One Ocean Hub – Ghana

Impact of mangrove selective logging upon estuarine trophodynamics in Ghana.

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Contents

1 Introduction 2
1.1.1 Mangrove Ecosystem Functioning and Services 2
1.1.2 Global Threats to Mangroves 3
1.1.3 Mangrove Forests of Ghana 3
1.2 Biodiversity, Ecosystem Functioning, and Ecosystem Services 5
1.3 Trophic Ecosystem Functioning 5
2 Methodology 7
2.1 Study Sites 7
2.2 Sample Collection 9
2.2.1 Basal Resources 9
2.2.2 Consumers 9
2.3 Analysis 10
2.3.1 Consumer Trophic Positioning 10
2.3.2 Niche Size and Overlap 12
2.3.3 Community-Wide Trophic Structure 12
3 Results 14
3.1 Stable Isotope Values of Food Sources 14
3.2 Stable Isotope Values of Consumers 14
3.3 Isotopic Niche 19
3.4 Community-Wide Trophic Structure 23
3.5 Trophic Position 25
4 Conclusions 26
4.1 Feeding Strategies 26
4.2 Trophic Diversity 27
4.3 Trophic Position 27
4.4 Final Remarks 28
5 References 29

1 Introduction

Mangroves are marine vascular plants with unique adaptations to brackish conditions and tidal incursions. The term 'mangrove' can refer to individual halophytic trees and shrubs that grow within the intertidal zone, as well as the entire ecosystem made up by these species. Existing in the intertidal zone, these forests support elements of both terrestrial and marine ecosystems, as well as having distinct ecological characteristics of their own (Alongi., 2009). However, their positioning along coastlines also exposes mangroves to exploitation and degradation from anthropogenic activities, resulting in them being threatened throughout most of their range (Friess et al., 2021; Polidoro et al., 2010). Their range is primarily in the tropics (Figure 1), with the region of West Africa account for 11% of the global mangrove area (UNEP, 2007).

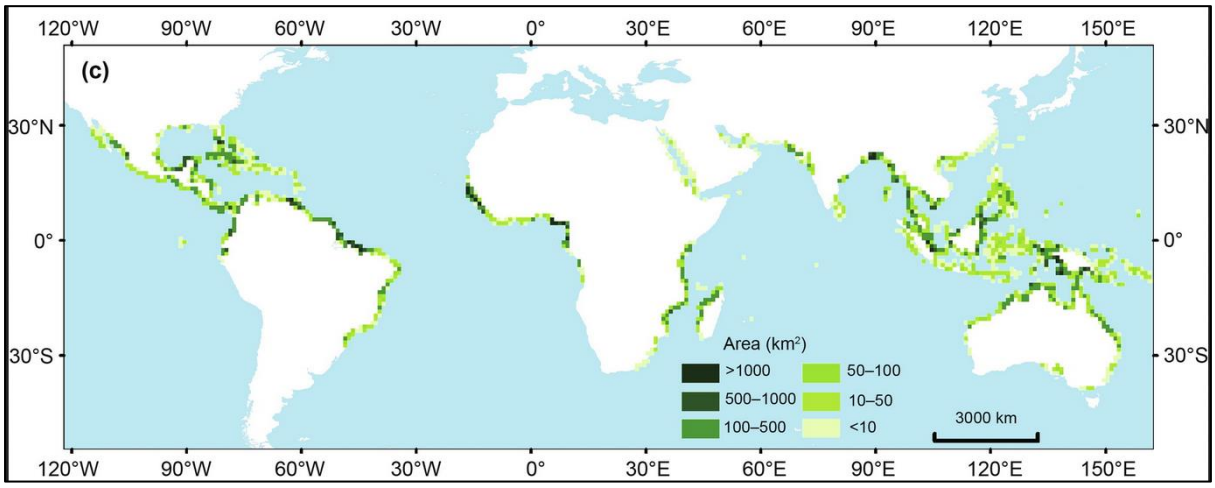

Figure 1: Global mangrove distribution map with areal cover in each decimal degree square from 2020 (Source: Jia et al., 2023).

1.1.1 Mangrove Ecosystem Functioning and Services

Due to their complex system of prop-roots and pneumatophores, mangroves act as highly effective ecosystem engineers, reducing the flow of water, trapping sediment and creating 3-D microhabitats, thereby supporting numerous ecosystem services including flood defence, protection against coastal erosion, carbon sequestration, and the improvement of water quality (Alongi, 2012; Dahdouh-Guebas et al., 2005; Valiela et al., 2002). These ecosystems also provide food and shelter for a variety of terrestrial and marine organisms (Igulu et al., 2014; Nagelkerken et al., 2008). This aspect of mangrove ecosystem functioning is reinforced by their connectivity with neighbouring ecosystems, facilitating trophic energy flow and the exchange of nutrients, as well as supporting ontogenetic shifts during the development of commercially important fish species (Cocheret de la Morinière et al., 2003; Nagelkerken et al., 2004; Saenger et al., 2013). The health and presence of mangroves has been shown to have an impact on both the abundance of certain fish species on adjacent reefs, as well as reef

health and resilience (Mumby et al., 2004, 2008). For coastal communities, mangrove ecosystems form a vital resource, and are relied upon for timber, fuel, medicine, and food (Alongi, 2002; Ellison, 2008).

1.1.2 Global Threats to Mangroves

The loss of mangrove forest is an issue of global importance with implications for the myriad of services provided by these ecosystems, and the communities which rely upon them. Mangroves extent has declined at an astounding rate, with estimates for global loss of area as high as 35% between 1980 and 2000, exceeding that of both coral reefs and tropical rainforests (Valiela et al., 2001). It is estimated that if current rates of exploitation continue, mangroves will disappear (at least functionally) within as little as 100 years (Duke et al., 2007). As coastal populations have increased, intensified resource extraction; conversion to aquaculture, agriculture, urban and industrial development; and rising levels of pollution all impact mangrove forest health and extent (Alongi, 2002; Giri et al., 2011; Valiela et al., 2001). Environmental changes linked to global warming – such as sea level rise and increased storm frequency – also have a negative effect (Asbridge et al., 2015; Di Nitto et al., 2014). In recent years, there has been a decline in the rate of mangrove area loss (FAO, 2020), but remaining mangroves are still threatened, with some areas where there has been little recent mangrove loss displaying high levels of degradation through fragmentation (Bryan-Brown et al., 2020). Increased levels of pollution and selective logging can both degrade mangrove ecosystems and impact their functioning, without causing a decrease in their extent (Barbanera et al., 2022; Bartolini et al., 2011; Costa et al., 2015).

1.1.3 Mangrove Forests of Ghana

Ghana has 550 km of coastline with over 100 estuaries and lagoons, and is home to six of the eight true species of mangrove trees found in West Africa (Ryan et al., 2000; UNEP, 2007). Mangroves are present across the coastline of Ghana, with the highest density of sites in the Volta Region in the East (Figure 2). Ghanaian mangroves are known to be of importance as nursery grounds for juvenile fish species (Aheto et al., 2014), which is notable as roughly 10% of the population of Ghana, over 2.6 million people, are reliant on the fisheries sector for their livelihoods (FAO, 2022). While it is known that healthy mangrove forests are important for carbon sequestration, and human physiological health in Ghana (Adotey et al., 2022; Awuku-Sowah et al., 2023), there has been little previous research into the loss of ecosystem functioning and services related to the degradation of mangrove forests in this country.

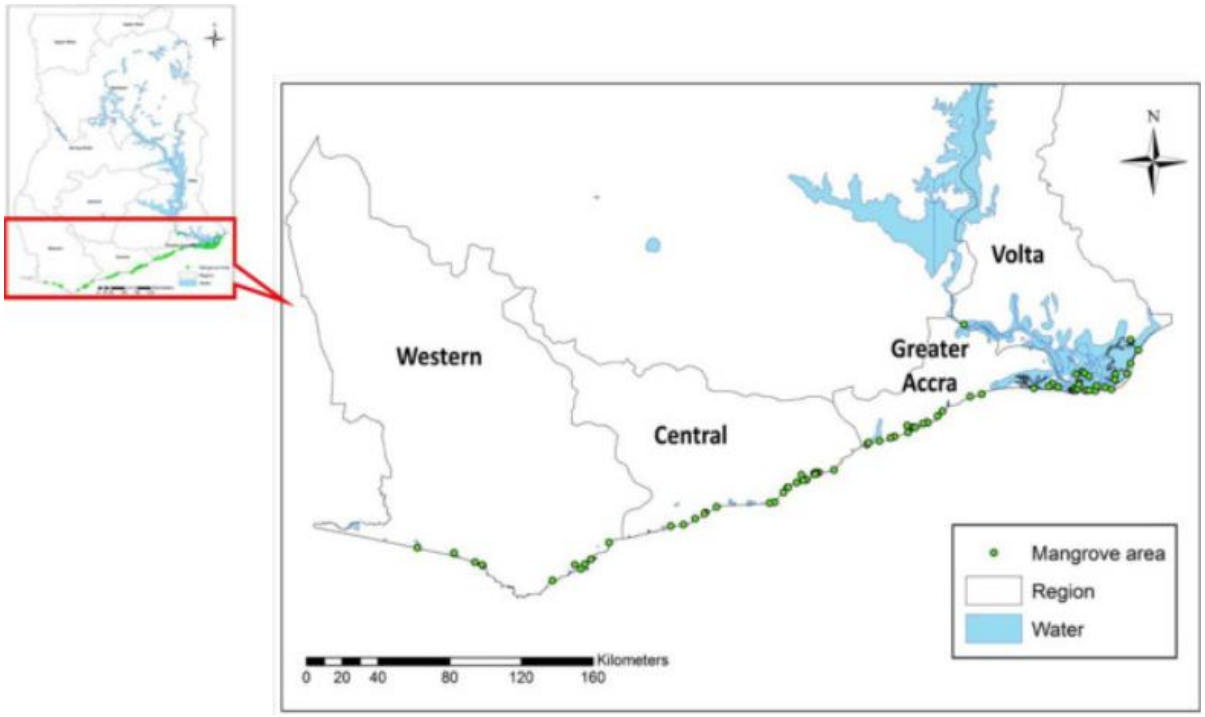

Figure 2: Mangrove locations along the coast of Ghana (Source: Awuku-Sowah et al., 2023)

Coastal development has been identified as the key driver in changes in mangrove forests on the coast of West Central Africa, alongside timber harvesting, conversion for agriculture, and biofuel plantation (Feka et al., 2011). Remaining mangroves can also suffer due to increased pollution from industrial and agricultural run-off, and insufficient sewage disposal, especially in countries where there is less stringent regulation (Adeel et al., 2002). Within Ghana, mangrove extent decreased by 24% between 1980 and 2005 (FAO, 2007) due to deforestation and over exploitation with little or no governmental control (Gordon et al., 2009). Most wetlands and their resources have historically been protected and regulated through traditional community practices in Ghana (Ajonina et al., 2014; UNEP, 2007). However, the rise in population along the coast has led to greater levels of exploitation and pollution in the mangrove forests, with many communities relying on them after losing their traditional source of livelihoods due to displacement (Macintosh et al., 2003). In some rural communities, mangroves are still protected due to their association with gods and spiritual powers (Adupong et al., 2013). However, in urban districts and areas where these old customs have largely been lost, mangroves are widely exploited. This is primarily for wood extraction, which is taking place at a rate that cannot be sustained by current mangrove productivity (Adanguidi et al., 2020). The intensity of this harvesting can alter forest structure and therefore functioning, with tree size, density, and regeneration all lower in sites in West Africa with higher harvesting pressure (Zanvo et al., 2021). The degradation of mangrove forests could have potentially devastating effects on the many vital services that the Ghanaian people rely on from these coastal ecosystems.

1.2 Biodiversity, Ecosystem Functioning, and Ecosystem Services

To explore the effect of ecosystem degradation on the delivery of key services, an understanding of the complex interactions between habitat, biota, and biogeochemical processes within multitrophic communities is required (Raffaelli, 2006; Snelgrove et al., 2014). The cumulation of biophysical and biogeochemical processes within an ecosystem can be described as its functioning, which is driven by the different functional roles or traits exhibited by the species present. This functioning supports the numerous ecosystem services that we as humans gain from the natural environment. The loss of marine vascular vegetation, including mangroves, is known to influence environmental conditions, including sediment grain size, organic matter content, temperature, and salinity (Alongi et al., 2008; Sweetman et al. 2010; Granek et al., 2008; Grellier et al., 2017). These changes can alter the communities present, and thereby influence the processes controlling the flow of energy through these systems (Levin et al., 2006; Sweetman et al., 2010; Whitcraft et al., 2007). Despite West Africa holding 11% of the worlds mangroves and being an area of high concern in terms of deforestation, the impact of native mangrove forest degradation on trophic ecosystem functioning in this region is relatively unstudied (Friess et al., 2019; UNEP, 2007).

1.3 Trophic Ecosystem Functioning

While, as of yet, there have been no studies focusing on how mangrove deforestation might affect fish diets, studies investigating the effects of forest dieback and restoration both display a relationship between canopy cover and the importance of mangrove matter to the food web, linked to changes in crab assemblages and the extent of microphytobenthos (MPB) (Harada et al., 2020; Then et al., 2021). Then et al (2021) found a distinct ecosystem response to mangrove reforestation between 5- and 15-years following deforestation, with a shift from microphytobenthos to mangrove derived organic matter at the base of the food web, coincident with increased canopy cover. This effect was seen most strongly in the crab and gastropod populations, but suspension feeders also displayed an increased mangrove organic matter uptake. Existing on the interface between terrestrial and aquatic systems, mangrove ecosystems may see a big change in trophic structuring with a move from primary producers being predominantly eukaryotic (i.e. mangrove trees) to unicellular (i.e. microphytobenthos). If the loss of mangroves alters the trophic structure in such a way that it becomes more similar to that of pelagic aquatic systems rather than terrestrial forest systems, then we may see changes in the relative importance of bottom-up vs top-down controls on the ecosystem, and therefore the overall ecosystem functioning (Shurin et al., 2005).

Strong synergistic relationships exist between mangrove trees and benthic fauna, influencing organic matter cycling (Kristensen, 2008; Kristensen & Alongi, 2006). The loss of mangroves can result in a

lower availability of labile organic matter within the sediment (Bulmer et al., 2015; Lovelock et al., 2011). As detrital pathways are often highly important in supporting mangrove food webs (e.g. Muro-Torres et al., 2020), the loss of mangroves could disrupt or reduce the flow of energy through the system, even if mangrove-derived organic matter is not a major component of the food web. Habitat degradation and consequential changes to the quality and quantity of detritus could alter numerous aspects of food web structure, including food chain length, prevalence of specialist vs. generalist feeders, and feeding behaviour relating to anti-predatory defences (Calizza et al., 2017; Henderson et al., 2020; Jaxion-Harm et al., 2012; Shurin et al., 2005). This, in turn, could lead to greater competition, and lower community stability (Calizza et al., 2017). There is also the potential for negative feedback cycles, where the loss of trophic diversity triggers a top-down cascade, reducing ecosystem functioning in terms of leaf litter decomposition and the cycling of nutrients (Jabiol et al., 2013; Wolkovich et al., 2014). It is therefore necessary to investigate differences in the importance of detrital and pelagic energy flow pathways within estuarine food webs with different degrees of mangrove degradation, as well as differences in trophic positioning and niche of the consumers reliant on these energy flow pathways.

The potential for mangrove deforestation to influence food webs is not only limited to their utilisation as a basal resource. As ecosystem engineers trapping allochthonous materials within their root and root-fibre matrix, mangroves can facilitate the inclusion of a more diverse range of basal resources within estuarine food webs, thereby increasing the trophic diversity present (Furukawa et al., 1997; Layman et al., 2007). As a biogenic structure, mangroves not only act as a nursery habitat for juveniles of many species, but also form a foraging habitat for others, while not necessarily acting as a food source to either (Nagelkerken et al., 2002; Sheaves et al., 2000). To assess the effect of mangrove loss on community wide trophic structure, the diversity of energy flow pathways, and redundancy of trophic niches can be compared using quantitive metrics describing the spread of taxa within isotopic niche space, based on the ratios of stable isotopes within their tissues (A. L. Jackson et al., 2011; Layman et al., 2007). A number of studies have investigated the effect of mangrove loss on community wide trophic structure, the diversity of energy flow pathways, and redundancy of trophic niches, and while all saw an effect of mangrove removal of community wide trophic structure, the nature of the effect was different. To date, no studies exist investigating the impact of mangrove loss on the community wide trophic structure of estuarine systems in West Africa. It is possible that the degradation of mangroves in this region may affect the trophic structure and resilience of these coastal ecosystems.

2 Methodology

2.1 Study Sites

Three study sites with varying degrees of mangrove loss were identified along the coast of Ghana for the comparison of benthic and trophic ecosystem functioning (Figure 3). These sites were all estuarine in nature, and of a relatively similar size (approximately 1.5km^2) and mangrove species composition. Two sites where selected in the Central region, located in the dry equatorial zone, where wet season maxima are from May to June and September to October, with a mean annual rainfall and temperature of 100mm and 27℃, respectively (Adotey et al., 2022). A third site was identified in the Western region, which is in the wet equatorial climate zone where wet season maxima are from May to June and October to November, and the average rainfall and temperature are 1600mm and 26℃ respectively (Ajonina et al., 2014). Two rounds of sampling were conducted in 2022, between 18/02/22 and 27/03/22 during the dry season, and 04/10/22 to 28/10/22 to capture the wet season in both regions. The Amanzule Estuary, in the Western region of Ghana, was identified as a relatively pristine site with mature forest and low anthropogenic pressure, partially due to the protection it has received through local customs for many years (Adupong et al., 2013) (Figure 3 A). This site is within the Ellembelle district, which has a population density of 121 people per km^2, based off the 2021 population census (Ghana Statistical Service, 2021). The Kakum Estuary is situated between Elmina and Cape Coast, in the Central Region of Ghana, and has been subject to long term resource exploitation, resulting in patchy, stunted, mangrove forest (Figure 3 B). The majority of the Estuary is within the Cape Coast Metropolitan district, which has a population density of 1557 people per km^2 (Ghana Statistical Service, 2021). Also in the Central region, the Narkwa Estuary has very few mangroves and is largely covered by mud and sand flats and was chosen as a control site (Figure 3 C). This site is subject to pollution from domestic waste, resulting in poor water quality (Takyi et al., 2022). The Narkwa Estuary sits within the Ekumfi district, which has a population density of 210 people per km^2 (Ghana Statistical Service, 2021).

Forest structure parameters of canopy cover, tree species, height, and diameter at breast height (dbh) (Table 1) were recorded in three 5x5m plots at each of the sites, following methods described by Kauffman and Donato (2012). Plot locations were chosen to be representative of the forest conditions along the mangrove-water interface at each site.

Table 1: Forest structure parameters from Amanzule (healthy mangrove forest), Kakum (degraded mangrove forest), and Narkwa (sand/mudflat with very sparse mangroves). Mean (± sd) canopy cover (%), tree height (m), and diameter at breast height (dbh) (cm), taken from measurements at three 5x5m plots at each of the sites

	CANOPY COVER (%)	HEIGHT (M)	DBH (CM)
AMANZULE	79.58 ± 6.32	7.08 ± 3.27	7.79 ± 4.66
KAKUM	18.42 ± 24.1	2.57 ± 1.21	5.18 ± 3.15
NARKWA	2 ± 4.47	1.18 ± 1.59	3.02 ± 4.81

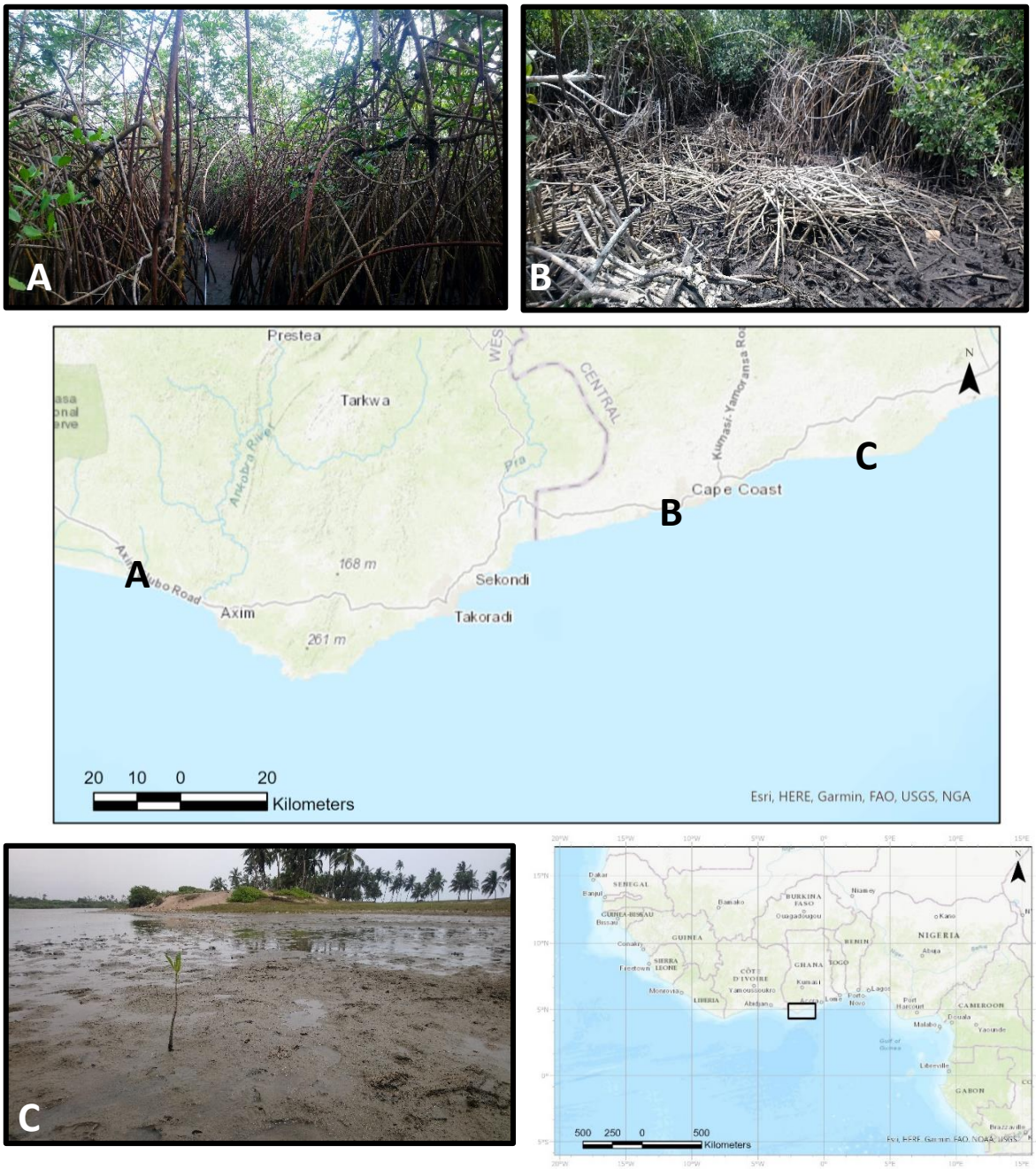

Figure 3: Study site locations along the coastline of Ghana. A - Amanzule, healthy mangrove forest; B - Kakum, mangrove forest subject to long term exploitation; C - Narkwa, a mudflat control site with few mangroves.

2.2 Sample Collection

2.2.1 Basal Resources

Mangrove leaves were collected at various stages of senescence, as their isotopic ratios and lability are known to vary between green, yellow, and decomposing brown leaves (Fourqurean et al., 2003). Samples of other abundant vegetation present at the different sites were also collected and identified with help of staff at the botanical department at the University of Cape Coast. These samples were dried at air temperature (30℃) for 4 days. Macroalgae samples were collected where present, and then cleaned of debris by hand under a dissecting microscope before being freeze dried. Surface sediment samples were taken for stable isotope analysis of the particulate organic matter. Sediments for $\delta^{13}C$ analysis were decalcified using 2M HCL. Where a conspicuous layer of microphytobenthos (MPB) was observed, sediment samples were collected. The MPB was extracted using Ludox (Levin et al., 2012) and filtered onto pre combusted (550°C for 1 hour) GF/F Whatman filters before being freeze dried. To collect phytoplankton and other suspended particulate organic matter (SPOM), a hand-held plankton net (20µm mesh) was dragged behind a small boat at ~2 knots for 10 mins, three times at each site, covering the target area. All samples were kept on ice for transport back to the laboratory. The filtrate from the plankton net drag was filtered through a 200µm mesh sieve in an attempt to separate the phytoplankton from other suspended matter (Levin et al., 2012). Both size fractions where then filtered onto pre combusted (550°C x 1 hour) GF/F Whatman filters and freeze dried. For all samples captured on filters, sections intended for $\delta^{13}C$ analysis were decalcified by fumigation with 2M HCL.

2.2.2 Consumers

Fish and larger invertebrates were sampled opportunistically, with larger invertebrates including oysters, gastropods, and crabs collected by hand where present. Fish and swimming crabs were brought from local artisanal fishers when they were observed fishing in the target areas. Fishing methods were recorded where possible, with a mixture of cast, seine, and gill netting used, and a mixture of methods at each site. Where possible, samples were collected on more than one day at each site to account for inter-diel variation caused by transient species. All samples were kept on ice for transport back to the laboratory. Individuals were identified, photographed, measured, and weighed, before being dissected for samples of white muscle tissue, which is known to be less variable in $\delta^{13}C$ and $\delta^{15}N$ than any other tissue (Pinnegar et al., 1999). All muscle tissue samples were then freeze dried for transport back to the UK. Back in the UK, samples were homogenised (and decalcified where necessary) before being analysed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ using IRMS analysis. Dry season samples are in the process of being analysed at NERCs National Environmental Isotope Facility, using a Thermo Delta V with EA IsoLink GC-IRMS, with various USGS and other standards. Results from this

facility have been delayed due to technical issues with their IsoLink machine, and consequently it was not possible to include them within this report. Wet season samples were analysed at the University of Southampton, on a Elementar Vario PyroCube Thermal Conversion Elemental Analyser interfaced with an Isoprime GeoVisION continuous flow IRMS. Vienna Pee Dee Belemnite (VPDB) was used as a reference material for $\delta^{13}C$, air N_2 for $\delta^{15}N$, and Canyon Diablo Troilite (CDT) for $\delta^{34}S$. Sulphur isotope data has been included to help distinguish between benthic and pelagic primary producers, and has been shown to separate producers with similar δ13C and δ15N values in over 40% of cases (Connolly et al., 2004).

2.3 Analysis

2.3.1 Consumer Trophic Positioning

All analyses were conducted in the R statistical programming environment (R Core Team, 2021). The isotopic signatures incorporated into the tissues of consumers can be altered relative to that of their prey, and the extent of this can be influenced by several factors including species, protein content of diet, and tissue type sampled (Caut et al., 2009; McCutchan et al., 2003; Stephens et al., 2022). This can be corrected for through the use of trophic discrimination factors (TDFs), which are subtracted from the isotope values of basal resources potentially contributing to the diet of a consumer. However, specific TDFs for consumers are typically unknown, and have been shown to be more variable between taxon, environment, and sample tissue than previously thought (Caut et al., 2009). As such, it is important to be aware of the sensitivity of results to variations in TDFs. The trophic position of the different taxa was estimated using the two baseline, full Bayesian model within the "*tRophicPosition*" package (version 0.8.0) in R (Quezada-Romegialli et al., 2022). This model allows for the inclusion of two baselines (terrestrial and aquatic basal resources) and TDFs for both nitrogen and carbon, as well as accounting for the variance associated with both of these (Quezada-Romegialli et al., 2018). To account for differences in discrimination factors based on protein in consumer diets, TDFs were applied based on consumer trophic guild using values from the McCutchan et al., (2003) meta-analysis (Table 2). A more recent meta-analysis of TDFs was considered, but the higher mean values appeared to be incompatible with this study when compared with local source and consumer stable isotope values (Stephens et al., 2022). To account for the variability of TDFs, as described above, the standard deviation of the TDFs was increased four-fold relative to the McCutchan values.

Table 2: *Trophic guild assignations for species sampled in the wet season, and Trophic Discrimination Factors used for each guild within the tRophic Position Model*

Species	Guild	Description	TDF-δ13C	TDF-δ15N	TDF-δ34S

Littorina angulifera (Mangrove periwinkle)	Herbivores	Feeding on vegetation	2.2 1.2	±	0.5 0.76	±	-0.5 2.6	±
Crassostrea tulipa (West African Mangrove Oyster) Ethmalosa fimbriata (Bonga shad)	Suspension Feeders	Feeding on Suspended organic matter	2.2 1.2	±	0.5 0.76	±	-0.5 2.6	±
Mugil sp. (Mullet) *Liza sp.* (Thinned lipped mullet) *Uca tangeri* (West African fiddler crab)	Detritivores	Feeding on detritus and associated microbial communities	2.2 0.8	±	0.5 0.56	±	1.9 1.68	±
Chiromantes angolense (Angola marsh crab) *Cardisoma armatum* (Lagoon land crab) *Penaeus* sp. (Penaeid prawn) *Carlarius* sp. (Sea catfish) *Coptodon zillii* (Redbelly tilapia) *Guinearma huzardi* (Red mangrove crab)	Omnivores	A mixture of carnivorous, detritivorous, and herbivorous tendencies	2.2 0.8	±	0.5 0.56	±	1.9 1.68	±
Periophthalmus barbarus (Atlantic mudskipper) *Sarotherodon melanotheron* (Blackchin tilapia) *Eucinostomus melanopterus* (Flagfin mojarra) *Dicologlossa cuneata* (Flatfish) *Pomadasys jubelini* (Sompat grunt)	Zoobenthivores	Carnivores feeding primarily on benthic fauna	2.4 0.88	±	0.6 0.64	±	1.9 2.04	±
Monodactylus sebae (African moony) *Pseudotolithus elongatus* (Bobo croaker) *Carlarius Gigas* (Freshwater Catfish) *Gobioides* sp. (Gobbie) *Lutjanus goreensis* (Gorean snapper) *Caranx* sp. (Jack) *Eleotris* sp. (Sleeper Gobie)	Carnivores	Generalist carnivores, including piscivores, molluscivores and invertivores.	2.4 0.88	±	0.6 0.64	±	1.9 2.04	±

Taxa were grouped into trophic guilds based on information in the literature (Table 2) (Carpenter et al., 2016; Dall et al., 1991; Froese et al., 2000; Longonje et al., 2014; Simier et al., 2021; Wolfrath, 1992). These groupings were then compared with those achieved through hierarchical cluster analysis (95% similarity) using Ward linkage on a Euclidean distance matrix, constructed from scaled stable isotope data.

To investigate differences in diet and the importance of different energy flow pathways between sites with varying degrees of mangrove loss, the contribution of different basal resources to the diet of consumers within each trophic guild will be estimated using Bayesian mixing models using the "*MixSIAR*" package (version 3.1.12) in R (Stock et al., 2018), including the residual and process error terms (Parnell et al., 2010; Stock et al., 2016). Unfortunately, due to delays in getting the full data set back from the stable isotope analysis facilities, these analyses are still being conducted and cannot be included in this report. Prior to running mixing models, consumer $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ signatures were checked for outliers using the Stable Isotope Mixing Polygon Simulation R script, which provides a quantitative basis for consumer exclusion and the correction of trophic discrimination factors in three-isotope systems (Smith et al., 2013). Only consumers that fell within the 95% mixing region were suitable for inclusion in the mixing models using the selected basal resources and trophic discrimination factors.

2.3.2 Niche Size and Overlap

To determine whether mangrove degradation influenced the niche width of different consumer groups, the three dimensional isotope data were used to quantifying the size and overlap of isotopic niches between trophic guilds using a Bayesian framework in the package "*nicheROVER*" (version 1.1.0.) (Lysy et al., 2021). This allows for the inclusion of a third isotope value, which reduces the risk of uncertainty relating to a 2D concept of niche overlap, such as defining the directionality of overlap between two groups by estimating the probability of one group falling in the niche of another (Swanson et al., 2015). Three-dimensional Bayesian elliptical niche regions were estimated for each trophic guild at each site by randomly selecting paired $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values using the default prior (Normal-Inverse-Wishart distribution). The probability of a randomly drawn individual from one trophic guild falling within the niche region of another was estimated using a Monte Carlo technique (Swanson et al., 2015). Little or no overlap in isotopic niches may indicate consumers have specialised and distinct dietary niches, while a high degree of overlap may indicate increased competition for limited resources. The suggested default value of α = 95% was used, though the sensitivity of the results to lower values of α was tested.

2.3.3 Community-Wide Trophic Structure

To characterise and compare community-wide trophic structure, a number of quantitative metrics can be calculated from the spread of mean stable isotope values for each group in 'isotopic niche space' (Layman et al., 2007). The total area of the convex hull encompassing all species (TA), and the average distance of each point to the centroid (CD) represent the spacing of species and the niche width occupied by the community. The $\delta^{15}N$ range (NR), suggests the presence of more trophic levels, while the $\delta^{13}C$ range (CR) represents the diversity of basal food sources, with a wider range reflecting a

higher number of food sources with distinct isotope signatures. The mean nearest neighbour distance (MNND) and the standard deviation of nearest neighbour distance (SDNND) measure the density and evenness of species packing, respectively.

One issue that has been identified with these 'Layman metrics' is that they vary with sample size and are therefore not reliable for comparisons between sites or season. A Bayesian approach to applying these metrics has been developed, which is less sensitive to variation in the number of groups (Jackson et al., 2011). This package, SIBER, also allows the full range of values for each group to be used, rather than just the mean, producing a posterior distribution of estimates for each Layman metric, thereby providing a measure of uncertainty in the results. Rather than calculating the TA, which encompasses all of the data and therefore is highly sensitive to sample size, SIBER quantifies the overall trophic diversity using Bayesian standard ellipse areas (SEA_B) which provide a better basis for comparison of community isotopic niche between sites than TA (Jackson et al., 2011). SEA_B, CD, NR, CR, MNND, and SDNND metrics were calculated for each community, grouping individuals by species, using the "*SIBER"* package (version 2.1.7.) in R (Jackson and Parnell, 2023).

3 Results

3.1 Stable Isotope Values of Food Sources

The stable isotope ratios of basal resources sampled in this study fell with the ranges seen within other studies (Henriques et al., 2021; Medina-Contreras et al., 2020; Nyunja et al., 2009; Sandoval et al., 2022; Viana et al., 2015). Sources at Narkwa (the sand/mudflat site) had the largest range of $\delta^{13}C$ values, from -27.9‰ to -6.8‰, compared to -32.5‰ to -12.2‰ at Amanzule (healthy mangroves) and -30.1‰ to -12.8‰ at Kakum (degraded mangroves). This was not the case for $\delta^{15}N$ values, which had the lowest range at Narkwa (4.2‰ to 7.8‰) compared with Amanzule (-0.4‰ to 7.2‰) and Kakum (1‰ to 8.53‰). The $\delta^{34}S$ range was greatest in the sources from Kakum (-16.8‰ to 21.11‰), followed by Amanzule (-13‰ to 20‰), and then Narkwa (-6‰ to 19.7‰). There are a small number of additional source samples yet to be analysed from Narkwa, which may increase the range of stable isotope values seen at this site. At Amanzule and Kakum (the healthy and selectively deforested sites) the stable isotope values for sediment organic matter were very close to that of the mangroves, while at Narkwa (the sand/mudflat site) they were more variable between samples, and closer in value to that of the terrestrial plants, indicating that mangrove organic matter makes up far less of the detrital pool at this site (to be expected given that there are very few mangroves there).

Table 3: Stable isotope values for source groups at each site (mean ± sd)

	Amanzule				Kakum				Narkwa			
	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)	n
Detritus	-26.44 ± 1.04	2.79 ± 0.3	-11.58 ± 1.29	3	-27.51 ± 0.12	4.45 ± 0.74	-11.74 ± 5.21	3	-9.21 ± 3.61	5.24 ± 0.32	-1.59 ± 4.75	3
Green Macroalgae	-22.01 ± 2.07	3.89 ± 1.42	19.21 ± 0.07	2	-18.52 ± 0.99	8.17 ± 0.52	20.79 ± 0.46	2				
Brown Macroalgae	-15.08 ± 0.29	2.05 ± 0.17	19.52 ± 0.57	3					-18.41 ± 0.06	7.66 ± 0.11	16.83 ± 0.59	3
Mangrove (C3 plants)	-30.23 ± 1.07	2.26 ± 1.4	4.97 ± 8.07	24	-27.95 ± 1.34	3.8 ± 0.87	7.91 ± 7.95	21	-27.04 ± 0.49	5.77 ± 0.48	17.06 ± 1.28	9
Terrestrial (C4 plants)	-12.7 ± 0.41	6.44 ± 1.13	16.7 ± 0.94	3	-13.34 ± 0.45	1.99 ± 1	10.29 ± 5.72	6	-16.29 ± 2.42	4.85 ± 0.68	18.37 ± 1.35	6

3.2 Stable Isotope Values of Consumers

Consumers were grouped by trophic guild based off of information in the literature and are outlined in Table 4. When grouped by HCA based on their stable isotope values, the resulting clusters matched fairly closely with the a priori guild assignations. This was particularly true at Amanzule, where there

was clearly a greater distinction between groups (Figures 3 & 4). As such, the *a priori* groupings were maintained. The grouping of species within trophic guilds at each site is displayed in Table 4

Table 4: Mean (± SD) stable isotope values for consumers sampled at the three sites during the wet season.

		n	δ13C (‰)	δ15N (‰)	δ34S (‰)
Amanzule					
Herbivore	Mangrove Periwinkle	10	-25 ± 0.51	3.22 ± 1.23	17.4 ± 0.87
Omnivore	Angola Marsh Crab	10	-24.1 ± 1.2	7.49 ± 3.1	13.7 ± 2.9
	Sea Catfish	9	-22.1 ± 2.36	10.7 ± 1.33	12.3 ± 2.84
Suspension Feeder	West African Mangrove Oyster	10	-16.7 ± 0.26	9.05 ± 0.34	14.9 ± 0.37
Detritivore	Mullet	10	-14.9 ± 0.81	10.8 ± 0.47	15.2 ± 1.13
	Thinned Lipped Mullet	10	-16.2 ± 2.62	11.4 ± 0.72	15.6 ± 1.55
Zoobenthivore	Sompat Grunt	10	-18 ± 1.13	12.1 ± 0.51	16.1 ± 1.54
Carnivore	Bobo Croaker	7	-18.4 ± 0.28	11.7 ± 0.095	17.9 ± 0.46
	African Moony	8	-18.2 ± 0.41	12.3 ± 0.39	18.1 ± 0.5
Kakum					
Omnivore	Angola Marsh Crab	9	-20.3 ± 1.16	8.25 ± 1.94	14.7 ± 1.13
	Red Mangrove Crab	10	-20.6 ± 2.4	11.8 ± 2.83	13 ± 2.14
	Lagoon Land Crab	10	-22 ± 1.06	12.9 ± 2.63	8.57 ± 3.14
	Redbelly Tilapia	10	-21.3 ± 1.34	14.9 ± 3.99	13.8 ± 2.64
	Blackchin Tilapia	10	-22.8 ± 2.03	16.3 ± 1.41	13.8 ± 2.33
Suspension Feeder	Bonga Shad	10	-18.3 ± 0.32	12.9 ± 0.39	17.9 ± 0.48
Detritivore	West African Fiddler Crab	10	-18.6 ± 1.2	6.88 ± 1.65	13.9 ± 1.09
	Mullet	10	-18.4 ± 2.34	12.9 ± 2.81	12.5 ± 1.83
Zoobenthivore	Flatfish	8	-19 ± 0.38	12 ± 0.25	18.1 ± 0.43
	Flagfin Mojarra	10	-21.2 ± 1.56	14 ± 2.38	12 ± 2.63
Carnivore	Freshwater Catfish	10	-22.2 ± 1.32	14.4 ± 0.72	13.6 ± 0.59
Narkwa					
Omnivore	Penaeid Prawn	10	-16.2 ± 1.82	9.66 ± 0.78	8.4 ± 2.62
	Blackchin Tilapia	10	-16.8 ± 1.23	10.4 ± 0.94	12.5 ± 3.06
Suspension Feeder	West African Mangrove Oyster	10	-16.5 ± 2.48	9.65 ± 0.88	15.7 ± 1.63
	Bonga Shad	10	-17.7 ± 1.17	11.9 ± 1.12	15.3 ± 3.2
Detritivore	Gobbie	10	-12.8 ± 3.27	6.97 ± 2.07	7.77 ± 5.51
	West African Fiddler Crab	10	-15.1 ± 4.2	8.34 ± 1.65	13.3 ± 2.62
	Mullet	10	-19.9 ± 4.8	11.4 ± 2.97	12.2 ± 3.52
Zoobenthivore	Atlantic Mudskipper	10	-14.2 ± 0.57	8.94 ± 2.01	8.54 ± 2.51
	Flatfish	10	-16 ± 1.16	11.4 ± 0.64	14.9 ± 3.28
	Flagfin Mojarra	10	-16.2 ± 1.36	13.3 ± 1.26	13.7 ± 1.44

Carnivore	Sleeper Gobie	10	-16.6 ± 1.13	11.4 ± 0.63	14.6 ± 1.24
	Jacks	10	-18 ± 0.85	11.5 ± 0.37	17.4 ± 0.75
	Gorean Snapper	10	-18.3 ± 1.4	12.2 ± 0.58	17.7 ± 2.4

Consumer stable isotope values fell within a broadly similar range between the three sites. Kakum had a higher mean δ15N, of 12.5 ‰, but a similar range (14.3‰) when compared with that of Amanzule (15.1‰) and Narkwa (14.3‰). Kakum and Amanzule had similar mean δ13C values (-20.5‰ and -19.3‰ respectively), and $\delta^{13}C$ ranges (11.8‰ and 13.5‰ respectively). Narkwa had a lower mean $\delta^{13}C$ of -16.5‰, and a larger range of 17.6‰. Mean consumer $\delta^{34}S$ was slightly higher at Amanzule (15.6‰), compared to that of Kakum (13.7‰) and Narkwa (13.2‰). Amanzule had the smallest $\delta^{34}S$ range, of 13.7‰, compared to 15.5‰ at Kakum, and 16.4‰ at Narkwa.

Amanzule appears to have quite a distinct trophic structure (Figures 4 & 5, A), with consumers in most trophic guilds displaying small isotopic niches, indicative of specialised feeding behaviour. Consumers of all guilds except for the omnivores also appear to be feeding at distinct trophic levels, as indicated by the groupings across the $\delta^{15}N$ range. The herbivores form the lowest trophic level, followed by the omnivores which span a wide range of $\delta^{15}N$ values, and then followed by the suspension feeders, detritivores, zoobenthivores and carnivores. At Kakum and Narkwa, however, most trophic guilds appear to occupy a much broader isotopic niche, spanning a wide range of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values (Figures 4 & 5, B & C). The mean stable isotope range within species was higher at Narkwa and Kakum, compared with Amanzule for all three stable isotopes. A pattern of larger intraspecies variation in all three stable isotope values moving successively from Amanzule to Kakum and then Narkwa can be seen for species within the detritivore, carnivore, zoobenthivore, and suspension feeder guilds. This indicates that these species adopt a more generalist feeding strategy at sites with lower mangrove cover. This pattern is most clear within the detritivore guild. It is a possibility that the wider range of $\delta^{13}C$ values for detritus at Narkwa has artificially increased the range of its consumers, without being indicative of an increased range of food sources exploited. However, this is not likely to be the case at Kakum, where the detritus has a narrower range of $\delta^{13}C$ values than at Amanzule.

There are fewer species within the carnivore trophic guild at Kakum than at Amanzule. Despite this, the spread of the consumer values within the isotopic biplots is larger at Kakum than at Amanzule, driven by greater intraspecies variation in isotope values for the carnivore species at Kakum than those at Amanzule. Differences in the zoobenthivore niche size between Amanzule and Kakum were largely driven by the broad niche of the Flagfin Mojarra (*Eucinostomus melanopterus*), which was only present at Kakum (Table 4).

Differences in the isotopic niche of the omnivore guild between sites appears to be driven more so by the number of species sampled at each site, rather than differences in the niche sizes of those species. The variability of stable isotope values was fairly similar across the three sites, with differences in species mean stable isotope values causing greater inter-site differences in guild niche size. Omnivorous species had similar variability within their stable isotope values at all three sites, aside for those for $\delta^{15}N$ at Narkwa, which were slightly smaller than those at the other sites (Table 4), indicating that the omnivorous species present at Narkwa occupied a more limited range of trophic positions compared to those at the other two sites. At Amanzule, the omnivorous species had higher intra-species variation in stable isotope values compared to species belonging to the other guilds. It is possible that omnivorous species present at the less degraded sites had already adopted generalist feeding strategies, so there would be little difference seen in their niche size between the sites.

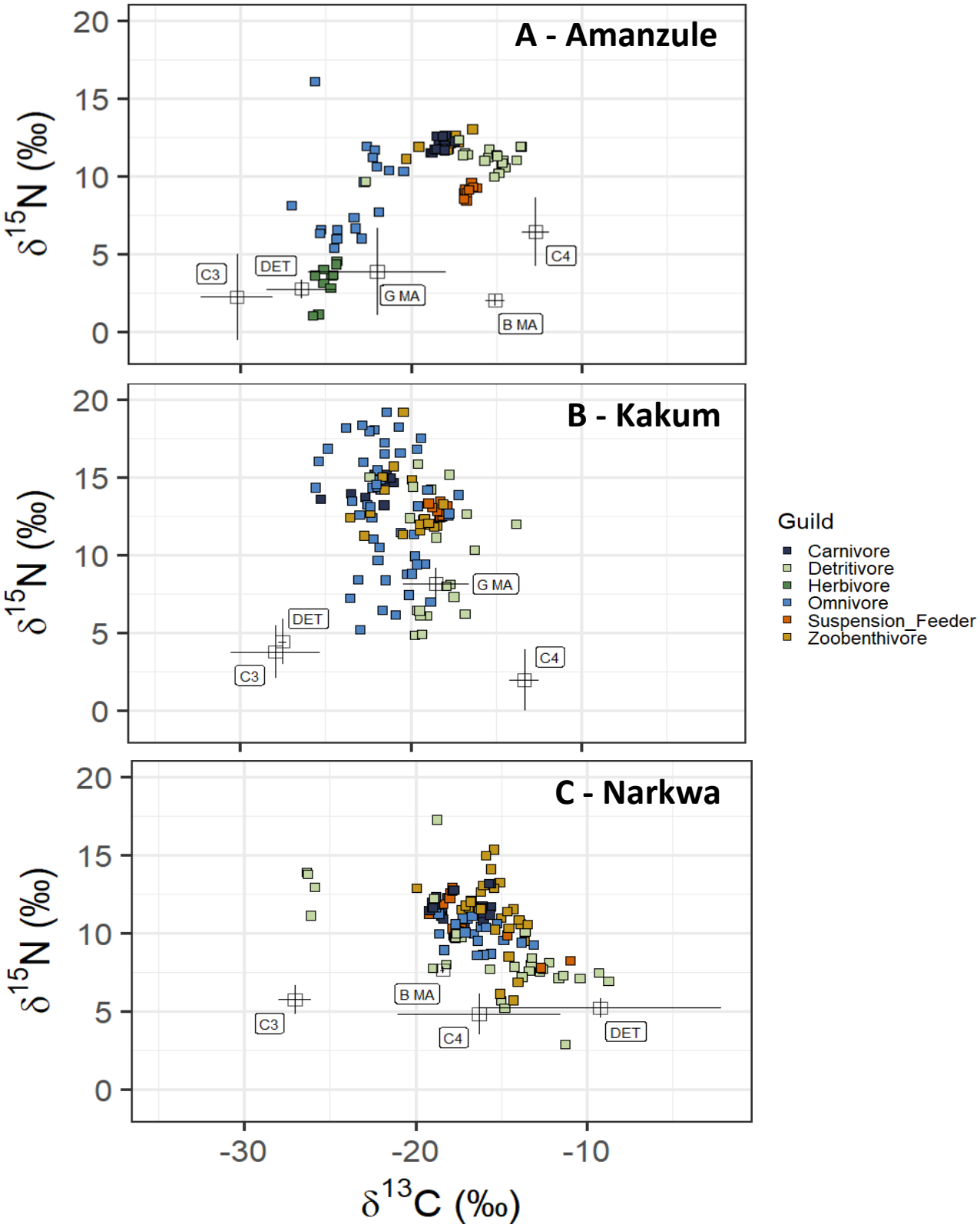

Figure 4: Isospace biplots for Amanzule (healthy mangroves), Kakum (degraded mangroves), and Narkwa (sand/mudflat) wet season communities. The $\delta^{13}C$ and $\delta^{15}N$ signatures of consumers are shown as coloured boxes, grouped by trophic guild. Mean values for the grouped food sources are displayed in labelled boxes, with the error bars representing the 95% confidence intervals. C3 = Mangrove (C3 Plants); C4 = Terrestrial (C4 Plants); DET = Detritus; B MA = Brown Macroalgae; G MA = Green Macroalgae. No corrections for trophic discrimination factors applied in this figure.

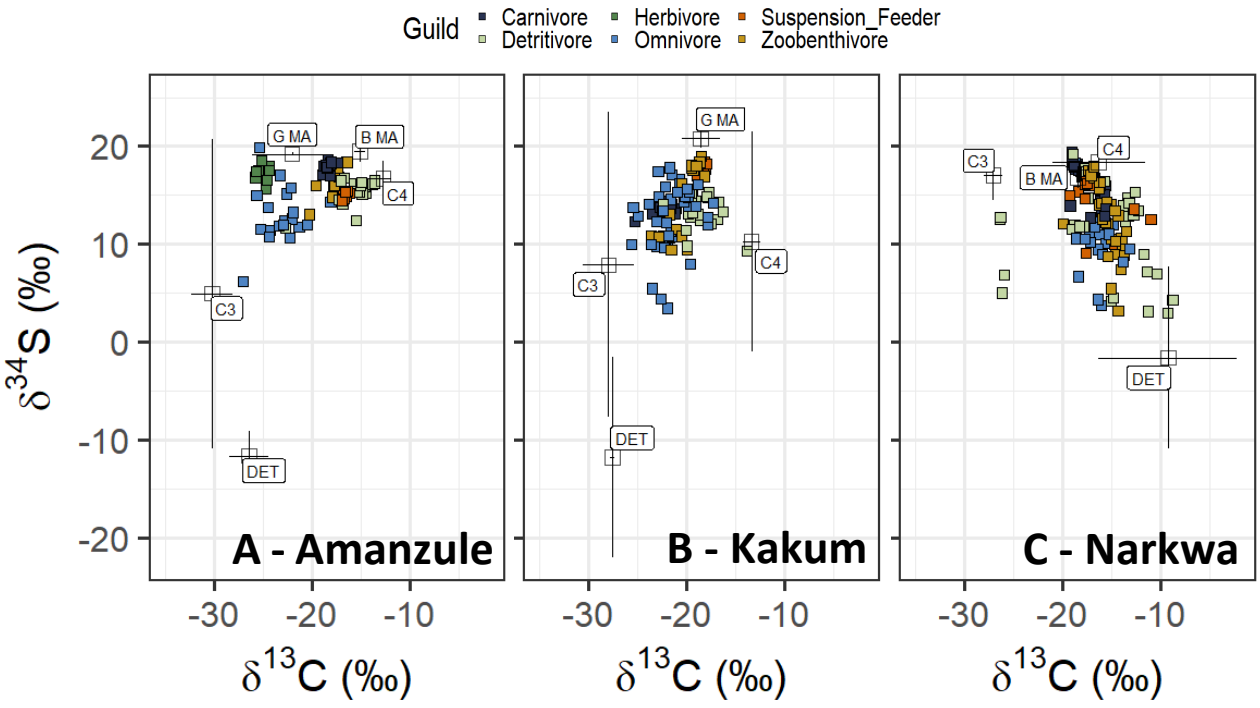

Figure 5: Isospace biplots for Amanzule (healthy mangroves), Kakum (degraded mangroves), and Narkwa (sand/mudflat) wet season communities. The $\delta^{13}C$ and $\delta^{34}S$ signatures of consumers are shown as coloured boxes, grouped by trophic guild. Mean values for the grouped food sources are displayed in labelled boxes, with the error bars representing the 95% confidence intervals. C3 = Mangrove (C3 Plants); C4 = Terrestrial (C4 Plants); DET = Detritus; B MA = Brown Macroalgae; G MA = Green Macroalgae. No corrections for trophic discrimination factors applied in this figure.

3.3 Isotopic Niche

At Amanzule and Kakum, the relative niche size of the trophic guilds followed a distinct pattern, with suspension feeders having the smallest niche, followed by the carnivores, zoobenthivores, detritivores, and then omnivores (Figure 6, A & B). In all cases, there was a probability of over 80% that each consecutive guild would have a larger niche region than the last. This pattern was not seen at Narkwa, where carnivores, omnivores, suspension feeders, and then zoobenthivores had consecutively larger niche sizes, with detritivores being largest by far (Figure 6, C). The niche regions of each trophic guild estimated through "*NicheROVER*" were significantly different from others within the same site, all with a large effect size ($p < 2x10^{-16}$, Cohen's $d > 1$). Effect size was checked to ensure that highly significant results were grounded in ecologically meaningful differences and not just a product of large posterior sample sizes ($n=10^3$). Statistical comparisons of guild niche size between sites were not made due to uncertainties in the potential effect of the variable ranges in the stable isotope values of available food sources on the values of consumers. However, it is clear that all guilds had a larger niche size at Kakum (the degraded mangrove site) when compared to their counterparts at Amanzule (the healthy mangrove site) (Figure 6), despite the food sources at Kakum having a 14.8% smaller $\delta^{13}C$ range.

In general, we see greater distinction in niche regions at Amanzule, compared to the more degraded sites. The probability of overlap between different trophic groups is lower than at the other sites, and notably, there are no instances where the niche region of one group is entirely within that of another. At Amanzule, there is a 14.12 ± 11.64% probability that an individual from the trophic group detritivore will be in the omnivore niche space, while at Kakum there is a 74.17 ± 10.75 % probability of this occurring (α = 95%). At Narkwa, this is lower again, at 16.99 ± 4.59 %, but the probability of an omnivore being found in the niche space of the detritivores is far higher than at the other sites, at 99.37 ± 1.28 % (See Tables 5-7). It is clear from both figures 5 & 6 that this can be explained by the niche regions of these trophic guilds at the different sites. At Amanzule, the omnivores have by far the largest niche region, with the detritivores displaying a partially distinct niche region, with a higher range of $\delta^{13}C$ values, indicative of a greater dietary contribution of marine algae's and C4 terrestrial plants (Figure 7). At Kakum, these two guilds have a similar niche region (Figure 6), and a broadly similar positioning in niche space (Figure 7). At Narkwa, the niche region of the omnivores is entirely encompassed by that of the detritivores, explaining the directionality of the probabilities of overlap between these two guilds.

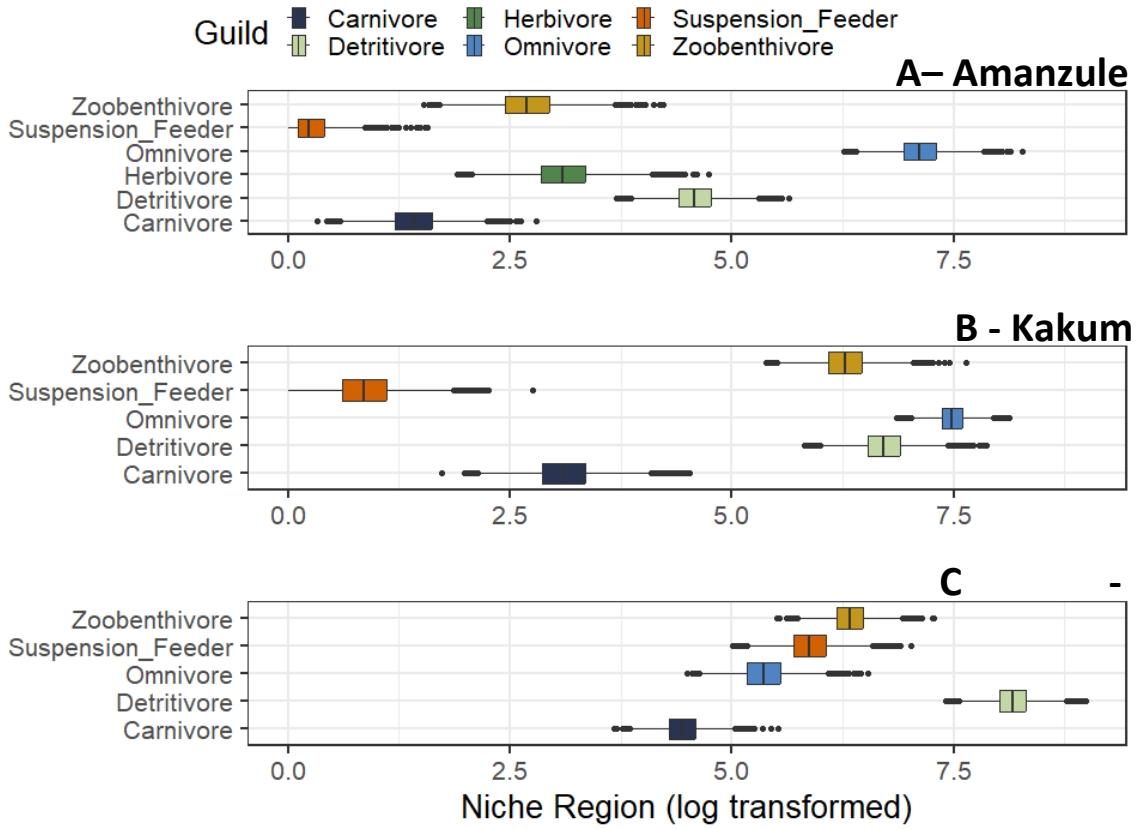

Figure 6: Niche region for trophic groups at Amanzule (healthy mangroves), Kakum (Degraded Forest), and Narkwa (sand/mudflat) wet season communities. Data were produced from 10^3 posterior estimates of probabilistic niche region, based off of all three stable isotope values for each consumer, and log transformed.

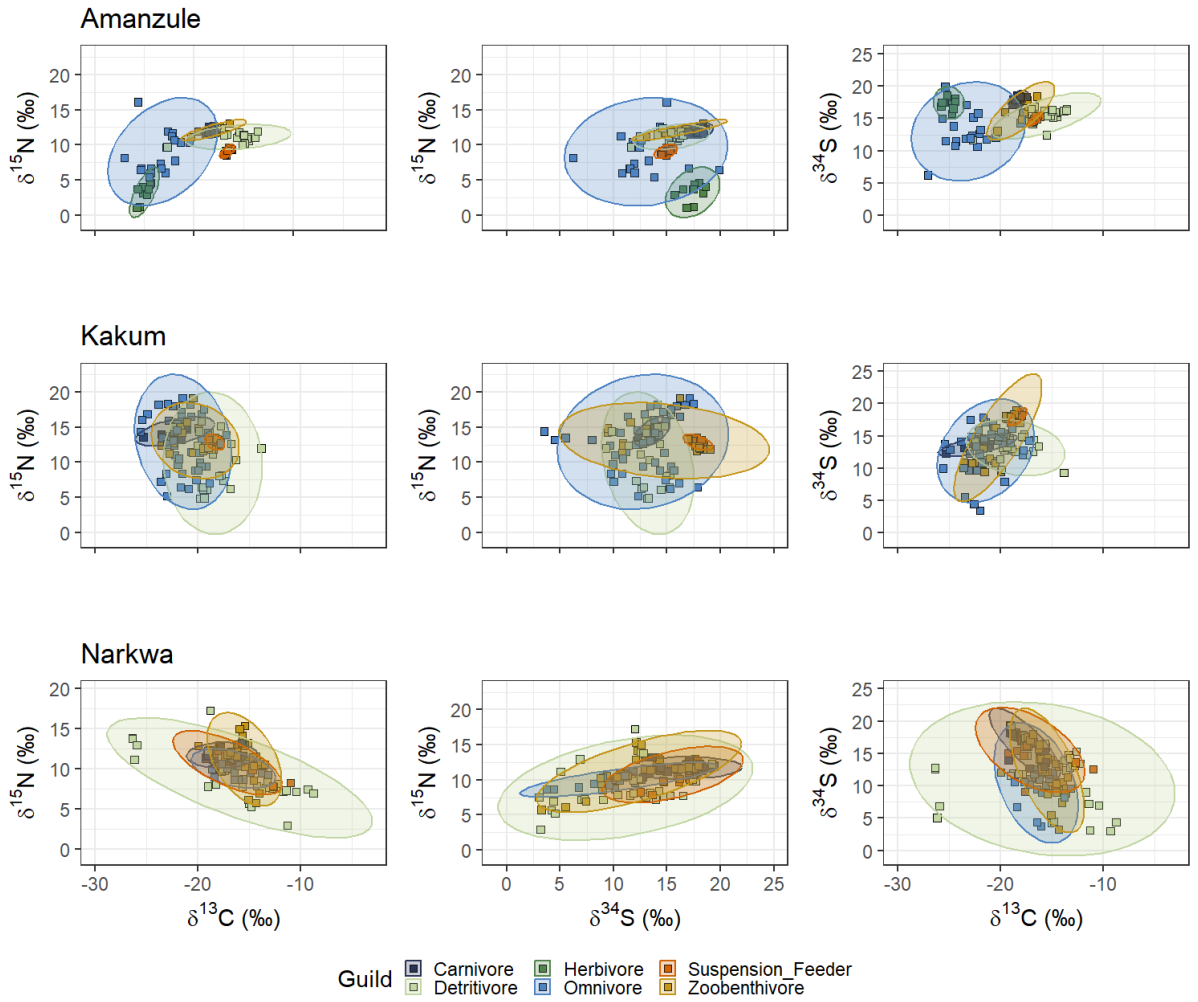

Figure 7: Isospace biplots for C/N, S/N, C/S with consumer values and trophic group 95% confidence interval ellipses plotted.

At Narkwa, the niche size of the detritivores is not only larger than that of all the other guilds, but also almost entirely encompasses them, with only a small portion of the Zoobenthivore niche region outside that of the detritivores, due to some individuals with both higher $\delta^{15}N$ and $\delta^{13}C$ values, suggestive that these individuals are feeding at a higher trophic level and are more reliant on terrestrial food sources compared to the high trophic level detritivores. Niche sizes and overlap probabilities are generally higher at Kakum when compared to Amanzule. However, there are far fewer trophic groups entirely encompassed within the niche region of another at Kakum when compared with Narkwa, and with no one clearly dominant group at this site. Omnivores, detritivores and zoobenthivores have the three largest niche regions at Kakum, with omnivores and detritivores having a larger $\delta^{15}N$ and $\delta^{13}C$ range than the zoobenthivores, while the niche region of the zoobenthivores is increased by their $\delta^{34}S$ range.

Table 5: Amanzule trophic group niche overlap probabilities (%), colour coded by value (mean overlap probability ± sd). The probability of an individual from Group A being within the niche of Group B. Alpha = 95%

		Group B					
		Carnivore	Detritivore	Herbivore	Omnivore	Suspension Feeder	Zoobenthivore
Group A	Carnivore	NA	1.06 ± 5.21	0 ± 0	35.55 ± 38.38	0 ± 0	25.88 ± 17.95
	Detritivore	0.03 ± 0.1	NA	0 ± 0	14.85 ± 12.69	0.16 ± 0.31	3.57 ± 2.97
	Herbivore	0 ± 0	0 ± 0	NA	40.18 ± 33.1	0 ± 0	0 ± 0
	Omnivore	0.05 ± 0.09	1.6 ± 1.72	0.38 ± 0.52	NA	0 ± 0.01	0.57 ± 0.59
	Suspension Feeder	0 ± 0	21.61 ± 25.02	0 ± 0	6.27 ± 22.05	NA	0 ± 0
	Zoobenthivore	5.37 ± 4.27	38.58 ± 21.77	0 ± 0	49.12 ± 25.82	0 ± 0	NA

Table 6: Kakum trophic group niche overlap probabilities (%), colour coded by value (mean overlap probability ± sd). The probability of an individual from Group A being within the niche of Group B. Alpha = 95%

		Group B				
		Carnivore	Detritivore	Omnivore	Suspension Feeder	Zoobenthivore
Group A	Carnivore	NA	63.2 ± 23.85	99.35 ± 1.61	0 ± 0	72.75 ± 15.06
	Detritivore	1.22 ± 0.96	NA	74.13 ± 10.43	0.01 ± 0.03	26.85 ± 9.28
	Omnivore	4.21 ± 1.61	43.87 ± 10.17	NA	0.09 ± 0.11	49.3 ± 8.83
	Suspension Feeder	0 ± 0	6.51 ± 16.04	97.53 ± 7.7	NA	99.89 ± 1.02
	Zoobenthivore	5.48 ± 2.74	51.73 ± 11.24	91.18 ± 5.98	1.14 ± 0.69	NA

Table 7: Narkwa trophic group niche overlap probabilities (%), colour coded by value (mean overlap probability ± sd). The probability of an individual from Group A being within the niche of Group B. Alpha = 95%

		Group B				
		Carnivore	Detritivore	Omnivore	Suspension Feeder	Zoobenthivore
Group A	Carnivore	NA	98.9 ± 1.8	59.14 ± 17.01	92.17 ± 5.63	75.48 ± 11.13
	Detritivore	3.78 ± 1.46	NA	17.37 ± 4.83	22.32 ± 6.39	26.87 ± 6.25
	Omnivore	15.49 ± 6.65	99.38 ± 1.26	NA	51.77 ± 13.34	73.93 ± 10.81
	Suspension Feeder	38.09 ± 8.53	98.63 ± 2.04	48.05 ± 11.78	NA	66.26 ± 11.76
	Zoobenthivore	21.72 ± 6.25	87.44 ± 7.72	38.39 ± 8.33	43.56 ± 11.48	NA

3.4 Community-Wide Trophic Structure

Differences between sites in SEA_B and each Bayesian Layman metric were statistically significant ($p<2.2 \times 10^{-16}$, Kruskal-Wallis test and Wilcox pairwise comparison), and all but two had a large effect size ($p < 2.2 \times 10^{-16}$, Cohen's $d > 1$) (Table 8). Amanzule had a smaller $\delta^{15}N$ range than Kakum, but the effect size was only small (Cohen's $d < 0.5$). Kakum had a larger standard deviation of nearest neighbour distance (SDNND) than Narkwa, but with only a small effect size (Cohen's $d < 0.5$). Amanzule (healthy mangroves) had the largest Bayesian Standard Ellipse Area (SEA_B), with a 94% and 100% probability of being greater than the SEA_B's of either Kakum or Narkwa (Table 8), respectively, indicative of a higher level of overall trophic diversity. Narkwa had a 99% probability of having a smaller SEA_B than Kakum. A similar pattern was observed for the metrics of mean Distance to Centroid (CD), with higher values indicative of higher spacing of species and therefor a greater diversity of energy flow pathways. The $\delta^{13}C$ range was highest at Amanzule, and lowest at Kakum, suggesting that a smaller range of basal food sources were used by consumers at the more degraded site. It is possible that this metric is confounded by a lower degree of distinction in basal resource $\delta^{13}C$ values. The

sources at Kakum occupy a slightly narrower $\delta^{13}C$ range than those at the other sites, 14% smaller than the range at Amanzule, and 18% smaller than that of the sources sampled from Narkwa.

The $\delta^{15}N$ range is indicative of the number of trophic levels, and is similar between Amanzule and Kakum, with only a 63% probability of Kakum having a higher value. This is far smaller at Narkwa than at either of these sites. This is backed up by the trophic position estimations, where Narkwa spans only three trophic levels, while Amanzule spans four, and Kakum five (Figure 9).

Communities with a more divergent trophic niches (and therefor a higher diversity of energy flow pathways) will exhibit higher MNND values compared to sites with species with similar trophic ecologies. This metric was consistently higher at Amanzule compared to the other two sites and had a 96% probability of being higher at Kakum than at Narkwa. The standard deviation of nearest neighbour distance (SDNND) was also higher Amanzule when compared to the other two sites, but similar between Kakum and Narkwa. This is suggestive of a greater range of trophic ecologies, but lower redundancy within trophic pathways at Amanzule compared to the site where the mangroves were degraded or not present.

*Table 8: Probability (%) of site A having a higher value for each metric than site B. SEA_B: Bayesian corrected Standard Ellipses Area; NR: $\delta^{15}N$ range; CR: $\delta^{13}C$ range; CD: mean distance to centroid; MNND: mean nearest neighbour distance; SDNND: standard deviation of the nearest neighbour distance. Figures marked with a * had large effect sizes (Cohen's d > 1)*

A	B	SEA_B	NR	CR	CD	MNND	SDNND
Amanzule	Kakum	94*	37	100*	100*	100*	100*
	Narkwa	100*	100*	100*	100*	100*	100*
Kakum	Narkwa	99*	100*	0.1*	100*	96*	58

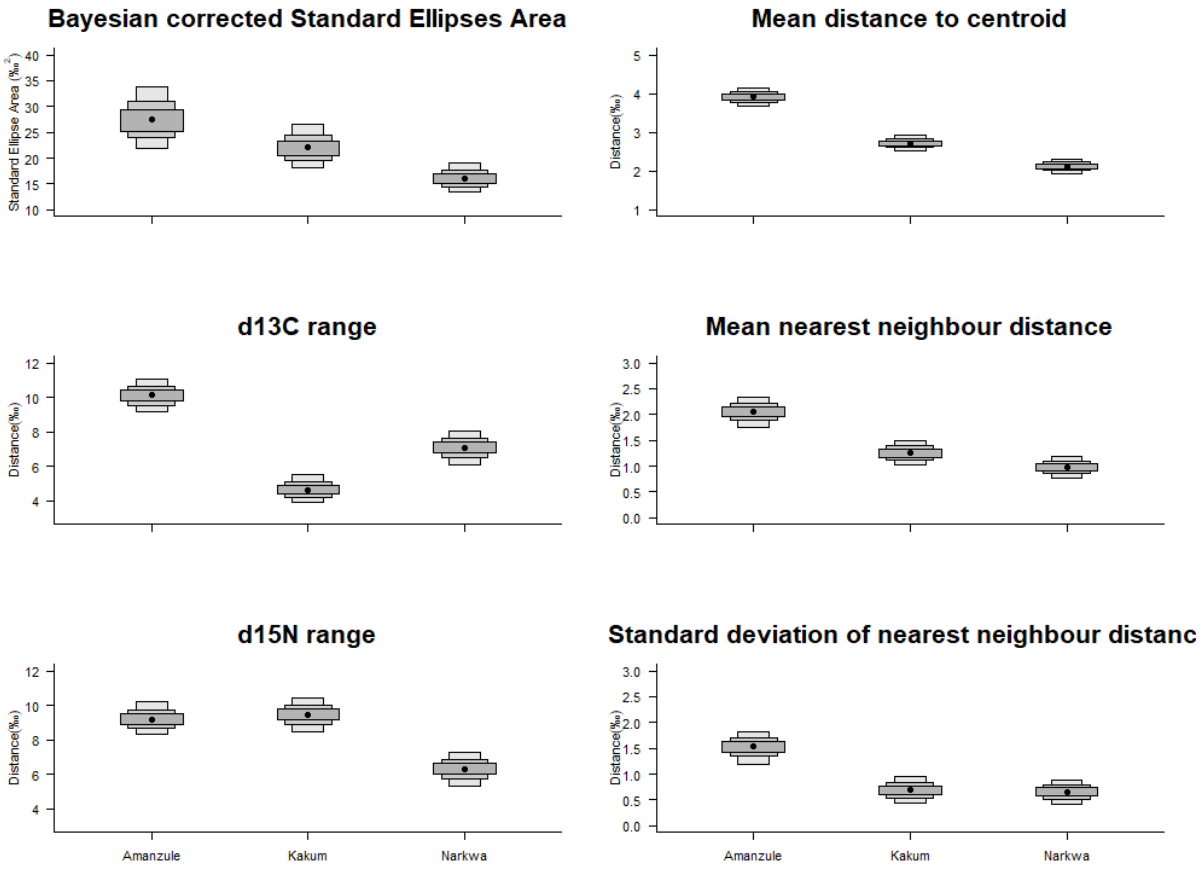

Figure 8: Density plots showing the credibility intervals of the Bayesian corrected Standard Ellipse Areas (SEA_B) and Bayesian results for the community-wide metrics at all three sites – d13C range (CR), d15N range (NR), mean distance to centroid (CD), mean nearest neighbour distance (MNND), and standard deviation of nearest neighbour distance (SDNND). Black dots display the mode and boxes indicate the 50%, 75% and 95% credibility intervals.

3.5 Trophic Position

The mode trophic position of consumers ranged from 1.2 to 4.7 at Amanzule, 2.4 to 6.6 at Kakum, and 1.7 to 4.1 at Narkwa (Figure 9). Kakum had the highest mean trophic position, of 4.9, compared to 3.8 at Amanzule and 3.1 at Narkwa. Fish in the genus *Mugil* were present across all three sites, and followed the same pattern seen in the overall mean trophic position at each site, with a modal trophic position of 5.2 at Kakum, 4.1 at Amanzule, and 3.6 at Narkwa.

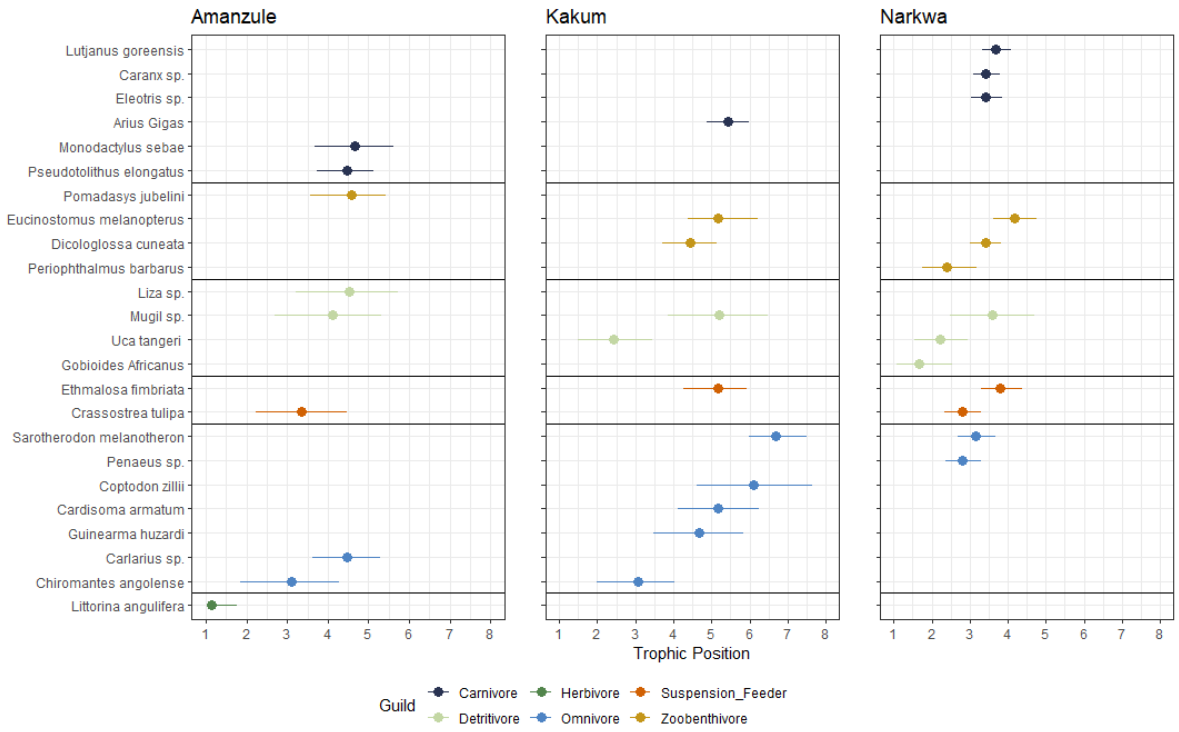

Figure 9: Trophic position estimations from posterior values of mode, and lower and upper 95% credibility intervals.

4 Conclusions

We assessed differences in the trophic niche and community-wide trophic structure of finfish and shellfish species at three sites with different degrees of mangrove cover along the coast of Ghana. There were clear differences between sites, indicative of an increased dominance of generalist feeding strategies, and decreased overall trophic diversity at sites with lower mangrove cover. We now present some conclusions drawn from these results, and briefly discuss the implications of these for communities reliant on coastal fisheries.

4.1 Feeding Strategies

Amanzule, the healthy mangrove estuary, was dominated by species with specialised feeding strategies, as demonstrated by the small niche size of trophic guilds at this site (Figures 6 & 7). Niches were also more distinct, with less overlap between guilds (Tables 5 to 7) and therefore reduced inter-species competition. By comparison, trophic guilds at Kakum, the degraded mangrove estuary, had far broader niches. It may be that at this more degraded site, reduced food availability has led to conspecifics employing divergent feeding strategies to reduce intraspecies competition, which is backed up by the greater variability in species stable isotope ranges (Table 4). Optimal foraging theory suggests that consumers will broaden their dietary niches when the availability of their preferred food

items is scarce (Pyke et al., 1977). Therefore, species with the ability to exploit more general diets are better able to adapt to degraded habitats when compared to species with small fundamental niches, and as such, it is possible that species with specialised feeding strategies may be lost (Pelage et al., 2022; Villéger et al., 2010). This would appear to be the case in this study, where the more degraded sites have fewer species employing specialised feeding strategies. While this may result in reduce intra-species competition, it is likely to lead to greater levels of inter-species competition, as can be seen by the far higher number of incidences and degree of overlap between trophic guilds at Narkwa and Kakum when compared with Amanzule. Degraded habitats, with high levels of inter-species competition, are often characterised by reduced food web resilience, and less stable relative abundances of different species (May, 1974; Rooney et al., 2006). As Narkwa displays a greater degree of overlap in trophic guild niches when compared with Kakum, it could be that continued loss of mangroves at the already degraded Kakum site will have a further negative impact on the stability of the food web, and consequently species abundance, biomass, and overall community structure.

4.2 Trophic Diversity

The healthy mangrove estuary had significantly higher trophic diversity (SEA_B) than the two more degraded sites (Table 8, Figure 8). It is theorised that the stability of complex ecosystems relies on the maintenance of distinct energy channels supporting higher level predators (Rooney et al., 2006). Notably, both the metrics describing the diversity of energy flow pathways (MNND and SDNND) were significantly higher at Amanzule, with less of a difference seen between Kakum and Narkwa. It is possible that the reduced number of energy flow pathways, and overall trophic diversity, at the more degraded sites may result in their food webs being less stable and more susceptible to collapse. A breakdown in trophic structure may trigger a reduction in benthic and demersal ecosystem functioning and the cycling of nutrients (Jabiol et al., 2013; Wolkovich et al., 2014). As discussed above, it may also lead to a decline in the stability of species abundances, with consequences for the local fishing communities reliant on these stocks.

4.3 Trophic Position

The only metric of community-wide trophic structure that was not higher at Amanzule was the $\delta^{15}N$ range, which is indicative of the range of trophic levels occupied by species within the community. This is backed up by the trophic position estimations, which used primary producer isotope values as a base, with a wider range and higher top level occupied at Kakum compared to Amanzule and Narkwa. It is not unexpected that Amanzule should support primarily species within the lower trophic levels, as healthy mangroves are known to form a key nursery habitat for juvenile fish (Nagelkerken et al., 2002). However, the smaller range of trophic levels at Amanzule compared to Kakum will almost

certainly lead to greater energy flow to higher trophic levels (including predatory fish) at Amanzule due to less energy (approximately 90%) being lost per trophic step.

4.4 Final Remarks

The results presented here suggest that a reduction in mangrove cover may be linked with a reduction in food web stability, decreased diversity and strength of energy flow pathways supporting higher level consumers that are sought after by artisanal fishermen, and increased inter-species competition. If mangrove degradation is allowed to take place in remaining healthy mangroves, then we may see the local loss of species with specialised dietary niches, as well as a decrease in the stability of relative population abundances. The results of this study also indicate that if mangroves are lost from areas already under pressure, then it is possible that the stability of food webs in these locations could be further degraded. As such, we recommend that local communities are encouraged, and assisted to manage mangrove resource extraction in a more sustainable manner, as part of the sustainable management of fisheries in this region. Further research on how this can be achieved is required, in consultation with local communities.

5 References

Adanguidi, J., Padonou, E. A., Zannou, A., Houngbo, S. B. E., Saliou, I. O., & Agbahoungba, S. (2020). Fuelwood consumption and supply strategies in mangrove forests - Insights from RAMSAR sites in Benin. *Forest Policy and Economics*, *116*, 102192. https://doi.org/10.1016/J.FORPOL.2020.102192

Adeel, Z., & Pomeroy, R. (2002). Assessment and management of mangrove ecosystems in developing countries. *Trees - Structure and Function*, *16*(2–3), 235–238. https://doi.org/10.1007/S00468-002-0168-4

Adotey, J., Acheampong, E., Aheto, D. W., & Blay, J. (2022). Carbon Stocks Assessment in a Disturbed and Undisturbed Mangrove Forest in Ghana. *Sustainability (Switzerland)*, *14*(19). https://doi.org/10.3390/SU141912782

Adupong, R., Nortey, D. D. N., & Asiedu, J. (2013). *Compilation of Customary Laws and Practices in the Greater Amanzule Wetland Areas. USAID Integrated Coastal and Fisheries Governance Initiative for the Western Region, Ghana.*

Aheto, D. W., Okyere, I., Asare, N. K., Dzakpasu, M. F. A., Wemegah, Y., Tawiah, P., Dotsey-Brown, J., & Longdon-Sagoe, M. (2014). A survey of the benthic macrofauna and fish species assemblages in a mangrove habitat in Ghana. *West African Journal of Applied Ecology*, *22*(1), 1–15.

Ajonina, G. N., Agardy, T., Lau, W., Agbogah, K., & Gormey, B. (2014). Mangrove Conditions as Indicator for Potential Payment for Ecosystem Services in Some Estuaries of Western Region of Ghana, West Africa. In S. Diop (Ed.), *The Land/Ocean Interactions in the Coastal Zone of West and Central Africa* (pp. 151–166). Springer, Cham. https://doi.org/10.1007/978-3-319-06388-1_13

Alongi., D. M. (2009). *The Energetics of Mangrove Forests*. Springer.

Alongi, D. M. (2002). Present state and future of the world's mangrove forests. *Environmental Conservation*, *29*(3), 331–349. https://doi.org/10.1017/S0376892902000231

Alongi, D. M. (2012). Carbon sequestration in mangrove forests. In *Carbon Management* (Vol. 3, Issue 3, pp. 313–322). Future Science LtdLondon, UK. https://doi.org/10.4155/cmt.12.20

Alongi, D. M., & de Carvalho, N. A. (2008). The effect of small-scale logging on stand characteristics and soil biogeochemistry in mangrove forests of Timor Leste. *Forest Ecology and Management*, *255*(3–4), 1359–1366. https://doi.org/10.1016/j.foreco.2007.10.051

Asbridge, E., Lucas, R., Accad, A., & Dowling, R. (2015). Mangrove response to environmental changes predicted under varying climates: Case studies from Australia. *Current Forestry Reports*, *1*(3), 178–194. https://doi.org/10.1007/S40725-015-0018-4/FIGURES/5

Awuku-Sowah, E. M., Graham, N. A. J., & Watson, N. M. (2023). The contributions of mangroves to physiological health in Ghana: Insights from a qualitative study of key informants. *Wellbeing, Space and Society*, *4*. https://doi.org/10.1016/J.WSS.2023.100137

Barbanera, A., Markesteijn, L., Kairo, J., Juma, G. A., Karythis, S., & Skov, M. W. (2022). Functional responses of mangrove fauna to forest degradation. *Marine and Freshwater Research*, NULL. https://doi.org/10.1071/mf21257

Bartolini, F., Cimò, F., Fusi, M., Dahdouh-Guebas, F., Lopes, G. P., & Cannicci, S. (2011). The effect of sewage discharge on the ecosystem engineering activities of two East African fiddler crab species: Consequences for mangrove ecosystem functioning. *Marine Environmental Research*, *71*(1), 53–61. https://doi.org/10.1016/J.MARENVRES.2010.10.002

Bryan-Brown, D. N., Connolly, R. M., Richards, D. R., Adame, F., Friess, D. A., & Brown, C. J. (2020). Global trends in mangrove forest fragmentation. *Scientific Reports 2020 10:1*, *10*(1), 1–8. https://doi.org/10.1038/s41598-020-63880-1

Bulmer, R. H., Lundquist, C. J., & Schwendenmann, L. (2015). Sediment properties and CO2 efflux from intact and cleared temperate mangrove forests. *Biogeosciences*, *12*(20), 6169–6180. https://doi.org/10.5194/bg-12-6169-2015

Calizza, E., Costantini, M. L., Careddu, G., & Rossi, L. (2017). Effect of habitat degradation on competition, carrying capacity, and species assemblage stability. *Ecology and Evolution*, *7*(15), 5784–5796. https://doi.org/10.1002/ece3.2977

Carpenter, K. E., & De Angelis, N. (2016). *Living Marine ressources of the eastern central atlantic: Volume 2 Bivalves, gastropods, hagfishes, sharks, batoid fishes and chimaeras* (Vol. 2). FAO.

Caut, S., Angulo, E., & Courchamp, F. (2009). Variation in discrimination factors (Δ15N and Δ13C): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology*, *46*(2), 443–453. https://doi.org/10.1111/J.1365-2664.2009.01620.X

Cocheret de la Morinière, E., Pollux, B. J. A., Nagelkerken, I., Hemminga, M. A., Huiskes, A. H. L., & Van der Velde, G. (2003). Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. *Marine Ecology Progress Series*, *246*, 279–289. https://doi.org/10.3354/MEPS246279

Connolly, R. M., Guest, M. A., Melville, A. J., & Oakes, J. M. (2004). Sulfur stable isotopes separate producers in marine

food-web analysis. In *Oecologia* (Vol. 138, pp. 161–167). https://doi.org/10.1007/s00442-003-1415-0

Costa, T. de M. M., & Soares-Gomes, A. (2015). Secondary production of the fiddler crab Uca rapax from mangrove areas under anthropogenic eutrophication in the Western Atlantic, Brazil. *Marine Pollution Bulletin*, *101*(2), 533–538. https://doi.org/10.1016/J.MARPOLBUL.2015.10.061

Dahdouh-Guebas, F., Jayatissa, L. P., Di Nitto, D., Bosire, J. O., Seen, D. Lo, & Koedam, N. (2005). How effective were mangroves as a defence against the recent tsunami? *Current Biology : CB*, *15*(12). https://doi.org/10.1016/J.CUB.2005.06.008

Dall, W., Hill, B. J., Rothlisberg, P. C., & Sharples, D. J. (1991). 9. Food and Feeding. In *Advances in Marine Biology* (pp. 315–332). Academic Press. https://doi.org/10.1016/S0065-2881(08)60175-3

Di Nitto, D., Neukermans, G., Koedam, N., Defever, H., Pattyn, F., Kairo, J. G., & Dahdouh-Guebas, F. (2014). Mangroves facing climate change: Landward migration potential in response to projected scenarios of sea level rise. *Biogeosciences*, *11*(3), 857–871. https://doi.org/10.5194/BG-11-857-2014

Duke, N. C., Meynecke, J.-O., Dittmann, S., Ellison, A. M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K. C., Field, C. D., Koedam, N., Lee, S. Y., Marchand, C., Nordhaus, I., & Dahdouh-Guebas, F. (2007). A World Without Mangroves? *Science*, *317*(5834), 41–42. https://doi.org/10.1126/SCIENCE.317.5834.41B/ASSET/B11BCCDB-E90E-45A2-9E46-DD1F4C59AF37/ASSETS/GRAPHIC/41B-1.GIF

Ellison, A. M. (2008). Managing mangroves with benthic biodiversity in mind: Moving beyond roving banditry. *Journal of Sea Research*, *59*(1–2), 2–15. https://doi.org/10.1016/J.SEARES.2007.05.003

FAO. (2007). The world's mangroves 1980-2005. *FAO Forestry Paper*, *153*, 89.

FAO. (2020). *Global Forest Resources Assessment 2020: Main report. Rome.* https://doi.org/https://doi.org/10.4060/ca9825en

FAO. (2022). *Fishery and Aquaculture Country Profiles. Ghana. Country Profile Fact Sheets. Fisheries and Aquaculture Division [online].Rome*. https://www.fao.org/fishery/en/facp/81/en

Feka, N. Z., & Ajonina, G. N. (2011). Drivers causing decline of mangrove in West-Central Africa: a review. *International Journal of Biodiversity Science, Ecosystem Services & Management*, *7*(3), 217–230. https://doi.org/10.1080/21513732.2011.634436

Fourqurean, J. W., & Schrlau, J. E. (2003). Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA. *Chemistry and Ecology*, *19*(5), 373–390. https://doi.org/10.1080/0275754031000160937O

Friess, D. A., Chua, S. C., Jaafar, Z., Krauss, K. W., & Yando, E. S. (2021). Mangroves and people: Impacts and interactions. *Estuarine, Coastal and Shelf Science*, *248*. https://doi.org/10.1016/j.ecss.2020.107155

Friess, D. A., Rogers, K., Lovelock, C. E., Krauss, K. W., Hamilton, S. E., Lee, S. Y., Lucas, R., Primavera, J., Rajkaran, A., & Shi, S. (2019). The State of the World's Mangrove Forests: Past, Present, and Future. *Annual Review OfEnvironment and Resources*, *44*, 89–115. https://doi.org/10.1146/ANNUREV-ENVIRON-101718-033302

Froese, R., & Pauly, D. (2000). *FishBase 2000: concepts, design and data sources.*

Furukawa, K., Wolanski, E., & Mueller, H. (1997). Currents and sediment transport in mangrove forests. *Estuarine, Coastal and Shelf Science*, *44*(3), 301–310. https://doi.org/10.1006/ecss.1996.0120

Ghana Statistical Service. (2021). *Ghana Population Census*.

Giri, C., Ochieng, E., Tieszen, L. L., Zhu, Z., Singh, A., Loveland, T., Masek, J., & Duke, N. (2011). Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography*, *20*(1), 154–159. https://doi.org/10.1111/j.1466-8238.2010.00584.x

Gordon, C., Tweneboah, E., Mensah, A., & Ayivor, J. (2009). The Application of the Ecosystem Approach to Mangrove management : Lessons for Ghana . *Nature & Faune*, *24*(June 2015), 30–41. https://www.academia.edu/24991742/The_Application_of_the_Ecosystem_Approach_to_Mangrove_management_Lessons_for_Ghana

Granek, E., & Ruttenberg, B. I. (2008). Changes in biotic and abiotic processes following mangrove clearing. *Estuarine, Coastal and Shelf Science*, *80*(4), 555–562. https://doi.org/10.1016/J.ECSS.2008.09.012

Grellier, S., Janeau, J. L., Dang Hoai, N., Nguyen Thi Kim, C., Le Thi Phuong, Q., Pham Thi Thu, T., Tran-Thi, N. T., & Marchand, C. (2017). Changes in soil characteristics and C dynamics after mangrove clearing (Vietnam). *Science of the Total Environment*, *593–594*, 654–663. https://doi.org/10.1016/j.scitotenv.2017.03.204

Harada, Y., Fry, B., Lee, S. Y., Maher, D. T., Sippo, J. Z., & Connolly, R. M. (2020). Stable isotopes indicate ecosystem restructuring following climate-driven mangrove dieback. *Limnology and Oceanography*, *65*(6), 1251–1263. https://doi.org/10.1002/lno.11387

Henderson, C. J., Gilby, B. L., Schlacher, T. A., Connolly, R. M., Sheaves, M., Maxwell, P. S., Flint, N., Borland, H. P., Martin, T. S. H., Gorissen, B., & Olds, A. D. (2020). Landscape transformation alters functional diversity in coastal seascapes.

Ecography, *43*(1), 138–148. https://doi.org/10.1111/ECOG.04504

Henriques, M., Granadeiro, J. P., Piersma, T., Leão, S., Pontes, S., & Catry, T. (2021). Assessing the contribution of mangrove carbon and of other basal sources to intertidal flats adjacent to one of the largest West African mangrove forests. *Marine Environmental Research*, *169*, 105331. https://doi.org/10.1016/j.marenvres.2021.105331

Igulu, M. M., Nagelkerken, I., Dorenbosch, M., Grol, M. G. G., Harborne, A. R., Kimirei, I. A., Mumby, P. J., Olds, A. D., & Mgaya, Y. D. (2014). Mangrove Habitat Use by Juvenile Reef Fish: Meta-Analysis Reveals that Tidal Regime Matters More than Biogeographic Region. *PLOS ONE*, *9*(12), e114715. https://doi.org/10.1371/JOURNAL.PONE.0114715

Jabiol, J., Mckie, B. G., Bruder, A., Bernadet, C., Gessner, M. O., & Chauvet, E. (2013). Trophic complexity enhances ecosystem functioning in an aquatic detritus-based model system. *Journal of Animal Ecology*, *82*(5), 1042–1051. https://doi.org/10.1111/1365-2656.12079

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*(3), 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson, A., & Parnell, A. (2023). *SIBER: Stable Isotope Bayesian Ellipses in R. R package version 2.1.7.* https://cran.r-project.org/package=SIBER

Jaxion-Harm, J., & Speight, M. R. (2012). Algal cover in mangroves affects distribution and predation rates by carnivorous fishes. *Journal of Experimental Marine Biology and Ecology*, *414–415*, 19–27. https://doi.org/10.1016/j.jembe.2012.01.007

Jia, M., Wang, Z., Mao, D., Ren, C., Song, K., Zhao, C., Wang, C., Xiao, X., & Wang, Y. (2023). Mapping global distribution of mangrove forests at 10-m resolution. *Science Bulletin*, *xxxx*, 17–21. https://doi.org/10.1016/j.scib.2023.05.004

Kauffman, J. B., & Donato, D. C. (2012). *Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests*.

Kristensen, E. (2008). Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *Journal of Sea Research*, *59*(1–2), 30–43. https://doi.org/10.1016/J.SEARES.2007.05.004

Kristensen, E., & Alongi, D. M. (2006). Control by fiddler crabs (Uca vocans) and plant roots (Avicennia marina) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. *Limnology and Oceanography*, *51*(4), 1557–1571. https://doi.org/10.4319/lo.2006.51.4.1557

Layman, C. A., Arrington, D. A., Montana, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, *88*(1), 42–48. http://aquaticecology.tamu.edu/files/2012/07/Layman_et_al-2007.pdf

Levin, L. A., & Currin, C. (2012). *Stable Isotope Protocols: Sampling and Sample Processing*. https://escholarship.org/uc/item/3jw2v1hh

Levin, L. A., Neira, C., Grosholz, E. D., & Grosholz2, E. D. (2006). *Invasive Cordgrass Modifies Wetland Trophic Function*. *87*(2), 419–432.

Longonje, S. N., & Raffaelli, D. (2014). Feeding ecology of mangrove crabs in Cameroon. *Applied Ecology and Environmental Research*, *12*(4), 959–973. https://doi.org/10.15666/aeer/1204_959973

Lovelock, C. E., Ruess, R. W., & Feller, I. C. (2011). CO2 Efflux from Cleared Mangrove Peat. *PLOS ONE*, *6*(6), e21279. https://doi.org/10.1371/JOURNAL.PONE.0021279

Lysy, M., Stasko, A. D., & Swanson, H. K. (2021). *nicheROVER: Niche Region and Niche Overlap Metrics for Multidimensional Ecological Niches.* (R package version 1.1.0.). https://cran.r-project.org/package=nicheROVER

Macintosh, D. J., & Ashton, E. C. (2003). *Report on the Africa Regional Workshop on the Sustainable Management of Mangrove Forest Ecosystems*. www.worldbank.org;

May, R. M. (1974). On the theory of niche overlap. *Theoretical Population Biology*, *5*(3), 297–332. https://doi.org/10.1016/0040-5809(74)90055-0

McCutchan, J. H., Lewis, W. M., Kendall, C., & McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, *102*(2), 378–390. https://doi.org/10.1034/j.1600-0706.2003.12098.x

Medina-Contreras, D., Arenas-González, F., Cantera-Kintz, J., Sánchez-González, A., & Giraldo, A. (2020). Food web structure and isotopic niche in a fringe macro-tidal mangrove system, Tropical Eastern Pacific. *Hydrobiologia*, *847*(15), 3185–3199. https://doi.org/10.1007/s10750-020-04295-x

Mumby, P. J., Edwards, A. J., Ernesto Arias-González, J., Lindeman, K. C., Blackwell, P. G., Gall, A., Gorczynska, M. I., Harborne, A. R., Pescod, C. L., Renken, H., C. C. Wabnitz, C., & Llewellyn, G. (2004). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature 2004 427:6974*, *427*(6974), 533–536. https://doi.org/10.1038/nature02286

Mumby, P. J., & Hastings, A. (2008). The impact of ecosystem connectivity on coral reef resilience. *Journal of Applied Ecology*, *45*(3), 854–862. https://doi.org/10.1111/J.1365-2664.2008.01459.X

Muro-Torres, V. M., Amezcua, F., Soto-Jiménez, M., Balart, E. F., Serviere-Zaragoza, E., Green, L., & Rajnohova, J. (2020). Primary sources and food web structure of a tropical wetland with high density of mangrove forest. *Water (Switzerland)*, *12*(11), 1–18. https://doi.org/10.3390/w12113105

Nagelkerken, I., Blaber, S. J. M., Bouillon, S., Green, P., Haywood, M., Kirton, L. G., Meynecke, J. O., Pawlik, J., Penrose, H. M., Sasekumar, A., & Somerfield, P. J. (2008). The habitat function of mangroves for terrestrial and marine fauna: A review. In *Aquatic Botany* (Vol. 89, Issue 2, pp. 155–185). Elsevier. https://doi.org/10.1016/j.aquabot.2007.12.007

Nagelkerken, I., Roberts, C. M., Van der Velde, G., Dorenbosch, M., Van Riel, M. C., Cocheret de la Morinière, E., & Nienhuis, P. H. (2002). How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series*, *244*, 299–305. https://doi.org/10.3354/MEPS244299

Nagelkerken, I., & van der Velde, G. (2004). Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. *MARINE ECOLOGY PROGRESS SERIES Mar*, *274*, 153–159. www.int-res.com

Nyunja, J., Ntiba, M., Onyari, J., Mavuti, K., Soetaert, K., & Bouillon, S. (2009). Carbon sources supporting a diverse fish community in a tropical coastal ecosystem (Gazi Bay, Kenya). *Estuarine, Coastal and Shelf Science*, *83*(3), 333–341. https://doi.org/10.1016/J.ECSS.2009.01.009

Parnell, A. C., Inger, R., Bearhop, S., & Jackson, A. L. (2010). Source partitioning using stable isotopes: Coping with too much variation. *PLoS ONE*, *5*(3), e9672. https://doi.org/10.1371/journal.pone.0009672

Pelage, L., Lucena-Frédou, F., Eduardo, L. N., Le Loc'h, F., Bertrand, A., Lira, A. S., & Frédou, T. (2022). Competing with each other: Fish isotopic niche in two resource availability contexts. *Frontiers in Marine Science*, *9*(December), 1–14. https://doi.org/10.3389/fmars.2022.975091

Pinnegar, J. K., & Polunin, N. V. C. (1999). Differential fractionation of δ13C and δ15N among fish tissues: Implications for the study of trophic interactions. *Functional Ecology*, *13*(2), 225–231. https://doi.org/10.1046/j.1365-2435.1999.00301.x

Polidoro, B. A., Carpenter, K. E., Collins, L., Duke, N. C., Ellison, A. M., Ellison, J. C., Farnsworth, E. J., Fernando, E. S., Kathiresan, K., Koedam, N. E., Livingstone, S. R., Miyagi, T., Moore, G. E., Nam, V. N., Ong, J. E., Primavera, J. H., Salmo, S. G., Sanciangco, J. C., Sukardjo, S., … Yong, J. W. H. (2010). The loss of species: Mangrove extinction risk and geographic areas of global concern. *PLoS ONE*, *5*(4). https://doi.org/10.1371/journal.pone.0010095

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). OPTIMAL FORAGING: A SELECTIVE REVIEW OF THEORY AND TESTS BY. *The Quarterly Review of Biology*, *5*(2), 137–154. http://deathfromadistance.org/content/Bingham_1999_QRB_74,_133-169_2M_version.pdf

Quezada-Romegialli, C., Jackson, A. L., & Harrod, C. (2022). *tRophicPosition: Bayesian Trophic Position Estimation with Stable Isotopes. R package version 0.8.0.*

Quezada-Romegialli, C., Jackson, A. L., Hayden, B., Kahilainen, K. K., Lopes, C., & Harrod, C. (2018). tRophicPosition, an r package for the Bayesian estimation of trophic position from consumer stable isotope ratios. *Methods in Ecology and Evolution*, *9*(6), 1592–1599. https://doi.org/10.1111/2041-210X.13009

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Raffaelli, D. G. (2006). Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Marine Ecology Progress Series*, *311*, 285–294. https://doi.org/10.3354/MEPS311285

Rooney, N., McCann, K., Gellner, G., & Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature 2006 442:7100*, *442*(7100), 265–269. https://doi.org/10.1038/nature04887

Ryan, J. M., & Ntiamoa-Baidu, Y. (2000). Biodiversity and ecology of coastal wetlands in Ghana. *Biodiversity and Conservation*, *9*, 445–446.

Saenger, P., Gartside, D., & Funge-Smith, S. (2013). A review of mangrove and seagrass ecosystems and their linkage to fisheries and fisheries management. In *Food and Agriculture Organization of the United Nations*. http://www.fao.org/docrep/018/i3355e/i3355e00.htm

Sandoval, L. A., Mancera-Pineda, J. E., Leal-Florez, J., Blanco-Libreros, J. F., & Delgado-Huertas, A. (2022). Mangrove carbon sustains artisanal fish and other estuarine consumers in a major mangrove area of the southern Caribbean Sea. *Marine Ecology Progress Series*, *681*, 21–35. https://doi.org/10.3354/MEPS13910

Sheaves, M., & Molony, B. (2000). Short-circuit in the mangrove food chain. *Marine Ecology Progress Series*, *199*, 97–109.

Shurin, J. B., Gruner, D. S., & Hillebrand, H. (2005). All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1582), 1–9. https://doi.org/10.1098/RSPB.2005.3377

Simier, M., Osse, O. J. F., Sadio, O., & Ecoutin, J. M. (2021). Biology and ecology of sea catfish (Ariidae) of estuarine, lagoon and coastal ecosystems in West Africa. *Journal of Fish Biology*, *99*(2), 629–643. https://doi.org/10.1111/jfb.14751

Smith, J. A., Mazumder, D., Suthers, I. M., & Taylor, M. D. (2013). To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. *Methods in Ecology and Evolution*, *4*(7), 612–618. https://doi.org/10.1111/2041-210X.12048

Snelgrove, P. V. R., Thrush, S. F., Wall, D. H., & Norkko, A. (2014). Real world biodiversity-ecosystem functioning: a seafloor perspective. *Trends in Ecology & Evolution*, *29*(7). https://doi.org/10.1016/j.tree.2014.05.002

Stephens, R. B., Ouimette, A. P., Hobbie, E. A., & Rowe, R. J. (2022). Reevaluating trophic discrimination factors (Δδ13C and Δδ15N) for diet reconstruction. *Ecological Monographs*, *92*(3), 1–20. https://doi.org/10.1002/ecm.1525

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, *2018*(6), e5096. https://doi.org/10.7717/PEERJ.5096/SUPP-3

Stock, B. C., & Semmens, B. X. (2016). Unifying error structures in commonly used biotracer mixing models. *Ecology*, *97*(10), 2562–2569.

Swanson, H. K., Lysy, M., POwer, M., Stasko, A. D., Johnson, J. D., & Reist, J. D. (2015). A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology*, *96*(2), 318–324. https://doi.org/10.1890/14-0235.1

Sweetman, A. K., Middelburg, J. J., Berle, A. M., Bernardino, A. F., Schander, C., Demopoulos, A. W. J., & Smith, C. R. (2010). Impacts of exotic mangrove forests and mangrove deforestation on carbon remineralization and ecosystem functioning in marine sediments. *Biogeosciences*, *7*(7), 2129–2145. https://doi.org/10.5194/bg-7-2129-2010

Takyi, R., El Mahrad, B., Nunoo, F. K. E., Adade, R., ElHadary, M., & Essandoh, J. (2022). Adaptive management of environmental challenges in West African coastal lagoons. *Science of the Total Environment*, *838*(December 2021). https://doi.org/10.1016/j.scitotenv.2022.156234

Then, A. Y. H., Adame, M. F., Fry, B., Chong, V. C., Riekenberg, P. M., Mohammad Zakaria, R., & Lee, S. Y. (2021). Stable Isotopes Clearly Track Mangrove Inputs and Food Web Changes Along a Reforestation Gradient. *Ecosystems*, *24*(4), 939–954. https://doi.org/10.1007/s10021-020-00561-0

UNEP. (2007). *The mangroves of West-Central Africa. UNEP-Regional Seas Programme/UNEP-WCMC.* http://www.archive.org/details/mangrovesofweste07corc

Valiela, I., Bowen, J. L., & York, J. K. (2001). Mangrove forests: One of the world's threatened major tropical environments. *BioScience*, *51*(10), 807–815. https://doi.org/10.1641/0006-3568(2001)051[0807:MFOOTW]2.0.CO;2

Valiela, I., & Cole, M. L. (2002). Comparative evidence that salt marshes and mangroves may protect seagrass meadows from land-derived nitrogen loads. *Ecosystems*, *5*(1), 92–102. https://doi.org/10.1007/s10021-001-0058-4

Viana, I. G., Valiela, I., Martinetto, P., Monteiro Pierce, R., & Fox, S. E. (2015). Isotopic studies in Pacific Panama mangrove estuaries reveal lack of effect of watershed deforestation on food webs. *Marine Environmental Research*, *103*, 95–102. https://doi.org/10.1016/J.MARENVRES.2014.10.003

Villéger, S., Miranda, J. R., Hernández, D. F., & Mouillot, D. (2010). Contrasting changes in taxonomie vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, *20*(6), 1512–1522. https://doi.org/10.1890/09-1310.1

Whitcraft, C. R., & Levin, L. A. (2007). Regulation of benthic algal and animal communities by salt marsh plants: Impact of shading. *Ecology*, *88*(4), 904–917. https://doi.org/10.1890/05-2074

Wolfrath, B. (1992). Field experiments on feeding of European fiddler crab Uca tangeri. *Marine Ecology Progress Series*, *90*(1), 39–43. https://doi.org/10.3354/meps090039

Wolkovich, E. M., Allesina, S., Cottingham, K. L., Moore, J. C., Sandin, S. A., & De Mazancourt, C. (2014). Linking the green and brown worlds: The prevalence and effect of multichannel feeding in food webs. *Ecology*, *95*(12), 3376–3386. https://doi.org/10.1890/13-1721.1

Zanvo, M. S., Salako, K. V., Gnanglè, C., Mensah, S., Assogbadjo, A. E., & Glèlè Kakaï, R. (2021). Impacts of harvesting intensity on tree taxonomic diversity, structural diversity, population structure, and stability in a West African mangrove forest. *Wetlands Ecology and Management*, *29*(3), 433–450. https://doi.org/10.1007/S11273-021-09793-W/FIGURES/5