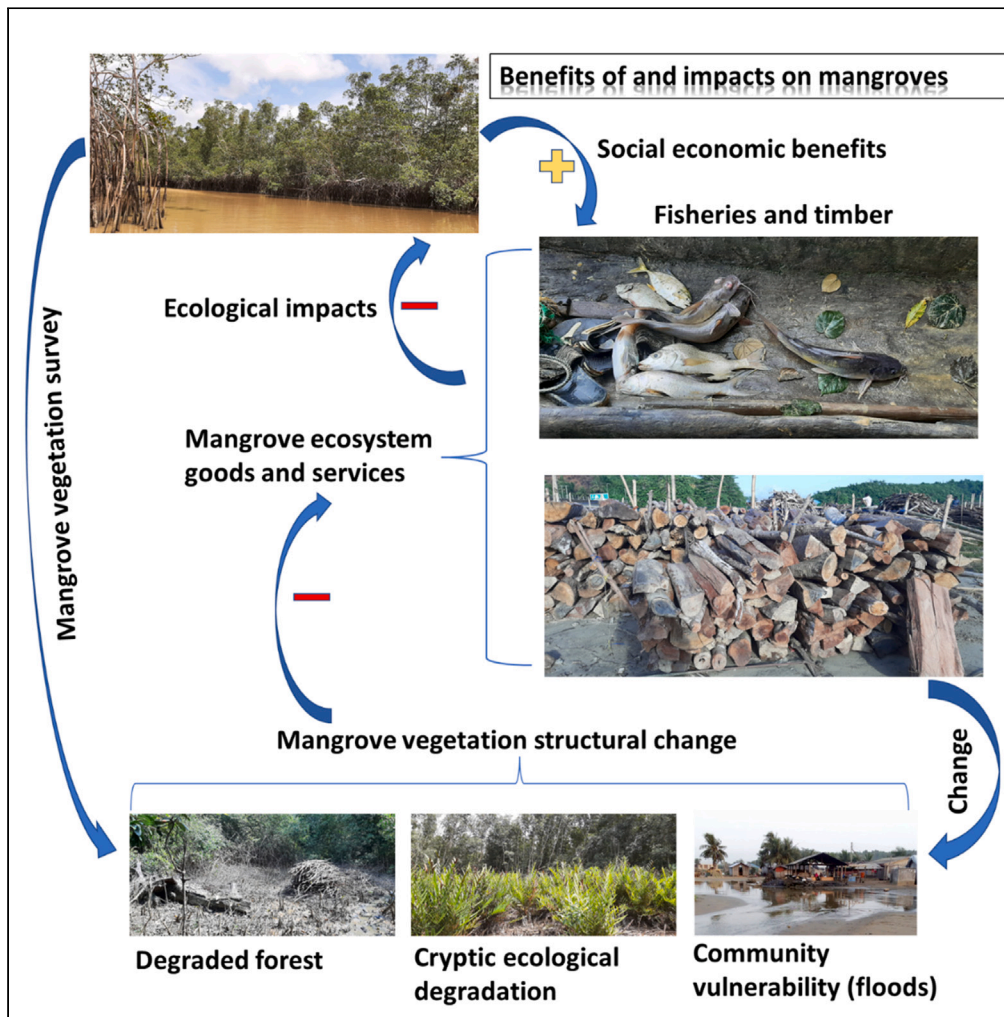


Article

Does mangrove vegetation structure reflect human utilization of ecosystem goods and services?



Frederick Asante, Jean Hugé, Noble K. Asare, Farid Dahdouh-Guebas

frederickasante34@gmail.com

Highlights

Assessing mangrove structure using local knowledge, resource use, and vegetation survey

Factors of change in mangroves include mangrove wood cutting and distance from river

People with very good knowledge on mangrove are more likely to cut mangrove wood

The overgrowth of *Acrostichum aureum* was found to inhibit mangrove juvenile growth

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Article

Does mangrove vegetation structure reflect human utilization of ecosystem goods and services?

Frederick Asante,^{1,2,9,*} Jean Hugé,^{1,3,4} Noble K. Asare,^{5,6} and Farid Dahdouh-Guebas^{1,2,7,8}

SUMMARY

Many coastal communities in developing countries depend on mangrove ecosystem services (ES). A combination of anthropogenic and environmental stresses threatens mangroves globally. This study at the Ankobra catchment communities in Ghana focused on the relation between ES utilization and mangrove forest structure. Through vegetation survey, we observed significant effects of selective logging, branch cutting, density of *Acrostichum aureum*, and water stress on tree stocking and sapling densities. We observed through interviews in five communities that about 98% and 88% of mangrove wood harvested are used for fuelwood and construction respectively. The vegetation structure of the forest areas receiving high harvesting pressures was less complex, with lower tree and sapling density, as well as lower seed-bearing trees than less-disturbed areas. Existing mangrove harvesting regulations are compromised to accommodate the needs of the surrounding communities. Recognizing these impacts is important to improve management decisions, address community needs, and reduce pressure on mangroves.

INTRODUCTION

Mangroves are (sub)tropical and warm temperate intertidal forests, providing a wide range of services supporting the well-being of humans.^{1,2} Found in >120 countries and territories,^{3–6} mangroves have about 80 so-called “true mangrove” species^{7,8} in 30 genera belonging to 17–20 families.^{8–10} These are ecologically functional species with an important ethnobiological value. Aside from their provisioning services, such as fuelwood, timber, medicine, fish, etc.,^{11–13} and defensive support against natural disasters, mangroves trap, and retain terrestrial sediments and recycle nutrients necessary for primary production in the marine environment, and help improve the health of other coastal ecosystems, such as seagrass beds, salt marshes, oyster reefs, and coral reefs.^{14–18} Mangrove ecosystems also serve as carbon sinks, sequestering over $226 \pm 39 \text{ g C m}^{-2}$ of “blue” carbon annually.^{19,20} Aesthetically, mangroves attract tourists, generating revenues for many countries.²¹ However, human pressure has led to significant threats to mangroves.^{2,5,22,23} In the last 30 years of the 20th century, the world lost about 35% of its mangrove cover.^{16,24} Typical causes of mangrove degradation globally have since been associated with aquaculture and agriculture expansions, harvesting of wood products, freshwater diversion, urbanization, and other coastal developments.^{25–27}

These processes that drive mangrove deforestation and degradation significantly differ geographically.²⁸ For example, in Latin America and Southeast Asia, aquaculture is the most important driver.^{2,28} Harvesting mangrove wood for charcoal production, fuelwood, and construction are on the other hand the paramount agents in sub-Saharan Africa.^{2,29} The impacts of these processes make mangrove deforestation and degradation a greater concern in developing countries, as coastal rural communities often directly depend on the services provided by mangrove ecosystems.^{16,25,28,30} Though the loss rate has reduced from $\approx 2\%$ in the 20th century to $<0.4\%$ annually in the 21st century,² the exploitation of mangrove services remains mostly unsustainable and mostly unregulated.^{15,28,31} This is due to the unceasing human population growth and the new development of human activities along the coasts. Until now, research on isolated topics has been insufficient to address issues of man and the environment in terms of achieving a better balance between mangrove resource utilization and ecosystem conservation.^{1,32}

The vegetation structure is one of the features of the mangrove ecosystem that is directly impacted by degradation. Likewise in terrestrial forests, the vegetation structure of mangroves refers to tree size,

¹Laboratory of Systems Ecology and Resource Management, Department of Organism Biology, Faculty of Sciences, Université Libre de Bruxelles – ULB, B-1050 Brussels, Belgium

²Laboratory of Plant Biology and Nature Management, Ecology and Biodiversity, Vrije Universiteit Brussel – VUB, B-1050 Brussels, Belgium

³Department of Environmental Sciences, Open University of the Netherlands, Valkenburgerweg 177, 6419 Heerlen, the Netherlands

⁴Centre for Environmental Science, Universiteit Hasselt, Martelarenlaan 42, 3500 Hasselt, Belgium

⁵Department of Fisheries and Aquatic Sciences, School of Biological Sciences, University of Cape Coast, Science Building Floor 3, Cape Coast, Ghana

⁶Centre for Coastal Management (CCM), Africa Centre of Excellence in Coastal Resilience (ACECoR), University of Cape Coast, Cape Coast, Ghana

⁷Interfaculty Institute of Social-Ecological Transitions, Université Libre de Bruxelles – ULB, Brussels, Belgium

⁸Mangrove Specialist Group (MSG), Species Survival Commission (SSC), International Union for the Conservation of Nature (IUCN), C/o Zoological Society of London, London, UK

⁹Lead contact

*Correspondence: frederickasante34@gmail.com

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growth, propagule production, density, and species composition.^{28,33,34} Previously, the structural properties of mangroves were viewed as being shaped by only abiotic processes, including hydrodynamic and hydrographic actions of the ocean.³⁵ While these actions of the ocean play a major role, the anthropogenic activities on mangrove have become more significant. Stresses such as clear-cut and/or selective logging can directly affect mangrove composition and other structural properties, thereby reducing tree stock.^{12,13,36} Regeneration, tree growth, and stock productivity and structure become compromised through the disruption of mangrove ecosystem functions by human activities.^{13,37,38} Transitions in mangrove species composition due to users' preferences from preferred to less preferred, and from vulnerable mangrove species to more disturbance-resistant ones and mangrove associates, have also become a real issue.^{15,34,39} Thus, mangrove vegetation structure may change in response to uncontrolled ecosystem service exploitation.²⁸ A sustainable vegetation structure of mangroves that transits over different generations is very important for many human reasons. For example, developing nations mostly depend -directly- on services that nature provides including the ability of mangroves to provide food, fuel, support for local income, and ecological benefits such as coastline protection and flood control.^{33,40,41} For these reasons, the vulnerabilities of coastal communities increase under reduced capacity of mangrove ecosystems to provide services.^{33,40} This makes mangrove vegetation structure assessment important as it allows us to also evaluate both coastal habitat resilience, and community vulnerabilities.^{33,41,42} Thus, the assessment of mangrove vegetation structure can serve as an early warning sign and help identify opportunities for reducing the risks associated with mangrove degradation on coastal communities.^{41,42} However, approaches that couple direct human impacts with vegetation dynamics are scarce considering the huge spatial differences in mangrove degradation rate across the globe. Therefore, to better make informed decisions for sustainable management, which improve our understanding of the impacts of human activities on mangroves,^{2,13,43,44} an integrated approach that relates mangrove resource users, resource distribution, utilization patterns, and the mangrove vegetation structure is urgently needed.^{28,45} A study of this kind that combines these factors helps to identify the needs of coastal communities, trends in mangrove resource use, shifts in mangroves, and management decisions that ensure proper human well-being and environmental justice.^{1,45}

Like in other developing countries, a high proportion of Ghana's population (39%) lives in coastal regions,⁴⁶ which creates pressure on coastal resources, especially on mangroves.^{11,47,48} Ghana has 7 mangrove species, 5 of which are true mangroves: *Rhizophora racemosa* Meyer; *Rhizophora harrisonii* Leechman; *Rhizophora mangle* L.; *Avicennia germinans* (L.) Stearn; and *Laguncularia racemosa* (L.) Gaertn. f.; and two are minor species or associates: *A. aureum* L.; and *Conocarpus erectus* L.^{48,49} However, as in other developing worlds like Indonesia, Nigeria, Cameroon, etc., mangroves are declining along the entire coastline in Ghana through felling for fuelwood and construction^{11,50} and through land reclamation.^{11,51} The Ankobra mangrove forest in Ghana also experiences these threats. We investigated the utilization pattern of mangrove resources and linked this pattern to the vegetation structure of the Ankobra mangrove forest. First, we gathered information on the household use of mangrove resources. Second, we investigated the local perception of the management and status of the mangrove. We ended by establishing the relationship between mangrove utilization and mangrove forest vegetation composition and structure. This study is significant because it provides baseline information on restoring mangrove structure especially in unmanaged systems within West Africa and beyond. It also provides information for stakeholders to improve sustainable management and future studies of mangroves.

RESULTS

Mangrove use, utilization pattern, and local knowledge

Survey of rural communities' level of knowledge on mangroves

The study identified three true mangrove species (*R. harrisonii*, *A. germinans*, and *L. racemosa*) and other minor or associate species. The respondents in the most mangrove cutting village (Sanwoma) (Figure 1) significantly had good knowledge (able to identify and name at least two) of true mangrove species, as opposed to the other communities ($z_{0.742} = 3.985$, $p = 6.74e-5$) who rather had fair knowledge (able to name at least one) about mangroves ($\chi^2 = 51.344$, $df = 4$, $p = 1.89e-10$). Knowledge of true mangrove species varied by collection frequency per week ($z_{0.047} = 2.017$, $p = 0.044$) and collection distance ($z_{0.052} = 2.11$, $p = 0.035$) when the models were fitted by Conway-Maxwell-Poisson. However, gender, age class, and the number of years one lives in the village had no significant correlation with the knowledge of mangroves (see Tables S1, S2, and Figure S1).

Mangrove use and preferred species

The percentage of the population who used mangrove plants for fuelwood and construction was significantly higher than the percentage who used mangrove plants for food, medicinal, and fishing activities ($\chi^2 = 78.77$, $df = 4$, $p = 3.18e-16$) (Figure 2). However, no significant difference was found between those who use mangroves for fuelwood and construction.

Regarding the preference of mangrove species, the number of people who use *L. racemosa* (19%) was significantly lower than those who used *R. harrisonii* and *A. germinans* for fuelwood ($\chi^2 = 24.89$, $df = 2$, $p = 3.94e-6$). However, no significant difference was found between those who use *R. harrisonii* (74%) and *A. germinans* (65%). Regarding the choice of mangrove species for fuelwood, 90% of the respondents reported *R. harrisonii* was the best, while for the second choice, 62.5% reported they would choose *A. germinans* (see Figure S2). Over 36% of the respondents indicated that the high calorific value of the mangrove species influences their choice for the first best fuelwood species, followed by little/no smoke (27% comparatively), but 18.4% mentioned that the taste of fish after smoking was also a reason (see Table S3). For mangrove as construction wood, the percentage of respondents who reported they use *A. germinans* (76%) and *R. harrisonii* (70%) for pillars was significantly higher than the percentage who use *L. racemosa* (22.5%) ($\chi^2 = 30.72$, $df = 2$, $p = 2.13e-7$). Over 56% of respondents indicated *A. germinans* as the first best mangrove species for construction, ahead of 25% that preferred *R. harrisonii*. The most influential factor for choosing construction wood species was durability (i.e., 6.37 ± 4.37 and 3.78 ± 3.31 years for first and second choices respectively), which was significantly different ($\chi^2 = 17.64$, $df = 1$, $p = 2.66e-5$). The respondents' ability to identify more true mangrove species (knowledge of mangrove) significantly correlated with the ability to select the best species ($z_{0.4491} = 2.187$, $p = 0.287$). Medicinally, the bark, roots, and leaves of *Avicennia* and *Rhizophora* were reported to cure different diseases, such as malaria, ulcer, cardiac problems, stroke, wounds, and stomach problems (see Figure S3). The use of mangroves for medicine had no significant variation with gender. On average, people travel 1.34 km for mangrove parts for medicine.

Chemically, *Rhizophora* bark and roots were reported to be used for tanning fishing nets, which was reported by 45% of respondents in Sanwoma (i.e., the most fishing and mangrove cutting village) and 10% of respondents from Ezium. Collection of mangrove parts for use as the dye was personally done by fathers who averagely travel the same distance as those who go for medicine. Mangrove was not used as fodder for animals, but rather the young roots of *Rhizophora* were reportedly eaten as food by fishermen or mangrove harvesters while on the field for fishing or mangrove wood collection. According to 25 (31%) of respondents in the most fishing village (Sanwoma), eating/chewing the root reduces hunger and thirst.

Fishing: The common activity that links all rural communities to the mangrove forest

Fishing was observed to be the commonest mangrove-dependent activity for all villages in this study where all villages catch the same fish types (see Table S4). However, four villages, Adelekezo, Eshiem, Ezium, and Kukuaville, do not fish from the open ocean and in unvegetated deep flats, as opposed to the most mangrove cutting village (Sanwoma). Mangrove forest creeks were the commonest locations for fishing by all villages (see Figure S4). However, communities were significantly separated by the type of fish species they catch ($F = 2.123$, $df = 4$, $p = 0.0001$). The results indicate a significant difference between Sanwoma and Kukuaville ($p_{adj} = 0.025$) and between Sanwoma and Eshiem ($p_{adj} = 0.020$) with respect to fish species caught. However, no significant difference was observed in the species of fish caught by the people of Sanwoma, Adelekezo, and Ezium. People with good knowledge of mangrove significantly correlated with the number of people in fishing ($z_{0.9390} = 2.02$, $p = 0.044$).

How respondents view mangrove benefits and mangrove management

The percentage of the population in Sanwoma, the most mangrove cutting village, who reported that mangroves were important to them, was significantly higher than percentages in other villages ($\chi^2 = 41.0$, $df = 4$, $p < 0.001$). Sixty-one percent of the population in Sanwoma together benefit from both fish and fuelwood, while 16% each for wood only or fish only respectively, were the most important benefits from mangrove. In the other villages, 60%, 67%, 80% and 8% of the people in Adelekezo, Eshiem, Ezium, and Kukuaville, respectively, reported only fish as their most beneficial resource from mangrove. In Ankobra, local regulations bind mangrove harvesters to go 50–100 m away from the river when cutting mangroves, replant after cutting, and usually best to cut dead woods. A significant proportion (73%) of the Sanwoma population, as

Table 1. Importance values of tree species of the Ankobra mangrove forest

Forest bank	Species	Relative values (%)			
		Relative density	Relative frequency	Relative dominance	I. V.
Eastern bank1 (EB1)	<i>A. germinans</i>	9.98	20.69	15.03	45.7
	<i>R. harrisonii</i>	86.46	65.52	79.7	231.67
	<i>L. racemosa</i>	1.9	6.9	2.08	10.88
	<i>Z. zanthoxyloides</i>	1.66	6.9	3.2	11.76
Eastern bank2 (EB2)	<i>A. germinans</i>	0.53	2.78	21.84	25.15
	<i>R. harrisonii</i>	84.24	58.33	68.6	211.18
	<i>T. populnea</i>	2.63	8.33	1.27	12.23
	<i>Z. zanthoxyloides</i>	0.88	8.33	0.32	9.53
	<i>A. glabra</i>	11.73	22.22	7.96	41.92
Western bank1 (WB1)	<i>A. germinans</i>	3.74	14.71	31.84	50.28
	<i>R. harrisonii</i>	91.5	55.88	60.44	207.82
	<i>L. racemosa</i>	0.68	2.94	1.56	5.18
	<i>T. populnea</i>	0.68	5.88	0.27	6.83
	<i>Z. zanthoxyloides</i>	3.06	17.65	5.75	26.46
	Others	0.34	2.94	0.14	3.42
Western bank2 (WB2)	<i>A. germinans</i>	0.34	10	17.75	28.09
	<i>R. harrisonii</i>	99.66	90	82.25	271.91

Note: Total number of plots (total area m²): Western bank 1 = 20 (2000 m²), Western bank 2 = 20 (2000 m²), Eastern bank 1 = 19 (1900 m²), and Eastern bank 2 = 21 (2100 m²). Total number of individuals sampled: Western bank 1 = 294, Western bank 2 = 592, Eastern bank 1 = 420, and Eastern bank 2 = 571.

All mangrove and non-mangrove trees larger than or equal to 2.5 cm in diameter (130 cm above ground, D_{130cm}) were measured inside 0.01 ha plots.

opposed to Adelekezo (60%), Eshiem (44%), Eziom (30%), and Kukuaville (58%), respectively, were aware of forestry regulations like the total ban on forest tree cutting, the requirement of permits, cutting mangrove far from riverbanks, a total ban on the felling of certain forest trees and animal hunt ($\chi^2 = 19.76$, df = 4, $p = 0.0006$).

Mangrove status: mangrove vegetation structure and regeneration

Forest structure

A total of 1,877 adult trees were sampled, the principal tree species of vegetation across all sites in the Ankobra mangrove forest being *R. harrisonii* (Table 1). However, with *A. aureum*'s inclusion in the importance value calculation (without relative dominance, RDo), *A. aureum* was the most important species across all the Western mangrove banks (56.6% and 53.4% in WB1 and WB2 respectively). However, in the Eastern bank forests, *R. harrisonii* remained the principal species.

The composition of species and the underlying factors controlling vegetation community in the Ankobra mangrove forest are illustrated in Figures 3A and 3B. The results indicate significant differences in species composition among sites (ANOSIM statistics $R = 0.1438$, $p = 0.0001$). No significant differences were however observed between the two forests of the eastern bank ($r^2 = 0.049$, $p = 0.114$), but between forests of different banks – Eastern bank 1 and Western bank 2 ($r^2 = 0.19$, $p = 0.006$); Eastern bank 2 and Western bank 1 ($r^2 = 0.15$, $p = 0.012$); Eastern bank 2 and Western bank 2 ($r^2 = 0.16$, $p = 0.012$) and Western bank 1 and Western bank 2 ($r^2 = 0.095$, $p = 0.024$). *A. aureum* and *R. harrisonii*'s contributions to the dissimilarities of species composition in the forest were 56.5% and 34.8% respectively, with a cumulative effect of 91.3%. Factors such as the average distance of plots from the Ankobra river (AvDistRiver: $p = 0.033$) and the total number of branches of trees cut (TotalCutBranches: $p = 0.002$) per plot had a significant association with species composition. Latitudinal and longitudinal changes, as well as the total number of trees cut per plot, had no significant association with species composition.

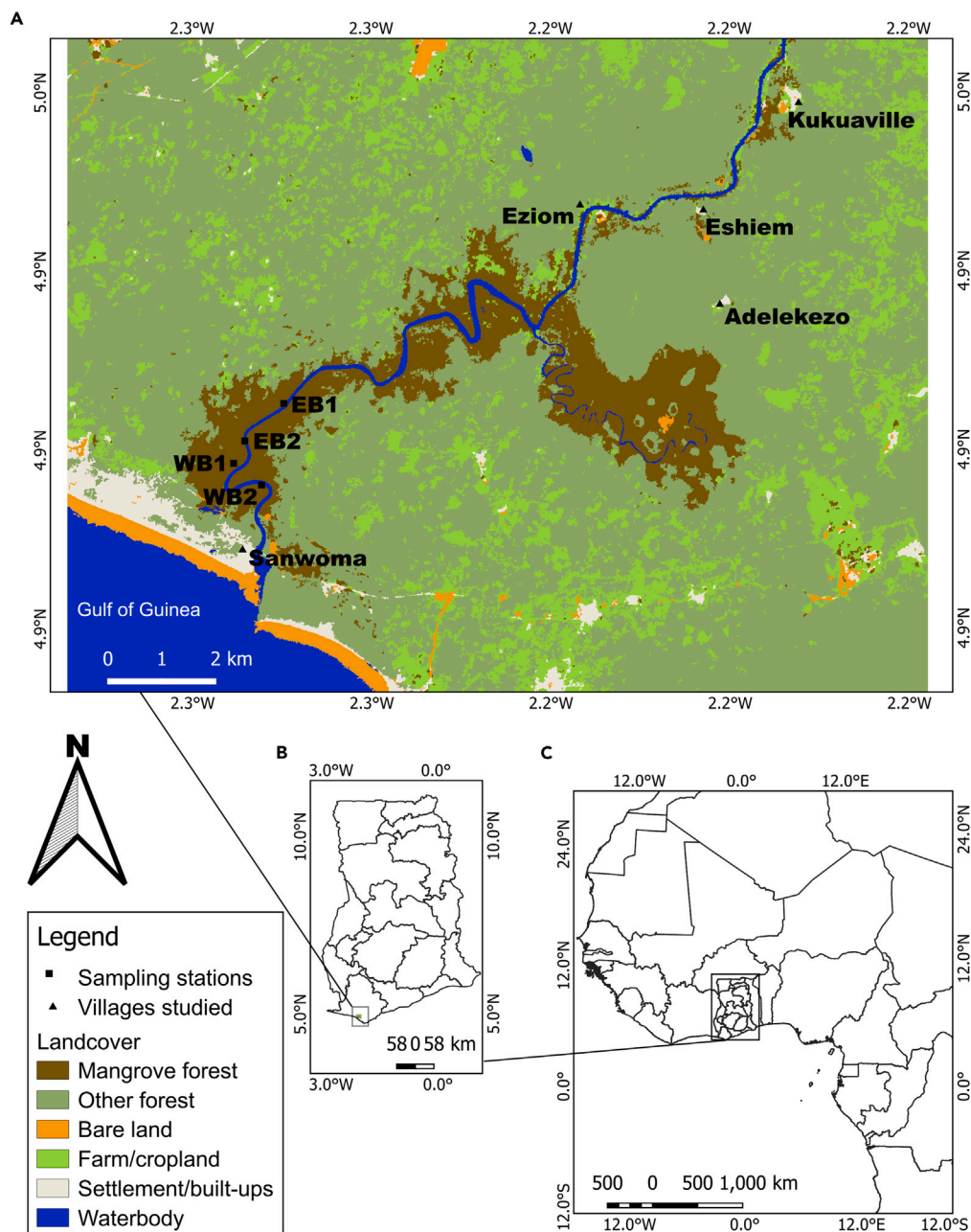


Figure 1. Study area map

(A) Study area map for Ankobra mangrove and surrounding villages: Kukuaville, Eziom, Eshiem, Adelekezo, and Sanwoma. WB1 (Western bank 1), WB2 (Western bank 2), EB1 (Eastern bank 1), and EB2 (Eastern bank 2) were areas of the mangroves surveyed (Sentinel 2A satellite image, 2018).

(B) Regional map of Ghana (Source: [AmeriGeo](#)), accessed on 21/02/2022 at 15h00 Central European Time (CET). The part of B linked to A is the Western region of Ghana.

(C) West and Central African map (Source: OCHA Services).

Stocking density

Figure 4A (see Table S5) shows the inventories of vegetation in the Ankobra mangrove forest. A total of 2,211 stems ha^{-1} were encountered in the Eastern bank 1 of which 86.4% and 10% were *Rhizophora* and *Avicennia*, respectively. In the Eastern bank 2, 2,719 stems ha^{-1} were encountered, of which 84.2% were *Rhizophora*, and 11.7% were *Annona glabra* L. The Western bank 1 and Western bank 2 contained 1,470 and 2,960 stems ha^{-1} ,

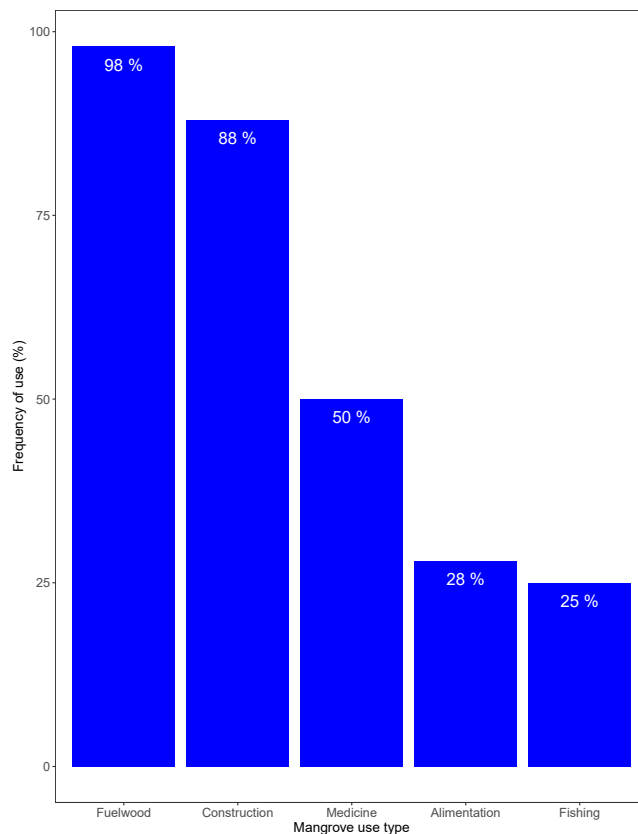


Figure 2. Main uses of mangroves by the population of Sanwoma

$n_{\text{fuelwood}} = 78$, $n_{\text{construction}} = 70$, $n_{\text{medicine}} = 40$, $n_{\text{alimentation}} = 22$, and $n_{\text{fishing}} = 20$, $N_{\text{total}} = 80$., where: n = number of respondents who use mangroves for a particular purpose, while N = total number of respondents interviewed in Sanwoma (see also Figures S2, S3, and Table S3).

respectively. Of the Western bank 1, 91.5% of the stems were *Rhizophora*, while only 3.7% were *A. germinans*. Also, for the Western bank 2, 99.7% were *Rhizophora*, and 0.3% were *Avicennia* stems. Diameter classes were significantly associated with sites ($\chi^2 = 146.37$, $df = 15$, $p = 1.27e-23$), thus trees with >20.0–30.0 cm diameter class were absent in the Eastern bank 2 and the Western bank 2, while class >30.0 cm was absent in Eastern bank 1 (see Figure S5). The total stem density ha^{-1} in the Western bank 1 was significantly lower than the stocking densities in other sites ($\chi^2 = 556.23$, $df = 3$, $p = 3.1e-120$). Trees with a diameter class above 6 cm were significantly lower in the Eastern bank 2 and all the Western bank mangroves. There was a significant difference in the total stem density ha^{-1} ($F = 18.67$, $df = 5$, $r^2 = 0.29$, $p = 2.76e-15$) between diameter classes. Stocking density was significantly associated with latitudinal gradients (estimate = -0.08546 , $z = -2.980$, $p = 0.002887$), total number of cut trees per plot (estimate = -0.11187 , $z = -3.432$, $p = 0.000599$) and the density of *A. aureum* per plot (estimate = -0.094 , $z = -2.682$, $p = 0.007321$). Unlike species composition, the distance between plots and the river, as well as the total number of cut branches per plot, had no significant association with the stocking density of diameter classes.

Also, the size class frequency distribution shows that in Western bank 1, the logarithmic relationship between species stem density and diameter class size is explained by 98% variation but have the lowest seed-bearing trees (3254.9) based on Equation 10 (i.e., De Liocourt's exponential model: $Y = ke^{-ax}$). This was opposite for Western block 2 which had the highest mortality rate of 1.667 and the most prolific seed-bearing rate of 15994 among all sites studied. The Eastern bank 1 on the other hand had both the lowest mortality rate of 1.093 and relationship (explaining 44% variation) (see Figure S5).

Forest regeneration

Natural regeneration was observed in all sites (but with very high intra-site and between-site differences), as seen in Figure 4B (see Table S6). All species showed clustered dispersion trends (Morisita index, $I_M > 1$),

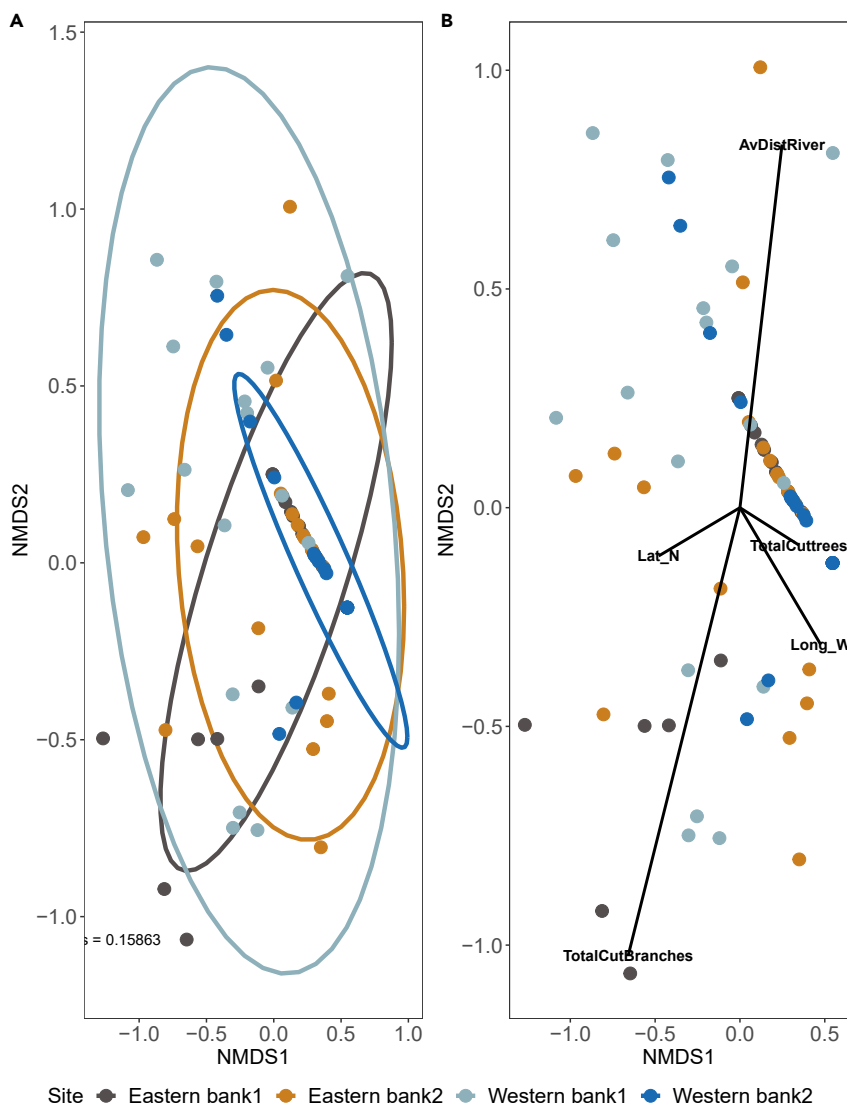


Figure 3. Non-metric multidimensional scaling (NMDS) of species composition and factors

(A) The species composition of vegetation in the Ankobra mangrove forest among sites.

(B) factors driving species composition in the Ankobra mangrove forests (where AvDistRiver means the average distance of plot from the Ankobra river; Lat_N = latitudinal gradients North; Long_W = longitudinal gradients to the West; Total Cut trees = total cut trees per plot; and Total Cut Branches = total cut trees. The dissimilarity distance applied was the Bray-Curtis, while the Envfit function was used to combine species abundance and the drivers on plot B.

except for *Thespesia populnea*, which displayed random distribution ($I_M = 0$). There was a significant difference in juvenile density among sites ($\chi^2 = 2773.7$, $df = 3$, $p = 2.2e-16$), with higher densities recorded again in the Western bank 2 (9,005 juveniles ha^{-1}), the Eastern bank 2 (6,192 juveniles ha^{-1}) and the Western bank 1 (6,167 juveniles ha^{-1}) and lowest density in the Eastern bank 1 forests (3,173 juveniles ha^{-1}). However, no significant difference was observed in juvenile density between the Eastern bank 2 and the Western bank 1, but the density of each of the two banks was significantly higher than in the Eastern bank 1 ($\chi^2 = 1164$, $df = 2$, $p = 1.75e-253$). There were higher densities of juveniles in regeneration class RCII than RCI, RCIII, and RCIV across all sites. The RCII had a percentage of not less than 68% of the total individuals ha^{-1} in any of the sites studied. The *R. harrisonii* had the highest percentage of juveniles in all sites, between 72% in Eastern bank 1 and 99% in the Western bank 2. Total juvenile density per plot had significant negative trends with the density of *Acrostichum* per plot (estimate = -0.203 , $z = -7.188$, $p = 6.60e-13$), tree branch cutting (estimate = -0.085 , $z = -3.320$, $p = 0.000899$) and latitudinal gradient

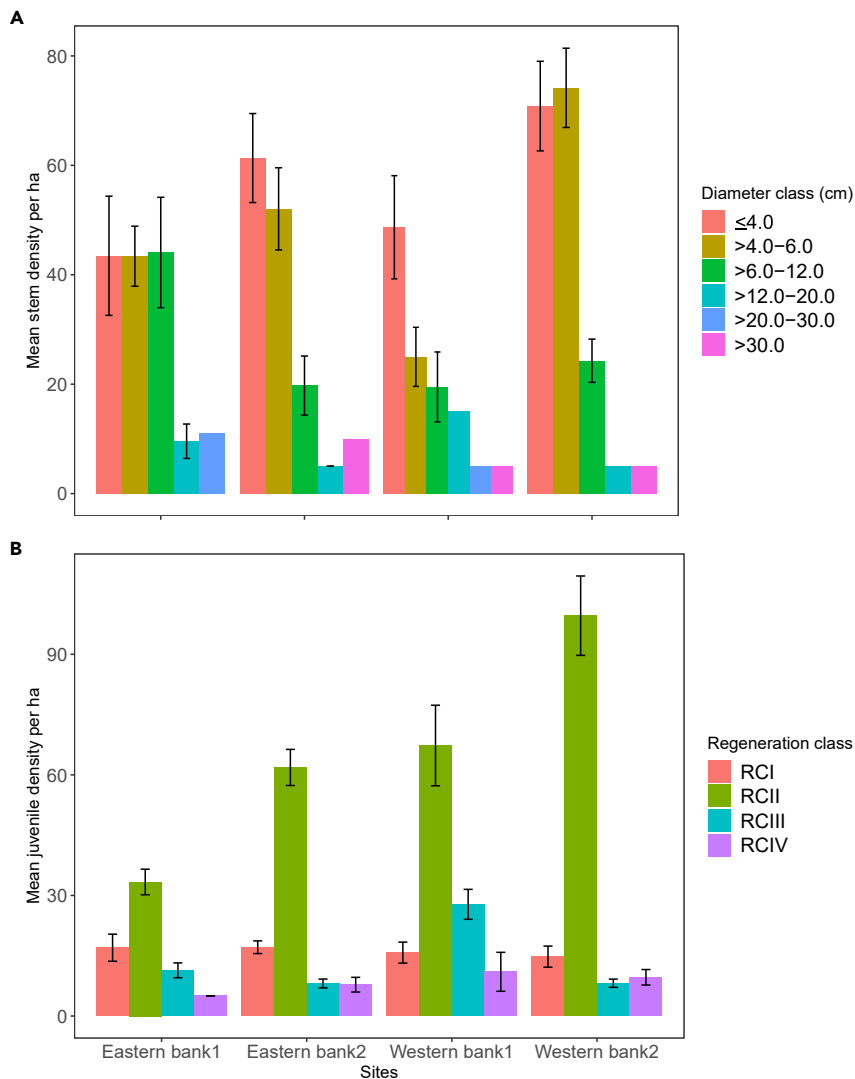


Figure 4. Mangrove vegetation structural properties

(A) Stacking density, which is the number of trees ha^{-1} in given diameter classes in studied sites of the Ankobra (see also Table S5).

(B) Sapling density is the number of juveniles in given height classes (natural regeneration classes) in the studied sites of the Ankobra mangrove forests. Bars and errors bars represent mean \pm SEM of the density of trees and juveniles ha^{-1} (see also Figure S6 and Table S6).

(estimate = -0.08841 , $z = -4.703$, $p = 2.56e-06$), but positively associated with the total number of trees available per plot (estimate = 0.12342 , $z = 6.135$, $p = 8.49e-10$), the average distance from river (estimate = 0.12342 , $z = 6.396$, $p = 1.60e-10$) and the total trees cut per plot (estimate = 0.06227 , $z = 2.861$, $p = 0.004227$) (see Figure S6).

The complexity index was also highest in the Western bank 2 (closest site to the landing beach of Ankobra) and lowest in the Eastern bank 2 mangrove forest. Generally, the Western mangrove forest had the highest complexity index. Stems with diameters between 4 and 6 cm had the highest complexity index and were more evident in the Western bank mangrove forest (Table 2).

Height-diameter distribution

The relationship between diameter and height of trees in the entire mangrove forest was statistically significant and positive ($F = 1160.25$, estimate = 5.93 , $p < 0.001$), explaining a substantial variation (R^2) of

Table 2. Structural attributes of the Ankobra mangrove forest

Forest bank	Attributes	Utilization/diameter class (cm)					
		≤4.0	>4.0–6.0	>6.0–12.0	>12.0–20.0	>20.0–30.0	>30.0
Eastern bank1	No of species	3	4	3	4	1	0
	Stem density	737	779	616	68	11	0
	mean height	4.100	6.078	9.944	14.185	21.500	0.000
	basal area	0.642	1.401	3.112	1.120	0.512	0.000
	Complexity index	0.019	0.066	0.191	0.011	0.001	0.000
Eastern bank2	No of species	4	2	2	2	0	1
	Stem density	1271	1090	314	19	0	10
	mean height	3.958	4.930	5.941	12.175	0.000	16.650
	basal area	0.011	0.020	0.013	0.004	0.000	0.012
	Complexity index	0.001	0.001	0.000	0.000	0.000	0.000
Western bank1	No of species	5	3	4	1	1	1
	Stem density	930	325	190	15	5	5
	mean height	3.255	6.061	7.501	7.757	18.200	20.500
	basal area	0.704	0.599	0.823	0.262	0.206	0.769
	Complexity index	0.107	0.035	0.047	0.000	0.000	0.001
Western bank2	No of species	2	1	1	1	0	1
	Stem density	1275	1335	340	5	0	5
	mean height	6.732	9.593	13.726	8.500	0.000	22.000
	basal area	1.125	2.404	1.424	0.094	0.000	1.070
	Complexity index	0.193	0.308	0.066	0.000	0.000	0.001

38%. Similar results were found in the separate bank forests, thus in the entire Eastern bank ($F = 1139.87$, estimate = 5.67, $p < 0.001$, $R^2 = 0.54$) and the Western bank ($F = 650.70$, estimate = 7.28, $p < 0.001$, $R^2 = 0.42$).

For *R. harrisonii*, which was the most dominant tree species in the forest, its tree diameter also varied significantly with tree height ($F = 1707$, estimate = 5.79, $p < 0.001$), which also explained a substantial variation of 35%. It was observed that a significant proportion of trees in the Eastern bank 2 and Western bank 1 forests were limited to heights below 12.0 m and diameters below 5.0 cm (Figure 5).

DISCUSSION

Local knowledge on mangroves

Coastal residents' botanical and ecological knowledge about mangrove forests is influenced by the use of mangroves.⁵² The results of this study support the observation by Walters,⁵³ where the village (Sanwoma) that visit the mangrove for fishing and cutting of mangrove wood had higher knowledge of mangrove compared to villages that only come into the mangrove forest to fish. Thus, apart from people in the village who visit the mangrove more often for both wood and fish, the other four mangrove-fringing villages are primarily farmers that only see fishing as a secondary activity, hence visit mangroves less often. Similar to this study, reviews by Otto and Pensini⁵⁴ and Parrotta et al.⁵⁵ observed that traditional knowledge of an ecosystem is gained through connectedness and experiences. For example, >60% of the population in the village closer to the mangrove forest, who cut mangroves, and also fish in the mangroves more often, could identify and specify the names and uses of at least two of the three true mangrove species (i.e., *Rhizophora spp.*, *Avicennia spp.*, and the *Laguncularia spp.*). On the other hand, populations who visit the mangrove forest secondarily for only fishing mostly identified any tree in the forest as *R. spp.*, construing a lack of high connectedness and experience on mangroves (see Figure S1). A similar account was the observations of Palacios and Cantera⁵⁶ in Colombia and Frank et al.⁵⁷ in Kenya, who found differences in mangrove knowledge among communities based on lack of connectedness. Comparing these two populations, we note that people who lack enough knowledge on mangroves may either have low preference for mangrove wood or have adequate alternative wood options, hence have indirect or low negative impact on mangrove forests.

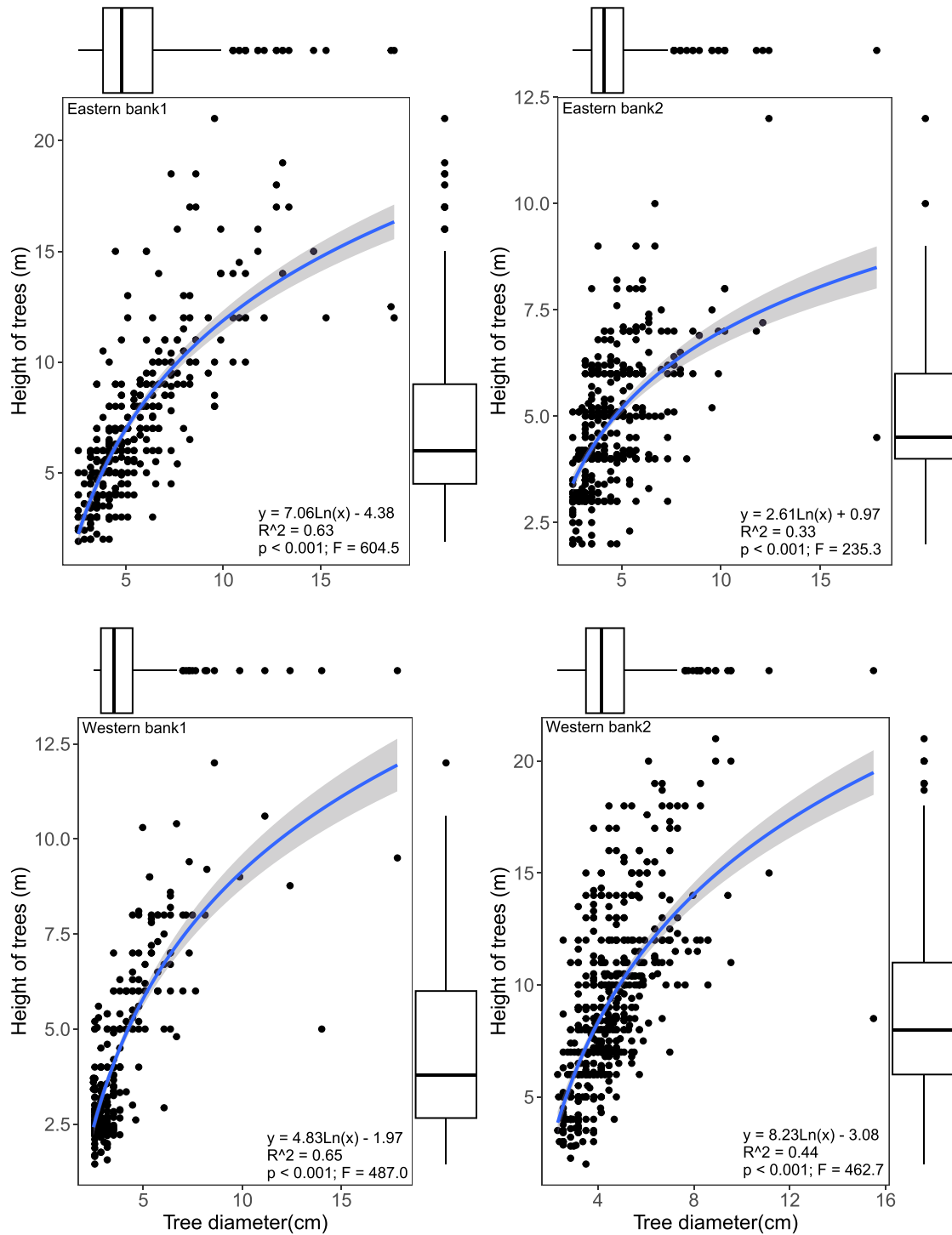


Figure 5. Height-diameter distribution of the dominant species, *Rhizophora harrisonii*

Tree diameter equals diameter of tree measured 130 cm above ground. The equation, ($p < 0.05$), correlation coefficients (R^2), and the F-statistics are given in each case. The boxplots display percentile distribution in each case. The ends of the box are positioned at the 25th and 75th percentiles of the dataset. The exact p values were $3.92e-79$, $1.74e-43$, $3.89e-62$, and $3.82e-76$ for Eastern bank1, Eastern bank 2, Western bank1, and Western bank2, respectively (see also Figure S5).

Like other vegetation types across the world, mangroves are known by different local names in different locations,⁵⁸ which mostly reflect their key biological features.⁵⁹ In this study, and in the local “Nzema” language, mangrove (“ngateke”) generally refers to *Rhizophora* due to its higher abundance in the forest and its usefulness. The same case where the name of the most abundant mangrove species was given to the entire mangrove in a community has been reported in India by Dahdouh-Guebas et al.,⁶⁰ Kovacs⁶¹ in Mexico, and by Nfotabong-Atheull et al.⁴⁰ in Cameroon. In the Ankobra catchment communities, the local name of *Rhizophora* (“ngatekeblew”) refers to female mangroves because they have more “legs” (roots) and “hands” (branches), hence are more useful, while *Avicennia* (“ngatekenyini”) means male mangroves (few roots and branches and less useful). *Acrostichum* (“kosinyansoa”) refers to leaves for a type of crab (known as “kosi” in the local language). This crab (i.e., the “kosi”) feeds on and takes refuge under the *Acrostichum* mostly during long low tide periods. The refuge behavior of the crabs and other shellfish, like the *Littorina* spp. are rather positive for hand-picking fishers (mostly females/women) who target shellfish. The meaning of the local name for *Laguncularia*, “kosibaka”, however, is not generally known, but in the Nzema language, “kosi” as used earlier is a species/genus of crab, while “baka” means tree, hence “tree of crab” (see Table S2). It is therefore important to note that the plant species that are more abundant or more useful to coastal communities can shape their knowledge of forest ecosystems.

Mangrove species preferences and utilization

As prevails in most developing countries,^{12,52,62,63} mangrove cutters in our study also exploit mangroves for fuelwood, construction, medicine, food, and chemical for tanning of fishing nets. The most important mangrove species recorded for fuelwood were *R. spp.* and *A. germinans*. To the indigenes of the most mangrove cutting village, Sanwoma (the known fishing community), mangrove wood is easier to get, cheaper, more calorific, and results in nicer/tastier smoked fish. These properties of mangroves have been reported by Kwarteng et al.⁶⁴ in Ghana and Nfotabong-Atheull et al.⁴⁰ in Cameroon where smoking is the most preservation means by market women. The better taste and reddish color of fish smoked using mangrove woods are also reported by Ajonina et al.⁵⁰ and Kwarteng et al.⁶⁴ In Colombia⁵⁶ and Malaysia,⁶⁵ *R. spp.* was reported as the main wood for fuel because of its high calorific value. Along the eastern coast of Ghana, mangroves are used for fuelwood.^{11,51} In several other African countries, including Guinea⁶⁶ and Madagascar,⁶⁷ mangroves are also used for fuelwood. From the findings of this study, *A. germinans*, considered the second-best choice as fuelwood, is rather not used by fish processors for smoking fish, but rather for other domestic uses, such as cooking, heating, bread baking, and frying of fish. This is because it darkens the fish when used for smoking, due to its high smoke production. The fish processors’ reports are comparable to Aritonang et al.,⁶⁸ who explained that the bark/shell of *A. spp.* contains liquid smoke (formed by burning bark or shell of the wood and condensing the smoke to liquid) but can be purified from its dark-charcoal color to gray and be used as a preservative against microbial growth on fish. The leaves of *A. spp.* have also been reported by Palawe et al.⁶⁹ to contain ethanol extracts, which are anti-microbial products, a benefit yet to be known by many mangrove users.

The aesthetics, straightness, resistance, durability, and availability were among the factors for selecting the best construction mangrove species. The durability of such selection was most important. Mangrove users from this study identified *Avicennia* as the most durable mangrove species because it is more resistant to insects – and this supports the anti-microbial findings of Palawe et al.⁶⁹ According to Kusmana and Sukristijono⁷⁰ the durability and strength of the genus *A. spp.* make them very useful as timber products in Indonesia. On the other hand, Friess et al.² also reported the durability and strength of *Rhizophora*, hence being preferred for house construction. In Colombia, *L. racemosa* and *A. germinans* are logged for construction, while *Rhizophora* was only best suited for fuelwood.^{56,71} In our study, *Rhizophora* was also preferred for construction to *Laguncularia*, but comes after *Avicennia*. Unlike mangrove users in Colombia, mangrove cutters in our study have less preference for *L. racemosa* for construction because of the very low abundance of the species in the Ankobra forest. Like this study, Ntyam et al.⁵¹ and Traynor and Hill⁷² reported the use of *Rhizophora* and *Avicennia* species for construction in Cameroon and South Africa, respectively. These descriptions of mangrove illustrate their importance to building, especially in communities with limited access to high-resistant building timber. However, the preference can somewhat regionally vary based on how an individual views the benefits for a particular mangrove species.

This study documents the use of *Rhizophora* and *Avicennia* for treating different ailments in Ghana. The barks, roots, and leaves are used for treatments (of malaria, stomach problems, ulcers, and diarrhea) by boiling or grinding and mixed with garlic and ginger. *Rhizophora* and *A. germinans* were also reported

for the treatment of malaria,⁷³ and haemorrhoids⁷⁴ in Benin. Nabeelah Bibi et al.⁷⁵ reported *A. germinans* to be used for treating ulcers, malaria, haemorrhoids, treatment for haemorrhages, and rheumatism. In Colombia, Palacios, and Cantera⁵⁶ found that leaves of *R. spp.* are chewed to compensate for alcohol, while *Avicennia* roots were used to heal wounds and diarrhea. This study did not find the use of mangroves to treat rheumatism and compensate for alcohol. However, the people of Sanwoma use *Rhizophora* for making “bitters” (a mixture of plant parts and alcohol to raise one’s appetite).

Dossou-Yovo et al.,⁷³ and Ahouangan et al.⁷⁶ in Benin, Dahdouh-Guebas et al.⁶⁰ in India, all reported the use of mangroves as fodder for livestock. We found that local people in our study area consume the new roots of *Rhizophora* to compensate for the absence of food while in the mangrove forest. While *A. spp.* are not species eaten as food by fishermen in our study, in Southeast Asia, countries such as India and Indonesia, their seedlings are eaten as vegetables.^{70,77} In East Africa, such as Kenya, *R. spp.* is used for tanning fishing nets.^{78,79} The Gambia¹² and India⁶⁰ are reported to use mangroves for tanning fish nets. The reason found in this study, which supports Satyanarayana et al.¹² was that the red pigments (tannins) in *Rhizophora* both strengthen the net and blind a shoal of fish when in use. The comparison of mangrove uses in this study to other studies indicates that mangrove uses may be similar around the world but differ depending on how they are used for the specific purpose(s).

Fishing was found to be the primary activity that connects all villages in the study area to mangroves, as often seen in most mangrove communities in the world (cf. Ehirim et al.,⁸⁰ Gallup et al.⁸¹ in Senegal, India, and Seary et al.⁸² in Bangladesh). Sanwoma, the main coastal community in this study, has fishing as its primary source of income. While fishing was a secondary income source for the other villages, fishing in all these communities varied with gender (male dominated). Adjei and Sika-Bright⁸³ and Uduji and Uduji and Okolo-Obasi⁸⁴ have reported gender-based division of tasks in fishing, and similar to this study more males (mostly sea fishing) are into fishing, and most females are fishmongers. Some of the different fishing gears and techniques used were also used elsewhere, e.g., in Bosomtwe-Sam in Ghana.⁸⁵ The information here is that while people may have inadequate knowledge of mangrove species, corresponding to low use of the wood, the multiple benefits of the ecosystem, including its fisheries, can still bring the different human populations together. This helps us understand better the diversities that lie in the mangrove ecosystem, the resource users, and the use patterns, as well as how every individual can impact the ecosystem.

Mangrove status: mangrove vegetation structure and regeneration

Globally, unregulated tree felling, and overexploitation of fisheries due to increasing human population density in coastal countries, have become major threats to all mangroves, including pristine types.^{39,41,86} These threats are widening across all tropical coasts.^{3,5} The sites studied here showed a significant correlation between mangrove species composition along the distance of plots from river and anthropogenic pressures such as tree branch cutting (the number of branches cut in a tree per plot). The change in species composition due to distance from the river could explain two major stresses, including salinity stress, which increases landward, and hydrological (inundation) stress. The study showed mangrove forests dominated by *R. harrisonii* and *A. aureum* with low and unproportionable composition of *A. germinans* and *L. racemosa*. This is true because in river estuaries as exemplified in Guinea,⁸⁷ low salinity tolerant mangrove species like *R. racemosa* and *R. harrisonii* predominate over species such as *L. racemosa*, and *A. germinans* that tolerate a high range of salinities. Also, cutting of branches of the trees of certain mangrove species may have an indirect effect on propagule abundance (and natural recruitment), since branches are normally the points of attachment for fruits and leaves. The degradation due to branch cutting of mangroves and the stresses of salinity and/or water could be advantageous for the colonization of opportunistic and non-useful vegetation species, including terrestrial plants.⁸⁸ In effect, among the three main true mangroves found in this study were four minor/associate mangrove species of terrestrial origin. For example, both *T. populnea* (L.) and *Sol. ex Correa*, a semi-mangrove^{89,90} and *A. aureum* L.^{91,92} are reported to colonize and increase on low saline soils in degraded mangrove forests. Qiu et al.⁸⁹ reported that *T. populnea* grows normally under saline conditions below 8 g kg⁻¹ (8 ppt)– with rather inhibited growth when the salinity is above 11 g kg⁻¹ (11 ppt) because of a reduction in chlorophyll production. In similar account in Brazil, Santos and Fabricante⁹⁰ report that *T. populnea* has invaded North-eastern Brazilian mangroves due to the influence of the Sergipe River, as the species thrives better in low salinity conditions, but also under high inundation, since the propagules are adapted to float in the water for long-distance dispersion. In highly disturbed areas of mangroves, herbaceous plant species like *A. aureum* secondarily

may appear providing distinctive composition because they can modify that habitat unfavorably for other successors (i.e., cryptic ecological degradation).⁸⁷ The dominance of *Acrostichum* in the western bank forests could be associated with high degradation, as *Acrostichum* is considered an opportunistic species that pioneers degraded and low saline sections of mangrove forests.⁹² In Sri Lanka, increasing freshwater conditions resulted in a >59% net increase in *A. aureum*.³⁹ The Ankobra estuary is a riverine type with low salinity range, therefore, in addition to mangrove tree felling, *Acrostichum* alone in this study contributed to about 56% of the dissimilarity in species composition among sites. Additionally, *A. aureum* spread sporadically, and they are not useful to people. Therefore, they have more advantage to spread over large areas against species preferred by humans—similar situations in the Small Island Developing States (SIDS).⁹³ In West African mangroves, *Zanthoxylum zanthoxyloides* (Lam.) Zepern. & Timler has also been reported in Nigeria,⁹⁴ Senegal⁹⁵ and in Benin they are harvested as fodder for livestock,⁷⁶ but act as opportunistic species in disturbed mangroves. The species, *A. glabra*, the second most abundant species found in only the Eastern Bank 2 forest, is mostly associated with terrestrial forests.³⁴ All these species invade mangrove forests under anthropogenic influence. Therefore, together with inundation and salinity stresses, the composition of degraded sites is altered as opposed to non-degraded areas.³⁴ This is very visible in Western bank 2, where only true mangrove species (*R. harrisonii* and *A. germinans*) occur (Table 1) together with *A. aureum*.

Stocking density of trees in the forests was negatively affected by latitudinal gradients, selective logging of trees, and the density of *A. aureum* per plot. This means that the northward movement of vegetation and the abundance of *Acrostichum* could inhibit the transition of young trees to mature trees. The effects of mangrove cutting in this study are not only a challenge in Ghana and in our study site, but also in other countries like Madagascar⁶⁷ and in the Colombian Pacific,⁵⁶ where cases of mangrove extraction by rural communities caused severe changes in species composition and vegetation structure. When there is high anthropogenic pressure, such as selective logging, species introgression becomes a major issue, leading to cryptic degradation, and this can make the “non-useful” species becoming more important.^{39,71} As we also observed the growing dominance of *A. aureum* in this study, a similar instance was observed by Scales and Friess²⁸ in Madagascar, where excessive harvesting of preferred mangrove species resulted in non-useful *Ceriops tagal* (Pers.) C.B.Rob becoming the most important species. In Colombia, Blanco et al.⁷¹ reported that massive selective clearing led to the introduction of antagonistic species such as *Laguncularia* and *Acrostichum*, thereby reducing the growth and abundance of native species of *Rhizophora* and *Avicennia* in different diameter classes in the Uraba Gulf mangrove forests. Although *Acrostichum* is not identified as invasive in Ghana, mangrove cutters confirmed its cover has significantly increased over historical years in areas where low abundance and small diameter trees occur. Therefore, as uncontrolled harvesting is happening, it paves way for the non-useful species which modify the habitats including the obstruction of light from reaching young generations of preferred and important species.^{34,39}

The low density of trees and juveniles in the upper classes for both diameter classes and natural regeneration classes has been similarly reported by Ntyam et al.⁵¹ in Ghana and Akpovwovo⁹⁶ in Nigeria as a response to selective logging which reduces propagule abundance in disturbed areas. Thus, when mature trees in higher diameter classes are mostly harvested either for construction or fuelwood, there is an indirect reduction in propagule formation and abundance. Young seedlings are also inhibited from transitioning through juvenile stages to maturity due to competition for light and space with less preferred or opportunistic species which secondarily pioneers degraded areas.^{39,87} Also, the differences in complexity index among the individual forests studied could reflect the effect of human pressure where some sites receive higher encroachment of mangrove cutters than others.³⁶ A similar account was given in both Sri Lanka and Kenya by Dahdouh-Guebas et al.,³⁹ Goessens et al.⁹⁷ in the Matang mangrove in Malaysia, and in India by Rasquinha and Mishra,⁹⁸ who found that less-disturbed mangrove forests become more structurally complex with higher density of trees than disturbed ones. In essence, the Western bank 2, which is about 1.5 km from the landing beach of Ankobra (in Sanwoma) and has both the highest stocking density ha^{-1} of stems and saplings, could be an indication of low wood harvesting. This is because cutting mangroves is somewhat not encouraged (though compromised due to limited livelihood options), so people who enter the mangrove forest for fuelwood and construction wood go beyond this point (i.e., the WB2) by an average of 3.2 km and 3.6 km respectively. Therefore, in forests of low mangrove harvesting, there is more advantage for higher natural seedling recruitments, leading to high stocking density and juvenile density, as observed in Kenya by Kairu et al.⁴⁵ and in Ghana by Ntyam et al.⁵¹ The relatively low stocking densities of 1,470 and 2,211 stems ha^{-1} in the Western bank 1 (≥ 2.5 km from the landing beach) and Eastern

bank 1 (≥ 3 km) reflect that WB1 and EB1 have youthful plants (with short heights and low diameters) because of high human disturbance,⁷⁸ which can be compared with Akpovwwo⁹⁶ in Nigeria. Ntyam et al.⁵¹ and Ajonina⁹⁹ all reported a *R. spp.* dominated forest in Amanzule in the western coast of Ghana, in terms of seedlings, saplings, and adult trees, but lowest for *Laguncularia* (which is similar to this study). According to Akpovwwo⁹⁶ and Sherman et al.,¹⁰⁰ mangroves dominated by *R. spp.* have high stocking density. This could explain why the Ankobra mangrove forest, which is *Rhizophora*-dominated, registered a higher density compared to the *Avicennia*-dominated (3627.7 stems/ha) Kakum forest reported by Adotey et al.¹⁰¹ However, despite the Western bank 2 having the highest stocking density, all forest banks in this study recorded relatively lower stem density especially compared to Ajonina et al.⁵⁰ in Amanzule forests and Adotey et al.¹⁰¹ in Kakum mangrove forests. This occurrence could be attributed to the high harvesting pressure on the forest, as fish smokers prefer *Rhizophora* in the surrounding villages.

Main,¹⁰² and Alemayehu, and Chemuku¹⁰³ state that at least 2,500 established seedlings per hectare are needed for sufficient regeneration. From this study, the density of established regeneration in each mangrove **bank** was higher than this threshold Kairu et al.⁴⁵ However, due to the intense pressure on the ecosystem through the collection of mature trees, there is no full reflection of a balanced mangrove structure with a good transition from juvenile-sapling regeneration to mature tree abundance. Therefore, the provision of alternative/supplementary livelihood as requested by the mangrove cutters could be the best option. These may include alternative sources of fuel, improved electricity, and cold stores (alternative fish processing means), and livelihood funds, which could help reduce the pressure on the mangroves. Technical and vocational training programmes and improved mangroves for tourism,¹⁰⁴ and payment for ecosystem services¹⁰⁵ in accordance with the needs of the communities¹ have also been suggested for mangrove-dependent communities.

Conclusion

The analysis of the spatial stocking and sapling densities from this study can be used as good inventory to gauge the structural properties of the Ankobra mangrove system. The present inventory revealed that areas closer to villages (within the first 1.5 km of the forest from the Sanwoma village) have high standing density (2,960 individual stems ha^{-1}) and high natural regeneration density (9,005 individual juveniles ha^{-1}). Sites further away from villages (beyond this limit, the 1.5 km), on the other hand, have a low standing and juvenile densities due to higher human encroachment). We see from this that when local regulations against mangrove cutting is restricted to only some parts of mangrove forests (where in our study was just a small area), the structure of the whole mangrove forest become structurally poor (i.e., leading to monospecific forest, and disproportional number of individuals in the different vegetation age groups/classes). The study also reveals that in mangroves with selective logging, where people prefer certain tree species more than others, species that are less preferred or non-used can later become a problem, especially when favored by environmental conditions. For this reason, the fern and herbaceous *A. aureum* abundantly occupied degraded portions of the forest and contributes 56% of the dissimilarity in species composition of the mangrove across all forest areas, covering about 59% of the western bank mangrove forests. This ecological impact has significant effects on both natural regeneration and stocking density of the forests, such as inhibition of seedling growth to mature trees. Selective logging negatively affected the standing density, while the cutting of branches was found to negatively impact juvenile density ($p < 0.05$). This study further reveals that the removal of adult trees affects not only tree standing density but also juvenile density, because areas with lower tree abundance correspondently had lower juvenile density ($p < 0.05$). The structure of the forest was also dependent on environmental factors like water availability, but this relationship was not consistent across the entire forest compared to mangrove cutting. For this reason, the forest has good natural regeneration with well-established seedlings (i.e., regeneration class RCII), but they are not reflected in the adult tree population. Thus, selective cutting resulted in significantly different mangrove diameter distributions, leading to the low number of mature trees in more disturbed locations. Monitoring mangrove diameter distribution classes can therefore inform scientists and managers of how much local communities rely on mangroves. Meanwhile, mangrove cutting is seen to benefit about 98%, 88%, and 50% of the population who use mangrove wood or wood products for fuelwood, construction, and medicine respectively, a situation which is common across the tropical mangrove nations. Therefore, communities whose daily needs, such as shelter and health, heavily depend on mangroves, must be well-recognized in the management of the ecosystem. Just like other developing world, the lack of alternative/supplementary livelihoods, such as arable land for farming, employment, cheap labor, and low fish catch were identified as the main forces driving mangrove cutting in communities with high

dependence on mangroves. We therefore recommend that capacity-building programmes, such as vocational training (i.e., tailoring, dressmaking, carpentry, driving, and other artworks), should be encouraged to support communities that depend solely on mangroves. Also, reintroducing the payment schemes for people devoted to mangrove afforestation programmes, as carried out by previous NGOs (i.e., the Hen Mpoano and the Sustainable Fisheries Management Project), could be effective to protect mangroves. This can help bring the mangrove structure into balance. Moreover, all these recommendations must parallel the provision of the community needs such as a better road network for transporting farm produce to markets, school facilities provided to reduce the number of mangrove harvesters, and provision of access to other fish processing facilities other than smoking. This research creates a basis for better management and conservation of mangroves, and a continuation of these assessments to predict the structural changes and impacts on their ecosystem services is recommended. This shows that management of mangrove forest anywhere in the world is highly dependent on addressing needs of communities.

Limitations of the study

We identified from this study that anthropogenic and environmental factors such as wood cutting and water stress have significant impacts on the structure of mangrove forests. We hold that these impacts favor non-useful vegetation such as mangrove ferns, which in turn significantly reduce natural regeneration and tree growth. However, we believe that the models developed to investigate these effects would be more improved if the study surveyed and included edaphic (soil) factors in mangrove forests. These parameters may include soil salinity, nutrients, temperature, etc., which are identified to have effects on plant growth. Also, due to time constraints for this study, which combined both a mangrove survey and interviews, the study did not extensively include greater portions of mangroves around the farming communities in the mangrove survey. In these areas, mangroves are not harvested. Therefore, including those areas of the mangrove forest would explain whether other indirect factors such as agriculture and pollution affect the mangrove structure. Finally, the study included fishery activities in mangrove forests. However, it was very difficult to use the scientific names of fish species caught in mangroves for our fishery analyses. This was due to two reasons: inconsistent local names for a particular fish species and the lack of time for laboratory identification of the fish species sampled.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.106858>.

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AUTHOR CONTRIBUTIONS

F.A.: Conceptualization, methodology, formal analysis, data curation, validation, investigation, writing – original draft, writing – review & editing, visualization; J.H.: Writing - review & editing, validation, supervision; N.K.A: Writing – review & editing, resources, supervision; F.D.-G.: Conceptualization, methodology, data curation, validation, resources, writing - review & editing, supervision, project administration.

DECLARATION OF INTERESTS

The authors declare no competing interest.

INCLUSION AND DIVERSITY

We worked to ensure gender balance in the recruitment of human subjects. We worked to ensure that the study questionnaires were prepared in an inclusive way.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
R	The R Development Core Team	https://cran.r-project.org
RStudio	Posit Software, PBC	https://posit.co/
PAST 4.03	The Palaeontological Association ¹⁰⁶	https://past.en.lo4d.com
Other		
Mangrove survey data	This paper	https://serm.ulb.be (serm@ulb.be)
Interview survey data	This paper	https://serm.ulb.be (serm@ulb.be)

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be answered by the lead contact, Frederick Asante (frederickasante34@gmail.com).

Materials availability

This study generated primary data from mangrove vegetation from field surveys and interviews, and the data associated with the results are available at the Systems Ecology and Resource Management Research Unit through the email address serm@ulb.be.

Data and code availability

All vital data and codes are included in the Excel-based platform and can be contacted via the SERM Lab, ULB (at <https://serm.ulb.be>) serm@ulb.be or via the lead author's email above. Any additional information required to reanalyse the data reported in this study can be requested from the lead author.

METHOD DETAILS

Study site description

The Ankobra estuarine mangrove wetland, located between 4° 59' 23.87"N, -2°18' 56.63"W and 4° 50' 15.05"N, -2° 9' 43.31807"W covers an area of 1.18 km².¹⁰⁷ The mangrove fringes the banks of the Ankobra river, flowing 190-209 km south of the Atlantic Gulf of Guinea.^{108,109} The Eastern bank of the estuary is almost free of settlement due to its highland nature, while the Western bank is gently sloping, enabling a high concentration of human settlements and easy access into the mangrove system with or without canoes. Five main villages surround the mangrove forest namely, Sanwoma, Ajomoro Eshiem (Eshiem, hereafter), Eziom, Kukuaville, and Adelekezo. The people of Sanwoma engage in fishing activities and mangrove cutting, with men as fishers and women as fishmongers.¹⁰⁹ Fish processors, domestic house constructors, and the community in general heavily depend on the mangrove.¹⁰⁸ On the other hand, Eshiem, Eziom, Kukuaville, and Adelekezo are mainly farming communities that plant food crops and commercial crops, and only engage in fishing as secondary activities mainly on subsistence bases. The sites selected for this study were randomly chosen distance referenced to the Ankobra beach landing in Sanwoma. The distance between the landing beach and Western bank2 was 1.5 km, while it was 2.5 km from the Western bank 1. For Eastern bank 1 and Eastern bank 2, the distances between them and the landing beach were 3.0 km and 4.0 km respectively.

Data collection techniques

Vegetation sampling

Mangrove vegetation data were collected using the methods employed by Kairo et al.,³⁶ and Bundotich et al.,¹¹⁰ who used a stratified sampling scheme on transect lines. The data were collected from two adjacent sites of the estuary, the Western bank, and the Eastern bank, relative to the landing beach of Ankobra.

An initial reconnaissance was conducted to demarcate the line transects (perpendicular to the coastline) and the river/estuarine bank. Four line transects were set – two on each side and 1.0 km apart (i.e., transects Western bank 1 and Western bank 2; and Eastern bank 1 and Eastern bank 2, respectively) (Figure 1). Along each transect, 10 m × 10 m adjacent quadrats were drawn to sample adult mangroves (trees with stem diameter ≥ 2.5 cm and stem girth ≥ 8 cm). The height of each tree within each plot was measured with Suunto™ clinometer in meters, whereas the girth G_{130} of each tree (in cm) was measured at 130 cm above the ground and along the stem with a measuring tape. For *Rhizophora* species, girth measurements were done at 30 cm above the highest prop root⁶⁰ but for other species, individual branches of a tree were treated as separate stems when the stem forked below 130 cm from the ground.³⁶ The position of each tree in the plot was also identified by measuring its x- and y-coordinates. Also, the number of dead/cut trees and cut branches were counted in each plot. Since *Rhizophora* spp. are cut very close to the ground, the remaining roots were counted from which the number of cut trees was estimated using the average number of roots from live trees. A total of 80 plots were sampled, which consisted of 20 plots on each line transect across the Western banks and 19 and 21 on EB1 and EB2 banks respectively. Only 19 plots were surveyed on EB1 as that was the limit of the line, behind the 19th plot was terrestrial land without mangroves. The GPS coordinates of each plot were recorded using the *GPS Status* (version 11.0.307) smartphone application with an average(range) error of 4.4(2-8) m. Mangroves were taxonomically identified to the species levels using identification keys by Tomlinson,¹¹¹ Duke and Allen,¹¹² and Stearn.¹¹³ The identification was also supported by “Plant identification applications” (i.e., PictureThis version 3.25.1, iNaturalist version 1.26.11, and PlantNet version 3.9.18). These Apps extract information from the pictures of the plant physiognomies provided and use machine learning and computational selection to identify the plant. For this study, pictures of the fruits, leaves, and full plants (where applicable) were used in the Apps. The plants identified were further confirmed from Ghana’s flora and the West African sub-regional flora database and the World Register of Marine Species, WORMS.

To assess the natural regeneration pattern, each of the 10 m × 10 m quadrats were subdivided into 5 m × 5 m subplots,^{102,114} and the occurrence of juveniles of each species were counted and categorized into different height-based classes.⁴⁵ Thus, all seedlings with heights below 40 cm belonged to class 1 (RCI), saplings with heights between 40 and 150 cm belonged to class 2 (RCII), and trees with heights greater than 150 cm but below 300 cm belonged to RCIII,^{102,110,114} and finally, trees with a height greater than 300 cm but with stem diameter less than 2.5 cm were grouped under class RCIV. It should be noted that all seedlings above 30 cm in height were referred to as established regeneration. It should be noted that the juveniles considered in this study refer to all live plants and propagules regardless of the number of leaves they contained.

To depict the structure of the forest types in the Ankobra mangrove system, the profiles of the 100 m² quadrats were drawn based on the tree density.¹¹⁴ The spatial pattern of trees and regeneration in the field was analysed inside 100 m² plots along the line transects.^{36,110}

Traditional mangrove use, utilisation patterns and local ecological knowledge data

Before beginning the data collection, ethical clearance was first obtained from the University of Cape Coast, Ghana. Together with the ethical clearance were the informed-consent forms which explained to every participant the purpose of the research and the voluntary participation in this study as well as the confidentiality of their responses as the information received from them was to be used anonymously for research. Therefore, every participant signed/thumb-printed the consent form.

The data collection was conducted by face-to-face interviews in the five main mangrove communities – Sanwoma, Eshiem, Ezium, Kukuaville, and Adelekezo, using the modified semi-structured questionnaire of Dahdouh-Guebas et al.⁶⁰ The questionnaire consisted of four (4) main parts:

- Socio-demographic and economic traits.
- The Main uses of mangroves as vegetation, and ecosystems.
- Fish-related activities; and
- Evolution of the mangrove area and local importance.

Each part contained open- and some close-ended questions to ensure that relevant and quality information was collected for comparative data analysis.¹¹⁵ Within each of the last three parts, questions regarding COVID-19 effects were surveyed.

Before data collection, a meeting was convened with the assemblymen and traditional leaders to explain to them the purpose of the research and also gain further knowledge about the households in the villages.

A total of 121 households were visited by employing systematic sampling by visiting every second house from a marked point, but in the absence of an empty house at the time of the survey, the third house was interviewed. "We defined household as a person or group of related or unrelated persons who live together in the same housing unit, sharing the same housekeeping and cooking arrangements and are considered as one unit, who acknowledge an adult male or female as the head of the household".¹¹⁶ The 121 respondents represent 80 from Ellembelle (i.e., Sanwoma) and 41 from Evalue-Ajomoro-Gwira (Eshiem-9, Eziom-10, Adelekezo-10, and Kukuaville-12 respondents). In Eziom, almost all households were visited due to its low population.⁷⁸ The GPS coordinates of all households visited were recorded to avoid double sampling in a single household. To avoid redundancy and achieve some level of consistency in answers from respondents in a household, only one person was interviewed.¹¹⁷ Participant in each household was randomly chosen only when individuals willing to partake were two or more. The whole interview was conducted in an Akan language (Twi) and then translated to English. Prior notices were given to all villages through the local information systems before the day of the interview.

The content of the questionnaire included questions to unearth the general information about the individuals of the community (respondents), questions to reveal how they conduct various activities in the mangrove forest (mangrove species use, and fishery-related activities) and what their preferences were, as well as questions aimed at drawing out the respondents' opinions about some socio-economic issues^{78,118} about the Ankobra mangrove system. For questions regarding mangrove knowledge, respondents were assisted with tree physiognomies such as leaves, fruits, and seeds of each mangrove species¹¹⁸ as well as pictures taken from the Ankobra mangrove forest. All interviews began by weighing the respondents' knowledge of mangroves to ensure that both the respondent and interviewer were discussing the same concept and subject area.

Because of COVID-19, all protocols laid down by the government for ensuring reduction in the viral spread were followed making sure that a nose mask was worn throughout the interviews – in the absence of a mask, the participant was given one for free. All questions were read loud and clear and explained to participants once they accept to partake in the research. Permission of each respondent was sought whenever necessary to do an audio voice recording.

QUANTIFICATION AND STATISTICAL ANALYSIS

Mangrove vegetation structure and regeneration

Forest composition and structural indices

From the tree count, the stem density of each species was determined to indicate the abundance of each species in each site (Equation 1). This was done for all the seven vegetation species including three true mangroves: *Rhizophora harrisonii*, *Avicennia germinans*, and *Laguncularia racemosa*; and four associate/minor mangroves: *Acrostichum aureum*, *Thespesia populnea* (L.) and Sol. ex Correa, *Zanthoxylum zanthoxyloides* (Lam.) Zepern. & Timler, and *Annona glabra* L. All other vegetation which was less abundant and non-mangrove were denoted "others". Absolute frequency (Equation 2) and absolute dominance/cover (Equation 3) were also calculated.

$$\text{Absolute density (De)} = \frac{\text{Number of trees of a species}}{\text{Area of plot in ha}} \quad (\text{Equation 1})$$

$$\text{Absolute frequency (F)} = \text{percentage of plots in which a species is found} \quad (\text{Equation 2})$$

$$\text{Absolute dominance (Do)} = \frac{\text{Total basal area of species}}{\text{Area of plot in ha}} \quad (\text{Equation 3})$$

where

$$\text{Basal area} = \frac{\sum (D)^2}{4} \quad (\text{Equation 4})$$

D = diameter ($D_{130 \text{ cm}}$) of each tree in a plot

Relative frequency (RF), relative density (RDe), and relative dominance/cover (RDo) were calculated for each species of mangrove.^{28,119} The importance value (IVI) of each species was estimated from the summation of the RF, RDe, and RDo. These statistics were done in Excel 365

$$\text{Relative density (RDe)} = \frac{\text{Total absolute density of a species}}{\text{Total absolute densities of all species}} \times 100 \quad (\text{Equation 5})$$

$$\text{Relative frequency (RF)} = \frac{\text{Absolute frequency of a species}}{\text{Total frequency of all species}} \times 100 \quad (\text{Equation 6})$$

$$\text{Relative dominance (RDo)} = \frac{\text{The absolute dominance of a species}}{\text{Total absolute dominance of all species}} \times 100 \quad (\text{Equation 7})$$

where

$$\text{Importance value (IVI)} = \text{RDe} + \text{RF} + \text{RDo} \quad (\text{Equation 8})$$

Complexity indices (in a 0.1 ha plot) were determined for the forest structure in each of the forest banks – as a function of the product of the number of species, basal area (m^2/ha), mean height of the tree (m) and the number of stems ha^{-1} .^{120,121} The stocking density was determined by grouping the mangrove trees into different diameter classes. The diameter classes were grouped considering the diameter of mangrove wood used in households. In RStudio version 4.2.1, statistical difference in the density of trees among the diameter classes was determined using a one-way analysis of variance.³⁶ To analyse the species composition among the sites studied, multivariate beta dispersion (using the betadisper function in R) was first done to identify the dispersion within forest banks, and a data composed of the abundance of each species of plant per plot. When the dispersion was significant within banks, analysis of similarity (ANOSIM) was used to find the statistical spatial difference in vegetation composition among forest banks in PAST¹⁰⁶ version 4.03, while pairwise multiple tests were performed with the combination of Bonferroni corrections to identify the differences between sites. In the ANOSIM tests, plots were set as blocking factors while the individual banks (EB1, EB2, WB1, and WB2) were fixed to reduce pseudo-replication. To identify the driving factors of the changes in species composition, ENVFIT function in RStudio in the vegan package was used to relate the covariates (average distance from river, total number of cut trees and total number of cut branches, latitudinal gradients, longitudinal gradients) against species abundance.

A generalised linear mixed model (random coefficient Poisson model) with Gauss-Hermite approximation in R was used to find which factors dictate the changes in stocking density of plants within diameter classes as well as factors that influence the density of regeneration classes per plot. This type of Poisson regression uses 100 points per axis to fit the model thereby improving accuracy. The fixed factors included the density of *Acrostichum aureum*, average distance from the river, total number of cut trees and the total number of cut branches, latitudinal gradients, and longitudinal gradients, but plots were as blocks/random factors for standing density whereas plots and subplots were random factors for the regeneration class's models. Differences in juvenile density among sites were assessed with a chi-square test.

According to De Liocourt,¹²² the number of trees in an uneven-aged forest stand (N) tends to decrease in successive diameter classes by a constant ratio q . Thus,

$$N = N_i / N_{i+1} \quad (\text{Equation 9})$$

which, q is the ratio between the number of trees in one diameter class and the next larger class. Here, N_i represents the number of trees in diameter class i , while N_{i+1} is the number of trees in the next diameter class $i+1$. This ratio, q is assumed constant for the entire life of the forest stand. Distribution in this form is called De Liocourt's distribution.¹²³ Therefore, assuming the Ankobra mangrove stand follows the above distribution, the stand density was harmonised by De Liocourt's model as $aq^n, aq^{n-1}, aq^{n-2}, aq^{n-3}, \dots, aq^3, aq^2, aq, a$, where a is the number of trees in the largest size class of interest and n is the number

of classes.³⁶ Formulated by Meyer¹²⁴ and used by Bundotich et al.,¹¹⁰ and Marín-Pageo and Rapp-Arrarás,¹²⁵ we plotted the logarithm of the frequency in successive classes against the size class to achieve an exponential model of the form,

$$Y = ke^{-ax} \quad \text{(Equation 10)}$$

where Y is the number of trees in diameter class x (i.e., the centre of the diameter), with k and a as constants. "Higher k means the forest contains prolific seed-bearing tree species, whereas higher a means high mortality in a light-demanding forest".³⁶

Analysis of the mangrove use, utilisation pattern and local knowledge

The socio-demographic characteristics of respondents were summarised and presented using descriptive statistics. Generalised linear mixed model (GLMMs - glmmTMB) in R⁶³ was used to test the relationships between the demographic characteristics (age, education, occupation, village, years of stay in the village, household size, household income, and gender of the communities), and their relationships with mangrove knowledge, mangrove use, and mangrove ecosystem use. We prefer to use GLMMs to test for comparisons because of the multilevel nature of our data. Secondly, the Fidelity level (FL) of the various uses of mangroves was calculated.

$$FL = n_i/N \quad \text{Equation 11}$$

where n_i = the number of respondents that claim to use a plant species for a particular 'i' purpose; and N = the total number of respondents that use mangrove to filter any given demand.

The FL helped us to know the percentage of respondents claiming the use of mangroves for the same purpose. Mangrove knowledge was ranked according to the number of true mangroves a particular age class could identify and name: on the levels Bad (no true species known), Fair (1 true species), Good (know 2 true species) and Very Good (know all the 3 true species). To assess the perception of degradation, the mangrove forest and the mangrove ecosystem goods and services, YES or NO answers backed with some explanations collected from the respondents were quantified and compared using the χ^2 test. Regarding the health benefits of mangroves, multinomial logistic regression was applied to identify which factor affects the choice of particular health care when one falls ill, a respondent variable had three levels: physicians, local drugs, and mangroves. Also, ordinal logistic regression was used to test which factor influenced one's rank of mangrove importance with four levels (0, 1, 2, 3). It must be acknowledged that all statistical analyses were performed at significant level (α) 0.05.