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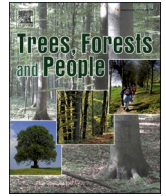
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Human-driven degradation impacts on mangroves in southern Sierra Leone

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ABSTRACT

Mangrove ecosystems remove carbon from the atmosphere and store it predominantly in soils constituting an important carbon sink. Additionally, they foster biodiversity and provide ecosystem services supporting local livelihoods and enhancing coastal protection. However, mangroves are declining in extent and experiencing degradation due to human activities as well as climate change impacts like sea-level rise and increasing frequency of extreme events. This study investigated how different levels of human-driven degradation affect forest structure, above- and belowground carbon stocks, tree species composition, and the population structures of dominant tree species. We investigated 19 transects of different degradation levels (pristine, moderately degraded, heavily degraded) in various locations (oceanic, riverine, interior) in the Sherbro river estuary in Sierra Leone.

Results showed that total carbon stocks of pristine mangroves amounted to 707 Mg C ha⁻¹ including soils to 1 m depth, which is higher than carbon stocks reported from many other regions in Africa.

Degradation resulted in declining basal area, decreasing density of large trees (≥ 30 cm diameter) but increasing stem density of small trees (5–10 cm diameter). All carbon pools declined with increasing degradation across all locations. While above- and belowground carbon decreased by 96 %, soil carbon (up to 1 m depth) decreased by 44 %. Heavy degradation resulted in a change in the dominating species from *Rhizophora racemosa* to *Rhizophora mangle* across all locations. Overall, we found major effects of degradation on mangrove characteristics and minor effects of location. We urge conservation of pristine forests, restoration of degraded mangroves, and the establishment of management systems that are ecologically informed and based on a comprehensive understanding of human-driven degradation impacts.

1. Introduction

Mangroves are salt-tolerant forest ecosystems growing in the intertidal zone in tropical and subtropical regions (Hamilton, 2020; Sudhir et al., 2022). Due to their high photosynthetic rate despite the salinity stress (Sudhir et al., 2022) and the anaerobic soil substratum that impedes decomposition (Shiau and Chiu, 2020), mangroves store carbon in trees but also in sediments that are trapped by roots and pneumatophores (Donato et al., 2011; Kathiresan, 2021). They thereby constitute one of the most carbon-rich ecosystems per unit area (Alongi, 2020; Twilley et al., 2018) and are receiving increased attention for their

potential contribution to climate change mitigation as part of the ‘Blue Carbon ecosystems’ (Leal and Spalding, 2022), which also include sea-grass beds and salt marshes (Alongi, 2020; Rao et al., 2021).

Apart from their role in climate change mitigation, mangroves protect coastal areas from erosion, tides, and tropical cyclones (Carugati et al., 2018; Kathiresan, 2021) and maintain water quality by filtering and trapping pollutants and sediments (Nunoo and Agyekumhene, 2022). In addition, mangroves can act as buffer for ocean acidification (Banerjee and Paul 2022) and coastal eutrophication (Zhao et al., 2019). Moreover, they serve as habitat, breeding, feeding and nursery sites for terrestrial and marine organisms including important commercial

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species, such as different fish species, oysters, or shrimps (Carugati et al., 2018; Dahdouh-Guebas et al., 2020; Nunoo and Agyekumhene, 2022). In addition to important regulating and supporting ecosystem services, mangrove ecosystems support local communities' livelihoods by providing them with provisioning services (such as food, fuelwood, medicine, or construction materials), and cultural services (identity, tourism etc.) (Ajonina et al., 2018; Jones et al., 2014; Kathiresan, 2021). In brief, mangroves are of key importance from local to global scales.

Despite their importance, more than 1 million hectares of mangroves were lost globally between 1990 and 2020 (FAO, 2020). Even though rates of decline have decreased in the past few years (Arumugam et al., 2020; Hamilton and Casey, 2016; Lee et al., 2021), mangroves diminish 3–5 times faster than other forest ecosystems (Dayal et al., 2022; UNEP, 2014). Distributed on 113 countries, there are 14.8 million hectares of mangroves left, of which about 21,200 hectares are lost annually (FAO, 2020). According to an estimate by Liu et al. (2021) 2,007,411 hectares of mangroves are found in West Africa, of which 170,341 hectares are located in Sierra Leone, which positions the country among the top ten countries in Africa when it comes to both mangrove extent and change in extent (UNEP, 2023). Compared to available research globally, there are few studies on mangroves in Africa, especially in West Africa. Mangroves in East and West Africa differ in species composition and usage pressures (Machava-António et al., 2022), so research needs to focus on all different regions.

Natural causes (e.g. tropical cyclones) can lead to mangrove loss in some sites. However, anthropogenic causes such as infrastructure development, conversion to agriculture, aquaculture, over-extraction of forest products, salt production, mining, and pollution are driving most mangrove loss across the tropics (Dayal et al., 2022; Goldberg et al., 2020; Goussard and Ducrocq, 2014; Islam et al., 2018; Jones et al., 2014; Yando et al., 2021).

Restoring areas from which mangroves have disappeared entirely, often requires planting nursery-raised mangrove seedlings, while passive restoration can be a viable approach for areas that are not yet fully degraded (Moudingo et al., 2018). Many restoration projects failed in the past, both due to financial constraints, institutional challenges in implementation and insufficiently addressed root causes of degradation, but also due to insufficient understanding of mangrove ecology and lack of locally adapted techniques (Leal and Spalding, 2022). In order to get a comprehensive picture of the effects of human-driven degradation on mangroves, to establish a baseline for restoration efforts, and to design effective restoration and conservation measures, impacts of degradation on forest structure, species composition, ecosystem functions, and related loss of ecosystem services should be investigated (Yando et al., 2021).

Some studies in Africa have already addressed certain effects of human-driven mangrove degradation. For instance, Ajonina et al. (2014a) studied mangroves in Cameroon, Gabon, the Republic of Congo (RoC), and the Democratic Republic of Congo (DRC). These authors showed that all carbon pools (aboveground (AGC), belowground (BGC), soil organic carbon (SOC)) decreased with increasing human-driven degradation pressures. While AGC decreased by 74–88 %, SOC decreased by 20–23 % (Ajonina et al., 2014a). However, Ajonina et al. (2014a) did not investigate effects on species composition. Indeed, very few studies considered the effect of degradation on species composition. A study in Gazi Bay in Kenya by Kihia (2014) reported changes in dominance and abundance of species when comparing disturbed and undisturbed sites. Additionally, population structures of species, the proportion of stems of different age or diameter classes, can provide knowledge about harvesting impacts and regeneration capacity as was demonstrated for different tropical forests including mangroves (Ajonina et al., 2014a; Batumike et al., 2022; Obiri et al., 2002). Other studies addressing mangrove degradation, either generally or specifically in Africa, often focused on loss of areal extent (e.g. Lee et al. 2021), impacts on flora and fauna (Carugati et al., 2018; Nunoo and Agyekumhene, 2022) or investigated drivers or narratives of degradation as

well as impacts on local livelihoods (Andrieu et al., 2020; Dayal et al., 2022). However, there is a lack of studies that comprehensively compare different degradation levels within the same region, rather than comparing differently degraded regions, as in the latter case degradation impacts can be confounded by location.

Depending on their location, mangroves are affected by rivers and tides to varying degrees (see e.g. Kathiresan 2021, Kjerfve 1990). Therefore, it is important to also consider potentially context-dependent effects of degradation on mangroves at different locations (e.g. oceanic, riverine, interior). When these impacts combined are considered to get a more complete picture of human-driven degradation, conservation and restoration plans can be improved, either preserving existing ecosystems or assisting the recovery of degraded ecosystems. If ecological requirements and ecological knowledge are neglected, fail of e.g. restoration projects is limited (Primavera and Esteban, 2008).

To fill these knowledge gaps this study focused on oceanic, riverine, and interior mangroves in the Sherbro river estuary in Sierra Leone and addressed the following research questions:

- (1) How does human-driven degradation affect mangrove forest structure and different carbon pools (aboveground, belowground, soil)?
- (2) How does human-driven degradation affect tree species composition?
- (3) How do different drivers of degradation affect population structures of dominant tree species?

2. Methods

2.1. Study Area

Our study focused on mangroves in the Sherbro river estuary (thereafter SRE) in southern Sierra Leone, on the Atlantic Coast of West Africa (see Fig. 1). The SRE constitutes one of four marine protected areas in Sierra Leone and encompasses about 50 % of the country's mangroves, about 90,000 hectares (estimate for 2016) (Feka and Sainge, 2022; Mondal et al., 2017). The climate is tropical and humid with annual rainfall at the coast ranging from 3000 to 5000 mm and average temperatures of 26 °C (SLMet, 2023). The rainy season extends from May to November (SLMet, 2023).

Compared to other estuaries in Sierra Leone, the SRE is characterized by low species diversity, higher number of large trees (defined as ≥ 30 cm diameter), and less disturbance and degradation over the past decades (USAID, 2020). The estimated human population of the SRE region comprises 223,230 people distributed among 105 villages and belonging mainly to Mende and Sherbro ethnic groups (Feka and Sainge, 2022). Pressures driving mangrove loss in the SRE are wood harvesting for fish smoking, cooking, and house construction as well as land conversion for agriculture (rice farming) and infrastructure development. Main species used are *Rhizophora mangle* (for cooking and construction of houses), *Rhizophora racemosa* (for fish smoking), *Rhizophora harrisonii* (for construction of houses and canoes) and *Avicennia* spp. (for construction of houses and fish smoking) (pers. observations, M.N. Sainge).

2.2. Data collection and analysis of soil samples

Data collection took place in November 2021 and during low tides. A total of 19 transects of 20 × 100 m were laid out across different parts of the SRE. The location of transects depended upon accessibility from existing villages located across four chiefdoms (Imperi, Bangruwa, Bendu Cha and Sittia), so they are not randomly distributed across the whole SRE (see Fig. 1). Based on calculations of distance to shoreline and closest rivers, transects were classified as riverine (all transects in Imperi, $n = 4$), interior (all transects in Bangruwa and transect S_P2, located in the interior of the Sherbro island in Sittia, $n = 6$) and oceanic

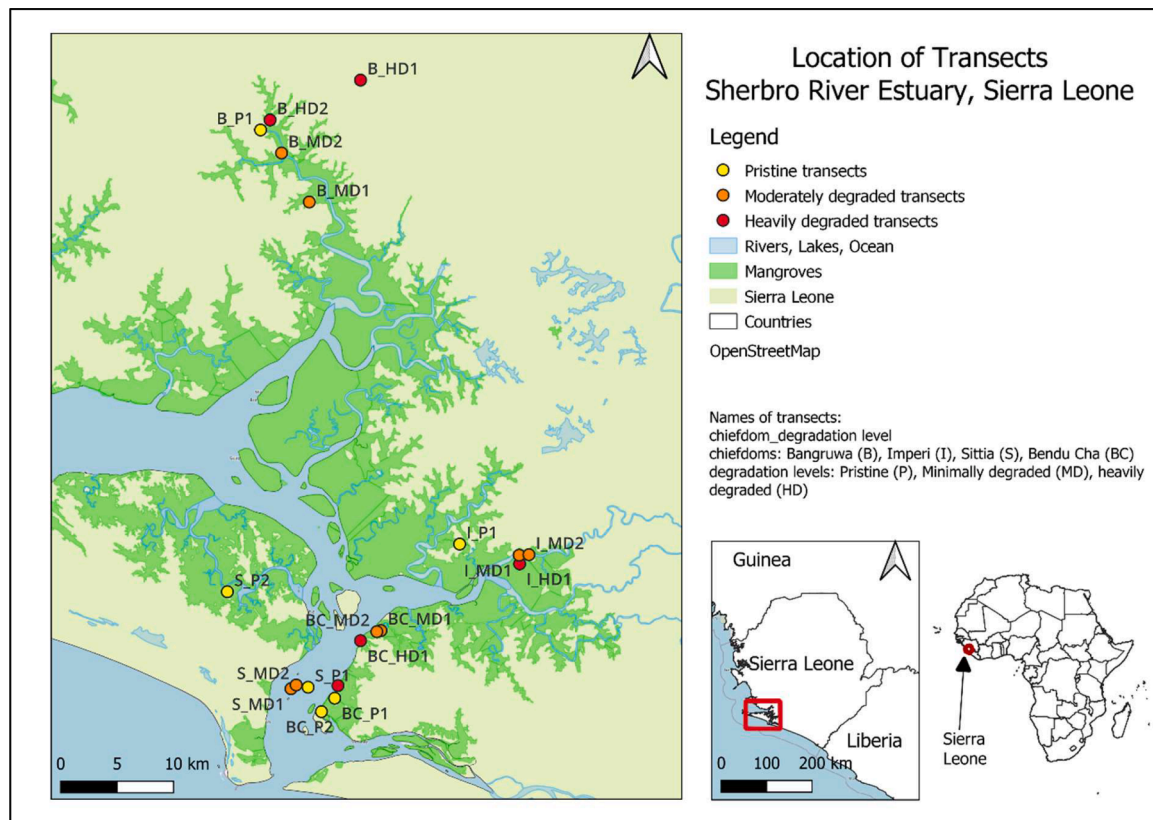


Fig. 1. Map of the Sherbro river estuary in Sierra Leone indicating transect locations and respective degradation level (data sources: OpenStreetMap, ICPAC Geoportal).

(all remaining transects in Sittia and all in Bendu Cha, $n = 9$). At each location, we distinguished sites of three different forest use regimes based on a priori descriptions of use by local communities: Pristine (thereafter P, intact or near intact, old-growth mangroves, without disturbance, $n = 6$ transects), moderately degraded (thereafter MD, in which wood extraction for fish smoking, building materials or firewood is common, $n = 8$ transects) and heavily degraded (thereafter HD, in which rice farming or heavy cutting of mangroves is or had been taking place, $n = 5$ transects). Note that due to time constraints, one pristine transect in Bangruwa was shorter (20×60 m).

In each transect, for each tree with ≥ 5 cm diameter at breast height (Dbh) or at 30–50 cm above the last stilt root, diameter (Dbh), height, and species were recorded adapting methods from the CIFOR protocol (Kauffman and Donato, 2012). The status of all observed species was checked on the IUCN Red List (IUCN, 2023). The results given in the following only refer to living trees.

In each of the four chiefdoms, one soil sample was taken with a cylindrical auger of known volume (10 cm diameter, 20 cm height) for each of the three degradation levels (except for Bangruwa, where there is no soil sample from pristine mangroves due to time constraints). Thereby, soil samples covered P ($n = 3$ transects), MD ($n = 4$ transects) and HD mangroves ($n = 4$ transects). Adhering to the recommendation given in de Jong Cleynndert et al. (2020), each location was sampled until 1 m depth, subdivided as 0–15 cm, 16–30 cm, 31–60 cm and 61–100 cm. Soil samples were air-dried and sieved through a 2 mm sieve. Soil carbon was determined using the Walkley-Black method (Walkley and Black, 1934) at the Njala University Quality Control Laboratory in Sierra Leone.

2.3. Data analysis

To investigate differences in forest structure between degradation

levels, we calculated stem density of all trees (≥ 5 cm diameter), stem density of large trees (≥ 30 cm diameter) and basal area ($\text{m}^2 \text{ha}^{-1}$) for each transect, and then computed the average per degradation level. For each transect, we further visualized species' abundances in terms of percentage of stems, using QGIS.

To estimate aboveground biomass (AGB), we used species-specific AGB equations where possible (for *Avicennia* spp., *Rhizophora mangle*, and *Rhizophora* spp.) (Fromard et al., 1998; Imbert and Rollet, 1989). For the other species (0.7 % of all stems), we used a general equation for mangroves (Komiyama et al., 2005). To estimate belowground biomass (BGB), the equation of Komiyama et al. (2005) was used (see Table A1 in Appendix for a list of all equations used). Following Kauffman and Donato (2012), aboveground carbon (AGC) was calculated as $0.5 * \text{AGB}$, and belowground carbon (BGC) as $0.39 * \text{BGB}$. As outlined in Kauffman and Donato (2012), soil carbon concentration per depth interval was calculated as: soil carbon (SOC) [Mg C ha^{-1}] = bulk density [g cm^{-3}] * soil depth interval [cm] * % C

Subsequently, total soil carbon was attained by summing the masses of sampled depth for each location.

Size class distributions (SCDs) at 5 cm diameter increments were created for the most abundant tree species at different degradation levels. Moreover, a simple linear regression was conducted using the natural logarithm of size classes and observations falling into the respective size class. Slope, coefficient of determination R^2 , and significance level were calculated and formed the bases for assessing whether a species showed continuous recruitment (see Young et al. 2017). A resulting negative slope points towards good recruitment, whereas a positive slope (more individuals in upper size classes) indicates impaired recruitment (Obiri et al., 2002).

Statistical analyses were carried out using R studio (version 4.2.1). The Kruskal-Wallis test was used to determine significant differences ($p < 0.05$) between degradation levels both regarding forest structure and

carbon stocks. Post-hoc pairwise comparisons of two degradation levels at a time were performed using Dunn's test.

3. Results

3.1. Forest structure

Basal area ($\text{m}^2 \text{ha}^{-1}$) ranged from $26.8 \text{ m}^2 \text{ha}^{-1}$ (P) to $14.5 \text{ m}^2 \text{ha}^{-1}$ (MD) and $1.7 \text{ m}^2 \text{ha}^{-1}$ (HD). Stem density ($\geq 5 \text{ cm}$) ranged from 540 stems ha^{-1} (P) to 732 stems ha^{-1} (MD) and 141 stems ha^{-1} (HD). Stem density of large stems ($\geq 30 \text{ cm}$) ranged from 129 stems ha^{-1} (P) to 38 stems ha^{-1} (MD) and 3 stems ha^{-1} (HD). Overall, degradation level had a significant effect on most forest structure variables studied (see Table 1).

Mean diameter at breast height (Dbh) [in cm], mean height [in m], basal area for $\geq 5 \text{ cm}$ Dbh, $5\text{--}10 \text{ cm}$ Dbh, $\geq 10 \text{ cm}$ Dbh, and $\geq 30 \text{ cm}$ Dbh [in $\text{m}^2 \text{ha}^{-1}$], stem density for $\geq 5 \text{ cm}$ Dbh, $5\text{--}10 \text{ cm}$ Dbh, $\geq 10 \text{ cm}$ Dbh, and $\geq 30 \text{ cm}$ Dbh [in stems ha^{-1}], compared between degradation levels (pristine (P), moderately degraded (MD), heavily degraded (HD))

Different letters within columns mark significant differences at $p < 0.05$ (displayed to the right of respective values to be compared for each row), whereas same letters indicate that there is no significant difference between the two columns.

3.2. Carbon stocks

Total carbon stocks ranged from $707.1 \text{ Mg C ha}^{-1}$ (P) to $435.8 \text{ Mg C ha}^{-1}$ (MD) and $271.9 \text{ Mg C ha}^{-1}$ (HD). AGC ranged from $182.0 \text{ Mg C ha}^{-1}$ in P transects to $70.0 \text{ Mg C ha}^{-1}$ in MD transects and 5.8 Mg C ha^{-1} in HD transects. Stems $\geq 10 \text{ cm}$ Dbh accounted for most of AGC (Table 2). Belowground carbon (BGC) decreased from $55.1 \text{ Mg C ha}^{-1}$ (P) to $25.7 \text{ Mg C ha}^{-1}$ (MD) and 2.2 Mg C ha^{-1} (HD). SOC decreased from $470.0 \text{ Mg C ha}^{-1}$ (P) to $340.1 \text{ Mg C ha}^{-1}$ (MD) and $263.9 \text{ Mg C ha}^{-1}$

Table 1

Forest structure compared between degradation levels of mangroves in the Sherbro river estuary, Sierra Leone.

Degradation level	Pristine (P)	Moderately degraded (MD)	Heavily degraded (HD)
Number of transects	6	8	5
mean Dbh [cm]	22.5 ± 4 a	13.7 ± 3.1 ab	11.6 ± 7.9 b
mean height [m]	23.6 ± 4.4 a	14.2 ± 2.9 b	9.3 ± 7.1 b
basal area [$\text{m}^2 \text{ha}^{-1}$]	26.8 ± 10.1 a	14.5 ± 5.2 a	1.7 ± 0.7 b
Basal area (5–10 cm) [$\text{m}^2 \text{ha}^{-1}$]	0.4 ± 0.2 a	2.1 ± 1.4 b	0.4 ± 0.3 a
Basal area ($\geq 10 \text{ cm}$) [$\text{m}^2 \text{ha}^{-1}$]	26.4 ± 10.2 a	12.7 ± 5.4 ab	0.9 ± 1.0 b
basal area ($\geq 30 \text{ cm}$) [$\text{m}^2 \text{ha}^{-1}$]	16.5 ± 9.7 a	4.5 ± 4.0 ab	0.4 ± 0.7 b
stem density ($\geq 5 \text{ cm}$) [stems ha^{-1}]	539.2 ± 129.2 a	731.9 ± 365.9 a	141 ± 82.3 b
stem density (5–10 cm) [stems ha^{-1}]	94.4 ± 58.0 a	365 ± 237.0 b	114 ± 75.0 a
stem density ($\geq 10 \text{ cm}$) [stems ha^{-1}]	418.1 ± 149.2 a	386.9 ± 161.5 a	27 ± 20.4 b
stem density ($\geq 30 \text{ cm}$) [stems ha^{-1}]	128.6 ± 71.4 a	38.1 ± 29.3 ab	3 ± 6.0 b

Table 2

Carbon stocks compared between degradation levels of mangroves in the Sherbro river estuary, Sierra Leone.

Degradation level	Pristine (P)	Moderately degraded (MD)	Heavily degraded (HD)
Number of transects	6	8	5
AGC ($\geq 5 \text{ cm}$) [Mg C ha^{-1}]	182.0 ± 77.3 a	70.0 ± 37.4 b	5.8 ± 6.6 b
AGC (5–10 cm) [Mg C ha^{-1}]	1.1 ± 0.6 a	4.2 ± 2.8 b	1.2 ± 0.9 a
AGC ($\geq 10 \text{ cm}$) [Mg C ha^{-1}]	180.9 ± 77.5 a	65.7 ± 36.2 a	4.7 ± 7.0 b
BGC [Mg C ha^{-1}]	55.1 ± 21.7 a	25.7 ± 11.2 ab	2.2 ± 1.8 b
SOC [Mg C ha^{-1}]	470.0 ± 105.7 a	340.1 ± 95.3 a	263.9 ± 119.3 a
Total Carbon [Mg C ha^{-1}]	707.1 ± 87.8 a	435.8 ± 99.4 ab	271.9 ± 121.3 b
SOC/Total Carbon [%]	65.6 ± 8.0 a	77.1 ± 8.3 ab	97.5 ± 1.6 b

(HD). Degradation had a significant effect ($p < 0.05$) on AGC and BGC but did not have a significant effect for SOC (Table 2).

Averaged across all transects, carbon stored in soils accounted for the largest share of total carbon stocks (75.2 %) followed by AGC (18.7 %) and BGC (6.1 %). The share of carbon stored in soils increased significantly with increasing degradation, while shares of AGC and BGC decreased (Fig. 2a, Table 2).

When comparing tree carbon stocks of pristine mangroves at different locations (Fig. 2b), an interior transect had the highest (Bangruwa, $>15 \text{ km}$ from ocean, AGC + BGC: $415.2 \text{ Mg C ha}^{-1}$), followed by an oceanic transect ($321.6 \text{ Mg C ha}^{-1}$ BC_P2, Bendu Cha) and an interior one ($206.8 \text{ Mg C ha}^{-1}$) (S_P2, Sittia). Riverine transects in Imperi exhibited lowest carbon stocks (Fig. 2b).

Aboveground carbon (AGC) for $\geq 5 \text{ cm}$ Dbh, $5\text{--}10 \text{ cm}$ Dbh, and $\geq 10 \text{ cm}$ Dbh [in Mg C ha^{-1}], belowground carbon (BGC) [in Mg C ha^{-1}], soil organic carbon (SOC) [in Mg C ha^{-1}], total carbon [in Mg C ha^{-1}], and proportion of soil organic carbon from total carbon [in %] compared between degradation levels (pristine (P), moderately degraded (MD), heavily degraded (HD))

Different letters within columns mark significant differences at $p < 0.05$ (displayed to the right of respective values, to be compared for each row), whereas same letters indicate that there is no significant difference between the two columns.

3.3. Species composition

All stems measured belonged to three families: *Rhizophoraceae* (86.5 %), *Acanthaceae* (12.8 %), and *Combretaceae* (0.7 %), and to six species: *Rhizophora racemosa* (77.0 %), *Rhizophora mangle* (8.4 %), *Rhizophora harrisonii* (1.1 %), *Avicennia africana* (11.8 %), *Avicennia germinans* (1.0 %), and *Conocarpus erectus* (0.7 %). All species were listed as least concern according to the IUCN Red List. Species diversity ranged from 1 to 4 tree species per transect. *R. racemosa*, *R. mangle*, *R. harrisonii* and *Avicennia ssp.* are portrayed with characteristic pictures in Fig. 3. As *Conocarpus erectus* only occurred in one site, it is not portrayed here.

Overall, we observed differences in species composition related to both location and degradation level (see Fig. 4). P transects across all locations were dominated by *R. racemosa*. MD transects were also dominated by *R. racemosa* in Imperi (riverine) and Bangruwa (interior), while *Avicennia africana* dominated in Sittia (oceanic on islands), and some variation was observed in MD transects in Bendu Cha (oceanic)

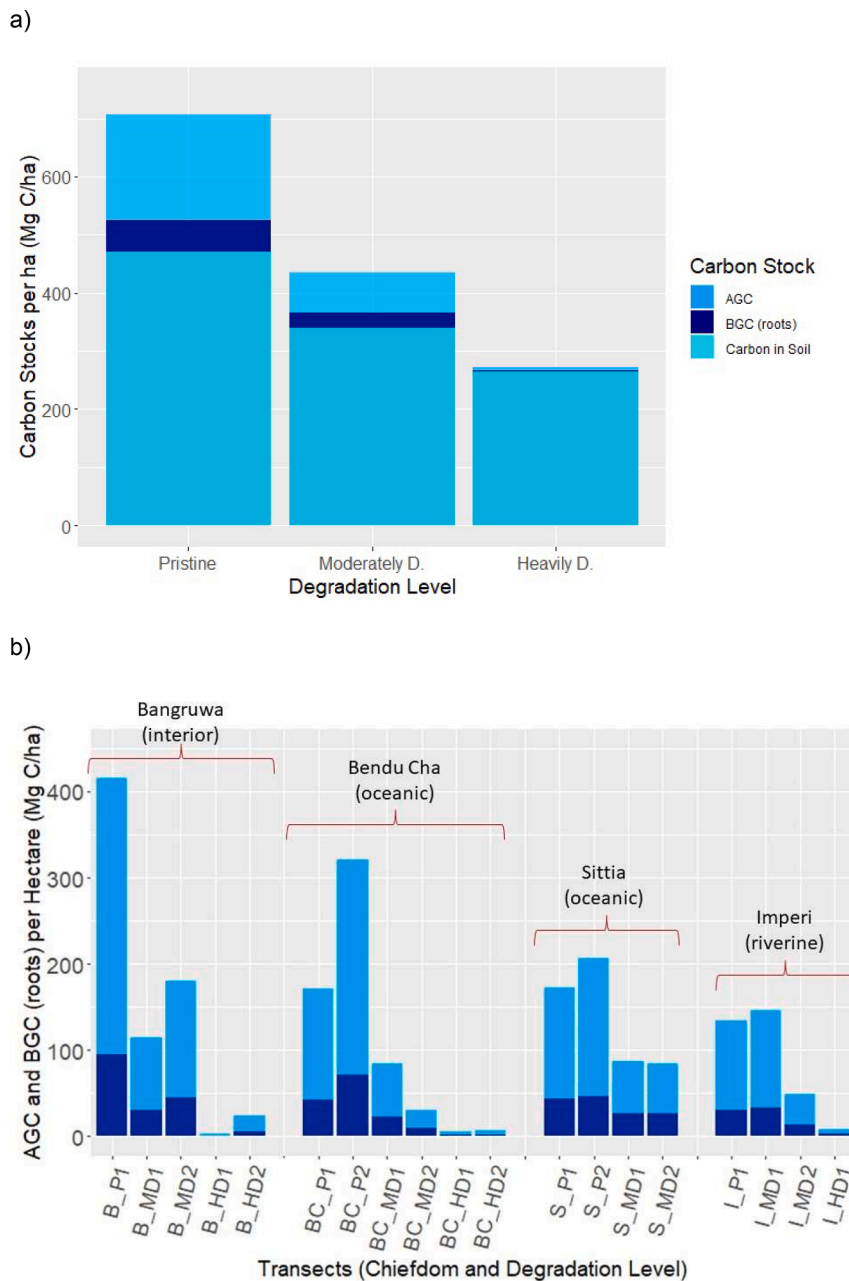


Fig. 2. a (top). Carbon stocks [in Mg C ha⁻¹] for different degradation levels of mangroves in the Sherbro river estuary, Sierra Leone Colors indicate different carbon pools (from top: aboveground carbon (AGC), belowground carbon of roots (BGC), and carbon in soil (SOC)) Fig. 2b (bottom): Comparison of aboveground carbon (AGC) (blue, top) and belowground carbon (BGC) (dark blue, bottom) between mangroves at different degradation levels and in different chiefdoms in the Sherbro river estuary, Sierra Leone [carbon pools in Mg C ha⁻¹]. Abbreviations of transects as combination of chiefdom (Bangruwa (B), Bendu Cha (BC), Imperi (I) and Sittia (S) and degradation levels (pristine (P), moderately degraded (MD) and heavily degraded (HD)).

(Fig. 4). *R. racemosa* was not found in HD transect in any location. Instead, *R. mangle* dominated in HD together with *R. harrisonii*, *Avicennia germinans* or *Conocarpus erectus* (Fig. 4).

Some variation in species composition could be explained by location, e.g. *Avicennia* being most abundant in Sittia (oceanic on small islands). However, the changes in the dominant species from *R. racemosa* to *R. mangle* could not be explained by location as in Imperi, Bangruwa and Bendu Cha transects dominated by *R. racemosa* and *R. mangle* were located in immediate proximity to each other (Fig. 4).

3.4. Population structures

For *Rhizophora racemosa*, the size class distributions (SCDs) showed negative slopes in both P and MD transects (Fig 5a, b), but fewer small stems were observed in P than in MD transects. This suggests that regeneration may be affected by light requirements and that prevalent uses for this species (fish smoking) target predominantly larger size classes.

For *Rhizophora mangle*, the SCDs showed negative slopes in both MD and HD transects with very similar distributions in both degradation categories (Fig 5c, d). For *Avicennia africana* in MD transects the SCD also showed a negative slope (Fig 5e). In all cases, SCDs could be

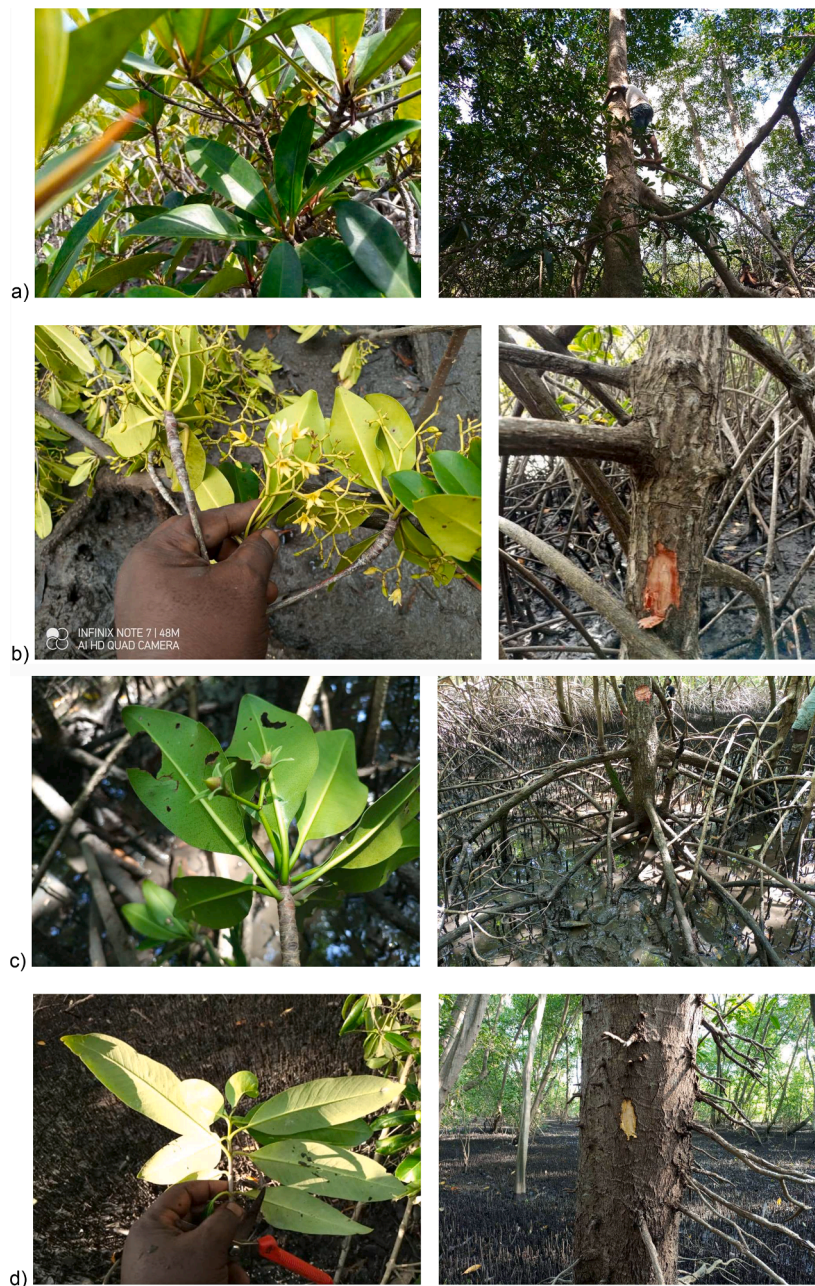


Fig. 3. Characteristic features of the four main occurring mangrove species in the Sherbro River Estuary (Pictures: Moses Nsanyi Sainge) a) *Rhizophora racemosa*: leaves and flower (left), stem and roots (right) b) *Rhizophora mangle*: leaves and flowers (left), bark, stem, and roots (right) c) *Rhizophora harrisonii*: leaves and flowers (left), bark, stem and roots (right) d) *Avicennia* spp.: leaves (left), bark, stem, and pneumatophores (right).

classified as reverse J-shapes and continuous recruitment (according to Young et al. 2017) (Appendix Table B1).

4. Discussion

4.1. Effects of human-driven degradation on forest structure

First, it should be noted that the pristine transects sampled in the SRE have many large trees with some of the highest basal areas reported on the African continent (higher than e.g. in Cameroon, Gabon, RoC, DRC (Ajonina et al., 2014a), Senegal, Liberia (Kauffman and Bhomia, 2017) or Tanzania (Njana et al., 2018)).

In our study, human-driven degradation significantly reduced basal area and density of large stems (≥ 30 cm). This becomes evident as larger stems are preferably harvested e.g. as wood for construction and

since basal area is correlated with the number of large trees. When stem density of all stems (≥ 5 cm) was considered, degradation increased stem density in MD, and decreased it in HD. The trend of decreasing number of large trees (≥ 30 cm) with increasing degradation levels aligns with findings from other studies, e.g. in Central Africa (Cameroon, Gabon, RoC, DRC) (Ajonina et al., 2014a) or Kenya (Kihia, 2014).

Comparisons of stem density to the literature is challenging due to ambiguities in thresholds used in previous studies. Therefore, we highlight the importance of stating the diameter threshold used and to preferably report estimates for different diameter thresholds separately (e.g. ≥ 5 cm, ≥ 10 cm, ≥ 30 cm Dbh), as suggested by de Jong Cleynert et al. (2020).

The issue of diverging diameter thresholds for reporting stem density is particularly challenging for study comparison across locations. For instance, a study by Ajonina et al. (2014a) from Cameroon, Gabon, RoC,

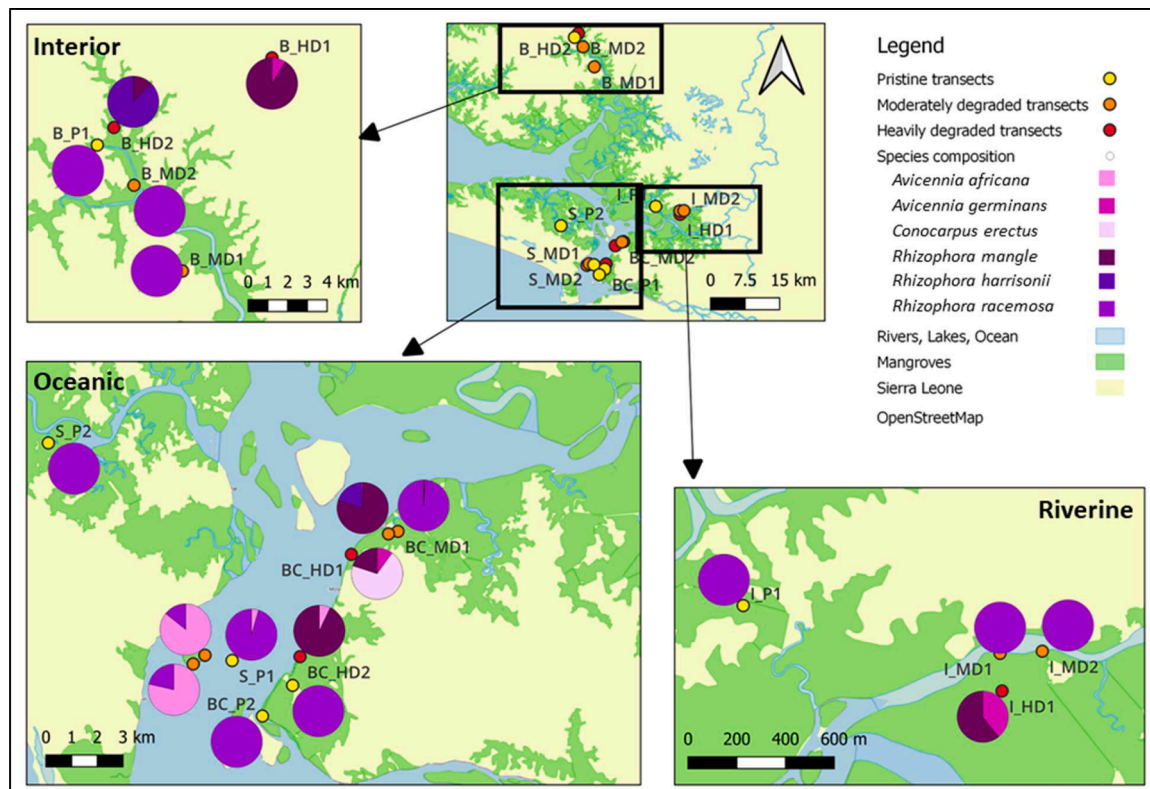


Fig. 4. Species composition of transects in the Sherbro river estuary in Sierra Leone (species abundances shown as proportions in pie chart for each transect). Abbreviations of transects as combination of chiefdom (Bangruwa (B), Bendu Cha (BC), Imperi (I) and Sittia (S) and degradation levels (pristine (P), moderately degraded (MD), and heavily degraded (HD)) (map data sources: OpenStreetMap, species: own investigations).

and DRC included all stems > 1 cm Dbh and reported values ranging from 450 stems ha^{-1} to 3,256 stems ha^{-1} for mangroves of different degradation intensities (from heavily degraded to undisturbed). A study from Tanzania by de Jong Cleynert et al. (2020) reported stem density of 242.5 stems ha^{-1} for 5–10 cm, 517.8 stems ha^{-1} for stems ≥ 10 cm and 1.3 stems ha^{-1} for ≥ 30 cm Dbh. Mangroves in that study had a history of exploitation and continued to be used e.g. for construction and firewood. While we report more large trees and fewer small trees in the SRE, their results most resemble the values found in our study for MD transects for 5–10 cm and ≥ 10 cm Dbh, which matches the similar usage pressures. When tying the findings related to stem densities to regeneration potential, the high stem density of small stems in MD areas points towards good conditions for passive restoration, while still some larger trees are present for shading and protection e.g. against flooding, and as source for seeds. In HD transects passive restoration is less likely to work due to changes in species' composition as well as in light and flooding.

4.2. Effects of human-driven degradation on carbon stocks

Total carbon stocks ranged from 707.1 Mg C ha^{-1} (P) to 435.8 Mg C ha^{-1} (MD) and 271.9 Mg C ha^{-1} (HD) on average. However, in some locations, e.g. pristine interior transects in Bangruwa, AGC+BGC amounted to more than twice the average of all pristine transects.

Carbon stocks in pristine transects in the SRE (with soils sampled up to 1m depth) are lower than the global mean of 865 Mg C ha^{-1} estimated by Kauffman et al. (2020). However, their estimate was derived from 190 sites across five continents with a greater average soil depths (216 cm) and 35 % of sites > 300 cm. Other authors reported similar values to ours: Alongi (2020) estimated global carbon stocks in mangroves to be around 738.9 Mg C ha^{-1} drawing on measurements from 52 countries worldwide that also included soils > 1 m depth. In this latter study,

estimates for SOC are higher than in our study, whereas AGC is lower (109.3 Mg C ha^{-1} in the study by Alongi (2020) and 182 Mg C ha^{-1} (P) in ours). As both global estimates considered SOC up to greater depths than our study, our results could underestimate total carbon stocks. In case greater soil depth was considered, carbon stocks of pristine mangroves in the SRE would most likely exceed global averages.

Aboveground carbon stocks found in pristine transects in our study exceed those reported by many studies in East African countries such as Cohen et al. (2013) or Gress et al. (2017) in Kenya, Fatoyinbo and Simard (2013), Siteo et al. (2014) or Stringer et al. (2015) in Mozambique or Njana et al. (2018) or de Jong Cleynert et al. (2020) in Tanzania. When compared to carbon stocks found in West Africa, findings from our study exceed estimates by Ajonina et al. (2014a) for Gabon, Carreiras et al. (2012) for Guinea Bissau, Egnankou et al. (2022) for Côte d'Ivoire, Alongi (2020) for Senegal, Togo, Ghana, Guinea, and Sierra Leone, Kauffman and Bhomia (2017) for Liberia and Senegal but are lower than estimates by Ajonina et al. (2014a) for Cameroon and Ghana.

Ratios between carbon pools were found to be on average 75 % SOC, 19 % AGC and 6 % BGC in our study. This aligns with typical ratios for mangrove forests like reported by Alongi (2020). Reasons for large SOC pools in mangrove ecosystems relate to high sedimentation rates, importance of soils as nutrient reservoirs and for stabilization, anoxic soils, and therefore slow decomposition (Alongi, 2014; Kathiresan, 2021).

Regarding location, high total carbon stocks of interior mangroves were observed in a study in Vietnam (Dung et al., 2016). The trend of increasing AGC with increasing seaward distance could be partly confirmed in this study, at least regarding high carbon stocks in Bangruwa (interior). In some studies, riverine sites were also reported as exhibiting higher aboveground carbon than oceanic sites (Donato et al., 2011; Kauffman et al., 2020). This could not be confirmed here.

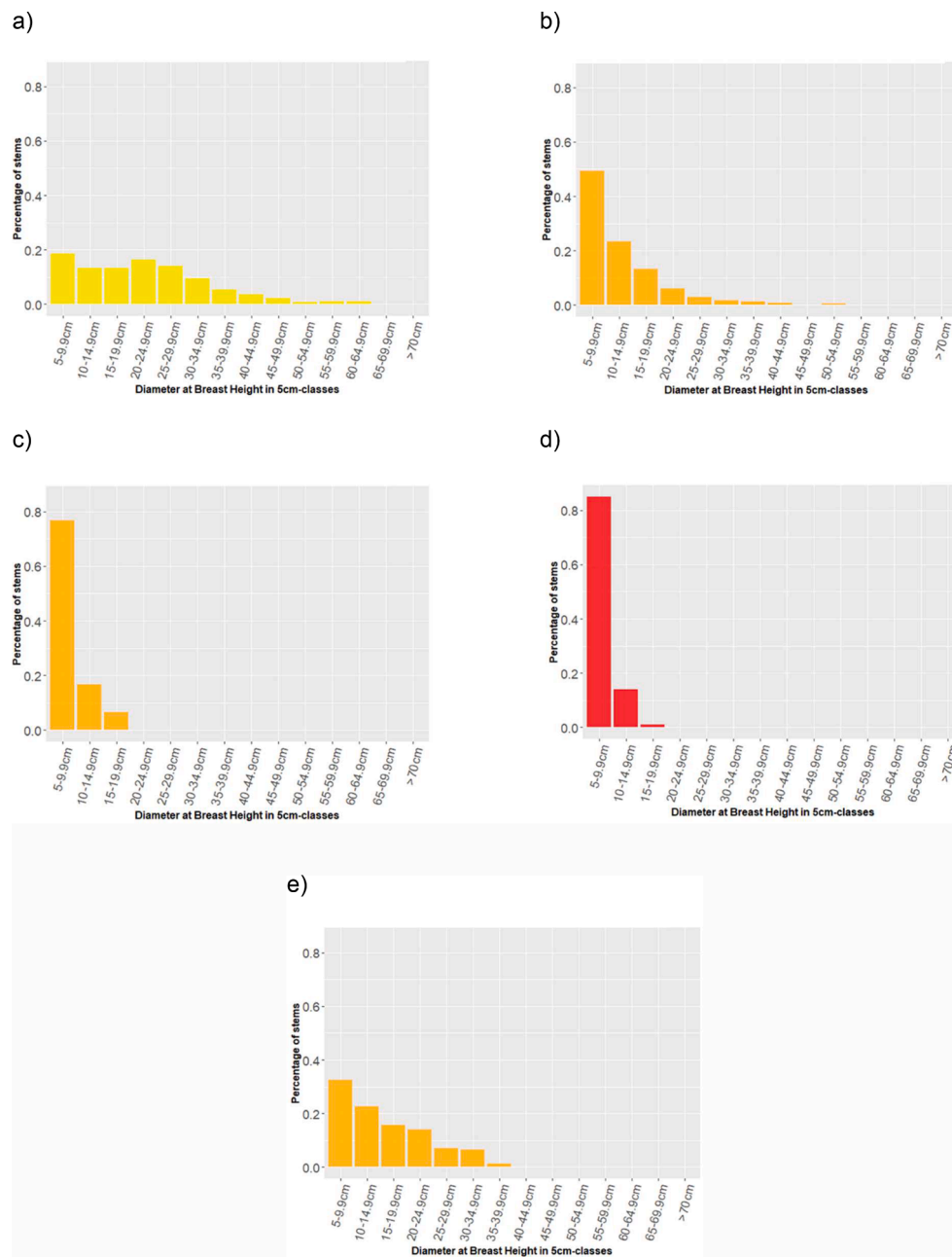


Fig. 5. Size class distributions (SCD) of most abundant species at different degradation levels of mangroves in the Sherbro river estuary, Sierra Leone (a) SCD of *Rhizophora racemosa* in pristine transects (b) SCD of *Rhizophora racemosa* in moderately degraded transects (c) SCD of *Rhizophora mangle* in moderately degraded transects (d) SCD of *Rhizophora mangle* in heavily degraded transects (e) SCD of *Avicennia africana* in moderately degraded transects.

However, as transects in Imperi (riverine) were most affected by degradation due to vicinity to roads and villages, results may be distorted by that. A study of mangroves in Tanzania found a significant correlation of decreasing SOC and associated total carbon stocks with increasing seaward distance (de Jong Cleynert et al., 2020). This was explained by areas closer to the shore experiencing greater tidal inundation, higher salinity levels, slower decomposition, and therefore higher SOC (de Jong Cleynert et al., 2020). This trend could not be confirmed here. However, in the study by de Jong Cleynert et al. (2020), transects were located at least 4 km away from the shoreline, so soil erosion was not an issue but likely plays a role closer to the shoreline as in transects measured in our study.

Concerning effects of human-driven degradation on different carbon pools, we found declines in AGC and BGC to exceed those of SOC. AGC decreased on average by 61.5 % from P to MD transects and by 96.8 % to

HD ones. BGC decreased slightly less by 53.4 % from P to MD and 96.0 % from P to HD. SOC decreased by 27.6 % from P to MD and 43.8 % from P to HD. This aligns with findings from other studies like for instance Ajonina et al. (2014a), who also reported declines in AGC and BGC to exceed those of SOC though generally the declines reported in their study were lower than ours, especially for SOC. AGC in their study decreased by 87.6 % in HD compared to P transects, BGC by 79.5 % and SOC by 24.6 % (Ajonina et al., 2014a). However, the study design of Ajonina et al. (2014a) differed from ours as a total of 15 regions distributed among four countries was considered rather than comparing different degradation levels within one region. Transforming mangroves to rice farms through burning can also exacerbate carbon loss from soils as was done in HD transects in the SRE. Release of carbon through degradation of mangroves depends mainly on how deeply the soils are affected (Donato et al., 2011). A variety of factors can play a role for the

less pronounced decreases in SOC compared to AGC and BGC. AGB is often purposefully removed from the ecosystem by humans (and used as firewood and building material), thereby leading to instant decreases of AGC and BGC: The decomposition of SOC, however, happens slowly and over a prolonged time when formerly anoxic soils are exposed and subjected to aerobic decomposition (Kauffman et al., 2020). Additionally, alluvial deposition by rivers and soils receiving carbon input from outside the system (flood water, tides, alluvial deposits) can be explanatory factors behind slower degradation of SOC (Ajonina et al., 2014a).

4.3. Effects of human-driven degradation on species composition

While location mattered for explaining some variety in species composition, degradation level seemed to be the main explanatory factor driving changes in species compositions, with heavy degradation driving changes from mono specific *Rhizophora racemosa* stands to *Rhizophora mangle* as dominant species in all locations.

Varying species composition in mangroves has mostly been studied in relation to zonation patterns, which are commonly linked to salinity gradients, tidal flushing, and soil type (Ukpong, 1995). *R. racemosa* commonly dominates mangroves in West Africa (Feka and Ajonina, 2011). While being tolerant of saline conditions (Numbere, 2018), this species is preferably found on sites of intermediate or low salinity (Duke et al., 1998) along rivers and streams especially in tidal estuaries, where it forms pure stands (Ajonina et al., 2018). Species distributions observed in our study align with findings from Ghana, where *Avicennia* tended to dominate in areas of high salinity, like lagoons, whereas *R. racemosa* was absent from these sites, but was found at less saline locations (Nunoo and Agyekumhene, 2022). In a study on the Aberdeen creek mangroves in Sierra Leone (located about 130 km north from SRE), *R. racemosa* was only found on sites without human influence (Gledhill, 1963). *R. mangle* is very salinity tolerant, a typical pioneer species in succession (Ellison, 2021), adapted to sandy soils and drier conditions (Numbere, 2018). On more human influenced sites in the Aberdeen creek mangrove swamp in Sierra Leone mainly *R. mangle* and *R. harrisonii* were found (Gledhill, 1963), which aligns with our findings for HD transects.

Consequently, possible explanations for observed changes in species composition are changed abiotic conditions that favour *R. mangle*. Disturbed areas have fewer sheltering larger trees, lower basal areas and are characterized by more extreme conditions like higher temperatures and irradiation (Carugati et al., 2018) and potentially higher salinity levels due to higher evaporation. As known from other studies of mangrove species composition (e.g. Numbere 2018), *R. mangle* is better suited for the conditions characterising the disturbed sites. Further reasons relate to natural succession starting in HD transects after they had been transformed to rice fields with *R. mangle* as pioneer species. Moreover, it plays a role for *R. racemosa*'s decreased importance and competitive ability that it is the most preferably used species for fish smoking.

There are few studies that focused on how mangrove degradation drives changes in species composition. Despite some studies looking at mangroves affected by different degradation intensities, they did not report any changes in species composition, e.g. Ajonina et al. (2014a). In a study on mangroves in Gazi Bay, Kenya by Kihia (2014), tree cutting, trampling by man, vehicles, and digging for fish bait by fishermen were the main disturbances. The study in Kenya reported changes in dominance and abundance of species comparing disturbed and undisturbed sites. However, differently to our study, all six recorded species were present in both disturbed and undisturbed sites (Kihia, 2014).

Yudha et al. (2021) also found logging to impact species composition in mangrove forests in West Papua, Indonesia. However, in this case, rather than changing species compositions or replacement of dominating species, the occurring species remained the same in primary and secondary forests and the dominant species (*Rhizophora apiculata*)

increased in dominance after logging (from 46 % to 69 %), while the shares of co-dominant species decreased in secondary forests despite *Rhizophora apiculata* being one of the targeted commercial species.

To put it briefly, degradation seems to be the main factor behind observed changes from *R. racemosa* to *R. mangle* as dominating species. Our findings stand out by documenting fundamental changes in species compositions from one mono-dominant species to entirely different dominating species rather than merely changed dominances and abundances within the same community of species.

4.4. Effects of human-driven degradation on population structures

Size class distributions (SCDs) of the three most abundant species showed negative slopes and were classified as having continuous recruitment for all degradation levels. Fewer large stems and more small stems were observed in degraded transects. Different drivers of degradation (wood extraction in MD transects, and conversion to rice farms in HD transects) had similar effects on population structures when comparing the same species. However, species compositions differed between degradation levels (see 3.3 and 4.3).

Other studies reported that various uses that target particular stem sizes, affect SCDs differently as e.g. species used for firewood exhibit fewer stems in smaller size classes, whereas species used for construction are characterized by a lack of large stems (Batumike et al., 2022; Obiri et al., 2002). Our findings correspond to studies by Ajonina et al. (2014a), who looked at mangroves of different degradation levels (as increasing intensity of wood extraction) in Cameroon, Gabon, RoC, and DRC. They also report reverse J-shaped curves for P, MD, and HD transects with HD transects exhibiting a particularly large number of small stems and no large stems (≥ 30 cm Dbh). Another study from the Greater Amanzule mangroves in Ghana showed similar findings to ours and additionally measured seedlings (0, 1 cm Dbh) and saplings (1–5 cm Dbh) (Ajonina et al., 2014). They reported reverse-J shaped distributions for both degraded and intact mangroves. While degraded ones exhibited many seedlings of 0, 1 cm Dbh and some stems up to 10 cm Dbh, pristine ones were characterized by fewer seedlings but more saplings and trees up to 50 cm Dbh.

The continuous recruitment visible in the SCDs of species analyzed in the SRE generally points towards good regeneration capacities and potential for passive restoration if degradation pressures are removed. However, changes in species composition as observed from MD to HD transects may impede passive restoration of HD transects back to pristine-like states with *Rhizophora racemosa* as dominant species.

4.5. Study limitations

Our study has some limitations. First, only four out of ten chiefdoms in the SRE area were sampled due to accessibility and time constraints. However, they covered a range of locations within the SRE. Although chiefdoms closest to roads and villages are likely to be those in which degradation is most prevalent, future work should consider other chiefdoms. Second, the classification of transects into only three use or degradation levels could be improved by differentiating a larger number of degradation levels.

Third, there are limitations of inferring population structures from size class distributions since static information about size class distributions may not provide a good picture of future population trends (Condit et al., 1998). Still, the relative proportion of small vs. large stems in a population can give an idea of the direction of future population change if it is applied to intraspecific differences and at a local level (Feeley et al., 2007) as it was done in this study. Additionally, measuring all stems ≥ 5 cm, instead of ≥ 10 cm as in many other studies, also provides a more accurate assessment of population dynamics as potential impairments of recruitment already become visible for stems < 10 cm. Additionally, counting seedlings in smaller sub-plots as done or recommended e.g. by Ajonina et al. (2014a) could have provided an

even more accurate picture.

4.6. Management implications

Our findings highlight that mangroves in the SRE store important quantities of carbon, in both living trees and soils. Total carbon stocks were higher than in many other mangrove forests in Africa and could even exceed global averages if SOC at greater depth (> 1 m) was considered. As demonstrated in our study, human activities have significant impacts on these carbon stocks. As there is considerable international focus on avoiding degradation of carbon-rich ecosystems, mangroves can play an important role if they are not degraded. In addition, size and spatial arrangement of remaining mangrove patches matter for regeneration capacity (Bryan-Brown et al., 2020), especially when considering changing species compositions and succession dynamics.

The negative effects of current human usage pressures are likely to be exacerbated by climate change impacts, especially sea level rise (Gilman et al., 2008; Goussard and Ducrocq, 2014). Considering these pressures and the dependence of surrounding communities on the multiple ecosystem services provided by mangroves in the SRE, more efforts should be made to increase both the conservation of remaining pristine mangroves, and the restoration of degraded ones. Pristine mangroves in the SRE should be a focus of conservation efforts due to their complex structure, the high number of large trees, as well as the high carbon stocks. As the success of mangrove restoration is never guaranteed (Leal and Spalding, 2022) conservation of still pristine mangroves should have top priority. However, we also showed that MD mangroves show potential for passive restoration approaches. This could form the basis for determining sustainable harvesting rates and long-term management strategies that allow a certain level of use by local communities without undermining the regenerative capacity of the mangrove ecosystems. In the case of HD mangroves in the SRE, restoration would probably have to include more active interventions, e.g. in the form of enrichment planting *R. racemosa* to help the succession process towards the original species composition.

5. Conclusion

This study assessed impacts of human-driven degradation on mangrove forest structure, carbon stocks, and species composition. Degradation had a significant effect on forest structure with declining basal area, fewer large trees, and higher stem density of small trees, with increasing degradation level. Notably, AGC of pristine mangroves was higher than in many other mangrove forests in Africa. All carbon pools (AGC, BGC, and SOC) decreased with increasing degradation, limiting the potential for climate change mitigation.

Results also showed that heavy degradation resulted in a change in the dominating species from *Rhizophora racemosa* to *Rhizophora mangle*, which other studies have not been focusing on when assessing degradation impacts. Intact, structurally complex, old mangrove stands of *Rhizophora racemosa* provide valuable habitats as well as coastal protection – and have higher carbon stocks as our study demonstrated. Overall, this study showed how human-driven degradation affects forest structure, carbon stocks, species composition, and the population structures of dominant species. Considering these various aspects combined for different degradation levels (forest structures, species composition, populations structures, carbon stocks), is unique to our study and provides a comprehensive basis for assessing management pathways, including pathways to restoration. Our study demonstrated the importance of conservation of the remaining pristine mangroves in the SRE and laid the basis for developing viable approaches both for restoration and sustainable management of the degraded patches.

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CRediT authorship contribution statement

Lea Christin Huber: Conceptualization, Formal analysis, Writing – review & editing. **Moses Nsanyi Sainge:** Data curation, Writing – review & editing. **Zebedee Njisuh Feka:** Funding acquisition, Data curation, Writing – review & editing. **Richard Abdoulaye Kamara:** Data curation, Writing – review & editing. **Alie Kamara:** Formal analysis, Writing – review & editing. **Martin Sullivan:** Formal analysis, Writing – review & editing. **Aida Cuni-Sanchez:** Conceptualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data can be shared for scientific purposes by the corresponding author upon reasonable request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2023.100445.

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