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).

47 Although there has been an increasing effort in defining forest degradation, there have also

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

62 to understanding the impact of degradation to forest dynamics and processes (Field *et al.* 2008;

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,

65 evenness) and composition (community structure) from degradation without coupling to

66 ground-based observations (Dalponte *et al.* 2018). Yet, there is relative scarcity of ground-

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
69 observations of structural degradation with measures of functional processes, despite ground-
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
82 family Ocypodidae (e.g., fiddler crabs) consume organic compounds derived from microalgal
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,
86 thereby boosting mangrove productivity (Cannicci *et al.* 2008). Crabs also affect the influx and
87 chemistry of groundwater, preventing sediment from becoming compacted (Wolanski *et al.*
88 1992), thereby increasing pore water exchange between swamp sediment and interstitial water
89 (Ridd 1996). Within the mangrove ecosystem, a large proportion of leaf biomass is processed
90 by Sesarmid crabs; ensuing organic-matter and energy pass through diverse microbial loops
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).

93

94 There is considerable research-emphasis on the roles of species traits to ecosystem functioning
95 (e.g., Richardson *et al.* 2017; Knoester *et al.* 2019; Freitas and Pagliosa, 2020) and on how
96 species diversity responds to anthropogenic stressors at taxonomical and functional levels (Lee
97 2008). Ecosystems that incorporate several species with similar or same functional roles (i.e.,
98 functional redundancy) will suffer less reduction to overall ecosystem functioning when species
99 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.
112
113   **Material & Methods**
114
115   *Study sites and experimental design*
116   Sampling was done in two bays in southern Kenya: Gazi Bay (4° 22′ S, 39° 30′ E) a semi-
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
122   at our sites, whilst keeping the influence of other mangrove environmental variation at a
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

141   used to assess forest functioning by quantifying: 1) mangrove forest structure, 2) epibenthic

142   faunal abundance and taxonomy, and 3) physical parameters (Fig.S1), as subsequently

143   described.

144

145   *Assessment of forest structure*

146   Tree stem diameter at breast height (DBH; 130cm above ground), tree height and density (trees

147   ha^{-1}) were recorded following Kauffman and Donato (2012). Canopy cover (%) was quantified

148   as the proportion of the forest floor that had overlaying canopy, as estimated by projecting tree

149   crowns to the forest floor (Korhonen *et al.* 2006). Tree stump density (stumps ha^{-1}) and number

150   of cut branches (branches ha^{-1}) were recorded as direct indicators of human disturbance to forest

151   (i.e,. cutting or forest clearing). An allometric equation specific to Kenya (Cohen *et al.* 2013)

152   converted DBH (cm) into above ground tree biomass (AGB; in Mg ha $^{-1}$):

153

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

155   where H is tree height (m) and ρ is wood density (g cm $^{-3}$) with values specific to each tree

156   species.

157   *Assessment of epibenthic faunal composition and assemblages*

158   Fauna was observed during spring tides when surface activity peaks (Skov *et al.* 2002). The

159   assessment involved two procedures (Fig. S1): 1) quantification of brachyuran crabs following

160   the two-step approach of Skov *et al.* (2002) and 2) quantification of non-crab Epibenthic faunal

161   abundance, including molluscs, echinoderms and other crustaceans. For procedure 1, three 1×1

162   m^2 randomly located sub-quadrats per plot were set out a day prior to observation. Visual counts

163   with binoculars from 3.5 m distance enumerated non-burrowing species, whereas burrow

164   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-

179   free area outside the plot: $\frac{Temperature(out) - Temperature(in)}{Temperature\ (out)}$, where 'in' is the average

180   temperature inside the plot and 'out' canopy-free temperature outside the plot. With this

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*

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

190   degradation among the multiple structural and physical forest variables observed (canopy

191   cover, tree biomass, density, soil pH, temperature, salinity, basal area etc) (Fig. 1) and 2) to

192   examine epibenthic faunal responses to variation in these degradation indicators.

193   For objective 1, we used a combination of principal component analysis (PCA) to summarise

194   forest and environmental variables to visualise what best indicator drives degradation (Method

195   Supplementary Material) and generalised linear mixed models (GLMMS) to understand the

196   relationship among forest variables. For objective 2, LMMs following the model *(Y ~ (x₁+ x₂+*

197   *x₃+ x₄...+ xn), random = ~ 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

212   Permutational Multivariate Analyses of Variance (PERMANOVA; Anderson, 2014) evaluated

213   the effect of canopy cover on crab community assemblage and functional groups. Data were

214   fourth-root transformed to highlight rarer species and reduce the asymmetry of species

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)

218   was conducted to detect differences in crab community composition among canopy cover

219   classes. Significant PERMANOVAs were followed by pairwise comparisons of crab

220   community composition among canopy classes (>500 permutations). Functional groups that

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$^{\circ}$ 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**

230   *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; β=1.36 Fig. S3a) and increased pH (F= 46.5; d.f= 45; p= 0.001;$R^2 = 0.5$; β=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*

241   Across sites, 17 families, comprising 60 distinct species of epifauna were identified, including

242   gastropods, bivalves, echinoderms and crustaceans. Our model selection identified canopy

243   cover as the best and consistent predictor for most of the community structure analysis, whereas

244   the multivariate LMMs (all forest variables as predictors included) did not show any clearer

245   trends (Table 1; Fig. 3, Fig. S4). Furthermore, the relationships of canopy cover with all other

246   forest variables and the model selections warranted its use as a proxy for degradation in

247   subsequent analyses.

248

249   *Responses of crab community assemblages, composition, traits and functional diversity to*

250   *canopy cover.*

251   Similarly, crab assemblages also showed a consistently clear association with canopy cover,

252   apart from species evenness which remained unaffected (p=0.3). The AIC ranking tables

253   showed that the best-fit model contained only canopy cover, which explained the greatest

254   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

261   species/trait) peaked either end of the canopy cover spectrum. For instance, predators (e.g.,

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

264 having overall the highest trophic diversity, and foli-detritivores significantly increasing from
265 5% to 50% canopy cover (PERMANOVA p=0.02; SIMPER: Average diss%=87.77). Yet,
266 dissimilarities were found between communities inhabiting 0% and 50% canopy cover
267 (PERMANOVA p=0.001), with the loss of foli-detritivores e.g. *Neosarmatium smithi* at 0%
268 canopy cover and detritivores *Uca urvillei*, *U. tetragonon* lost at 50% canopy cover (SIMPER:
269 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
273 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
278 young trees and cut stumps, related to reduced shading, and decreased soil pH. The incremental
279 change in canopy cover was a good proxy of degradation and related well to key faunal
280 community responses, conforming its usefulness as an indicator of forest health and quality
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
284 influence mangrove ecosystem processes, including nutrient cycling, carbon storing and forest
285 regeneration (Skov and Hartnoll 2002; Lee *et al.* 2008; Kristensen 2008). The negative
286 response of species richness and diversity to degradation may imply a reduction of habitat
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
290 of efficient use of resources and higher productivity, as species exploit resources differently
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).

297   Degradation of mangroves is globally pervasive (Wilkinson and Salvat, 2012; Brown *et al,*

298   2020) and while there has been ample and justifiable emphasis on forest loss (e.g., Olander *et*

299   *al.* 2012; Richards *et al.* 2020; Turschwell *et al.* 2020), there has been less focus on how the

300   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^o 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
332 the environmental parameters, we measured were relatively homogenous across the
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 response

363   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

374   improve the understanding of how small-scale anthropogenic disturbances interact with

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

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400 **Data Availability Statement**

401 The data that support this study will be stored securely in the Main Frame facility of Bangor

402 University, United Kingdom. The data can be obtained, upon request, by contacting

403 Dr Martin Skov, School of Ocean Sciences, Askew Street, Bangor University, LL59 5AB,

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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 ΔAICc < 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	AIC$_c$	logLik	ΔAICc	wi
		Epibenthic fauna		
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

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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 ΔAICc < 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$_c$	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

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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	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			

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828   Figure 1: Functional implications of degrading mangroves from primary forest to fully

829   deforested (<10% above-ground biomass remaining: FAO 2011). We depict a linear decline in

830   function with degradation, although responses could be non-linear, invariant, or positive,

831   depending on the functional process considered. Stressors to trees and fauna (e.g., desiccation

832   risk, salinity, hydrological forcing) are predicted to increase with reduction in biomass and

833   canopy cover through feedback-loop change to bio-physical properties. We expect canopy loss

834   to diminish litterfall-food for fauna and to alter faunal composition and diversity.

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836   Figure 2: The study area in South-east Kenya, showing (a) Gazi Bay including the Mikoko

837   Pamoja protected section in the white square and (b) Vanga Bay with Sii Island located 6 km

838   off the coast.

839

840   Figure 3: Mixed linear regressions of epibenthic composition with canopy cover (%) on the top

841   panel and crab composition at the bottom. (a) epibenthic abundance (F=3.7; SE=0.06; p=0.001;

842   R^2=0.2), (b) epibenthic richness (F=2.8; SE=0.04; p=0.008; R^2=0.1) and (c) epibenthic

843   diversity (F=3; SE=0.02; p=0.004, R^2=0.2); (c) crabs abundance (F=3.3; SE= 0.01; p=0.002;

844   R^2=0.2), (b) crabs richness (F=2.2; SE=0.002; p=0.0; R^2=0.1) and (c) crabs diversity (F=2.4;

845   SD=0.01; p=0.02; R^2=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).*

854   Bubble plots illustrate differences in (b) *T. crenata*, (c) *U. occidentalis*, (d) *P. guttatum* and (e)

855   *C. eulimene* abundance by canopy cover classes. Variation in bubble sizes represent from 100%

856   stepping down to 0 % canopy cover.

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858   Figure 5: Functional composition of mangrove crabs in a Multi-Dimensional Scaling

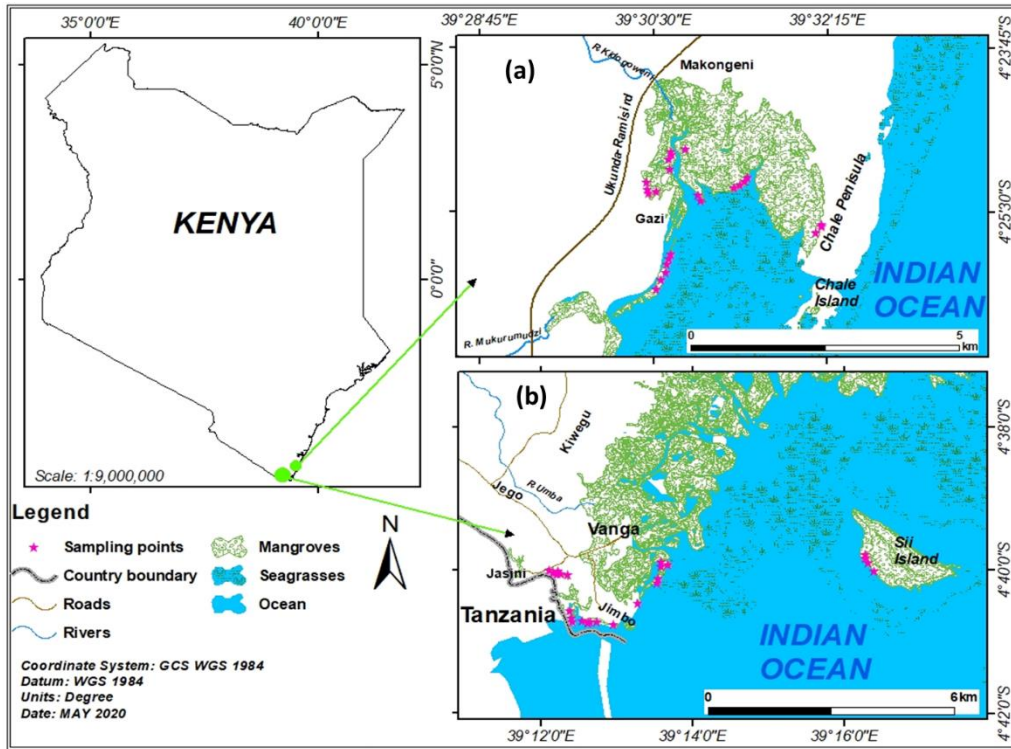859   ordination, with vectors based on Pearson correlations <0.2.

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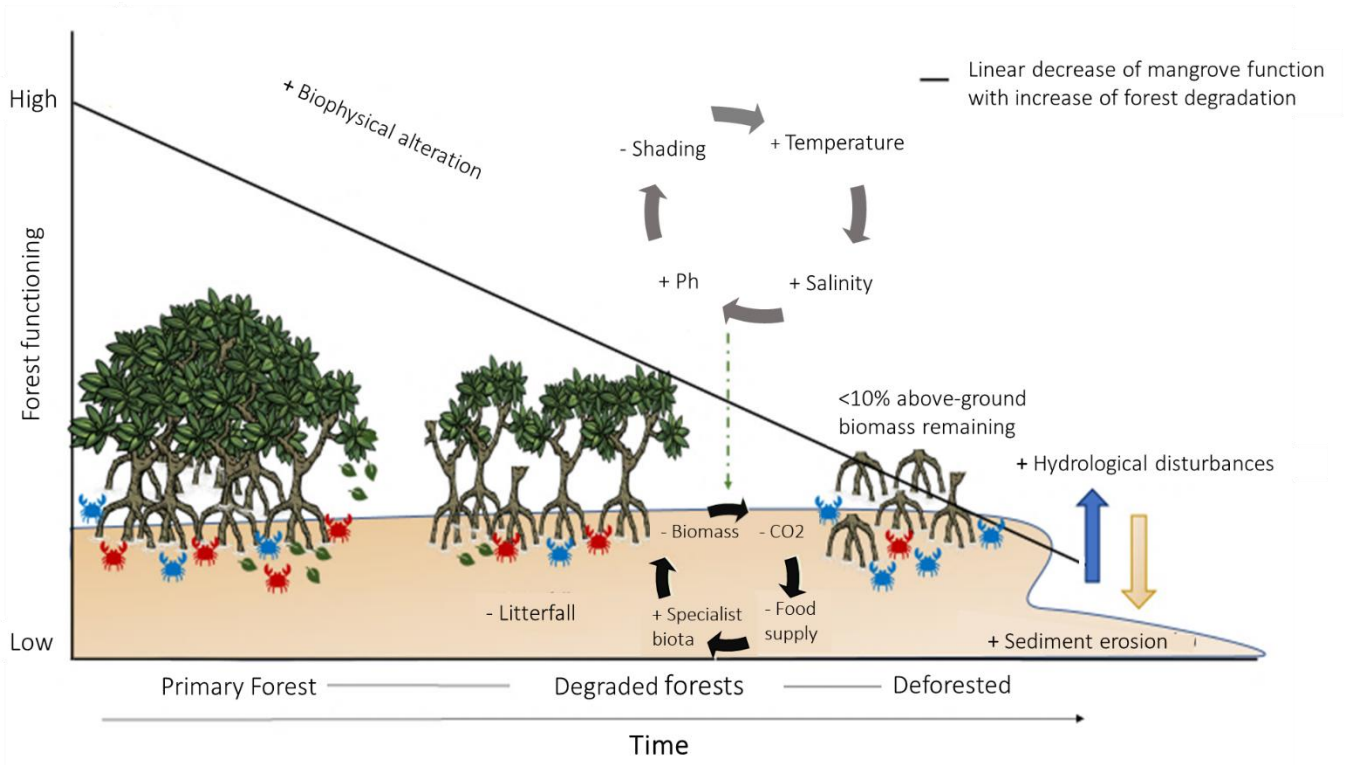
862   Fig.1

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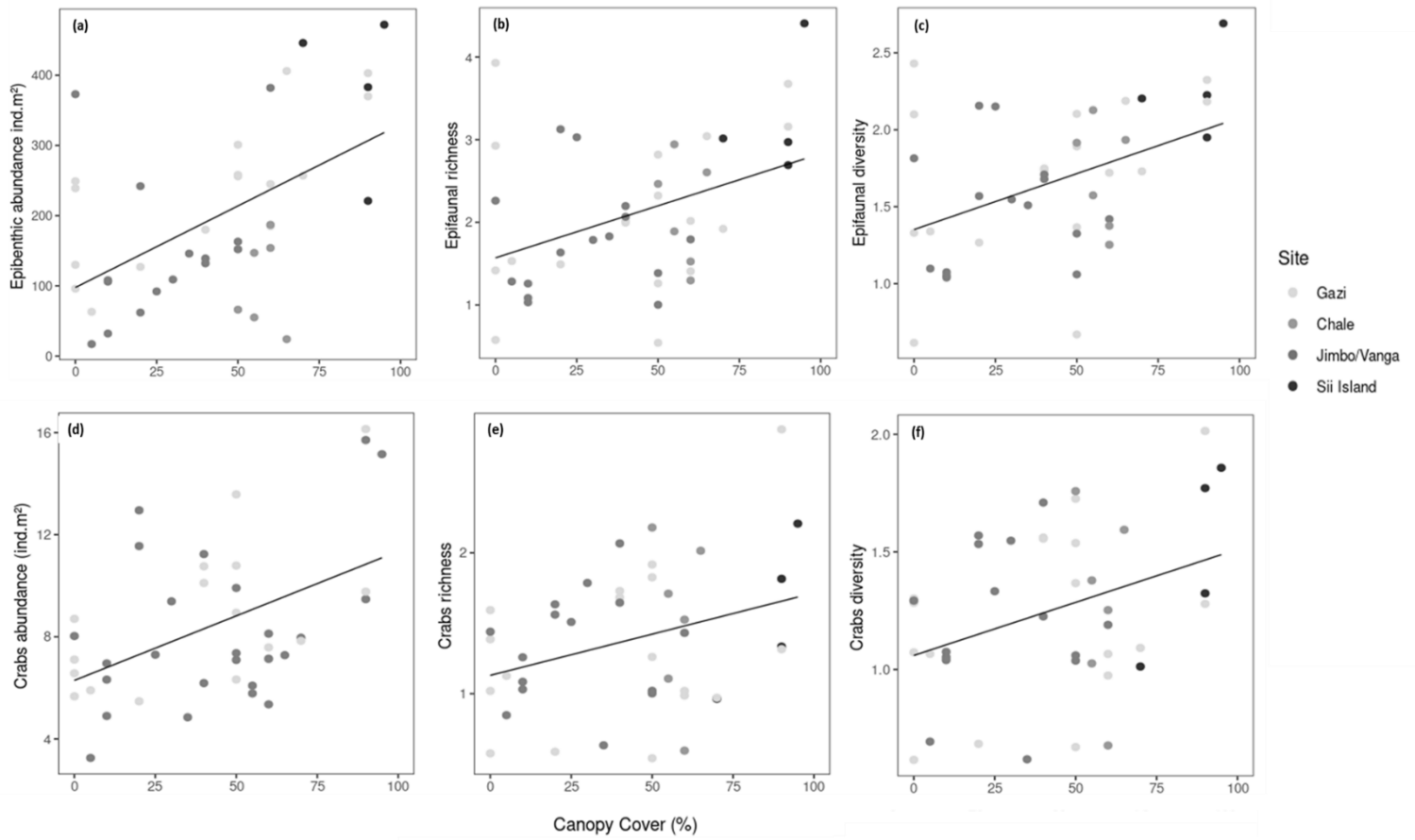864   Fig. 2
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867   Fig.3
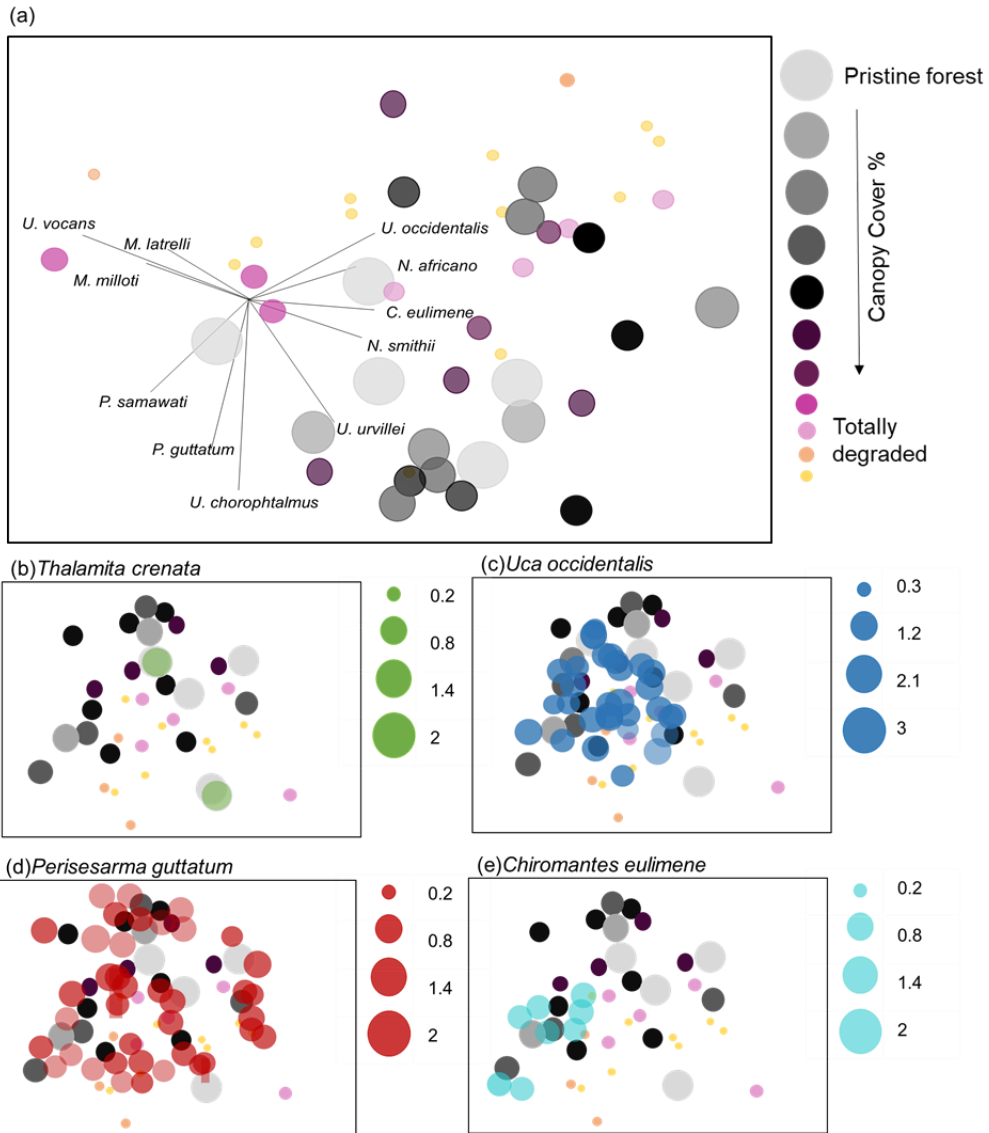
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887 Fig.4

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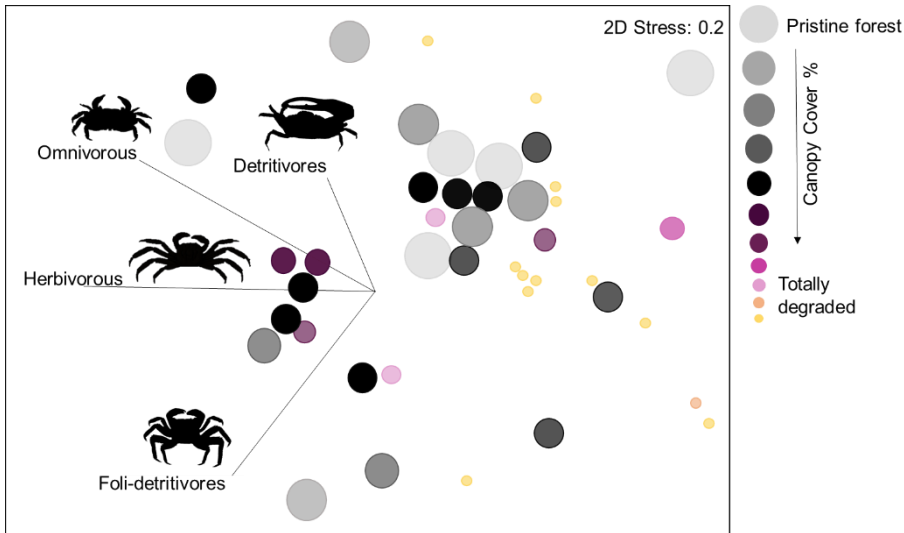892

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899   Fig 5.

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917 Supplementary Materials:

918 Functional responses of mangrove fauna to a gradient in forest degradation

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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
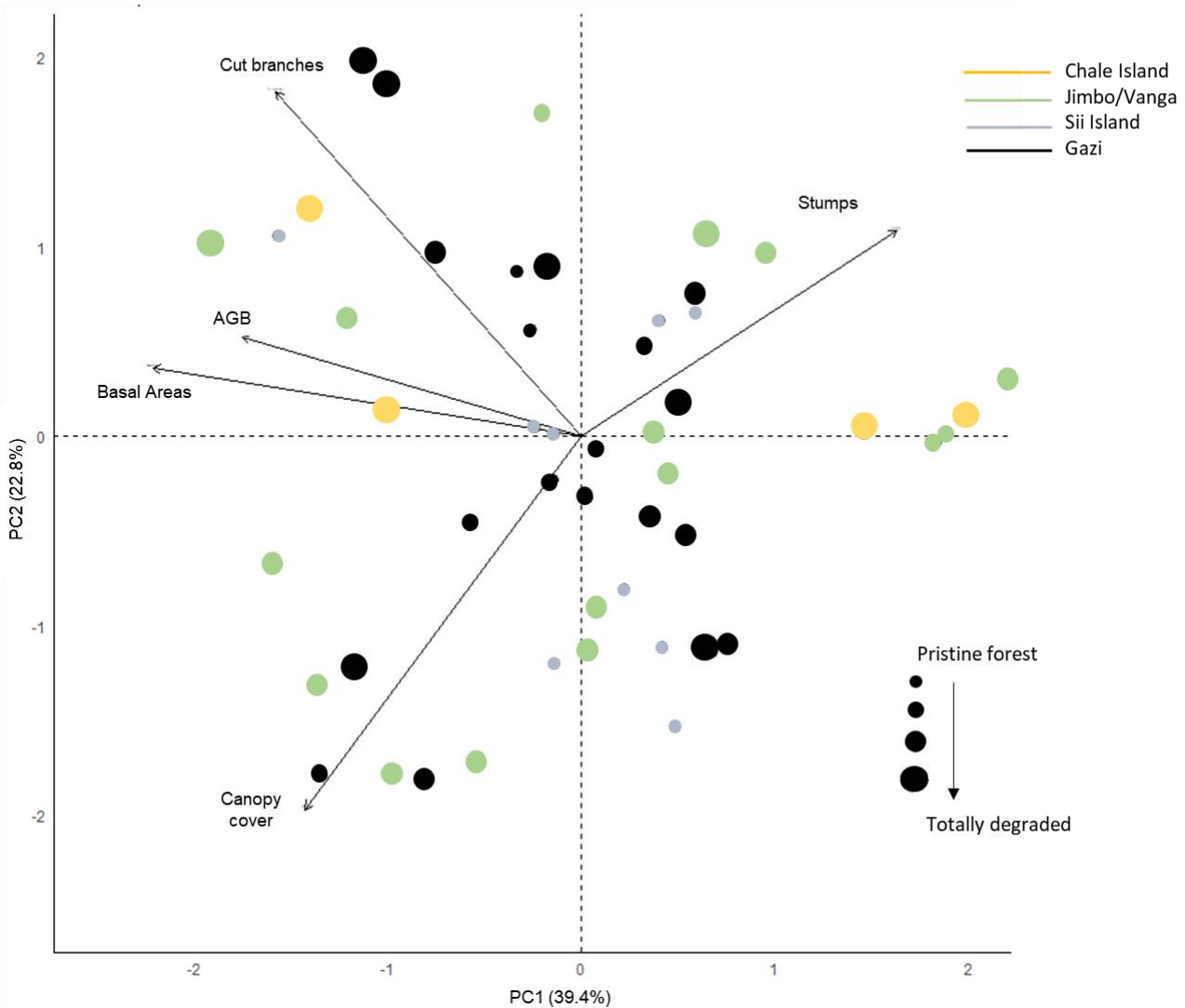939 diversity. C) Biophysical parameters were measured at three points within the plot.
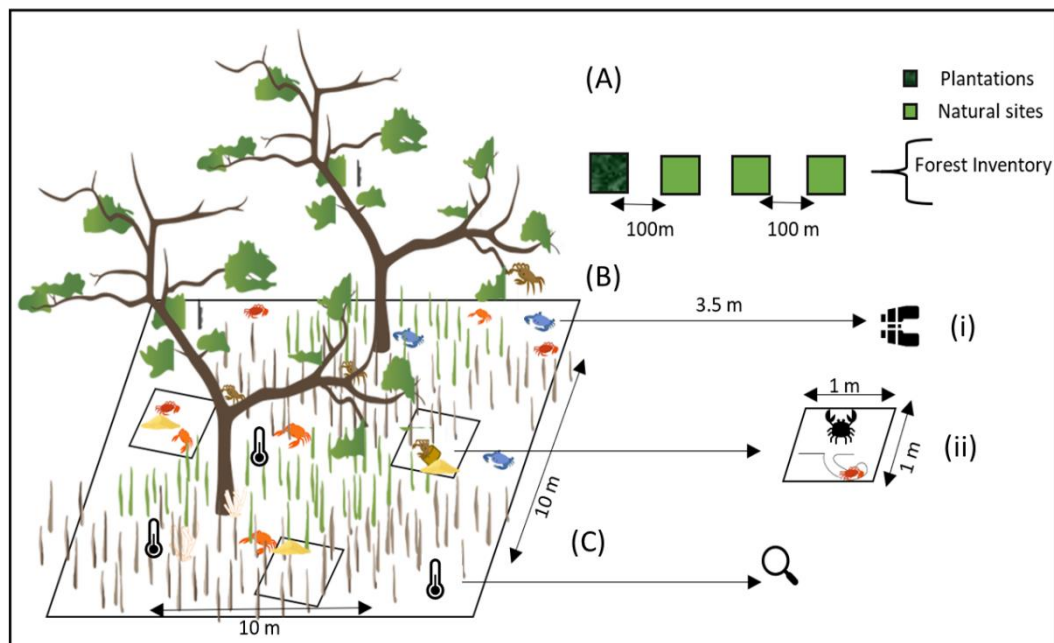
940 Figure S2: Principal component analysis (PCA) showing relationships among mangrove forest
941 variables. Each dot in the PCA represents mangrove plots based on normalised data.
942
943
944 **Results**

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
949 present a maximum number of components. A clustering algorithm (K-means) analysis was
950 used to reduce the number of data-points and identify classes of degradation (Faber 1994).
951 Exploratorily analyses showed that assumptions of homogeneity of variance and normality of
952 residuals were met. Plot differentiation along PC1, which explained 39.4% of the variation

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

955   variation) was explained by canopy cover (%), cut branches (branches/ha); with basal area (m2

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

961   the strongest correlation to each other and to PC1, with the other correlations being only

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).

968   Mixed linear models were used to test for relationships of biophysical variables (temperature,

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 (p

971     $=0.13$) and grain size ($p =0.12$). Shading diminished with a reduction of canopy cover ($F=37.1$,

972     $d.f= 45$ $p = 0.001$, $R^2 = 0.4$, $\beta=1.36$, Figure S3a), whereas pH increased ($F= 46.5$, $d.f= 45$ $p =$

973   0.001, $R^2 = 0.5$, $\beta=0.6$, Figure S3b)

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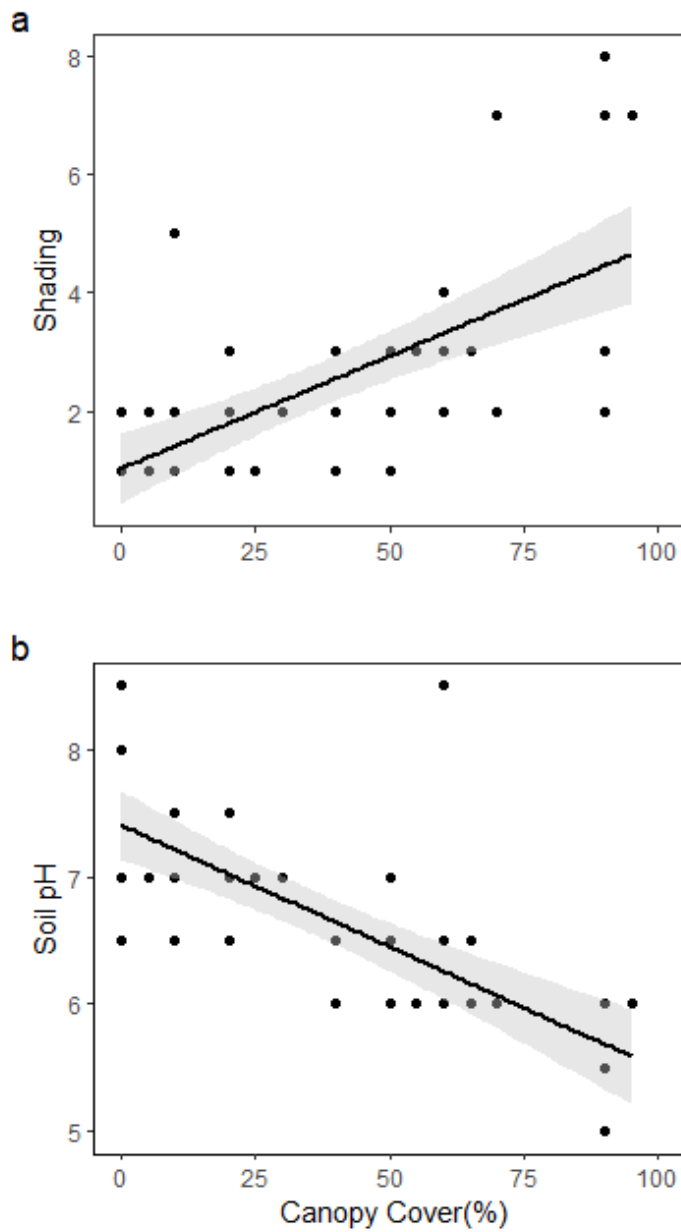
Figure S3: Relationships of (a) Shading (the difference between outside and inside canopy temperature and (b) Soil pH and mangrove Canopy Cover (%)

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

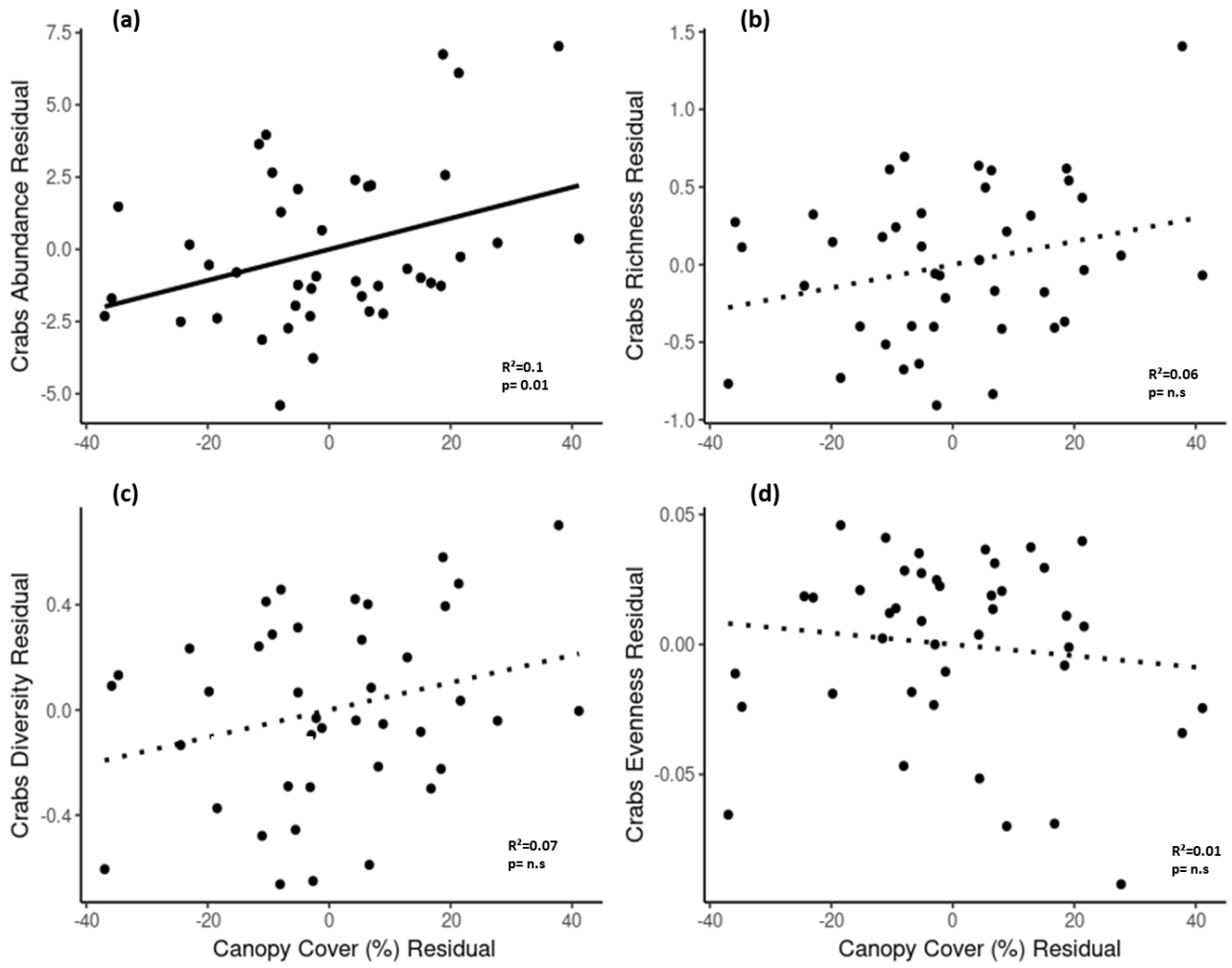|					
Gazi (19)	Canopy Cover (%)	44.5	27.6	90	0
	Cut branch density (m^{-2})	11.6	10.6	36	0
	Stump density (m^{-2})	4.6	6.7	26	0
	Basal area (m^2 ha^{-1})	108.1	169.5	1300.3	4.2
	AGB (Mg ha^{-1})	1453.1	988.8	3985.8	320.8
Chale (4)	Canopy Cover (%)	28.8	33.3	60	0
	Cut branch density (m^{-2})	2.8	3.4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

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995 Figure S4. Partial regression plots showing the influences of epibenthic fauna residuals
996 composition with canopy cover residual:(a) abundance, (b) richness, (c) diversity and (e)
997 evenness.
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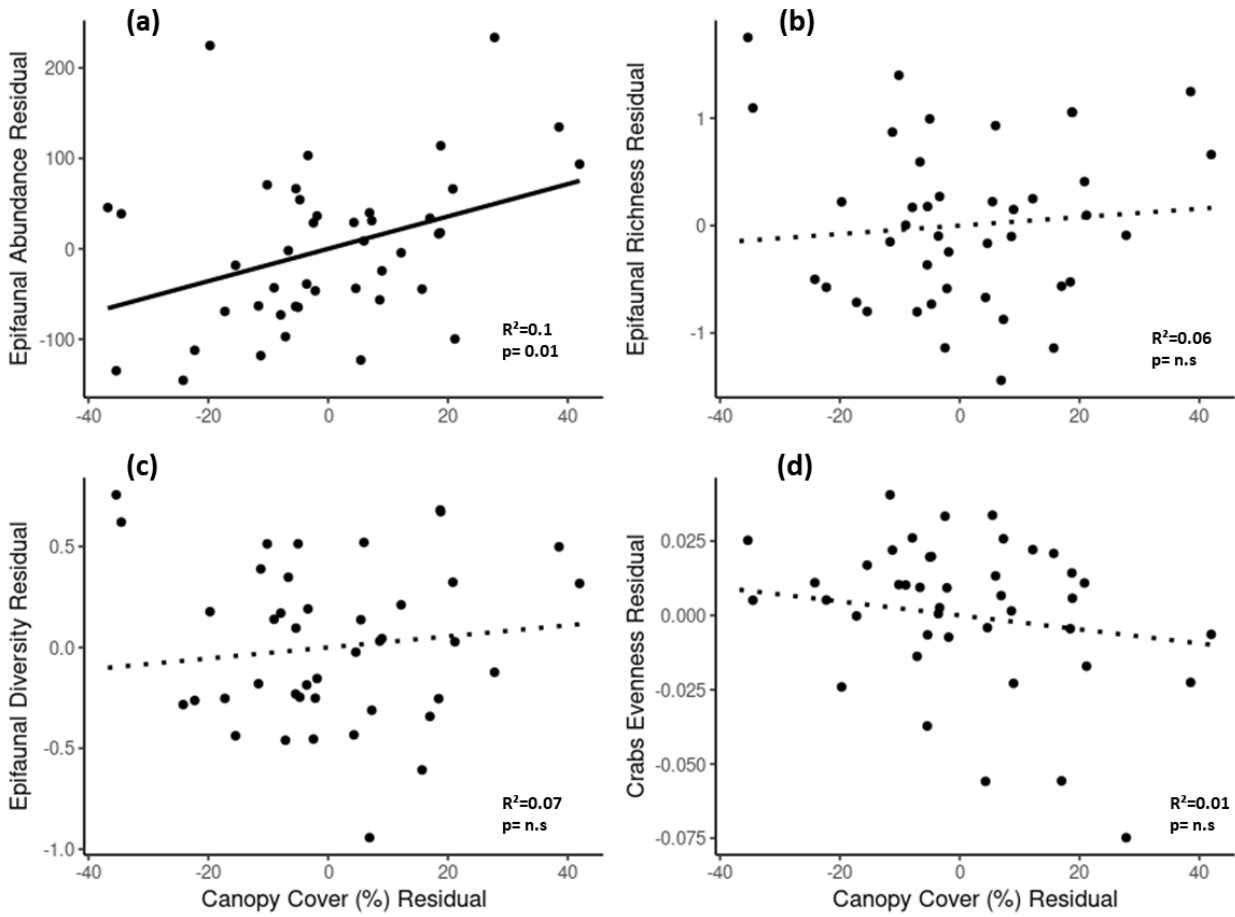
1000
1001 Figure S5: Partial regression plots showing the influences of crabs residuals composition with
1002 canopy cover residual: (a) abundance, (b) richness, (c) diversity and (e) evenness.
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