

# Functional responses of mangrove fauna to forest degradation

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1	Functional responses of mangrove fauna to forest degradation
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15	Summary text for the Table of Contents.
16	Animals living in mangroves on tropical coastlines are threatened by forest clearing. In Kenya,
17	we investigated how the degree of mangrove forest clearing (i.e. degradation) affects species'
18	presence and abundance and found that specialist species decrease while generalists increase
19	in abundance with degradation. Most epibenthic faunal species play important roles in keeping
20	mangroves healthy, and a taxonomic and functional reduction and/or increased generalism in
21	species composition can negatively affect ecosystem functioning and benefits to humans.
22	
23	Abstract
24	Structural degradation of mangroves through the partial removal of trees is globally pervasive
25	and likely to affect ecological functioning, including habitat provisioning for biodiversity.
26	Biodiversity responses will depend on the severity of degradation, yet few studies contrast and
27	quantify several degradation states. Addressing this knowledge gap, we sampled faunal
28	diversity across a range of mangrove forests in southern Kenya. Canopy cover was the strongest
29	predictor of faunal responses among forest structural variables. Faunal abundance, species
30	richness and biodiversity all decreased with reduction in canopy cover, while taxonomic and
31	functional composition changed. The trophic diversity of crabs peaked at intermediate canopy
32	cover, with degraded habitats having more generalist species and fewer specialists. Functional
33	redundancy was unaffected by canopy thinning. The decline in functional diversity and richness
34	of brachyuran crabs with canopy cover implies resource-use efficiency weakens with increased

35 degradation. Our results are indicative of significant alterations to forest functioning with

36 degradation, as epibenthic faunal are important regulators of mangrove ecosystem processes,

- 37 including nutrient cycling and carbon.
- 38

39 Key words: functional plasticity, forest quality, functional redundancy, tropical forests

40

# 41 Introduction

42 Mangrove forests are disappearing globally at a rate of 0.2-0.7% per annum due to coastal 43 development, over-exploitation and land-use change, with larger areas estimated to be in some 44 state of degradation (Brown et al., 2020). In the tropics alone, degraded forest cover 500 million 45 hectares (ITTO 2012; Putz and Romero, 2014). The effect of degradation is of growing concern, 46 as 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 47 48 been difficulties in disentangling degradation from deforestation (Olander et al. 2008; Ferreira 49 and Lacerda, 2016; Murdiyarso et al. 2009). Some authors recognise tropical forests to be 50 degraded once the forest has been logged (Sierra 2001), while others take this into consideration 51 only when the forest has been heavily burned and/or logged (Thompson et al. 2013). The 52 existence of several competing definitions of degradation has led to ambiguity and 53 misconceptions, hindering the implementation of a clear conceptual framework for moving 54 forward (IPCC 2006; Schoene et al. 2007; Sasaki and Putz, 2009; Ghazoul et al. 2015). In most 55 cases, degradation is considered in terms of a loss of some attributes, function and/or services 56 in response to disturbance (Fig.1, Murdiyarso et al. 2008; Putz and Romeo, 2014; Ghazoul et 57 al. 2015) with societal and cultural perspectives largely determining what is considered 58 'degraded' (Souza et al. 2005).

59 In addition to the difficulties in defining degradation, further challenges are encountered when 60 assessing degraded forests. Recent studies highlighted the importance of quantifying responses 61 to ecosystem functioning (e.g. productivity, carbon sequestration and nutrient cycling) as key to understanding the impact of degradation to forest dynamics and processes (Field et al. 2008; 62 63 Ghazoul et al. 2013). While remote sensing is widely used to detect changes in forest cover, it 64 cannot assess the breadth of changes to forest quality or faunal assemblage (diversity, richness, evenness) and composition (community structure) from degradation without coupling to 65 ground-based observations (Dalponte et al. 2018). Yet, there is relative scarcity of ground-66 67 based studies which quantify structural degradation directly (tree stumps, branches removed,

68 tree density/size compositional change, etc) and even fewer studies which combine observations of structural degradation with measures of functional processes, despite ground-69 70 based observations being essential for estimating threshold-responses of forest functioning to 71 degradation (Perry et al. 2018). While ground-observations have evident limitations (scale of 72 study, time/economically costly, lack of repetitive references, Cremer et al. 2019), it does 73 provide opportunity for determining how ecological functioning, such as habitat provisioning 74 for fauna, changes in response to alteration in forest structure (Field et al. 2008). Here, we 75 explore the implications of mangrove degradation to faunal composition, diversity and 76 functional make-up.

77 Across both terrestrial and marine ecosystems, structural degradation is typically associated 78 with a loss of biodiversity (Primavera et al. 2019; Richardson et al. 2020). Diverse macrofauna 79 inhabit mangrove forests, with crabs and gastropods as the dominant epifauna, and annelids 80 and nematodes as key infauna organisms (Fondo and Martens, 1998; Cannicci et al. 2008). 81 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 microalgal 82 83 and bacterial primary production (Cannicci et al. 2008). In addition to their habitat 84 specialisations, mangrove crabs play a crucial role in ecosystem functioning and processes, 85 such as decreasing ammonium and sulphide concentration in the soil through bioturbation, thereby boosting mangrove productivity (Cannicci et al. 2008). Crabs also affect the influx and 86 87 chemistry of groundwater, preventing sediment from becoming compacted (Wolanski et al. 1992), thereby increasing pore water exchange between swamp sediment and interstitial water 88 89 (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 90 91 and are transported to the higher trophic levels through detritivores and bacterivores populating 92 the benthos (Skov and Hartnoll 2002; Nagelkerken et al. 2008; Carugati et al. 2019).

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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, 2010; Leung 2015).

100 We examined the consequences of mangrove degradation on the biodiversity responses of 101 marine epibenthic faunal, given their ecological importance to mangrove ecosystem 102 functioning (Nagelkerken et al. 2008). We hypothesised that increased degradation would 103 cause a decrease in the taxonomic diversity, richness and abundance, and in taxonomic 104 evenness of benthic fauna overall (Bernardino et al. 2018; Freita and Pagliosa, 2020). We also 105 anticipated degradation to change the taxonomical and functional assemblages of brachyuran 106 crabs, increasing Ocypodidae and decreasing Sesarmidae abundances. We expected this 107 because sesarmid crabs have a high dependency on leaf fall for food (Skov et al. 2002), which 108 would diminish with loss of tree cover, while deposit-feeding ocypodids extract fine detritus 109 and biofilm from the substrate (Cannicci et al. 2008), which is less liable to diminish with 110 reduced mangrove cover. Finally, we expected crab evenness, functional diversity, richness, 111 and redundancy to decrease with degradation.

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# 113 Material & Methods

114

# 115 Study sites and experimental design

Sampling was done in two bays in southern Kenya: Gazi Bay (4° 22' S, 39° 30' E) a semi-116 117 enclosed shallow bay, 40 km south of the city of Mombasa, and Vanga Bay (4° 10' S, 39° 27' 118 E) at the border with Tanzania (Fig.2). Gazi comprised a 661-ha mangrove forest complex, 3.3 119 km across and concentrated along the northern shores of the bay (Matthijs et al. 1999). Vanga 120 Bay held 4,428-ha mangrove spread across a series of creeks and including Sii Island, 6 km off 121 the coast (Fig.2b). The study aspired to capture the range of mangrove degradation occurring at our sites, whilst keeping the influence of other mangrove environmental variation at a 122 123 minimum. Observations focused exclusively on the low mangrove to minimise the influence of 124 shore elevation and mangrove zonation on faunal responses. Sampling areas within the two 125 bays were selected without *a priori* quantification of degradation levels or the expectation of 126 certain sites being particularly degraded or undegraded. Instead, we observed within our plots 127 forest variables such as those shown in Table S1, which we used, through a posteriori analysis, 128 to assess the severity of degradation within every observation plot. Thus, our design relied on 129 the *a posteriori* assessment of faunal responses to degradation, in which degradation was 130 expressed on a continuous scale (e.g. values of variables in Table S1). This design relied on the 131 opportunistic encountering of a range in the levels of degradation amongst plots, rather than 132 the contrasting of sites with different levels of pre-ordained, categorical levels of degradation,

133 as done by past studies (e.g. Huxam et al. 2004; Sjoling et al. 2005; Carugati et al. 2019). 134 Because of this design, the within-site variation in forest degradation-indicators was often as 135 great as the between-site variation (Table S1). Plot positions were randomised within study 136 areas, although kept >100 m apart and away from mangrove silviculture and protected areas. 137 A total of fifty 10×10 m plots were observed in the two bays: 23 in Gazi Bay, from the west by 138 the village to the east on Chale Peninsula (Fig 2a), and 27 in Vanga, from Jimbo and Vanga 139 villages on the main coast to Sii Island (Fig 2b, Table S1). 140 Sampling was carried out from February until July 2019. Per plot, a three-step approach was

- used to assess forest functioning by quantifying: 1) mangrove forest structure, 2) epibenthicfaunal abundance and taxonomy, and 3) physical parameters (Fig.S1), as subsequently
- 143 described.
- 144

### 145 Assessment of forest structure

Tree stem diameter at breast height (DBH; 130cm 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; in Mg ha <sup>-1</sup>):

153

# 154 $AGB = DBH * H + \rho$

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

# 157 Assessment of epibenthic faunal composition and assemblages

Fauna was observed during spring tides when surface activity peaks (Skov *et al.* 2002). The assessment involved two procedures (Fig. S1): 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  $1\times1$  $m^2$  randomly located sub-quadrats per plot were set out a day prior to observation. Visual counts with binoculars from 3.5 m distance enumerated non-burrowing species, whereas burrow counts quantified burrowing species in four burrow size-classes: small (<4 mm), medium (4-8

165 mm), large (8-20 mm) and extra-large (>35 mm Skov et al., 2002). Size-classification 166 facilitated allocating crabs-burrow counts to crab families, with ocypodid crabs assumed to 167 account for the small burrows. Crabs were classified into four functional groups based on their 168 trophic traits:"foli-detritivores" (feeding on fallen mangroves propagules and leaf litter), 169 detritivores (including deposit feeders), omnivores and predators (Fratini et al. 2000; Gillikin 170 et al. 2004; Cannicci et al. 2008). For procedure 2, epifauna abundance was recorded per 171 quadrat (1x1m) and identified at species level (fauna climbing trees were excluded from 172 estimation).

173

### 174 Assessment of physical variables

175 Air and soil (30cm below surface) temperature were measured at three random points using a 176 Hanna Combo multi-meter (Fig. S1 C). To reduce the effect of variation in ambient temperature 177 between sampling days and time of day, air temperature under the canopy inside the plot was 178 standardised to temperature in the absence of canopy cover, measured at the nearest canopy-Temperature(out)-Temperature(in), where 'in' is the average 179 free area outside the plot: Temperature (out) temperature inside the plot and 'out' canopy-free temperature outside the plot. With this 180 181 approach, air temperature was a measure of the reduction in ambient temperature incurred by 182 the plot canopy cover (or the lack thereof). Sediment grain size was derived from three 183 randomly distributed, 30cm deep, 6cm diameter soil cores per plot, pooled and homogenised, 184 before wet-analysing a 5 g subsample in a Mastersizer 3000 laser particle-size analyser. Soil 185 pH, water and soil salinity were measured in situ with a Hanna HI 98129. Sampling was 186 conducted at low tide during spring tide periods.

187

#### 188 Data analysis

The analysis had 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 to visualise what best indicator drives degradation (Method Supplementary Material) and generalised linear mixed models (GLMMS) to understand the relationship among forest variables. For objective 2, LMMs following the model ( $Y \sim (x_{1+} x_{2+} x_{3+} x_{4-} + x_{1})$ , *random* =  $\sim 1 / site$ ) were used to determine which combination of forest variables

198 best predicted variation in faunal community assemblage and composition responses. Models 199 were constructed using the lme function of the nlme package in R studio (version 3.6). Initial 200 model selection was conducted to identify potential variance structures using restricted 201 maximum likelihood (REML) estimates, followed by the selection of the fixed effects using 202 maximum likelihood (ML) estimation (Zuur et al. 2007). We used stepwise exclusion analysis, 203 with variables (fixed effects) not adding to improving the model fit (Akaike information 204 criterion (AIC) value) subsequently removed and analyses re-run. The analyses showed that 205 models with canopy cover only had the best-fit and that canopy cover was the most consistent 206 predictor of variation in faunal community responses. Therefore, we used canopy cover as a 207 single proxy for degradation in subsequent LMMs to be related to faunal community 208 composition responses. GLMMs were preferred to ordinary linear regression models to 209 accommodate non-stable variances and alternative exponential residual distributions (Zuur et 210 al. 2007).

211

Permutational Multivariate Analyses of Variance (PERMANOVA; Anderson, 2014) evaluated 212 213 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 214 215 distribution (Clarke et al. 2006). Responses of crab community composition and assemblages 216 to variation in canopy cover classes was illustrated using Multidimensional Scaling (MDS) 217 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 218 219 classes. Significant PERMANOVAs were followed by pairwise comparisons of crab community composition among canopy classes (>500 permutations). Functional groups that 220 221 differed among canopy classes were identified using Similarity Percentage analysis (SIMPER) 222 on a Bray–Curtis matrix of dissimilarities (Clarke, 1993). Variation in the trophic community 223 structure was expressed through three indices of functional diversity: functional richness (n° of 224 unique functional traits), functional evenness (regularity of functional traits based on 225 abundance) and functional redundancy (calculated as the ratio of functional to taxonomic 226 diversity, following Villéger et al. 2008). Analyses were performed using the packages qpcR, 227 princomp, lme4 and stats.

- 228
- 229 **Results**

<sup>230</sup> Canopy cover as a proxy of degradation

231 GLMMs models showed that overall, canopy cover had a positive, although minimal 232 association with the other observed forest factors (GLMM; AGB F=3,15; SD=0.6; SE=0.2; 233 p=0.01; Basal Area F=2.04; SD=0; SE=0; p=0.05; Stumps F=-2.5; SD=0.04; SE=0.06; p=0.05). 234 Forest structural variables varied considerably across sites, with Sii Island and Gazi showing 235 the least signs of degradation, and Jimbo (Vanga) and Chale (Gazi Bay) showing the highest 236 (Table S1). Reduction in canopy cover diminished shading (F=37.1; d.f= 45; p= 0.001,  $R^2$  = 237 0.4;  $\beta = 1.36$  Fig. S3a) and increased pH (F= 46.5; d.f= 45; p= 0.001; R<sup>2</sup> = 0.5;  $\beta = 0.6$ , Fig. S3b) 238 but did not affect soil temperature, salinity or grain size (Result Supplementary material).

239

#### 240 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, Fig. 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.

248

# Responses of crab community assemblages, composition, traits and functional diversity tocanopy 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, Fig. S5).

255 Crab community composition changed with canopy cover (Fig.4 Table 3), with communities 256 of very low (5%) and medium-high (70%) canopy cover being most dissimilar (SIMPER 257 pairwise test: diss%=94.36). Key species accounting for this dissimilarity were the foli-258 detritivores Chiromantes eulimene (94.84%) and Neosarmatium smithi (pairwise test: 259 diss%=83.42), which were linked to higher canopy-cover, and the omnivorous *Metopgrapsus* 260 thukuhar that preferred low to mid canopy cover (89.46%). Functional groups (no. of species/trait) peaked either end of the canopy cover spectrum. For instance, predators (e.g., 261 262 Thalamita crenata) were only found at 90% canopy cover (SIMPER: cumulative diss %= 263 92.77, Fig.4b, Table 3). Diversity increased from canopy cover of 5% to 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 e.g. *Neosarmatium smithi* at 0% canopy cover and detritivores *Uca urvillei*, *U. tetragonon* lost at 50% canopy cover (SIMPER: cumulative diss%= 83.17 and 96.45; Fig.5).
- 270 Functional richness and functional diversity increased with canopy cover and varied among
- 271 sites (LMM; |t|=8.8; p=0.001; d.f=45; |t|=2.8; p=0.001; d.f.=45), while functional redundancy
- 272 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.
- 274

# 275 **Discussion:**

276 This study reveals clear effects of forest structure and degradation on epibenthic faunal 277 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 278 279 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 280 281 (Joshi et al. 2006; Chen et al. 2019; Wu et al. 2020). Epibenthic faunal community composition 282 and assemblages responded positively with the increase in canopy. These faunal responses are 283 symptomatic of over-arching changes in mangrove functioning from degradation, as fauna influence mangrove ecosystem processes, including nutrient cycling, carbon storing and forest 284 285 regeneration (Skov and Hartnoll 2002; Lee et al. 2008; Kristensen 2008). The negative response of species richness and diversity to degradation may imply a reduction of habitat 286 287 availability and resources (Lee 2008; Carugati et al. 2019; Freita and Pagliosa, 2020). Notably, 288 degradation reduced functional diversity and functional richness, as the variation in trophic 289 composition declined with a reduction in canopy cover. High functional diversity is indicative of efficient use of resources and higher productivity, as species exploit resources differently 290 291 through niche complementary - functional groups occupied distinct niches and used food 292 resources in a complementary way.) (Petchey 2003; Petchey and Gaston, 2006). High 293 functional diversity and richness invariably underpin ecosystem functioning and stability 294 (Rasher et al. 2013; Richardson et al. 2017). Hence, the observed loss in functional richness 295 and assumed associated decline in niche complementarity among species is likely to have 296 important consequences for mangrove ecosystem functioning (Bellowood et al. 2003).

Degradation of mangroves is globally pervasive (Wilkinson and Salvat, 2012; Brown *et al*, 2020) and while 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.

301

302 We found complex faunal responses with degradation (i.e. percentage of canopy cover, our best 303 proxy), which could not have been detected by simply comparing a degraded to an undegraded 304 forest, as is most often done. Faunal species assemblages and functional composition, which 305 we explored through the responses of forest-floor crabs, particularly changed at the extremes 306 of the degradation gradient. Thus, species feeding on leaves and litter from trees (foli-307 detritivores) unsurprisingly peaked at high canopy cover, while omnivores preferred moderate 308 canopy cover. Predators were very rare, yet only found at the highest canopy cover. These 309 observations echo previous studies showing that declines in crab species richness or diversity 310 were associated with loss of specialists (Carrete et al. 2010; Velliger et al. 2010). In fact, 311 functional groups frequency (n° of species/functional traits) differed most markedly between 312 the highest and lowest canopy covers, peaking at high canopy and slumping at low canopy 313 cover. Such modifications in the composition of functional groups among communities, in line 314 with previous studies, could occur due to the reduction in habitat complexity with degradation 315 and the aversion of some groups to the conditions found and low habitat versatility (Mouillot 316 et al. 2007; Bernardino et al. 2018: Freita and Pagliosa, 2020).

317 Here, canopy cover was the best degradation-associated predictor of faunal responses. Studies 318 carried out in Mozambique also found that the presence of biota in mangrove forests was strictly 319 linked to tree cover and not to other biogenic structures of the mangrove trees, such as roots 320 and trunk morphology (Fondo and Martens, 1998), which might vary with tree species 321 composition. Here, we did not test for the effect of tree species composition on faunal 322 responses, because our exclusive focus on the low mangrove naturally restricted the between-323 site variation in tree assemblage, and since the distribution of epi-benthic mangrove fauna is 324 largely governed by their biophysical tolerance to the environmental stressors of their zone 325 (Fondo and Martens, 1998). However, epibenthic fauna can undeniably be responsive to 326 variation in forest root morphology and density (Leung 2015), which we did not quantify here 327 and which can vary between sites with the same tree species composition. We therefore cannot 328 fully dismiss that some of the between-site variation in faunal responses were due to site 329 differences in root and pneumatophore structure and density. Mangrove epibenthic faunal 330 species are distributed according to their biophysical tolerance to environmental stressors like 331 salinity, temperature, and desiccation (Fondo and Martens, 1998). Although we found most of the environmental parameters, we measured were relatively homogenous across the 332 333 degradation gradient, shading, which obviously declined with a decrease in canopy cover, 334 might have been a key factor responsible for the decline in faunal richness and diversity. Under 335 shadier conditions, due to denser canopies, mangroves produce more leaf litter, cycles more 336 nutrients and maintain higher soil moisture (Tolhurst et al. 2020). Heavy shading can 337 significantly modify processes and properties at the sediment-water interface, such as increased 338 carbohydrate accumulation on the burrow surface, which may affect faunal abundance and 339 distribution (Khon et al. 2010; Tolhurst et al. 2020), as was shown Similar patterns were also 340 observed by Ruwa (1988), who found species diversity greater in moderate shade conditions. 341 Canopy cover is also a yardstick indicator of the state of a collective of forest biogenic structural 342 variables.

343

344 In mangrove ecosystems, biogenic structures, especially dense roots, may act as an 345 environmental filter (exclusion) for large body-size crabs, leading to trait convergence (i.e. 346 reduction in functional niches – the ecological volume occupied in the ecosystem, based on the 347 species' impact (Brandl and Bellwood, 2013), causing root-dense areas to display low 348 functional diversity and redundancy (Leung 2015). Yet, while we found that functional 349 diversity and richness decreased with degradation and likely reduction of habitat heterogeneity, 350 functional redundancy varied independently. These patterns indicate a consistent overlap of 351 functional niches among species, even at the most degraded sites, and also suggest functional 352 plasticity and functional accommodation - the lack of variation in functional rates (Needham et 353 al. 2010; Bingham et al. 2018). Several studies have highlighted how trait variation within 354 species improves the acclimation to changing environments (Okuyama 2008) and reduce 355 extinction risks (Bolnick et al. 2011). Many mangrove macrofauna do exhibit trait variations 356 to promote opportunistic feeding behaviours (see Fratini et al. 2000; Poon et al. 2009). In 357 mangroves, omnivorous crabs foraging in open-canopy forests exhibit enhanced functional 358 plasticity across trophic traits to counter otherwise challenging environmental conditions 359 (Giraldes et al. 2019). On the flip side, species of the normally litter-dependent species 360 (Sesarmidae) alter their diets with season, climate and food availability (Poon et al. 2009). The 361 extent to which the community turnover was affected by diet variation was not recorded here.

362 Nevertheless, it is plausible that the faunal assemblage changed feeding behaviour in response363 to forest degradation.

364

365 The observed changes in epibenthic faunal communities with degradation are likely to alter 366 mangrove ecosystem functions through modification of the benthic habitat. For instance, 367 micro-epiphytic biomass can bloom in the absence of grazing (Kristensen and Alongi, 2006) 368 causing indirect variation to the meiofaunal communities that feed on the micro-epiphytes 369 (Carlen and Olafsoon, 2002). The connection and provision of a food source to secondary 370 consumers and food-web dynamics with adjacent fisheries may also be affected by the lack of 371 food availability, from microphytes to macrofauna (Nagelkerken et al. 2008; Sheaves 2009; 372 Olds et al. 2013). There is much uncertainty about the effects of mangrove degradation on 373 epifaunal community and functional composition. We encourage more research in this area to improve the understanding of how small-scale anthropogenic disturbances interact with 374 375 ecosystem functioning and services (Lee 2008; Goldenberg et al. 2018), for the promotion of 376 effective and pragmatic management of mangroves. Forest degradation is an undeniable 377 challenge to the global biodiversity crisis (Primavera et al. 2019; Richardson et al. 2020). The 378 early stages of degradation that precede the clear felling of trees are subtle and difficult to detect 379 remotely. Yet, they provide the means towards early warning signs of impeding losses to wider 380 environmental functioning and are likely prevalent in developing countries, such as Kenya, 381 where wood extraction is a survival necessity to subsistence living. Without accelerating the 382 extent of ground-based observations, we will not gain clarity on the extent of the problem.

383

# 384 **Conflicts of interest**

385 The authors declare that they have no other conflicts of interest.

386

# 387 Declaration of Funding

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- 399

# 400 Data Availability Statement

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).

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- 806

807 Table 1: Model ranks for the Linear mixed effect model (LMM) of epibenthic faunal

808 assemblage (diversity, abundance, richness and evenness). Models are ranked by corrected

- 809 Akaike's information criteria (AICc), with all models within  $\Delta AICc < 2$  of the top ranked
- 810 models. The relative likelihood (logLik) and weight (wi) of evidence between each model and
- 811 the variables present in each model are given.

Model rank	AICc	logLik Epibenthic fauna	ΔΑΙCc	wi
Abundance ~ Canopy + BA+ stem cuts + 1 site	522.7	1	0	0.26
Abundance ~ Canopy + $1$  site	522.7	0.9	0.01	0.25
Abundance~ Canopy + $BA + 1$  site	522.8	0.9	0.1	0.24
Abundance ~ Canopy + BA + stem cuts+ stumps 1 site	523.4	0.8	0.7	0.17
Abundance ~ Canopy + BA + stem cuts+ stumps+ AGB 1 site	525.3	2.7	0.3	0.06
Richness ~ Canopy 1 site	111.3	1	0	0.3
Richness ~ Canopy + BA+ 1 site	111.7	0.7	0.7	0.2
Richness ~ Canopy + BA + stem cuts + 1 site	112	0.8	0.3	0.2
Richness ~ Canopy + BA+ stem cuts + Stumps + 1 site	112	0.7	0.7	0.2
Richness ~ Canopy + BA+ stem cuts + Stumps +AGB+1 site	113	0.2	2.5	0.08
Diversity ~ Canopy + 1 site	57	1	0	0.3
Diversity ~ Canopy + stem cuts + $BA + 1$  site	56.9	0.8	0.7	0.2
Diversity~ Canopy + stem cuts + 1 site	57.4	0.7	0.2	0.2
Diversity ~ Canopy + stem cuts + BA+ Stumps + 1 site	57.3	0.7	0.6	0.2
Diversity ~ Canopy + stem cuts + BA+ Stumps + AGB+ 1 site	59.2	0.3	2.5	0.07
12				

Fauna and mangrove degradation

- 814 Table 2: Model ranks for Linear mixed effect model (LMM) of crab assemblage (diversity,
- 815 abundance, richness and evenness). Models are ranked by corrected Akaike's information
- 816 criteria (AICc), with all models within  $\Delta AICc < 2$  of the top ranked models. The relative
- 817 likelihood (logLik) and weight (wi) of evidence between each model and the variables present
- 818 in each model are given.

Model rank	AIC <sub>c</sub>	logLik	ΔAICc	wi
		Crabs		
Abundance ~ Canopy + 1 site	203.1	1	0	0.5
Abundance~ Canopy + BA + 1 site	204.3	0.5	1.2	0.2
Abundance ~ Canopy + stem cuts + $BA + 1$  site	205.1	0.4	1.9	0.2
Abundance ~ Canopy + stem cuts + BA+ Stumps + 1 site	206.9	0.05	3.8	0.06
Abundance ~ Canopy + stem cuts + BA+ AGB+ Stumps + 1 site	208.9	0.05	5.8	0.02
Richness ~ Canopy + BA+ 1 site	66.3	0.5	1.4	0.2
Richness ~ Canopy + stem cuts + BA + 1 site	68.3	0.2	3.3	0.1
Richness ~ Canopy + stem cuts + BA+ Stumps + 1 site	70.3	0.07	5.3	0.03
Richness ~ Canopy + stem cuts + BA+ AGB+ Stumps + 1 site	72.3	0	9.3	0.005
Diversity ~ Canopy + $1$  site	34	1	0	0.6
Diversity~ Canopy + stem cuts + 1 site	37.8	0.4	1.9	0.3
Diversity ~ Canopy + stem cuts + $BA + 1$  site	37.8	0.1	3.8	0.09
Diversity ~ Canopy + stem cuts + BA+ Stumps + 1 site	39.8	0.05	5.8	0.03
Diversity ~ Canopy + stem cuts + BA+ AGB+ Stumps + 1 site	41.8	0.01	7.8	0.01
819				

0.00

Fauna and mangrove degradation

- 821 Table 3: Effects of mangrove canopy cover class on (i) crab community composition and (ii)
- 822 the composition of crab trophic traits, tested using Permutational Multivariate Analyses of
- 823 Variance on a Bray–Curtis similarity matrix of fourth-root transformed data. Perms=number of
- 824 permutations.
- 825

Variables	Source	df	MS	Pseudo- F	Р	Perms
Community	Canopy	10	3028.1	1.42	0.05	998
composition	Residual	36	2135.1			
Trophic troits	Canopy	10	631.0	1.73	0.05	999
Tropfile traits	Residual	36	366.9			

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Figure 1: Functional implications of degrading mangroves from primary forest to fully deforested (<10% above-ground biomass remaining: FAO 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 bio-physical properties. We expect canopy loss to diminish litterfall-food for fauna and to alter faunal composition and diversity.

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Figure 2: The study area in South-east 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.

839

Figure 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; SE=0.06; p=0.001; R<sup>2</sup>=0.2), (b) epibenthic richness (F=2.8; SE=0.04; p=0.008; R<sup>2</sup>=0.1) and (c) epibenthic diversity (F=3; SE=0.02; p=0.004, R<sup>2</sup>=0.2); (c) crabs abundance (F=3.3; SE= 0.01; p=0.002; R<sup>2</sup>=0.2), (b) crabs richness (F=2.2; SE=0.002; p=0.0; R<sup>2</sup>=0.1) and (c) crabs diversity (F=2.4; SD=0.01; p=0.02; R<sup>2</sup>=0.01); Degree of freedom= 45.

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847 Figure 4: (a)Variation in crab species composition with canopy cover classes, as described by 848 MDS ordination, with vectors based on Pearson correlations <0.2. Crab community 849 assemblages include species from families: Sesarmidae (Perisesarma guttatum, Perisesarma 850 samawati, Neosesarmatium smithi, N. africanum (ex.Neosesarmatium meinerti), Chiromantess 851 eulimene), Ocypodidae (Uca occidentalis, U. urvillei, U. chlorophtalmus, U. vocans, U. 852 inversa, U. tetragonon), **Portunidae** (Thalamita crenata), **Macrophtalmidae** (Macrophtalmus 853 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) 854 855 C. eulimene abundance by canopy cover classes. Variation in bubble sizes represent from 100% 856 stepping down to 0 % canopy cover.

857

Figure 5: Functional composition of mangrove crabs in a Multi-Dimensional Scaling
ordination, with vectors based on Pearson correlations <0.2.</li>



862 Fig.1









887 Fig.4



- .....



917 Supplementary Materials:

918	Functional responses of mangrove fauna to a gradient in forest degradation
919	
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931	
932	Corresponding author: barbanerada@gmail.com
933	
934	Material & Methods
935	Figure S1: Overview of the three-step approach per forest plot. A) Mangrove forest structure
936	assessment using plots kept 100 m apart from each other and plantation sites, B) macrofaunal

937 abundance and taxonomy quantification in three sub-quadrats (1x1m) using: (i) binoculars

- 938 observations of crab species and (ii) counts of crab burrows and assessment of epifaunal
- 939 diversity. C) Biophysical parameters were measured at three points within the plot.



- 940 Figure S2: Principal component analysis (PCA) showing relationships among mangrove forest
- 941 variables. Each dot in the PCA represents mangrove plots based on normalised data.
- 942
- 943
- 944 **Results**



945 A principal component analysis (PCA) was executed on the whole forest factors and 946 biophysical parameters with previous normalisation of data. The PCA aimed to reduce the 947 number of forest and biophysical factors to cover as much inter-site variability as possible. 948 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 949 950 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 951 residuals were met. Plot differentiation along PC1, which explained 39.4% of the variation 952

953 among plots, was mainly driven by the higher loading of basal area (m2) and AGB (Mg ha-1 954 ) 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 (m2 955 956 ) and AGB (Mg ha-1) have little influence to the PC2. In effect, canopy cover (%) and stump 957 density (stumps ha-1) were negatively correlated to each other, and although they contribute 958 to both axes, were more influenced by PC2 and PC1 respectively. The right angle created 959 between cut branches (branches/ha) and stump density (stumps ha-1) suggested the small 960 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 961 962 marginals. Overall, the PCA indicated canopy cover had a positive, although minimal 963 association with the other observed forest factors.

964 Environmental factor analysis:

965 Canopy cover was tested against the other remaining forest factors as a proxy for forest and 966 showed a positive regression with AGB (Mg ha-1), basal area (m2 ha-1) and stump density 967 (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, 968 969 salinity, grain size, pH) with canopy cover. Comparison along the gradient in canopy cover 970 showed that there were no significant trends for soil temperature (p = 0.14), soil salinity (p971 =0.13) and grain size (p = 0.12). Shading diminished with a reduction of canopy cover (F=37.1, 972 d.f=45 p = 0.001, R2 = 0.4,  $\beta=1.36$ , Figure S3a), whereas pH increased (F= 46.5, d.f= 45 p = 973  $0.001, R2 = 0.5, \beta = 0.6, Figure S3b)$ 

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Figure S3: Relationships of (a) Shading (the difference between outside and inside canopy
temperature and (b) Soil pH and mangrove Canopy Cover (%)

Table S1: The mean, ± standard deviation, minimum and maximum range in the values of forest
variables, clustered under four sampling sites.

Sites/Plots n°	Variables	Mean	SD	Max	Min	

	Canopy Cover (%)	44.5	27.6	90	0
	Cut branch density (m <sup>-2</sup> )	11.6	10.6	36	0
Gazi (19)	Stump density (m <sup>-2</sup> )	4.6	6.7	26	0
	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	108.1	169.5	1300.3	4.2
	AGB (Mg ha <sup>-1</sup> )	1453.1	988.8	3985.8	320.8
	Canopy Cover (%)	28.8	33.3	60	0
	Cut branch density (m <sup>-2</sup> )	2.8	3.4	7	0
Chale (4)	Stump density (m <sup>-2</sup> )	8.0	9.8	20	0
	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	81.9	101.6	463.5	0
	AGB (Mg ha <sup>-1</sup> )	610.9	706.8	1275.7	0
	Canopy Cover (%)	21.2	19.8	60	0
	Cut branch density (m <sup>-2</sup> )	15.3	17.5	75	0
Jimbo/Vang a (18)	Stump density (m <sup>-2</sup> )	10.5	21.0	100.0	0
	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	257.4	517.8	4899.2	0
	AGB (Mg ha <sup>-1</sup> )	2331.5	3648.3	16221.3	0
	Canopy Cover (%)	72.5	17.9	95	50
	Cut branch density (m <sup>-2</sup> )	0.9	2.5	7	0
Sii Island (9)	Stump density (m <sup>-2</sup> )	0.4	0.7	2	0
	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	11936.9	2417.3	13136.6	42.2
	AGB (Mg ha <sup>-1</sup> )	36867.3	46184.2	119230.3	1762.7

Figure S4. Partial regression plots showing the influences of epibenthic fauna residuals
composition with canopy cover residual:(a) abundance, (b) richness, (c) diversity and (e)
evenness.

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> (b) (a) Epifaunal Abundance Residual 200 Epifaunal Richness Residual 100 0 0 R<sup>2</sup>=0.1 -100 R<sup>2</sup>=0.06 p= 0.01 p= n.s -20 -40 -20 ò 20 40 -40 20 40 Ó (d) (c) Epifaunal Diversity Residual 0.025 0.5 Crabs Evenness Residual 0.000 0.0 -0.025 -0.5 -0.050 R<sup>2</sup>=0.07 R<sup>2</sup>=0.01 p= n.s p= n.s -0.075 -1.0 -20 -20 ò -40 20 40 20 40 Ò -40 Canopy Cover (%) Residual Canopy Cover (%) Residual

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Figure S5: Partial regression plots showing the influences of crabs residuals composition withcanopy cover residual: (a) abundance, (b) richness, (c) diversity and (e) evenness.





