

**Where to fish in the forest? Tree characteristics and contiguous seagrass features predict mangrove forest quality for fishes and crustaceans**

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1 **Where to fish in the forest? Tree characteristics and**  
2 **contiguous seagrass features predict mangrove forest**  
3 **quality for fishes and crustaceans**  
4

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## 1 Abstract

- 1) Mangroves often support rich fish and crustacean communities, although faunal abundance and diversity show strong spatio-temporal variability. Consistent patterns in mangrove animal communities might be dictated by forest characteristics, by seascape context, or by some combination of these factors. Predicting drivers of spatial heterogeneity in mangrove faunal communities can better support the zoning of forests for management purposes, for example by identifying sites important for fisheries nursery provision.
- 2) We sampled 14 sites within a large (4000 ha) mangrove forest in Kenya, quarterly over a period of two years. There were clear and consistent differences in the quality of sites for fish and crustacean abundance and diversity.
- 3) Forest characteristics (as summarised by the complexity index, CI) and seascape metrics (the presence, area and configuration of contiguous seagrass) were strong predictors of site differences. However, they showed opposite influences on dominant members of the fish and crustacean faunas, with CI correlated negatively with fishes and positively with crustaceans, and seagrass area correlated positively with fishes and negatively with crustaceans.
- 4) *Synthesis and applications.* Sites within the same mangrove forest exhibit consistent differences in fish and crustacean abundance. However, the fish and crustacean communities (and particularly dominant species within them) act differently in response to forest and seascape characteristics. Old growth, mature forest, set in a seascape of seagrass patches with bare sediment, was associated with highest crustacean abundance. In contrast, denser smaller trees and seascapes with larger, continuous areas of seagrass correlated better with fish abundance. Zoning for management, as mandated in new Kenyan policy, will need to consider these differences in seascape use between fish and crustaceans.

**45 Keywords**

46 Nursery habitat, ecosystem services, shrimp, juveniles, mosaic, East Africa, complexity

47

**48 2 Introduction**

49

50 Abundant evidence supports the notion that mangroves are usually important habitats for  
51 crustaceans and juvenile fishes (Faunce & Serafy, 2006). Meta-analysis demonstrate a positive  
52 relationship between mangrove presence or area and local fisheries catches at regional (10-100 km)  
53 scales (Carrasquilla-Henao & Juanes, 2016). Studies comparing areas with and without mangroves  
54 have provided convincing tests of nursery function (Nagelkerken et al., 2002; Mumby et al., 2004).  
55 Work at very local (1–100 m) scales has identified a range of plausible mechanisms that could  
56 underlie this effect. Dominant amongst these is the predator refuge hypothesis (Heck et al., 2003)  
57 which predicts that structurally complex habitats allow juveniles to hide from their larger predators.  
58 A large literature documents this in a range of habitats (e.g. Cocheret de la Morinière et al., 2004;  
59 Vnce et al., 1996). Dense mangrove stands provide a striking example of structural complexity and  
60 experimental and comparative studies have shown how the density of mangrove roots and stems is  
61 positively related with fish abundance and diversity (MacDonald & Weis, 2013; Nagelkerken &  
62 Faunce, 2007; Sheridan & Hays, 2003).

63

64 Despite these insights much remains uncertain about the roles of mangroves as habitat for mobile  
65 aquatic fauna. There is large, unexplained variability at the meso scale (100 m – 10 km). For  
66 example, research that samples fish beneath the mangrove canopy reports large temporal and spatial  
67 variability among sites (e.g. Crona & Rönnbäck, 2007; Huxham et al., 2004; Vance et al., 1996)  
68 which is not simply correlated with root density. Equally dense mangrove plots, in the same forest  
69 but separated by a few hundred metres, may have very different fish communities. Some of this  
70 uncertainty may be related to other variables that change at local scales, such as turbidity, salinity,

71 shade and temperature (Barletta et al., 2003; Macia, 2004; Verweij et al., 2006) but no one variable  
72 is consistently important. In general, it remains difficult or impossible to predict what areas of a  
73 forest are most valuable as fish habitats. Identifying whether some areas of mangroves are  
74 consistently better at providing nursery functions, and understanding why, would allow  
75 management to focus on conserving these areas.

76

77 An emerging perspective that can help to illuminate meso scale variability comes from landscape  
78 ecology. For example, [Bradley et al., \(2019\)](#) describe how, at the small scale (1-10 m), habitat  
79 characteristics related to structure and complexity were important predictors of fish presence in  
80 their study of coastal fish communities in Australia. As expected, greater complexity correlated  
81 with higher numbers of fish. However, the identities of these fish differed between marine and  
82 estuarine sites separated by ~ 10 kms, as did the nature of the features that provided habitat  
83 complexity (such as mangrove roots, seagrass, and cobble). They concluded that faunal – habitat  
84 relationships are context-dependent and stress the need to investigate the environmental context of  
85 habitats to understand their function, which links local scale variability with meso-scale  
86 characteristics. The seascape approach, adapted from landscape ecology, may shed light on what  
87 determines the quality of nearshore nursery habitats (Nagelkerken et al., 2015); in particular, it  
88 promises to help fill the knowledge-gap at the meso-scale. In the seascape, connectivity is  
89 determined by the extent to which patches allow or deter movement of resources and individuals  
90 between or across patches. Coastal ecosystems are not isolated, and their ecological status and  
91 resilience could be determined by their functional linkage with other habitats (Olds et al., 2016).

92

93 In the Caribbean and the Indo – Pacific, juvenile fishes have been recorded to use mangrove and  
94 seagrass habitats while adults utilise coral reefs (Dorenbosch et al., 2006; Mumby et al., 2004). In  
95 most forests, mangrove-dependent fish tend to move to adjacent seagrass habitats during low tides  
96 when the intertidal zone is not inundated (Jelbart et al., 2007; Sheaves, 2005). Fish may also seek

97 refuge in mangroves during the day, when they are vulnerable to visually hunting predators, and  
98 later move to seagrass beds for nocturnal feeding (Nagelkerken et al., 2000; Verweij et al., 2006). In  
99 the Western Indian Ocean region, a diverse range of species from different trophic levels have been  
100 found to utilise nearshore habitats (including mangroves and seagrasses) as juvenile habitats  
101 (Berkström et al., 2012; Lugendo et al., 2005) but the ecological requirements and movements of  
102 individual species are often unknown.

103

104 In the current work, we test the prediction that mangrove forest structure and adjacent seascape  
105 composition, in particular the presence and extent of seagrass, interact to shape the abundance and  
106 diversity of fishes and crustaceans. Our first objective was to use repeated sampling to search for  
107 predictable patterns among a range of sites within a single large mangrove forest in southern Kenya.  
108 Mangrove habitat variables, and the setting of the site in the seascape, may both be important in  
109 explaining habitat use by mobile aquatic fauna. Our second objective was to combine measures of  
110 habitat quality and seascape context, consisting of forest characteristics and data on extent and  
111 shape of contiguous seagrass coverage, to help explain variation amongst these sites and increase  
112 the predictability of meso-scale variation and hence the ability to identify sites of high fisheries  
113 importance.

114

## 115 3 Materials and methods

116

### 117 3.1 Study area

118

119 The study area is Vanga Bay on the south coast of Kenya (4° 39' 38.42"S, 39° 13' 9.71"E). Sea  
120 surface temperatures range between 24 °C and 29 °C and salinity varies between 34.5 and 35.4,  
121 with lowest salinities during the rainy Southeast Monsoon (SEM) and the highest during the dry

122 Northeast Monsoon (NEM) season (UNEP, 1998). The tidal regime is semi diurnal with amplitudes  
123 from 1.5m at neap to 4m at spring tides.

124

125 The Vanga mangrove forest covers an area of ~ 4000 ha and six species of tree are found there:  
126 *Avicennia marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Rhizophora mucronata*, *Sonneratia alba*  
127 and *Xylocarpus granatum* (Figure 1) (GoK, 2017). Fishing is the major economic activity with  
128 fishing grounds being a complex of mangroves, seagrass and coral reef ecosystems. The fishery in  
129 Vanga is mostly artisanal, multi gear and multi species (Fortnam et al., 2021).

130

131 INSERT FIGURE 1 HERE

132

### 133 3.2 Sampling sites and methods

134

135 Fishes and crustaceans were sampled at fourteen mangrove creek sites chosen using three criteria:  
136 First, to create a wide geographical coverage within the forest whilst still being accessible enough to  
137 allow regular sampling. Second, to sample creeks within the mangrove canopy of broadly similar  
138 size (3-4 m width) and hydrology, so that any differences between sites were due to location rather  
139 than hydrology. Third, to sample across a range of forest characteristics (particularly using the  
140 Complexity Index (CI) as a summary variable; see below) that captured features of tree diversity,  
141 maturity, and density. We used structural data collected by the Kenya Marine and Fisheries  
142 Research Institute (KMFRI) in 2015, according to the protocol developed by Diefenback & Fritsky  
143 (2007), which allowed us to see average CI for areas of the forest close to all the sites we selected;  
144 we subsequently directly measured and confirmed CI for each site during our own sampling (see  
145 below) . Site locations were recorded with a Garmin GPS World Geodetic System (WGS) 1984 and

146 projected onto the Universal Transverse Mercator (UTM) 37S. Sites were, on average, 0.7 km from  
147 their nearest neighbouring site (with a maximum of 1.17 and minimum of 0.3 km); this ensured that  
148 the sampling of forest characteristics surrounding each site did not include any overlapping areas  
149 (Figure 1). Faunal sampling was done using fyke nets, every three months during spring tides from  
150 September 2015 to September 2017 (excepting March 2017 for logistical reasons). Nets were  
151 deployed in the morning at low tide and collected 24 hours later. Nets had two wings, each of length  
152 9.55 m, height 1m, and body frame length 3.6 m. The main frame measured 1 m x 1 m. There were  
153 three rings of diameter 0.9m, 0.7 m, and 0.62 m along the body frame and a net of mesh size 1.9 cm  
154 when stretched.

155

156 Sampling all the sites typically took five consecutive days; the order in which sites were sampled  
157 was changed on each date. Eight replicate samples were taken from each of the 14 sites across the  
158 2-year study period, resulting in a total of 112 samples. Samples were placed in a cool box and  
159 identified to the lowest taxon possible using Richmond (2011) and Anam & Mostarda (2012). Fish  
160 and crustacean abundance, biomass, and number of species per net were obtained. Fish standard and  
161 total lengths and individual mass were recorded. Crustaceans were counted and weighed to the  
162 nearest 0.1 g. The maximum length of each species was sourced from FishBase (Froese & Pauly,  
163 2022). Fishes with total length  $\leq 1/3$  maximum length were classified as small juveniles, between  
164  $>1/3$  to  $\leq 2/3$  maximum length as large juveniles/sub adults and those  $>2/3$  maximum length as  
165 adults (Nagelkerken & Velde, 2002). All samples were removed to the laboratory and used for  
166 additional data collection including for parasite fauna and stomach-content analysis (Wanjiru et  
167 al.,2022). Sampling and subsequent handling did not require formal ethical approval.

168

### 169 3.3 Forest quality measurements

170



171 The floral and structural characteristics of the forest contiguous to each sampling site were captured  
172 using plots measuring 100 m<sup>2</sup> and 400 m<sup>2</sup>. Plots were located within a semicircle of forest, centered  
173 on the sampling site with radius of maximum 100m, and situated upstream or to the sides of the  
174 site. Following standard forestry protocols (Diefenback & Fritsky, 2007) the plot size depended on  
175 the tree size and density; for large trees, 20 x 20 m was used but where trees were small and densely  
176 clustered 10 × 10 m plots were used, giving more comparable numbers of trees between each plot.  
177 At each site, data from between 2 - 5 plots were used to summarise forest structure. Within each  
178 plot, the diameter at breast height (dbh, measured at around 1.3 m) (cm) and height (m) were  
179 measured for all trees with a dbh greater than 2.5 cm using a tree calliper and a graduated pole  
180 respectively. Mean tree height, basal area, stem density and number of tree species were recorded,  
181 and used to calculate the complexity index (CI), according to Holdridge (1964):  $CI=10^{-3 \times (d) \times (s) \times (h) \times (b)}$   
182 where d is the stand density, s is the number of tree species, h is the mean tree  
183 height and b is the basal area. The CI is often used to infer forest quality; degraded and younger  
184 stands tend to have lower CI compared to undisturbed ones (Roth, 1992).

185

### 186 3.4 Spatial analysis of seascape features

187

188 A cloud-free Sentinel-2 image of the Vanga area at low tide was acquired from 27/03/2017. The  
189 spatial analysis was conducted in ArcGIS. A false colour composite was created using the Near  
190 Infrared (NIR), red and green bands. To differentiate land, sea and the intertidal, we calculated the  
191 Normalised Difference Water Index (NDWI) using the NIR and red bands and a threshold was set  
192 to detect the transition from land to water. Using a previously derived mask of the ocean at high tide  
193 (Harcourt et al., 2018), we differentiated the intertidal and subtidal regions. This was subsequently  
194 used to remove land from the analysis. Areas where seagrass was dominant were mapped by  
195 applying the technique of Harcourt et al. (2018) to the Sentinel-2 scene used in this study.

196

197 In the absence of any biological information on the movements of the main species we used a  
198 simple empirical approach to obtain a maximum relevant distance from each site to be used in this  
199 analysis. For each of the 14 sampling sites, a set of buffers with intervals of 0.5 km were  
200 constructed, extending seawards to a maximum distance of 19 km from the sampling point (Figure  
201 2). These buffers were used to calculate the distance between each mangrove field site to various  
202 seagrass points. To exclude land from these buffers, the ocean mask was used to extract only those  
203 regions covered by water. We calculated the direction from each field point at increments of 20  
204 degrees to isolate regions immediately in front of a sampling point (Figure 2b) and extracted the  
205 oceanic section of these direction buffers. This was computed for each of the sites making 14  
206 directional polygons. To extract the final datasets for statistical analysis, the intersection between  
207 seagrass presence and each of the directional and distance buffers was computed. The geometry of  
208 these patches was calculated to avoid including large seagrass patches that extend across multiple  
209 buffer boundaries and intersections. To establish the maximum distance to use in subsequent  
210 analyses, cumulative curves of the proportions of total seagrass habitat recorded in the bay allocated  
211 against each site were plotted. After 9km there was only around 50% difference between sites in the  
212 proportions of cumulative area implying that beyond this distance more than half of the seagrass  
213 measured for any given site would be shared with another. Hence, 9km was set as the maximum  
214 distance used from any given site for this study.

215

216 INSERT FIGURE 2 HERE

217

218 

### 3.5 Statistical analyses

219

220 Differences in fish and crustacean communities between sites were explored using analyses of  
221 ranked abundance (to remove variability between times and seasons) and univariate correlations.  
222 Means and total counts, for each site across all sampling dates, of abundance and biomass of fishes

223 were correlated against total species count for each site, to explore whether large biomasses or  
 224 abundances might be driven by high catches of just one or a few species. For crustaceans, which  
 225 had low total species counts, the same approach was taken for abundance vs biomass.

226

227 The main relationships between predictor and response variables were explored and summarised  
 228 with a principal components analysis (using the 'prcomp' command on R). Regression analyses were  
 229 used to explore relationships between forest characteristics, seascape predictors, fish and crustacean  
 230 variables, using a range of possible predictor and response variables (Table 1). The seagrass  
 231 predictors were available for a range of total potential areas, up to and including 9 km distance.  
 232 Stepwise regressions, with addition and subtraction approaches, were used to identify distances that  
 233 consistently showed no or little evidence of effects; these were excluded from subsequent models.  
 234 Best multiple regression models (on  $\log_{10}$  transformed data when necessary) were chosen by  
 235 comparing  $R^2$  values, p values, the strength of coefficients, and variance inflation factors (VIF) for  
 236 multicollinearity, with a VIF of  $>5$  deemed unacceptable. The strongest models incorporating forest  
 237 and seagrass predictors were compared using the Akaike Information Criterion (AIC). Finally,  
 238 simple linear regressions were performed between those predictors and response variables shown to  
 239 have the strongest relationships through the multiple regressions and by visual inspection of the  
 240 plots. Given the collinearity inherent in some of the predictor variables and the dangers of inflated  
 241 Type 1 error following multiple tests, the results were examined for key signals rather than  
 242 interpreted simply as significant or non-significant relationships.

243

244 **Table 1:** All predictor and response variables explored

Predictor variables	Seagrass area, seagrass perimeter, cumulative seagrass area, cumulative seagrass perimeter, seagrass perimeter/area ratio, forest complexity index, mean tree height, number of tree species, tree basal area, stem density
---------------------	---

Response variables (fish)	Total fish abundance, total fish biomass, species richness, <sup>1</sup> dominant fish species abundance: <i>Yarica hyalosoma</i> , <i>Acropoma japonicum</i> , <i>Gerres oyena</i> , <i>Gerres filamentosus</i>
Response variables (crustaceans)	Total abundance, total biomass, species richness, <sup>2</sup> dominant species abundance: <i>Penaeus semisulcatus</i> , <i>Penaeus monodon</i> , <i>Penaeus indicus</i>

245 <sup>1</sup> 62% of all individuals. <sup>2</sup> 88% of all individuals

246

247 Moran's 'I' was calculated using GeoDa software to test for spatial autocorrelation; there were no  
248 significant improvements after correction using spherical error terms, thus correction for auto  
249 correlation was found unnecessary.

250

251 Statistical analyses were performed using Minitab 15 and R v 4.2.0 software.

252

## 253 4 Results

254 A total of 1879 fishes and 1132 crustaceans were sampled belonging to 59 and 16 species,  
255 respectively. The most abundant fish species were *Y. hyalosoma*, *A. japonicum*, *G. oyena* and *G.*  
256 *filamentosus* (62% of the total individuals caught) while the most abundant crustacean species were  
257 *P. semisulcatus*, *P. indicus* and *P. monodon* (88% of all crustacean individuals). 61.8 % of all fish  
258 caught were juveniles, 38.1 % were large juveniles/sub-adults and only 0.2% were adults (from just  
259 two species, *Zenarchopterus dispar* and *Stolephorus commersonii*). All dominant species are of  
260 direct importance for local fisheries, with the exception of *Y.hyalosoma*. Full information on fauna  
261 is given in [Wanjiru et al. \(2022\)](#).

## 262 4.1 Differences among sites

263

264 There were large and consistent differences between sites, with some having predictably higher  
265 diversity and abundance than others. Species richness for fishes ranged from 7 (at site 14) to 24 (site  
266 7). The strong positive correlation between mean fish biomass and total number of species per site  
267 ( $R^2=0.93$ ,  $df= 1, 12$ ,  $p<0.001$ ; Figure 3) demonstrates that sites with high fish biomass were not  
268 simply characterised by one or two dominant species, but rather tended to be better for most  
269 species. Species richness counts for crustaceans ranged from 3 (site 7) to 9 (sites 4 and 10),  
270 however only three species (*P. semisulcatus*, *P. monodon* and *P. indicus*) dominated the catch with  
271 88% of all individuals. Hence there was no relationship between abundance and species count for  
272 crustaceans. As expected, there were large differences between times, with catches during SEM  
273 around three times higher than NEM (Wanjiru et al., 2022). However, the rank order of sites  
274 remained broadly consistent, as shown by significant differences among median ranks across all  
275 eight dates for both fishes and crustaceans (Figure 4; Kruskal Wallace tests for fishes, Chi-squared  
276 = 31.9, d.f. = 13,  $p = 0.0025$ ; for crustaceans, Chi-squared = 40.8, d.f. = 13,  $p = 0.0001$ ). Sites that  
277 supported high fish abundance did not necessarily support high crustacean abundances.

278

279 INSERT FIGURES 3 AND 4 HERE

## 280 4.2 Relationships between mangrove forest characteristics, seagrass coverage, fish 281 and crustacean variables

282

### 283 *Summary PCA*

284 A principal components analysis was used to visualise the main relationships between predictor and  
285 response variables (Figure 7). The first 5 principal components explained 80 % of the variability,  
286 with PC1 contributing 29.9 % and PC2, 25.7 %. Principal component 1 aligns with seascape  
287 (seagrass) variables including SG1 and SG2 (seagrass area at 1 and 2 kilometres) whilst PC2 aligns  
288 with the forest variables CI and basal area (which are themselves co-dependent). Key fish variables

289 (total abundance, abundance of dominant species *Y.hyalosoma* and *A.japonicum*) were negatively  
 290 related to the complexity index (CI) and basal area of the forest while crustaceans (total abundance,  
 291 *P. monodon* and *P. semisulcatus*) were positively correlated. By contrast, important fish variables  
 292 were positively correlated with seagrass area while crustaceans generally showed negative  
 293 relationships with seagrass area (but positive ones with perimeter/area and perimeter measures).  
 294 Four of the univariate relationships informing these patterns are illustrated in Figure 5.

295

296 INSERT FIGURE 5 HERE

297

298 *Univariate and multivariate regressions*

299 CI was the most important floral variable in univariate analyses. Important seascape predictors were  
 300 seagrass area and perimeter/area ratio (P/A) at 1.5 km and 3.5 km distance (Table 2).

301 Table 2. Selected univariate regression results

Predictor variable	Response variable	Coefficient	F	R <sup>2</sup> (%)	p
CI	Total fish abundance	-160	5.71	32.22	0.034
	Total crustacean abundance	+110	9.66	44.60	0.009
	<i>P. monodon</i> abundance	+6	8.51	41.50	0.013
	<i>P. semisulcatus</i> abundance	+96	8.21	40.63	0.014
Seagrass area 1.5 km	log (x+1) <i>Yarica hyalosoma</i>	+23	23.44	66.11	<0.001
Seagrass P/A 1.5 km	<i>P. indicus</i> abundance	+13	13.03	52	0.004
Seagrass P/A 3.5 km	<i>G. filamentosus</i> abundance	-0.96	10.72	0.47	0.007

302

303 Combining variables in multiple regressions and using best subsets and AIC analyses to select the  
 304 best fit models resulted in four final, highly significant models (Table 3). The exact combination of  
 305 predictors and responses differed from those highlighted by the key univariate regressions but were

306 consistent with the main trends they showed. For example, abundance of the dominant fish species  
 307 *Y. hyalosoma* was positively correlated with the area of contiguous seagrass and negatively related  
 308 with tree basal area (a key part of the CI). Abundance of the dominant shrimp species *P. indicus*  
 309 correlated positively with perimeter/area ratio of seagrass and with mean tree height (a positive  
 310 contributor to CI).

311 Table 3. Best fit multiple regression models

Response variable	Predictor variable	Coefficient	Model F	Model R <sup>2</sup> (%)	p
<i>P. indicus</i>	Seagrass P/A 2.5 km	1.69	13.48	86	0.001
	Mean tree height	20.2			
	Tree species	12			
	Stem density	0.01			
<i>P. indicus</i>	Seagrass P/A 1.5 km	0.25	11.94	68	0.002
	No. tree species	9.74			
<i>Y. hyalosoma</i>	Seagrass area 1 km	146	16.42	75	<0.001
	Stem density	-0.02			
<i>Y. hyalosoma</i>	Seagrass perimeter 1 km	3.81	11.28	80	0.001
	Seagrass area 1 km	-140.3			
	basal area	-28.7			

## 313 5 Discussion

314

315 In this study we addressed two research gaps: first, are there consistent differences in the fish  
316 and crustacean fauna found among different sites within the same mangrove forest, sampled  
317 over two years? Second, can measures of forest structure, or context in the seascape, or  
318 combinations of both, be used to predict these differences?

319

### 320 5.1 Consistency of mangrove forest sites as habitats for fishes and crustaceans

321

322 Our results revealed predictable patterns within the Vanga mangrove ecosystem. Some sites  
323 showed higher species richness, abundance and biomass than others, a pattern that persisted  
324 between years and seasons as shown by the significantly different rankings of the sites for  
325 these variables. This has important practical implications. Different services (such as carbon  
326 storage, fisheries habitat or nutrient filtration) may be associated with different locations in a  
327 habitat (Huxham et al., 2017). In principle, such patterning would allow differentiated use  
328 and protection of an ecosystem, for example through designating some parts of the forest for  
329 extractive use whilst protecting other areas as nursery sites or carbon stores. Indeed, zoning is  
330 already in place in the Vanga forest, which is home to Vanga Blue Forest, a mangrove carbon  
331 project that uses 450 ha as protected areas for carbon benefits (ACES, 2022). The National  
332 Mangrove Ecosystem Management Plan, developed for application along the whole coast,  
333 mandates similar zoning for all Kenyan mangrove forests (GoK, 2017). Hence it would be  
334 useful if areas important as nursery sites could be clearly identified and there is a  
335 presumption in policy that this will be done. However, our results suggest that any simple  
336 classification of the forest into relatively 'good' and 'bad' areas for fisheries is not possible  
337 because of the contrasting responses of different species and faunal groups. There was a



338 distinction between the main fish and crustacean species, with sites best for fish generally  
339 poor for crustacea, and *vice versa*.

340

## 341 5.2 Fish, crustacea and mangrove structural variables

342

343 Enhanced biomass and diversity of coastal fish assemblages are often associated with more  
344 structurally complex habitats (Lefcheck et al., 2019) and a substantial literature explores what  
345 structural features of mangroves might attract fish at very local scales (Cocheret de la  
346 Morinière et al., 2004; Laegdsgaard & Johnson, 2001; Loneragan et al., 2005). For example  
347 field studies and laboratory experiments have shown complex mangrove roots provide refuge  
348 for juvenile fish by deterring predators from attacking them (Laegdsgaard & Johnson, 2001;  
349 Macia, 2004; Sheridan & Hays, 2003). Here, total fish abundance, and the abundance of  
350 dominant fish species, were negatively associated with complexity index (CI), whilst the  
351 opposite pattern was seen for crustaceans. On first impressions, this may seem to contradict  
352 the association between structural complexity and juvenile fish found at other sites and  
353 scales. However, the CI is positively related to basal area, which is positively related to the  
354 size of trees (Roth, 1992). Therefore, high CI implies older, less dense trees with a more  
355 diverse mangrove species mix, as found in mature, old-growth forests. In Kenya, the old  
356 growth forests with high CI values have the highest stocks of carbon and are thus the most  
357 important carbon sinks (Huxham et al., 2015). However, these results suggest that a lower CI  
358 is better for fish, and this is consistent with the idea that fish prefer very dense stands, which  
359 are often younger and less likely to be multi-species. Maintaining and enhancing the range of  
360 ecosystem services, including carbon storage and fisheries provision, that are provided by  
361 mangroves will require recognition of these spatial differences and caution about allowing  
362 single services, such as carbon sequestration, to dominate policy decisions.

363

364 In contrast, crustaceans (and specifically the dominant species of shrimp, *P. indicus*, *P.*  
365 *monodon* and *P. semisulcatus*) showed positive associations with CI suggesting that they are  
366 using the mangrove habitat in a different way than fishes. Whilst most literature on shrimps  
367 in mangroves emphasises the importance of structural complexity, the type of complexity that  
368 matters may be different from that for fishes. For example, [Rönnbäck et al. \(1999\)](#) found  
369 fishes were more likely to associate with areas of dense pneumatophores rather than prop-  
370 roots, with shrimp preferring the latter. [Macia et al. \(2003\)](#) showed an interaction between  
371 turbidity and habitat complexity for *P. indicus*; in turbid waters (such as those at Vanga)  
372 protection from predation decreased with increasing complexity. Hence, penaeid shrimp can  
373 use turbidity as a refuge from predators and are also able to burrow into suitable substrates to  
374 reduce their susceptibility to predation (Dall et al., 1990). This could imply a preference for  
375 more open habitats with substrates suitable for burrowing (Mohan & Siddeek, 1996;  
376 Rönnbäck et al., 2002; Vance et al., 1996) .

377

### 378 5.3 Fish, crustacea and seagrass seascape features

379

380 Context in the seascape may be more important in explaining tropical fish assemblages than  
381 habitat characteristics of specific patches (Goodridge Gaines et al., 2022; Green et al., 2012);  
382 indeed Bradley et al. (2019) conclude that the context-dependency of animal-habitat  
383 relationships in the coastal zone is of ‘over-riding importance’. Most previous studies on how  
384 seascape context affects mangrove fauna have considered different scales and more  
385 fragmented mosaics than the current work, for example looking at patches of mangroves with  
386 varying degrees of isolation. Here, we looked at a single, continuous forest and considered  
387 how features of the seagrass growing next to it might influence vagile faunal communities.  
388 Some of the fish and crustacean variables were strongly associated with seagrass metrics. The  
389 perimeter/area ratio of seagrass - which increases with increasing fragmentation and

390 decreasing patch size of seagrass - proved the best predictor. Fish and crustacean variables  
391 were generally negatively and positively associated with this metric, respectively. The  
392 abundance of *P. indicus* gave the strongest association at 1.5 km ( $R^2=0.52$ ) and *P. monodon*  
393 abundance was also significantly positively correlated to perimeter/area ratio ( $R^2=0.43$ ). Fish  
394 variables were mostly negatively correlated with perimeter/area ratio and positively  
395 correlated with seagrass area. This generally positive influence of seagrass coverage on fish  
396 abundance was expected, as seagrass is well known as important habitat for many juvenile  
397 fish (Heck et al., 2003; Swadling et al., 2019). Here, we assume that fish found at the  
398 mangrove sites during high tide are conducting tidal migrations, to or through seagrass  
399 patches. Similar migrations, with site fidelity at high and low tide, have been demonstrated  
400 for juvenile Lutjanidae in Zanzibar (Dorenbosch, 2004) and Jelbart et al., (2007)  
401 demonstrated how patches of seagrass closer to mangroves in Australia supported higher  
402 densities of juvenile fish, including Ambassidae, at low tide.

403

404 The apparently negative relationship between shrimp and the area of contiguous seagrass may  
405 be linked to the use by shrimp of bare substrates, as discussed above. Even when seagrass has  
406 been shown to encourage higher invertebrate densities or diversities, the relationships are not  
407 always simple. For example, crustaceans sometimes have higher densities in smaller rather  
408 than large patches sizes of artificial seagrass (Eggleston et al., 1999). Different species are  
409 likely to interact with both the components and their spatial organisation of the seascape  
410 mosaic in different, and species-specific, ways. This suggests that these relationships cannot  
411 be generalised but must be considered separately for each species.

412

413 The spatial area over which seascape features exert influence on the structures of  
414 communities caught at any site is in most cases unknown. Relevant information informing

415 study design includes the home range and daily movement patterns of target species. For  
416 most taxa (including most of those in this study) such detail is missing, although information  
417 from tagging studies is slowly becoming available on the movements of some taxa such as  
418 *Haemulon* sp (Appeldoorn & Bouwmeester, 2022) and Lutjanidae (Dorenbosch et al., 2004).  
419 The smallest ambit applied to seagrass metrics in the current study was 0.5 km from a catch  
420 site, and most of the faunal variables showed the strongest responses to seagrass metrics  
421 within 3 km.

422

#### 423 5.4 Combining seascape and habitat predictors

424

425 For one of the dominant fish species – *Y. hyalosoma* – and one of the shrimp – *P. indicus* – a  
426 combination of seascape and habitat factors produced very strong and highly significant  
427 regression models that explained up to 86% of the variance between sites. We recognise that  
428 correlative work like this can never demonstrate causality, and that there are other potentially  
429 relevant variables at the habitat (such as abiotic drivers like turbidity) and seascape (such as  
430 macroalgae coverage) levels that could in principle be included in analyses like these.  
431 However, the strength of these relationships and the corroboration of similar work in the  
432 literature suggests that these findings capture important features of the ecology of these  
433 species.

434

#### 435 5.5 Conclusions

436

437 We show that sites within the same large mangrove forest, with similar hydrological features,  
438 are significantly and predictably different in their faunal communities. However, there is no  
439 simple classification into ‘good’ and ‘bad’ places for fauna in general, since those with  
440 highest abundances for fishes often showed lower abundances of crustaceans. A combination

441 of forest characteristics and measures of seagrass area and shape within 3 km of the catch  
442 sites were able to explain much of the variation between sites. Our results support the broad  
443 literature demonstrating the importance of mangroves as sites for juvenile fish and crustacean  
444 species, and the connectivity of mangroves with nearby seagrass. Sustaining rich faunal  
445 communities in mangrove and seagrass seascapes such as at Vanga requires not only the  
446 maintenance of the different habitat types but also the seascape diversity and connectivity  
447 that allows different species to flourish.

448

### 449 **Author contributions**

450 CW, MH, IN and SR conceived the ideas and designed the main methodology. WH led on  
451 GIS design and analysis. CW collected data. CW and MH led on writing, but all authors  
452 contributed and gave final approval for the manuscript.

453

### 454 **Statement on Inclusion**

455

456 Our study was led by a Kenyan scientist and includes authors from Europe and Australia. It  
457 responds directly to a Kenyan, as well as international, policy agenda and contributed to  
458 training and capacity building for Kenyan students and citizen scientists.

459

### 460 **Conflict of Interests**

461

462 We declare no conflicts of interest

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464

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470

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629

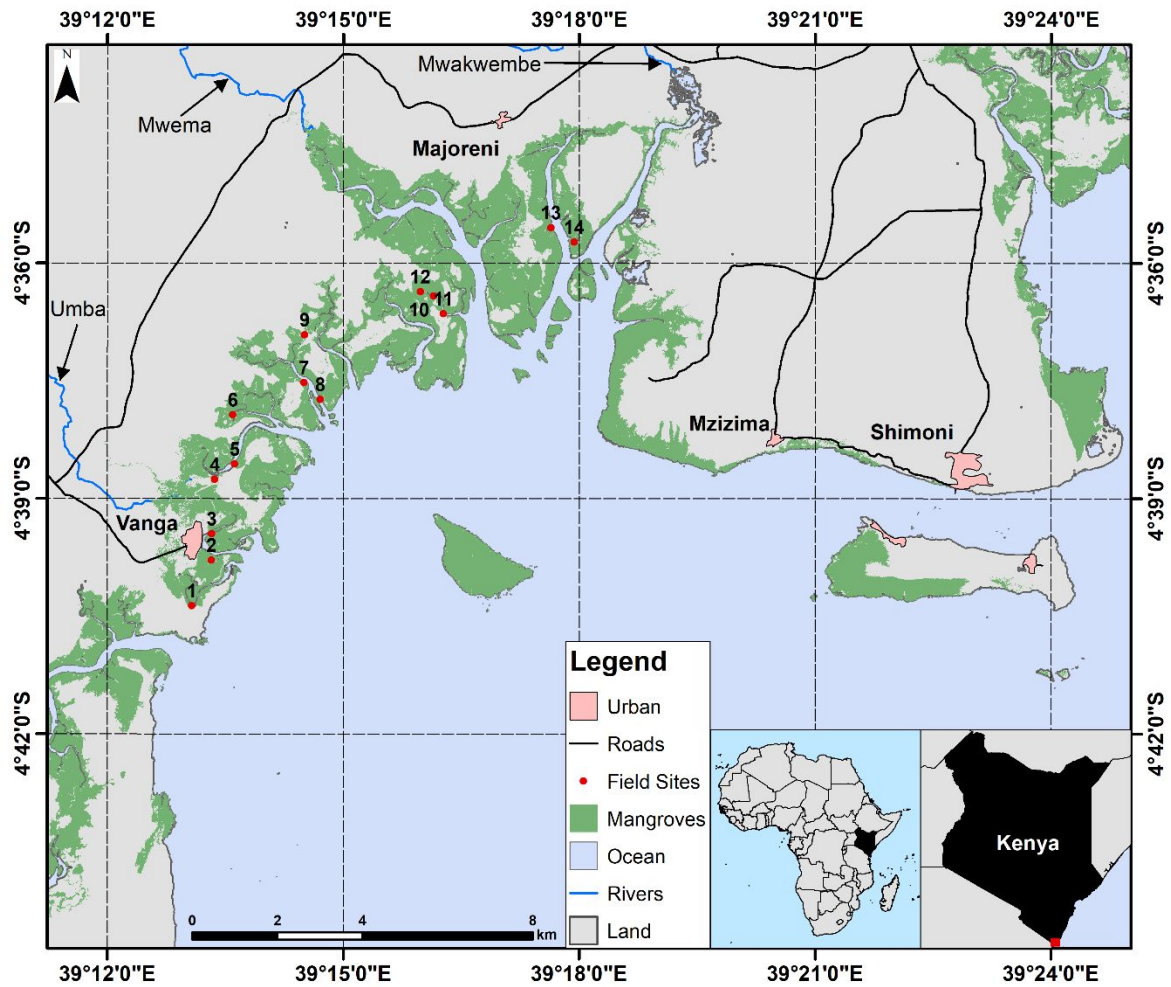


Figure 1. The Vanga mangrove forest (green) with sampling sites (red).

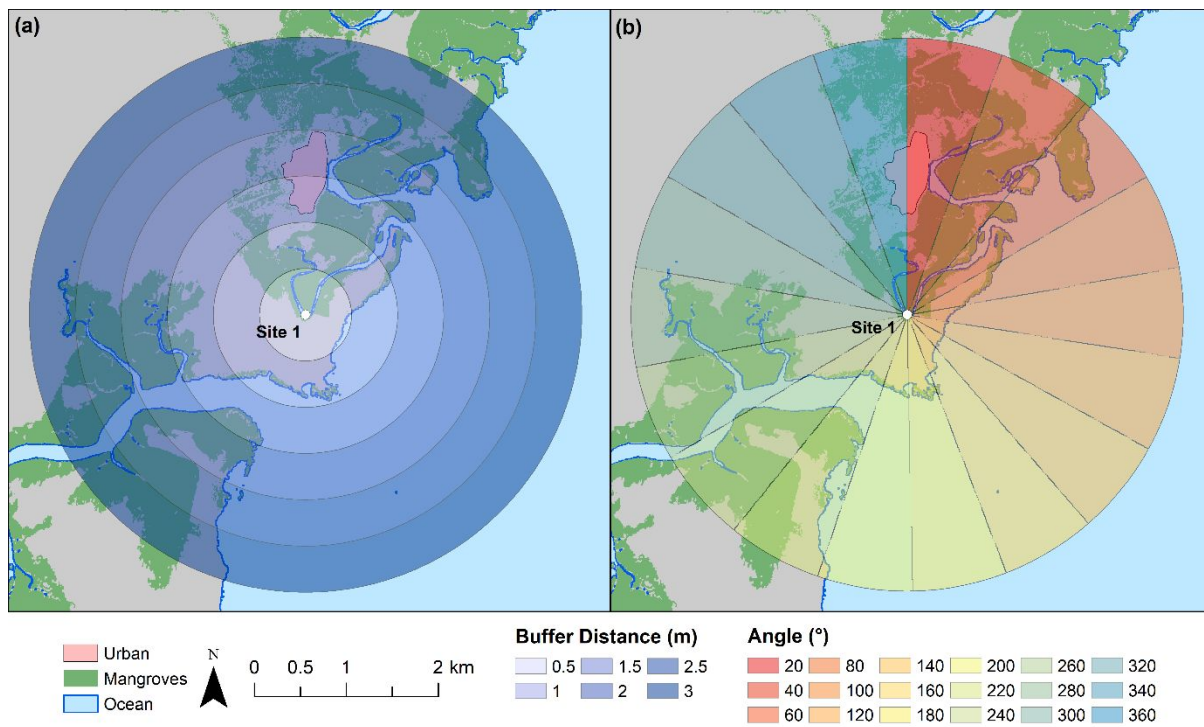


Figure 2: Example distance buffers at intervals of 0.5km (a) and angular directions at 20-degree intervals (b) from site 1.

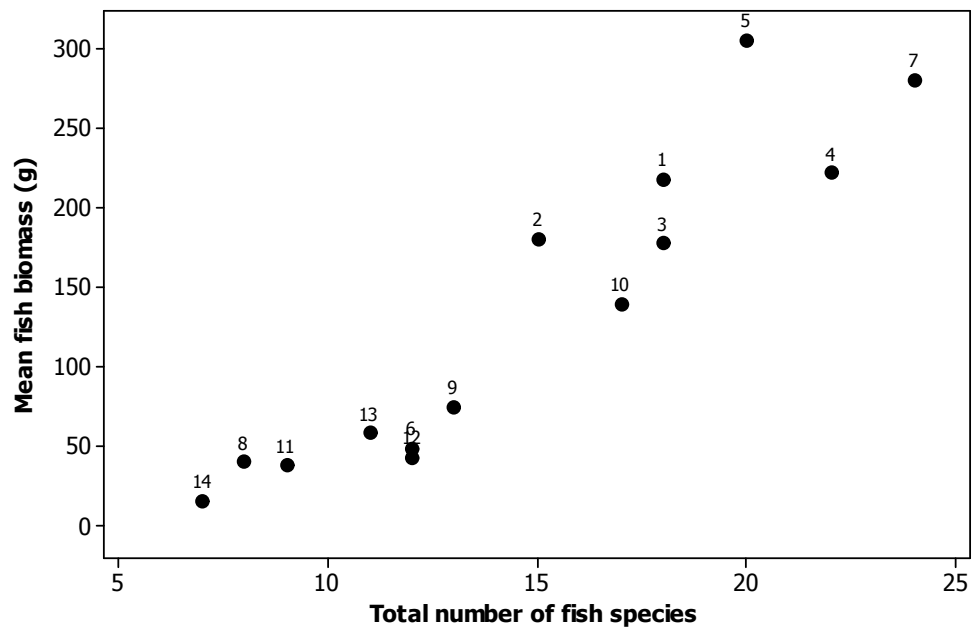


Figure 3: Mean fish biomass caught at each site versus total number of fish species, showing sites with high biomass also tended to support many species.

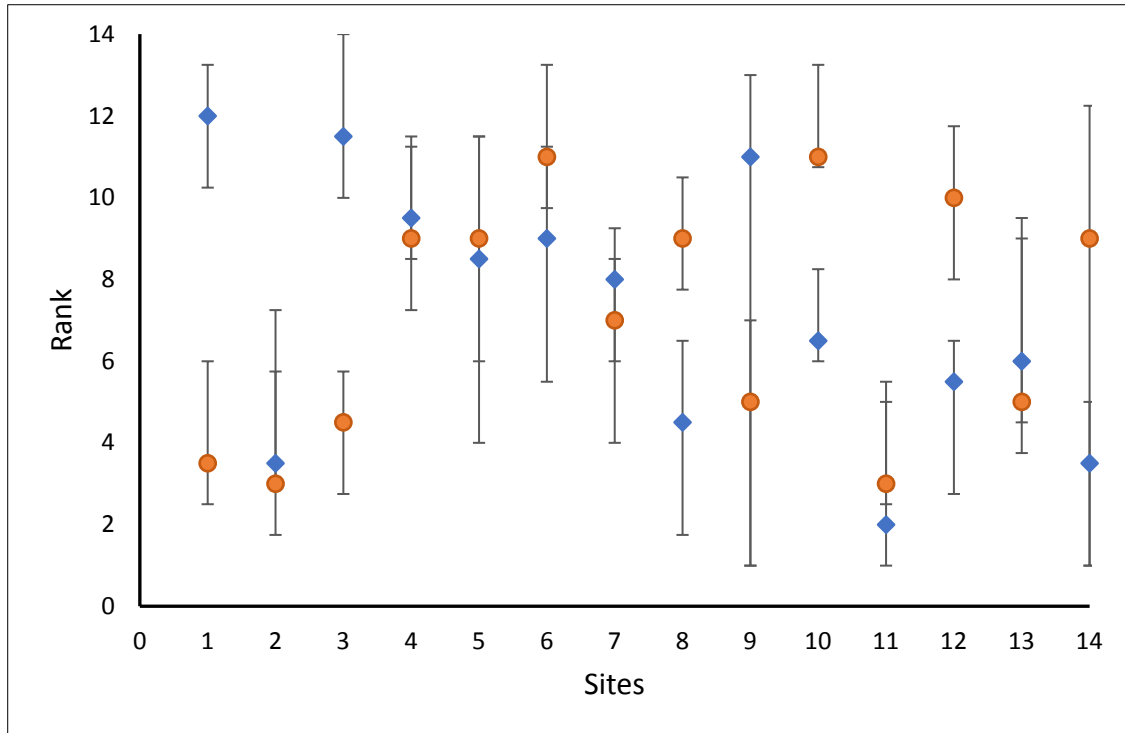


Figure 4: Median ranks of sites for fish (blue diamond) and crustacean (orange circle) abundance, with inter-quartile ranges, across 8 sampling times, ranked from highest to lowest on each sampling date.



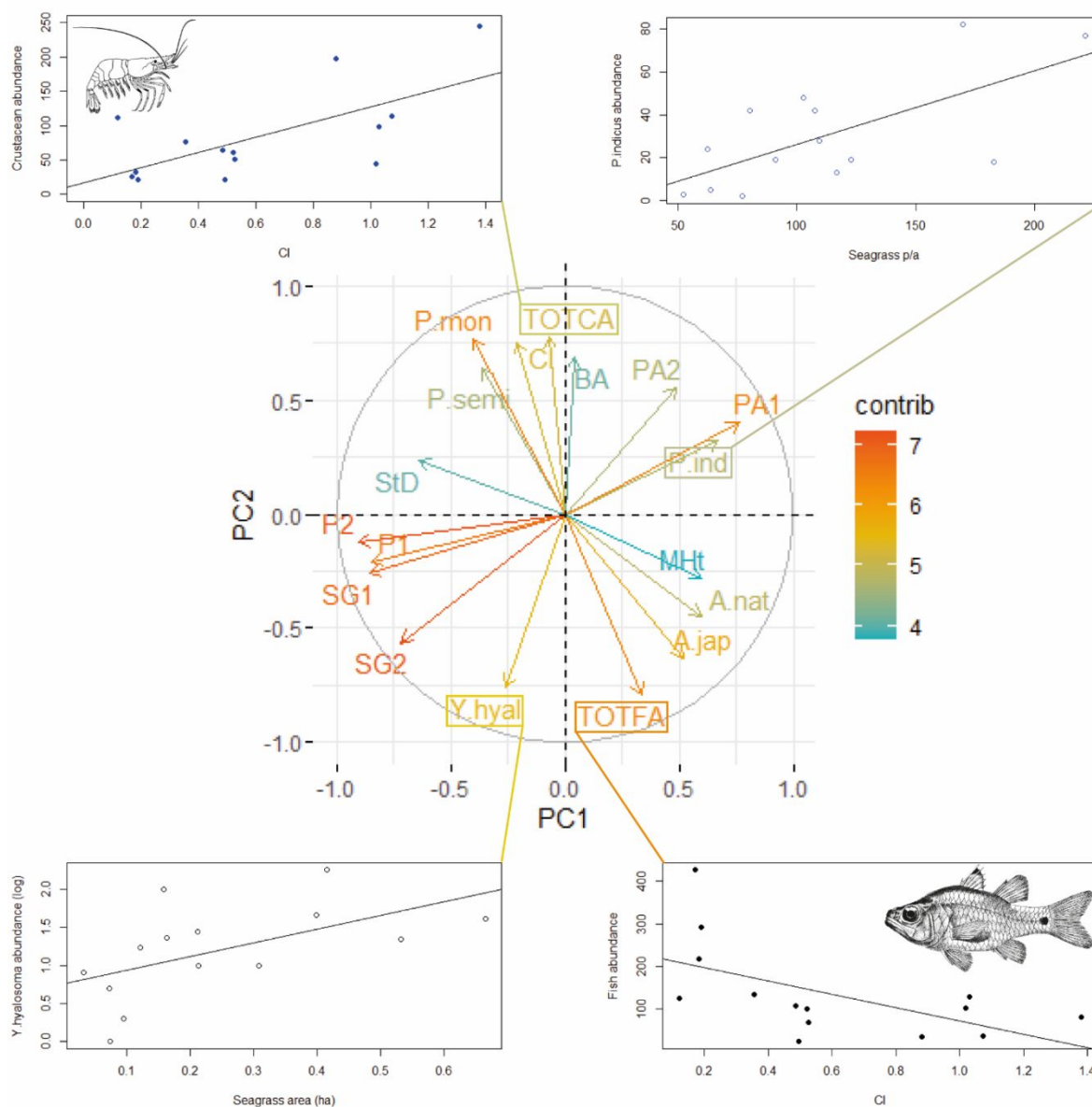
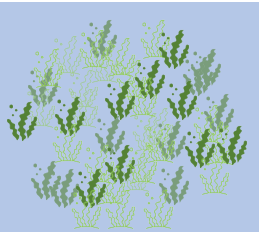


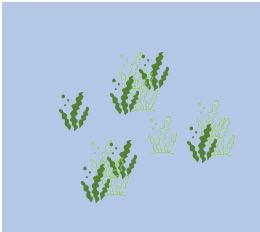
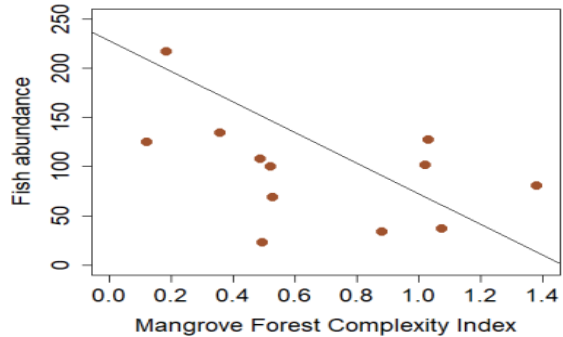
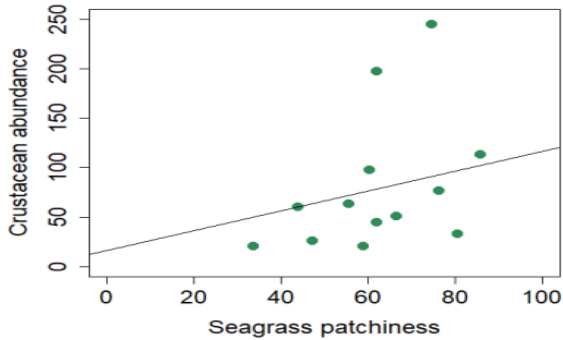
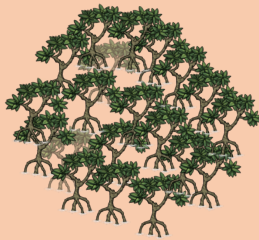
Figure 5. Principal Components Analysis showing the most important variables. Fauna: TOTCA total crustacean abundance; TOTFA total fish abundance; P. mon *P. monodon* abundance; P.semi *P. semisulcatus* abundance ; Y.hyal *Y. hyalosoma* abundance; A.jap *A. japonicum* abundance; A.nat *Ambassis natalensis* abundance; P.ind *P. indicus* abundance. Forest variables: CI complexity index; StD stand density; MHt mean tree height; BA basal area. Seagrass variables: P2 perimeter at 2 km; P1 perimeter at 1 km; SG1 area at 1 km; SG 2 area at 2 km; PA1 perimeter/area ratio at 1 km; PA2 perimeter/area ratio at 2 km. The four panels show key, significant univariate relationships. Table 2 gives model results for these regressions.



DENSE  
CONTINUOUS  
SEAGRASS

ABUNDANT FISH  
FEWER SHRIMP

DENSE SMALL  
MANGROVES



SPARSE  
PATCHY  
SEAGRASS

ABUNDANT  
SHRIMP  
FEWER FISH

SPARSE LARGE  
MANGROVES





390x292mm (300 x 300 DPI)