forest functioning to degradation (Perry *et al.* 2018). Although ground observations have evident limitations (scale of study, time and economically costly, lack of repetitive references; F. Cremer, M. Urbazaev, C. Schmulius, and C. Thiel, unpubl. data), they provide opportunity for determining how ecological functioning, such as habitat provisioning for fauna, changes in response to alteration in forest structure (Field *et al.* 2008). Here, we explore the implications of mangrove degradation to faunal composition, diversity and functional make-up.

Across both terrestrial and marine ecosystems, structural degradation is typically associated with a loss of

biodiversity (Primavera *et al.* 2019; Richardson *et al.* 2020). Diverse macrofauna inhabit mangrove forests, with crabs and gastropods as the dominant epifauna, and annelids and nematodes as key infauna organisms (Fondo and Martens 1998; Cannicci *et al.* 2008). Brachyuran crabs of the family Sesarmidae are leaf-litter specialists, whereas members of the family Ocypodidae (e.g. fiddler crabs) consume organic compounds derived from micro-algal and bacterial primary production (Cannicci *et al.* 2008). In addition to their habitat specialisations, mangrove crabs play a crucial role in ecosystem functioning and processes, such as decreasing ammonium and sulfide concentration in the soil through bioturbation, thereby boosting mangrove productivity (Cannicci *et al.* 2008). Crabs also affect the influx and chemistry of groundwater, preventing sediment from becoming compacted (Wolanski *et al.* 1992), thereby increasing pore-water exchange between swamp sediment and interstitial water (Ridd 1996). Within the mangrove ecosystem, a large proportion of leaf biomass is processed by sesarmid crabs; ensuing organic matter and energy pass through diverse microbial loops and are transported to the higher trophic levels through detritivores and bacterivores populating the benthos (Skov and Hartnoll 2002; Nagelkerken *et al.* 2008; Carugati *et al.* 2018).

There is considerable research emphasis on the roles of species traits to ecosystem functioning (e.g. Richardson et al. 2017; Knoester et al. 2019; Freitas and Pagliosa 2020) and on how species diversity responds to anthropogenic stressors at taxonomical and functional levels (Lee 2008). Ecosystems that incorporate several species with similar or same functional roles (i.e. functional redundancy) will suffer less reduction to overall ecosystem functioning when species are lost (Rosenfeld 2002; Hoey and Bellwood 2009; Leung 2015).

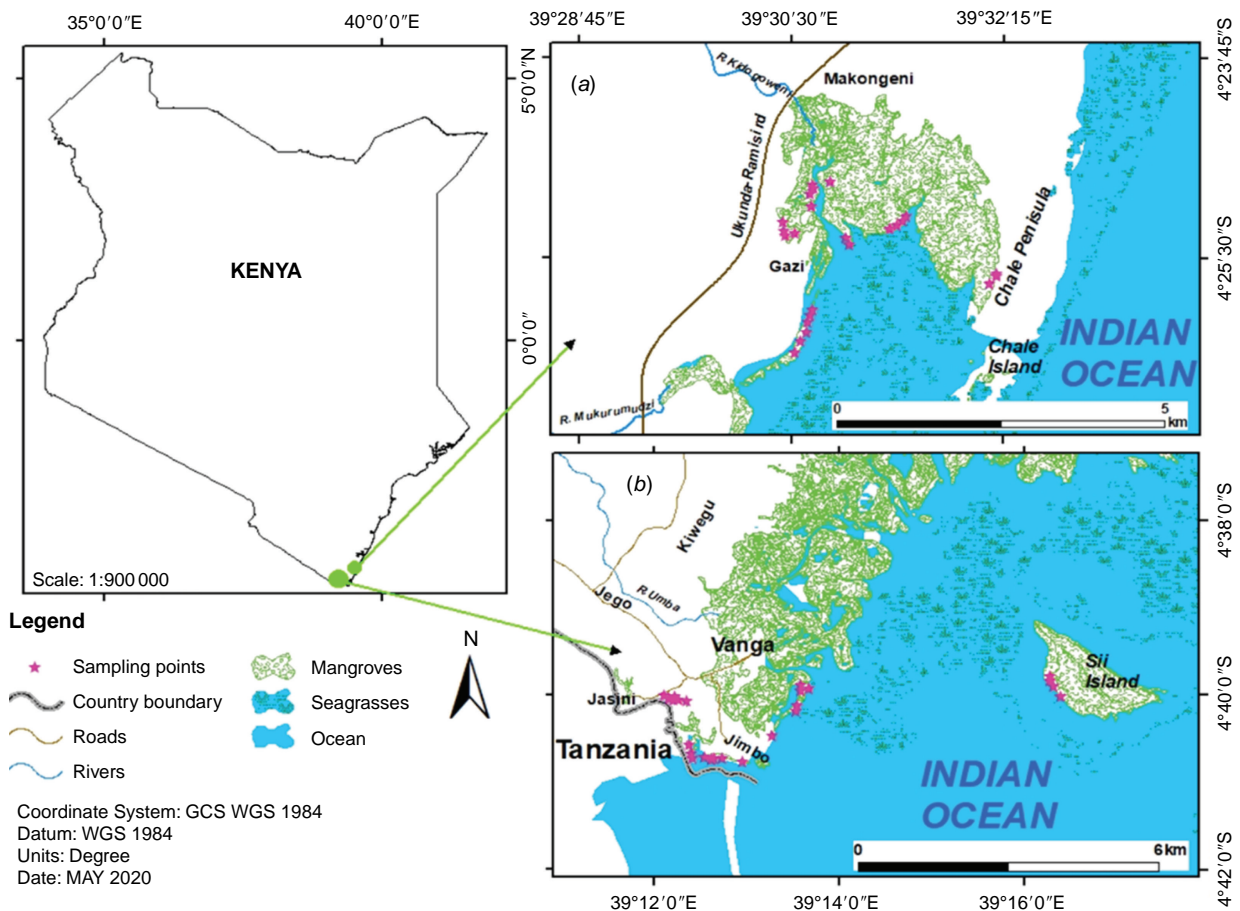
We examined the consequences of mangrove degradation on the biodiversity responses of marine epibenthic fauna, given their ecological importance to mangrove ecosystem functioning (Nagelkerken et al. 2008). We hypothesised that increased degradation would cause a decrease in the taxonomic diversity, richness and abundance, and in taxonomic evenness of benthic fauna overall (Bernardino et al. 2018; Freitas and Pagliosa 2020). We also anticipated degradation to change the taxonomical and functional assemblages of brachyuran crabs, increasing Ocypodidae and decreasing Sesarmidae abundances. We expected this because sesarmid crabs have a high dependency on leaf fall for food

(Skov et al. 2002), which would diminish with loss of tree cover, whereas deposit-feeding ocypodids extract fine detritus and biofilm from the substrate (Cannicci et al. 2008), which is less liable to diminishing with a reduced mangrove cover. Finally, we expected crab evenness, functional diversity, richness, and redundancy to decrease with degradation.

## Materials and methods

### Study sites and experimental design

Sampling was conducted in two bays in southern Kenya: Gazi Bay (4°22'S, 39°30'E) a semi-enclosed shallow bay, 40 km south of the city of Mombasa, and Vanga Bay (4°10'S, 39°27'E) at the border with Tanzania (Fig. 2). Gazi comprised a 661-ha mangrove forest complex, 3.3 km across and concentrated along the northern shores of the bay (Matthijs et al. 1999). Vanga Bay held 4428-ha mangrove spread across a series of creeks and including Sii Island, 6 km off the coast (Fig. 2b). The study aspired to capture the range of mangrove degradation occurring at our sites, while keeping the influence of other mangrove



**Fig. 2.** The study area in south-eastern Kenya, showing (a) Gazi Bay, including the Mikoko Pamoja protected section in the white square, and (b) Vanga Bay, with Sii Island located 6 km off the coast.

environmental variation at a minimum. Observations focused exclusively on the low mangrove to minimise the influence of shore elevation and mangrove zonation on faunal responses. Sampling areas within the two bays were selected without *a priori* quantification of degradation levels or the expectation of certain sites being particularly degraded or undegraded. Instead, we observed within our plots forest variables such as those shown in Supplementary Table S1, which we used, through a *posteriori* analysis, to assess the severity of degradation within every observation plot. Thus, our design relied on the *a posteriori* assessment of faunal responses to degradation, in which degradation was expressed on a continuous scale (e.g. values of variables in Table S1). This design relied on the opportunistic encountering of a range in the levels of degradation among plots, rather than the contrasting of sites with different levels of pre-ordained, categorical levels of degradation, as has been undertaken by past studies (e.g. Huxham *et al.* 2004; Sjöling *et al.* 2005; Carugati *et al.* 2018). Because of this design, the within-site variation in forest degradation indicators was often as great as the between-site variation (Table S1). Plot positions were randomised within study areas, although kept >100 m apart and away from mangrove silviculture and protected areas. In total, 50 plots 10 × 10 m in size were observed in the two bays, including 23 in Gazi Bay, from the west by the village to the east on Chale Peninsula (Fig. 2a), and 27 in Vanga, from Jimbo and Vanga villages on the main coast to Sii Island (Fig. 2b, Table S1).

Sampling was performed from February until July 2019. Per plot, a three-step approach was used to assess forest functioning, by quantifying (1) mangrove forest structure, (2) epibenthic faunal abundance and taxonomy, and (3) physical parameters (Supplementary Fig. S1), as subsequently described.

### Assessment of forest structure

Tree stem diameter at breast height (DBH; 130 cm above ground), tree height and density (trees ha<sup>-1</sup>) were recorded following Kauffman and Donato (2012). Canopy cover (%) was quantified as the proportion of the forest floor that had overlaying canopy, as estimated by projecting tree crowns to the forest floor (Korhonen *et al.* 2006). Tree stump density (stumps ha<sup>-1</sup>) and number of cut branches (branches ha<sup>-1</sup>) were recorded as direct indicators of human disturbance to forest (i.e. cutting or forest clearing). An allometric equation specific to Kenya (Cohen *et al.* 2013) converted DBH (cm) into above-ground tree biomass (AGB; Mg ha<sup>-1</sup>):

$$\text{AGB} = \text{DBH} \times H + \rho$$

where  $H$  is tree height (m) and  $\rho$  is wood density (g cm<sup>-3</sup>), with values specific to each tree species.

### Assessment of epibenthic faunal composition and assemblages

Fauna were observed during spring tides when surface activity peaks (Skov *et al.* 2002). The assessment involved two procedures (Fig. S1), namely (1) quantification of brachyuran crabs following the two-step approach of Skov *et al.* (2002) and (2) quantification of non-crab epibenthic faunal abundance, including molluscs, echinoderms and other crustaceans. For Procedure 1, three 1 × 1-m<sup>2</sup> randomly located subquadrats per plot were set out a day before observation. Visual counts with binoculars from 3.5-m distance enumerated non-burrowing species, whereas burrow counts quantified burrowing species in the following four burrow size classes: small (<4 mm), medium (4–8 mm), large (8–20 mm) and extra-large (>35 mm; Skov *et al.* 2002). Size classification facilitated allocating crab-burrow counts to crab families, with ocypodid crabs being assumed to account for the small burrows. Crabs were classified into the following four functional groups on the basis of their trophic traits: ‘foli-detritivores’ (feeding on fallen mangrove propagules and leaf litter), detritivores (including deposit feeders), omnivores and predators (Fratini *et al.* 2000; Gillikin and Schubart 2004; Cannicci *et al.* 2008). For Procedure 2, epifaunal abundance was recorded per quadrat (1 × 1 m) and epifauna was identified at the species level (fauna climbing trees were excluded from estimation).

### Assessment of physical variables

Air and soil (30 cm below surface) temperatures were measured at three random points using a Hanna Combo multimeter (Fig. S1c). To reduce the effect of variation in ambient temperature among sampling days and times of day, air temperature among sampling days and times of day, air temperature under the canopy inside the plot was standardised to temperature in the absence of canopy cover, measured at the nearest canopy-free area outside the plot:

$$\frac{\text{Temperature (out)} - \text{Temperature (in)}}{\text{Temperature (out)}}$$

where ‘in’ is the average temperature inside the plot and ‘out’ canopy-free temperature outside the plot. With this approach, air temperature was a measure of the reduction in ambient temperature incurred by the plot canopy cover (or the lack thereof). Sediment grain size was derived from three randomly distributed, 30-cm-deep, 6-cm-diameter soil cores per plot, pooled and homogenised, before wet-analysing a 5-g subsample in a Mastersizer 3000 laser particle-size analyser. Soil pH, water and soil salinity were measured *in situ* with a Hanna HI 98129. Sampling was conducted at low tide during spring tide periods.

### Data analysis

The analysis had the following two main objectives: (1) to establish the best indicators of mangrove degradation

among the multiple structural and physical forest variables observed (canopy cover, tree biomass, density, soil pH, temperature, salinity, basal area etc.; Fig. 1) and (2) to examine epibenthic faunal responses to variation in these degradation indicators.

For Objective 1, we used a combination of principal component analysis (PCA) to summarise forest and environmental variables, so as to visualise which indicator best drives degradation (see the 'Method' section in the Supplementary material) and generalised linear mixed models (GLMMs) to understand the relationship among forest variables. For Objective 2, LMMs following the model ( $Y \sim (x_1 + x_2 + x_3 + x_4 \dots + x_n)$ , random =  $\sim 1$ |site) were used to determine which combination of forest variables best predicted variation in faunal community assemblage and composition responses. Models were constructed using the lme function of the nlme package in R studio (ver. 3.6.0, RStudio PBC, Boston, MA, USA, see <https://rstudio.com/>). Initial model selection was conducted to identify potential variance structures by using restricted maximum likelihood (REML) estimates, followed by the selection of the fixed effects by using maximum-likelihood (ML) estimation (Zuur et al. 2007). We used stepwise exclusion analysis, with variables (fixed effects) not adding to improving the model fit (Akaike information criterion (AIC) value) subsequently being removed and analyses re-run. The analyses showed that models with canopy cover only had the best-fit and that canopy cover was the most consistent predictor of variation in faunal community responses. Therefore, we used canopy cover as a single proxy for degradation in subsequent LMMs to be related to faunal community composition responses. GLMMs were preferred to ordinary linear regression models to accommodate non-stable variances and alternative exponential residual distributions (Zuur et al. 2007).

Permutational multivariate analyses of variance (PERMANOVA; Anderson 2014) evaluated the effect of canopy cover on crab community assemblage and functional groups. Data were fourth-root transformed to highlight rarer species and reduce the asymmetry of species distribution (Clarke et al. 2008). Responses of crab community composition and assemblages to variation in canopy cover classes were illustrated using multidimensional scaling (MDS) based on a Bray–Curtis similarity matrix. A canonical analysis of principal coordinates (CAP) was conducted to detect differences in crab community composition among canopy cover classes. Significant PERMANOVAs were followed by pairwise comparisons of crab community composition between canopy classes (>500 permutations). Functional groups that differed among canopy classes were identified using similarity percentage analysis (SIMPER) on a Bray–Curtis matrix of dissimilarities (Clarke 1993). Variation in the trophic community structure was expressed through the following three indexes of functional diversity: functional richness (number of unique functional traits), functional evenness (regularity

of functional traits based on abundance) and functional redundancy (calculated as the ratio of functional to taxonomic diversity, following Villéger et al. 2008). Analyses were performed using the packages *qpcR*, *princomp*, *lme4* and *stats*.

## Results

### Canopy cover as a proxy of degradation

GLMM models showed that, overall, canopy cover had a positive, although minimal association with the other observed forest factors (GLMM; AGB  $F = 3.15$ ; s.d. = 0.6; s.e. = 0.2;  $P = 0.01$ ; basal area  $F = 2.04$ ; s.d. = 0; s.e. = 0;  $P = 0.05$ ; Stumps  $F = -2.5$ ; s.d. = 0.04; s.e. = 0.06;  $P = 0.05$ ). 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 S1). Reduction in canopy cover diminished shading ( $F = 37.1$ ; d.f. = 45;  $P = 0.001$ ,  $R^2 = 0.4$ ;  $\beta = 1.36$ , Fig. S3a) and increased pH ( $F = 46.5$ ; d.f. = 45;  $P = 0.001$ ;  $R^2 = 0.5$ ;  $\beta = 0.6$ , Fig. S3b) but did not affect soil temperature, salinity or grain size (see the Results section in the Supplementary material).

### Variation of epibenthic faunal diversity

Across sites, 17 families, comprising 60 distinct species of epifauna, were identified, including gastropods, bivalves, echinoderms and crustaceans. Our model selection identified canopy cover as the best and consistent predictor for most of the community structure analysis, whereas the multivariate LMMs (all forest variables as predictors included) did not show any clearer trends (Table 1, Fig. 3, S4). Furthermore, the relationships of canopy cover with all other forest variables and the model selections warranted its use as a proxy for degradation in subsequent analyses.

### Responses of crab community assemblages, composition, traits and functional diversity to canopy cover

Similarly, crab assemblages also showed a consistently clear association with canopy cover, apart from species evenness, which remained unaffected ( $P = 0.3$ ). The AIC ranking tables showed that the best-fit model contained only canopy cover, which explained the greatest amount of variation (Table 2, Fig. 3, S5).

Crab community composition changed with canopy cover (Fig. 4, Table 3), with communities of very low (5%) and medium–high (70%) canopy cover being most dissimilar (SIMPER pairwise test: diss% = 94.36). Key species accounting for this dissimilarity were the foli-detritivores *Chiromantes eulimene* (94.84%) and *Neosarmatium smithi* (pairwise test: diss% = 83.42), which were linked to higher

**Table 1.** Model ranks for the linear mixed-effect model (LMM) of epibenthic faunal assemblage (diversity, abundance, richness and evenness).

Model rank	AIC <sub>c</sub>	logLik	ΔAIC <sub>c</sub>	wi
<b>Epibenthic fauna</b>				
Abundance ~ canopy + BA+ stem cuts + I site	522.7	1	0	0.26
Abundance ~ canopy + I site	522.7	0.9	0.01	0.25
Abundance ~ canopy + BA + I site	522.8	0.9	0.1	0.24
Abundance ~ canopy + BA + stem cuts + stumps I site	523.4	0.8	0.7	0.17
Abundance ~ canopy + BA + stem cuts + stumps + AGB I site	525.3	2.7	0.3	0.06
Richness ~ canopy I site	111.3	1	0	0.3
Richness ~ canopy + BA + I site	111.7	0.7	0.7	0.2
Richness ~ canopy + BA + stem cuts + I site	112	0.8	0.3	0.2
Richness ~ canopy + BA+ stem cuts + stumps + I site	112	0.7	0.7	0.2
Richness ~ canopy + BA+ stem cuts + stumps + AGB + I site	113	0.2	2.5	0.08
Diversity ~ canopy + I site	57	1	0	0.3
Diversity ~ canopy + stem cuts + BA + I site	56.9	0.8	0.7	0.2
Diversity ~ canopy + stem cuts + I site	57.4	0.7	0.2	0.2
Diversity ~ canopy + stem cuts + BA + stumps + I site	57.3	0.7	0.6	0.2
Diversity ~ canopy + stem cuts + BA + stumps + AGB + I site	59.2	0.3	2.5	0.07

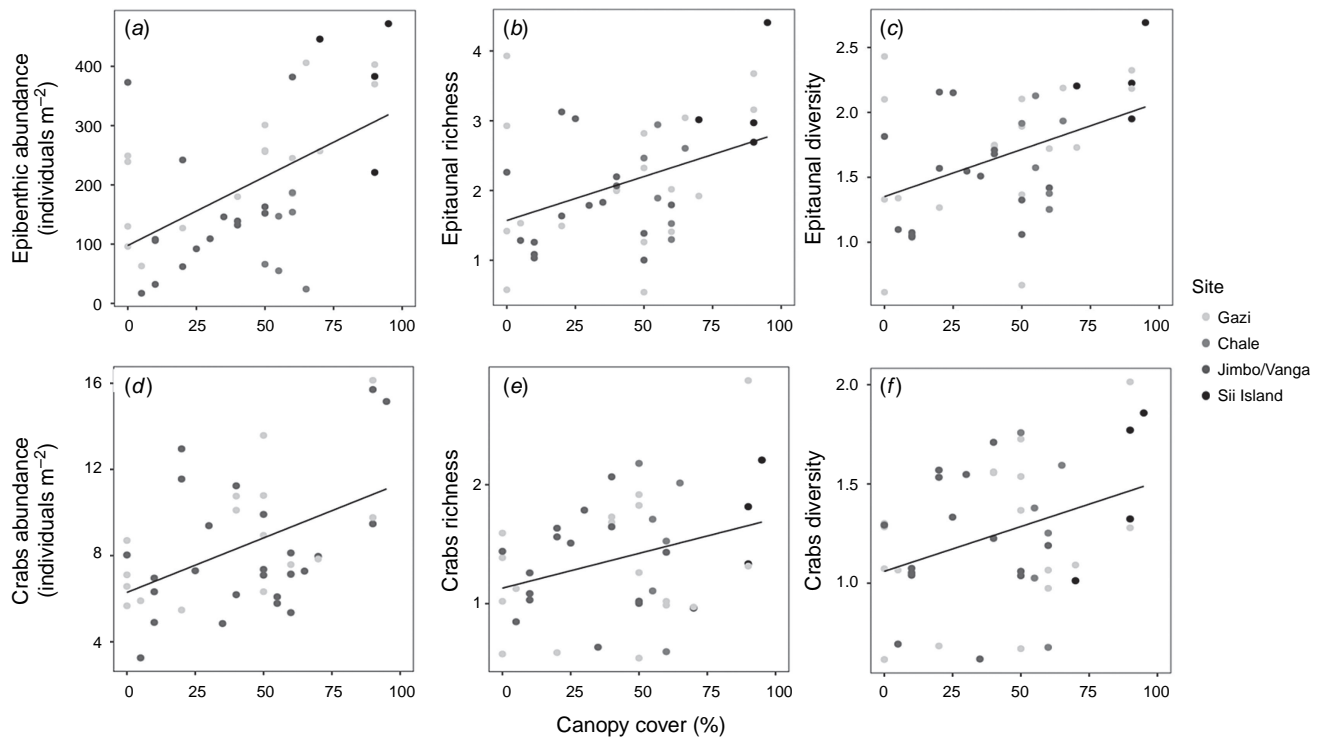
Models are ranked by corrected Akaike's information criteria (AIC<sub>c</sub>), with all models within ΔAIC<sub>c</sub> of <2 of the top-ranked models. The relative likelihood (logLik) and weight (wi) of evidence between each model and the variables present in each model are given.

canopy cover, and the omnivorous *Metopograpsus thukuhar* that preferred low to moderate canopy cover (89.46%). Functional groups (number of species ÷ trait) peaked at either end of the canopy cover spectrum. For instance, predators (e.g. *Thalamita crenata*) were found only at 90% canopy cover (SIMPER: cumulative diss% = 92.77, Fig. 4b, Table 3). Diversity increased from canopy cover of 5–50%, with 50% cover having overall the highest trophic diversity, and foli-detritivores significantly increasing from 5 to 50% canopy cover (PERMANOVA  $P = 0.02$ ; SIMPER: average diss% = 87.77). Yet, dissimilarities were found between communities inhabiting 0 and 50% canopy cover (PERMANOVA  $P = 0.001$ ), with the loss of foli-detritivores, for example, *Neosarmatium smithi* at 0% canopy cover and detritivores *Uca urvillei* and *U. tetragonon* being lost at 50% canopy cover (SIMPER: cumulative diss% = 83.17 and 96.45; Fig. 5).

Functional richness and functional diversity increased with canopy cover and varied among sites (LMM;  $|t| = 8.8$ ;  $P = 0.001$ ; d.f. = 45;  $|t| = 2.8$ ;  $P = 0.001$ ; d.f. = 45), whereas functional redundancy and evenness (LMM;  $|t| = 1.5$ ;  $P = 0.4$ ; d.f. = 45;  $|t| = -1.2$ ;  $P = 0.08$ ; d.f. = 45) were not significantly affected by change in canopy cover.

## Discussion

This study showed clear effects of forest structure and degradation on epibenthic faunal communities. Degradation was evident at sites through scarce canopy cover, dense stands of young trees and cut stumps, related to reduced shading, and decreased soil pH. The incremental change in canopy cover was a good proxy of degradation and related well to key faunal community responses, conforming its usefulness as an indicator of forest health and quality (Joshi *et al.* 2006; Chen *et al.* 2019; Wu *et al.* 2020). Community composition and assemblages of epibenthic fauna responded positively with the increase in canopy. These faunal responses are symptomatic of over-arching changes in mangrove functioning from degradation, because fauna influence mangrove ecosystem processes, including nutrient cycling, carbon storing and forest regeneration (Skov and Hartnoll 2002; Kristensen 2008; Lee 2008). The negative response of species richness and diversity to degradation may imply a reduction of habitat availability and resources (Lee 2008; Carugati *et al.* 2018; Freitas and Pagliosa 2020). Notably, degradation reduced functional diversity and functional richness, because the variation in trophic composition declined with a reduction in canopy

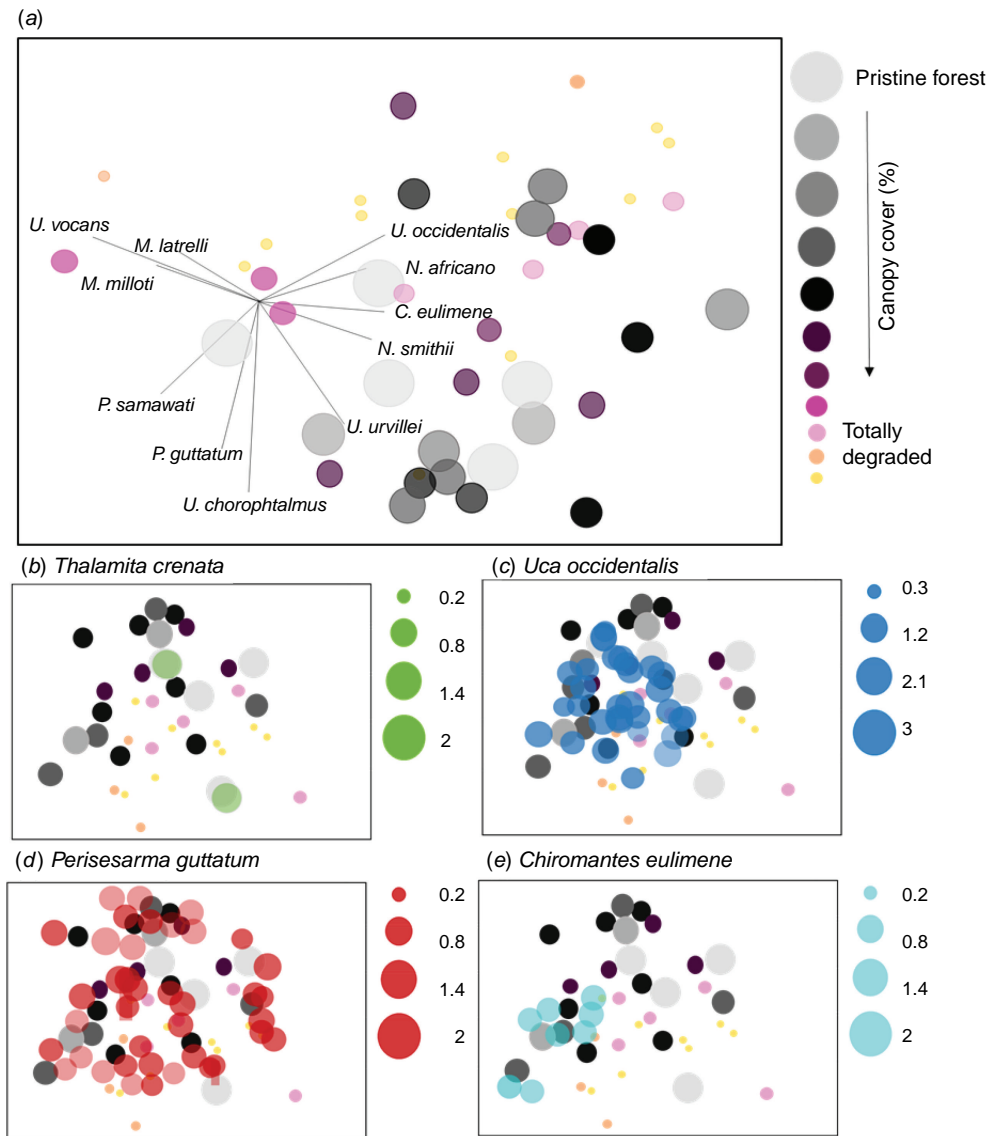


**Fig. 3.** Mixed linear regressions of epibenthic composition, with canopy cover (%) on the top panel and crab composition at the bottom: (a) epibenthic abundance ( $F = 3.7$ ; s.e. = 0.06;  $P = 0.001$ ;  $R^2 = 0.2$ ), (b) epibenthic richness ( $F = 2.8$ ; s.e. = 0.04;  $P = 0.008$ ;  $R^2 = 0.1$ ), (c) epibenthic diversity ( $F = 3$ ; s.e. = 0.02;  $P = 0.004$ ,  $R^2 = 0.2$ ), (d) crab abundance ( $F = 3.3$ ; s.e. = 0.01;  $P = 0.002$ ;  $R^2 = 0.2$ ), (e) crab richness ( $F = 2.2$ ; s.e. = 0.002;  $P = 0.0$ ;  $R^2 = 0.1$ ) and (f) crab diversity ( $F = 2.4$ ; s.d. = 0.01;  $P = 0.02$ ;  $R^2 = 0.01$ ); degrees of freedom = 45.

**Table 2.** Model ranks for linear mixed-effect model (LMM) of crab assemblage (diversity, abundance, richness and evenness).

Model rank	AIC <sub>c</sub>	logLik	ΔAIC <sub>c</sub>	wi
		Crabs		
Abundance ~ canopy + I site	203.1	1	0	0.5
Abundance ~ canopy + BA + I site	204.3	0.5	1.2	0.2
Abundance ~ canopy + stem cuts + BA + I site	205.1	0.4	1.9	0.2
Abundance ~ canopy + stem cuts + BA+ stumps + I site	206.9	0.05	3.8	0.06
Abundance ~ canopy + stem cuts + BA + AGB + stumps + I site	208.9	0.05	5.8	0.02
Richness ~ canopy + BA + I site	66.3	0.5	1.4	0.2
Richness ~ canopy + stem cuts + BA + I site	68.3	0.2	3.3	0.1
Richness ~ canopy + stem cuts + BA + stumps + I site	70.3	0.07	5.3	0.03
Richness ~ canopy + stem cuts + BA + AGB + stumps + I site	72.3	0	9.3	0.005
Diversity ~ canopy + I site	34	1	0	0.6
Diversity ~ canopy + stem cuts + I site	37.8	0.4	1.9	0.3
Diversity ~ canopy + stem cuts + BA + I site	37.8	0.1	3.8	0.09
Diversity ~ canopy + stem cuts + BA + stumps + I site	39.8	0.05	5.8	0.03
Diversity ~ canopy + stem cuts + BA + AGB + stumps + I site	41.8	0.01	7.8	0.01

Models are ranked by corrected Akaike’s information criteria (AIC<sub>c</sub>), with all models within ΔAIC<sub>c</sub> of <2 of the top-ranked models. The relative likelihood (logLik) and weight (wi) of evidence between each model and the variables present in each model are given.



**Fig. 4.** (a) Variation in crab species composition with canopy-cover classes, as described by MDS ordination, with vectors based on Pearson correlations of <math><0.2</math>. Crab community assemblages include species from families Sesarmidae (*Perisesarma guttatum*, *P. samawati*, *Neosesarmatum smithi*, *N. africanum* (ex. *N. meinerti*), *Chiromantes eulimene*), Ocypodidae (*Uca occidentalis*, *U. urvillei*, *U. chlorophthalmus*, *U. vocans*, *U. inversa*, *U. tetragonon*), Portunidae (*Thalamita crenata*), Macrophtalmidae (*Macrophtalmus latrelli*, *M. milloti*) and Grapsidae (*Metopograpsus oceanicus*, *M. thukuhar*, *M. messor*). Bubble plots illustrate differences in (b) *T. crenata*, (c) *U. occidentalis*, (d) *P. guttatum* and (e) *C. eulimene* abundance by canopy-cover classes. Variation in bubble sizes represents from 100% stepping down to 0% canopy cover.

cover. High functional diversity is indicative of efficient use of resources and higher productivity, because species exploit resources differently through niche complementary; functional groups occupied distinct niches and used food resources in a complementary way (Petchey 2003; Petchey and Gaston 2006). High functional diversity and richness invariably underpin ecosystem functioning and stability (Rasher et al. 2013; Richardson et al. 2017). Hence, the observed loss in functional richness and the assumed

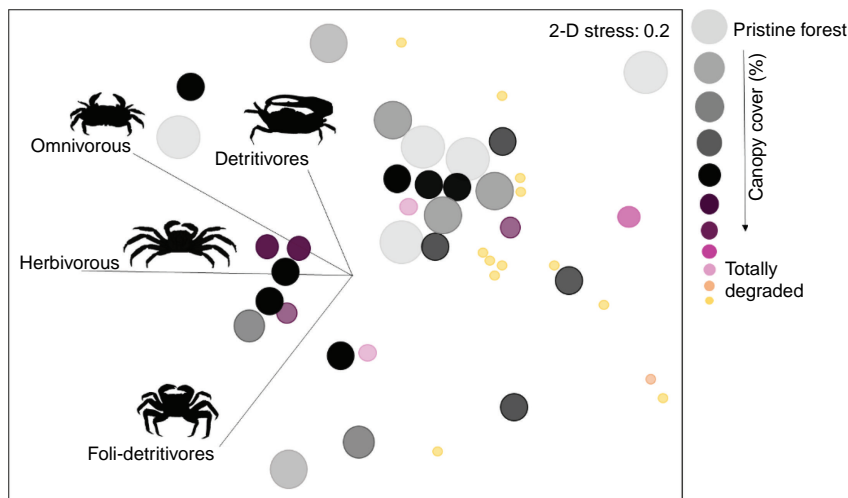
associated decline in niche complementarity among species are likely to have important consequences for mangrove ecosystem functioning (Bellwood et al. 2003). Degradation of mangroves is globally pervasive (Wilkinson and Salvat 2012; Bryan-Brown et al. 2020) and although there has been ample and justifiable emphasis on forest loss (e.g. Olander et al. 2012; Richards et al. 2020; Turschwell et al. 2020), there has been less focus on how the partial removal of forest structure influences ecosystem functioning.



**Table 3.** Effects of mangrove canopy-cover class on crab community composition and the composition of crab trophic traits, tested using permutational multivariate ANOVA on a Bray–Curtis similarity matrix of fourth-root transformed data.

Variables	Source	d.f.	MS	Pseudo-F	P	Perms
Community composition	Canopy	10	3028.1	1.42	0.05	998
	Residual	36	2135.1			
Trophic traits	Canopy	10	631.0	1.73	0.05	999
	Residual	36	366.9			

Perms, number of permutations.

**Fig. 5.** Functional composition of mangrove crabs in a multi-dimensional scaling ordination, with vectors being based on Pearson correlations of <0.2.

We found complex faunal responses with degradation (i.e. percentage of canopy cover, our best proxy), which could not have been detected by simply comparing a degraded to an undegraded forest, as is most often done. Faunal species assemblages and functional composition, which we explored through the responses of forest-floor crabs, particularly changed at the extremes of the degradation gradient. Thus, species feeding on leaves and litter from trees (foli-detritivores) unsurprisingly peaked at high canopy cover, whereas omnivores preferred moderate canopy cover. Predators were very rare, yet found only at the highest canopy cover. These observations echo previous studies showing that declines in crab species richness or diversity were associated with loss of specialists (Carrete et al. 2010; Villéger et al. 2010). In fact, functional-group frequency (number of species ÷ functional traits) differed most markedly between the highest and lowest canopy covers, peaking at high canopy and slumping at low canopy cover. Such modifications in the composition of functional groups among communities, in line with previous studies, could occur because of the reduction in habitat complexity with degradation and the aversion of some groups to the conditions found and low habitat versatility (Mouillot et al. 2007; Bernardino et al. 2018; Freitas and Pagliosa 2020).

Here, canopy cover was the best degradation-associated predictor of faunal responses. Studies conducted in Mozambique also found that the presence of biota in

mangrove forests was strictly linked to tree cover and not to other biogenic structures of the mangrove trees, such as roots and trunk morphology (Fondo and Martens 1998), which might vary with tree species composition. Here, we did not test for the effect of tree species composition on faunal responses, because our exclusive focus on the low mangrove naturally restricted the between-site variation in tree assemblage, and because the distribution of epibenthic mangrove fauna is largely governed by their biophysical tolerance to the environmental stressors of their zone (Fondo and Martens 1998). However, epibenthic fauna can undeniably be responsive to variation in forest root morphology and density (Leung 2015), which we did not quantify here and which can vary between sites with the same tree species composition. We, therefore, cannot fully dismiss that some of the between-site variation in faunal responses was due to site differences in root and pneumatophore structure and density. Mangrove epibenthic faunal species are distributed according to their biophysical tolerance to environmental stressors such as salinity, temperature and desiccation (Fondo and Martens 1998). Although we found that most of the environmental parameters we measured were homogenous across the degradation gradient, shading, which obviously declined with a decrease in canopy cover, might have been a key factor responsible for the decline in faunal richness and diversity. Under shadier conditions, owing to denser canopies, mangroves produce more leaf

litter, cycle more nutrients and maintain higher soil moisture (Tolhurst *et al.* 2020). Heavy shading can significantly modify processes and properties at the sediment–water interface, such as increased carbohydrate accumulation on the burrow surface, which may affect faunal abundance and distribution (Tolhurst *et al.* 2020). Similar patterns were also observed by Ruwa (1988), who found that species diversity was greater in moderate shade conditions. Canopy cover is also a yardstick indicator of the state of a collective of forest biogenic structural variables.

In mangrove ecosystems, biogenic structures, especially dense roots, may act as an environmental filter (exclusion) for large body-size crabs, leading to trait convergence (i.e. reduction in functional niches – the ecological volume occupied in the ecosystem, on the basis of the species' impact; Brandl and Bellwood 2014), causing root-dense areas to display low functional diversity and redundancy (Leung 2015). Yet, whereas we found that functional diversity and richness decreased with degradation and the likely reduction of habitat heterogeneity, functional redundancy varied independently. These patterns indicate a consistent overlap of functional niches among species, even at the most degraded sites, and also suggest functional plasticity and functional accommodation – the lack of variation in functional rates (Needham *et al.* 2010; Bingham *et al.* 2018). Several studies have highlighted how trait variation within species improves the acclimation to changing environments (Okuyama 2008) and reduces extinction risks (Bolnick *et al.* 2011). Many mangrove macrofauna do exhibit trait variations to promote opportunistic feeding behaviours (see Fratini *et al.* 2000; Poon *et al.* 2010). In mangroves, omnivorous crabs foraging in open-canopy forests exhibit enhanced functional plasticity across trophic traits to counter otherwise challenging environmental conditions (Giraldes *et al.* 2019). On the flip side, species of the normally litter-dependent species (*Sesarmidae*) alter their diets with season, climate and food availability (Poon *et al.* 2010). The extent to which the community turnover was affected by diet variation was not recorded here. Nevertheless, it is plausible that the faunal assemblage changed feeding behaviour in response to forest degradation.

The observed changes in epibenthic faunal communities with degradation are likely to alter mangrove ecosystem functions through modification of the benthic habitat. For instance, micro-epiphytic biomass can bloom in the absence of grazing (Kristensen and Alongi 2006), causing indirect variation to the meiofaunal communities that feed on the micro-epiphytes (Carlén and Ólafsson 2002). The connection and provision of a food source to secondary consumers and food-web dynamics with adjacent fisheries may also be affected by the lack of food availability, from microphytes to macrofauna (Nagelkerken *et al.* 2008; Sheaves 2009; Olds *et al.* 2013). There is much uncertainty about the effects of mangrove degradation on epifaunal community and functional composition. We encourage more research in this area to improve the understanding of how small-scale anthropogenic disturbances interact with

ecosystem functioning and services (Lee 2008; Goldenberg *et al.* 2018), for the promotion of effective and pragmatic management of mangroves. Forest degradation is an undeniable challenge to the global biodiversity crisis (Primavera *et al.* 2019; Richardson *et al.* 2020). The early stages of degradation that precede the clear felling of trees are subtle and difficult to detect remotely. Yet, they provide the means towards early warning signs of impending losses to wider environmental functioning and are likely to be prevalent in developing countries, such as Kenya, where wood extraction is a survival necessity to subsistence living. Without accelerating the extent of ground-based observations, we will not gain clarity on the extent of the problem.

## Supplementary material

Supplementary material is available online.

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**Data availability.** The data that support this study will be stored securely in the Main Frame facility of Bangor University, United Kingdom. The data can be obtained, upon request, by contacting Dr Martin Skov, School of Ocean Sciences, Askew Street, Bangor University, LL59 5AB, United Kingdom (mwskov@bangor.ac.uk).

**Conflicts of interest.** M. Skov is an editor for *Marine and Freshwater Research* but did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Marine and Freshwater Research* encourages its editors to publish in the journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

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