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Impacts of harvesting intensity on tree taxonomic diversity, structural diversity, population structure, and stability in a West African mangrove forest

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Abstract Understanding the impacts of wood harvesting intensity on the diversity and structure of ecosystems such as mangroves is essential for defining actions for their sustainable management. We compared tree taxonomic diversity, structural diversity and dominance patterns, density, growth characteristics, size class distribution-SCD and stand stability in West African mangroves subject to low *vs.* high wood harvesting intensity. Data on tree species identity, total height, diameter (dbh), and conditions (logged, topped or pruned) were collected from ten mangrove sites per harvesting intensity. We found seven species of which two true mangroves species (*Rhizophora racemosa* and *Avicennia germinans*) that were dominant across all sites. As expected, there were significantly 3–4, 3–7, and 2–4 times more logged, topped and pruned trees respectively in high-harvesting sites than in low-harvesting sites. Taxonomic diversity was less affected than structural diversity (dbh and height-based diversity metrics). Tree density was

significantly 1.3–5 times higher in low-harvesting sites than in high-harvesting sites for the whole stand and each of the dominant species. Total regeneration density was also low in high-harvesting sites. However, regeneration density was relatively higher in high-harvesting sites for *R. racemosa* contrary to *A. germinans*. Trees were also significantly smaller and shorter in high-harvesting sites. The SCD indicated inverse J-shaped distributions, irrespective of the harvesting intensity and showed that tree harvesting targeted mostly dbh classes 10–30 cm. The density of this class was 2.6–6.2 times lower in high-harvesting sites. This study provides important information on impacts of wood harvesting in a marginally studied mangroves' area.

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Introduction

Mangroves are forest ecosystems that occur at the confluence of the land and sea interface (Spalding 2010). Biogeographically speaking, they are limited to the tropical and subtropical coastlines of the world (Feka et al. 2008; Joshi et al. 2014). These ecosystems provide a wide variety of goods and services for

human well-being, in particular within coastal communities. They contribute to livelihoods by providing forest resources such as firewood, timber, medicine, and thatching materials as well as fisheries (fish, crabs, shrimps, oysters, etc.) and other non-timber products (Chang-yi et al. 1997; Ong and Gong 2013; Teka et al. 2019). Mangroves are also an important greenbelt and carbon sink that contributes to mitigate the adverse effects of climate change and protect coastal areas from natural disasters such as tsunamis, cyclones and erosion, which could result from the rise in sea-level (Hutchinson et al. 2014, Donato et al. 2011; Dahdouh-Guebas 2001; Walters et al. 2008). Further, they serve as breeding and spawning grounds for fish and sites for the nesting of migratory birds (Vovides et al. 2011).

While it is well established that mangroves are important by the nature of the services they provide to humans, their sustainability is still uncertain. Like most tropical forests, they are being degraded and destroyed (Feka et al. 2008). The importance of mangrove forests has caused increasing rates of exploitation and deforestation which reduce their productivity at global level (Duke et al. 2007). For instance, in 2005, the global area of mangrove forests was about 15.2 million ha, as a result of a loss of 3.6 million ha during the previous 25 years (FAO 2007). This decline is due to both anthropogenic disturbances and natural disasters, but anthropogenic factors have been identified as the main driver (Alongi 2002). The anthropogenic activities include overexploitation, tree cuttings, aquaculture, agriculture and coastal development projects which threaten mangrove forests and the diverse services they provide (Alongi 2002).

Human disturbances such as clear cut or selective logging can directly affect mangrove composition and structure by reducing tree stock. Selective logging may reduce stock of a given tree size class thereby affecting stand-level growth patterns. Regular pruning or topping may also affect tree growth. Further, human activies (e.g. pollution and agriculture) may also indirectly disrupt functioning of mangroves by affecting the soil properties and other abiotic conditions (e.g. light intensity) which may in turn affect the regenerations, tree growth and ultimately stand productivity and structure (Ngole-jeme 2016). Nevertheless, the impacts of human disturbances on ecosystem structure depend on the intensity and the type of the disturbances. For example, according to the intermediate disturbance hypothesis (Connell 1978), some intermediate levels of disturbance would allow a community of plants to be maintained, with a higher number of species recovering from that disturbance (Catford et al. 2012; Huston 1979). Understanding impacts of human disturbances on the ecosystem diversity and structure is therefore essential for defining actions for their sustainable management. This is particularly important in areas where a dual goal of conserving natural ecosystems and satisfying daily needs of people that depend on these ecosystems is challenging.

Several studies have examined the impacts of anthropogenic activities such as harvesting, on mangroves' diversity and/or population structure (e.g. Rajkaran and Adams 2010; Zhila et al. 2014; Ajonina et al. 2014; Ngole-Jeme et al. 2016). These studies consistently found that mangrove tree harvesting significantly reduce tree density. However, the impacts of harvesting on other structural parameters are inconsistent. For example, Rajkaran and Adams (2010) found that tree harvesting did not affect tree growth characteristics and size class distribution in Malaysia while Ngole-Jeme et al. (2016) reported negative impacts of harvesting on tree growth characteristics in Cameroon. Similarly, Ngole-Jeme et al. (2016) found that logging in mangrove ecosystems reduced plant taxonomic diversity whereas Zhila et al. (2014) found high taxonomic diversity in degraded mangroves compared to natural ones. These findings illustrate that the impacts of anthropogenic activities may not be straightforward and might depend on other factors including the socio-ecological context of the studied mangroves. Further, mangrove species may not have the same resilience to anthropogenic activities. For example, in South Africa, Gaoué and Yessoufou (2019) found that *Rhizophora mucronata* was more resilient to harvesting than others species such as *Bruguiera gymnorrhiza* and *Avicennia marina*, indicating that impacts at stand level might hide great discrepancies among species. Stand level and species-specific analyses are therefore important in assessing the impacts of anthropogenic activities on mangrove forests.

In Benin, mangroves' ecosystems cover 66 km^2 (Spalding 2010) and host various fauna and flora species along the coast (Ajonina et al. 2014). More than 15% of the mangrove cover has been lost in the past three decades (Orekan et al. 2019). These mangroves are exposed to increasing anthropogenic

activities due to the increasing human population density in coastal areas. In southern Benin, local people harvest mangrove trees for domestic fuel wood, traditional fish trap locally named "Acadja", salt extraction, and construction (Teka et al. 2019; Adangidi et al. 2020). A recent assessment has shown that the current demand for mangroves' wood cannot be sustained by their current productivity (see Adangidi et al. 2020). However, we still know little on how anthropogenic activities such as wood harvesting in mangrove forests affect mangrove tree diversity, in terms of taxon and structure, as well as their growth characteristics, size class distribution, and stability. Such information may guide actions that limit impacts of harvesting on the ecosystem conditions (Rajkaran and Adams 2010). The main objective of this study was to assess the impacts of wood harvesting intensity on mangroves' population structure. In particular, the study compared tree (i) taxonomic diversity, structural diversity and dominance patterns, (ii) density, and growth characteristics, (iii) size class distribution-SCD and stability in mangrove forests subject to low vs. high harvesting intensities. The comparison was done at the whole stand level (all species together) but also at species level, focusing on dominant species.

Materials and methods

Study area

This study was conducted in the coastal area of Benin (Fig. 1), particularly where mangroves are concentrated within a wetland complex area that includes Lac Ahémé, Chenal Aho, Lagune Cotière, and Bouche du Roy, named the Ramsar site 1017 (7°N and 1°35°–2°30E) (UNEP 2007). The climate is of equatorial type with two rainy and two dry seasons, and a mean annual rainfall of 1200 mm. The average daily temperature is 27 °C, relative humidity ranging from 78 to 95%. The region has a dense hydrological network with three major rivers: the Couffo, Mono, and Sazué. Mangrove vegetation is dominated by species such as *Rhizophora* spp and *Avicennia germinans* (L.) L. The mangroves are subject to high anthropogenic pressures which include collection of wood for domestic firewood and construction, salt extraction, fish traps ("Acadja"; Fig. 2), and commercialization (Teka et al. 2019; Adanguidi et al.

2020). These anthropogenic pressures lead to increased erosion, ecological change affecting biodiversity, etc. (Teka et al. 2019). The most prominent human activities in the study area are fishing, and salt extraction. Agricultural activities include vegetable and arable crop farming, especially tomatoes, beans, onions, pepper, maize, and cassava. Small livestock systems (domestic poultry, goats, and sheep) are mostly based on free-ranging systems around homesteads. The large amounts of clay in the mangrove area are also used in local pottery industry (Ajonina et al. 2014).

Sampling

An exploratory survey was first conducted to identify major sites of mangroves presence. Each visited mangrove site was considered either of low wood harvesting intensity or high harvesting intensity. High-harvesting sites were identified as frequently visited by local people and subject to "proscribed" mangroves cutting or wood collection for domestic uses, construction, sale, local intensive fishing system ("Acadja"), or salt extraction (Fig. 2a, b, c). Low-harvesting sites were sites where mangroves are sacralized i.e. sites protected by local divinities (e.g. "Zangbeto", Fig. 2d) or sites identified by local forest departments, conservation NGOs, or authorities as pristine mangroves sites and subject to no or little human exploitation, apart from fishing, and touristic visits in some cases. "Zangbéto" is a widespread traditional Divinity widely used to conserve mangrove ecosystems in Benin (see Teka et al. 2019; Teka and Vogt 2010). In mangrove sites protected by "Zangbéto", fishing and tourism are activities that are allowed. Tree cutting is prohibited and anyone who breaks these rules suffers punishments from the "Zangbéto". The first punishment is that some sacrifices are required to appease the divinity, and these sacrifices are expensive, up to 100 $ US, which is already too much considering that more than half the population (53.9%) lives with less than USD 1.00 per day (EMICoV 2011). Not doing these sacrifices will lead to misfortunes (death, getting foolish, uncurable disease, etc.) that will befall on family of the person who breaks the rules. In places where there these divinities do not exist, mangroves have been severely degraded (FAO 2020). A previous study by Ajonina et al. (2014) determined the disturbance status for a
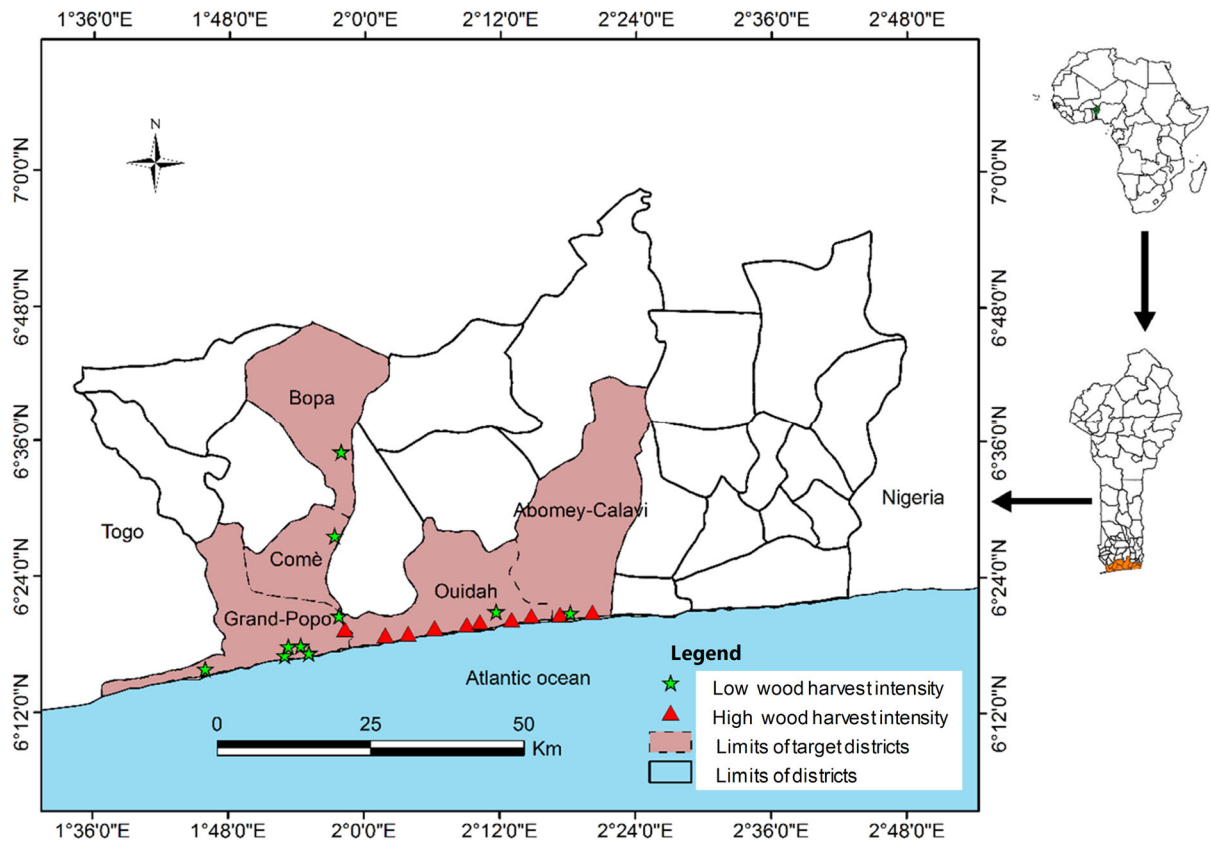
Fig. 1 Map of the study area showing the distribution of sampled low- and high-harvesting sites

number of sites, some of which were also considered in this study. The exploratory survey made it possible to record 25 mangrove sites of low-harvesting and 32 of high-harvesting. From these lists, ten sites of each harvesting intensity (low *vs* high) were selected, making a total of 20 sites. The study was carried out during the low tide, when the mangrove ecosystem was easily accessible. Quantitative data on mangrove vegetation structure at each site was collected using quadrat-sampling along transects. On each site, six transects of 200 m long × 10 m width (0.2 ha) were established following a random azimuth from a random fixed point. Each transect was then divided into five plots of 0.015 ha (15 m × 10 m) separated by 25 m (Abino et al. 2014), making a total of 600 plots. Within each plot, five sub-plots of 2 m × 2 m size were established (four in the corners and one at the center) to count individuals of dbh < 1 cm, considered as regeneration.

Data collection

Diameter at breast height (dbh), total height, and species identity of all trees with dbh (or diameter above the highest prop root in the case of *Rizophora* spp) greater than 1 cm, were recorded in each plot. In each 2 m × 2 m sub-plot, all regenerations were counted and identified at species level. In addition, we collected information on the tree condition, in particular, whether it was toped, logged, or pruned.

Data analysis

We first described the patterns of tree harvesting between low and high harvesting sites. Then we compared tree diversity (taxonomic and structural) and dominance, density, growth patterns, dbh size class distribution and stand stability between mangrove forests subject to low and high harvesting intensity.

Fig. 2 A disturbed mangrove site at Togbin **a**, *R. racemosa* individuals logged for firewood **b**, traditional system of salt production using mangrove trees as source of energy **c**, a mangrove site proected by the *Zangbéto* as local measure to mangrove conservation **d**, branches of mangroves harvested for fish trap "Acadja" **e**

Patterns of tree harvesting

To describe patterns of mangrove trees harvesting between low and high harvesting sites, densities of logged trees, pruned trees, and topped trees, were calculated per plot.

Tree diversity and dominance patterns

Species richness i.e. the number of distinct species, Shannon diversity, and Pielou evenness indices (Daget 1976) were used as measures of taxonomic diversity (see Table 1). As measures of structural diversity, we computed Shannon diversity and Pielou evenness indices based on dbh and height classes (Dănescu et al. 2016; Mensah et al. 2018). The dbh and height data

Table 1 Diversity and structure metrics to be computed for the structural analysis

Parameters	Formula	Formula details	Interpretation	References
Diversity parameters				
Shannon–Weiner Index, H	$H = -\sum_{i=1}^{s} \frac{ni}{n} \log_2 \frac{ni}{n}$	n_i is the number of individuals of the ith species; n is the total number of individuals considering all species	Measures species diversity in a community	Mac Arthur (1969)
Pielou's evenness index, Eq	$Eq = \frac{H}{H_{max}}$ with $H_{max} = \log_2 S$	H is the Shannon–Weiner Index and S is the species richness	Measures evenness in the distribution of individuals among species	Mac Arthur (1969)
Dominance parameters				
Relative density, RD	$RD = \frac{N}{TN}$	N is the number of individuals of a species and TN is the total number of individuals considering all species	Measures abundance of a species relative to abundance of all species	Cintron and Schaeffer-Novelli (1984)
Relative frequency, RF	$RF = \frac{F}{TS}$	F is the number of sampling units where the species occurs and TS is the total number of sampling units	Measures how often a species is observed in sampling units	Cintron and Schaeffer-Novelli (1984)
Relative dominance, RDo	$RD_0 = \frac{TA}{BA}$	TA is the basal area of a species and BA is the total basal area of all species	Measures how a given species dominates in a community	Cintron and Schaeffer-Novelli (1984)
Importance value index, IVI	$IVI = RD + RF + RD_0$	RD, RF, and RDo are defined as above	Ecological parameter wich determine the most representative species	Cintron and Schaeffer-Novelli (1984)
Stand structure parameters				
Basal area, G (m².ha⁻¹)	$G = \frac{10000\pi}{4s} \sum_{i=1}^{n_s} d_i^2$	d_i is the diameter of the tree ith of the plot	Dendrometric parameter wich inform to basal area distribution	Cintron and Schaeffer-Novelli (1984)
Mean diameter, D (cm)	$D = \sqrt{\frac{1}{n}\sum_{i=1}^{n} d_i^2}$	d_i is the diameter (in cm) of the tree ith of the plot	Measures horizontal growth of a species	Cintron and Schaeffer-Novelli (1984)
Simpson Index, SI	$SI = 1 - \sum n (n-1)/N (N-1)$	$\sum$ = sum of (total); n = the number of individuals of each different species; N = the total number of individuals of all the species	Measures if the size class distribution is even, regardless of the order in which the size classes are positioned	Wiegand et al. (2000)
Permutation index, P	$P = \sum_{i=1}^{n} |j_i - i|; j_i = 1...n$	J_i is the rank of size class i (i = 1 for the smallest class) with the top rank J_i = 1 given to the most frequent size class, and *n* is the number of classes	Measures the degree of deviation from the monotonic decline expected in an undistributed population	Wiegand et al. (2000)
Quotients between consecutive size classes, Q	$Q = N_{(i-1)}/N_i$	N_i is the number of individuals in class *i* and $N_{(i-1)}$ is the number of individuals in the class before class *i*	Measures population stability	Wiegand et al. (2000)

Table 2 Tree harvesting patterns across the study mangrove sites: variation between low- and high-harvesting sites

Structural parameters		Low-harvesting	High-harvesting	*p-value*	ICC_{Site}
Density of logged tree (stems.ha^{-1})					
All species	m	34.44	135.56	0.013	7.53
	se	6.03	8.09		
A. germinans	m	2.56	7.33	0.021	16.98
	se	1.24	1.85		
R. racemosa	m	35.78	121.11	0.010	20.00
	se	5.82	7.41		
Density of pruned tree (stems.ha^{-1})					
All species	m	43.56	86.22	0.011	4.08
	se	6.15	8.09		
A. germinans	m	13.56	21.33	0.043	4.65
	se	2.40	5.11		
R. racemosa	m	12.67	48.44	0.017	4.97
	se	3.20	5.00		
Density of toped tree (stems.ha^{-1})					
All species	m	17.11	55.78	0.040	40.92
	se	2.13	5.25		
A. germinans	m	0.44	3.11	0.033	12.71
	se	0.31	0.92		
R. racemosa	m	15.78	50.22	0.032	42.73
	se	2.00	5.01		

Table 3 Tree species and size diversity in mangrove forests in relationships to harvesting intensity

Harvesting intensity		Species			Dbh		Height	
		S	H_s	E_s	H_d	E_d	H_h	E_h
Low	m	4.30	0.67	0.32	0.98	0.36	1.82	0.75
	se	0.26	0.08	0.04	0.14	0.03	0.06	0.01
High	m	3.90	0.79	0.40	0.77	0.21	1.77	0.72
	se	0.10	0.06	0.02	0.13	0.05	0.07	0.02
p-value	–	0.641	**0.001**	**0.001**	**0.001**	**0.021**	0.528	0.669
Low harvesting	–	7	0.91	0.32	1.33	0.47	2.04	0.72
High harvesting	–	4	0.79	0.39	0.94	0.47	2.11	0.75

Values inbold indicate significant difference between sites of low and high harvesting intensity

m mean, *se* standard error

were arranged in seven classes of 10 cm and 3 m amplitudes respectively. These parameters were computed for each of the twenty sites and then averaged for each harvesting intensity. Linear model was used to test the effect of harvesting intensity on the taxonomic and structural diversity parameters. Species dominance was assessed using the importance value index (IVI; Table 1) calculated for each species as the sum of its relative density, relative frequency and relative dominance. Values of IVI vary from 0 to 3, higher values indicating higher dominance in the stand.

Tree density and growth patterns

Densities of regenerations, and of trees of dbh $\geq$ 1 cm were calculated per plot. Quadratic mean dbh, basal area, height, maximum diameter and maximum height (see Table 1) were also calculated. To assess the impacts of harvesting intensity on these structural parameters, we performed separate linear mixed models with harvesting intensity as the fixed factor and site as the random factor. For all mixed models, the intra-class correlation (ICC_{Site}) was calculated for
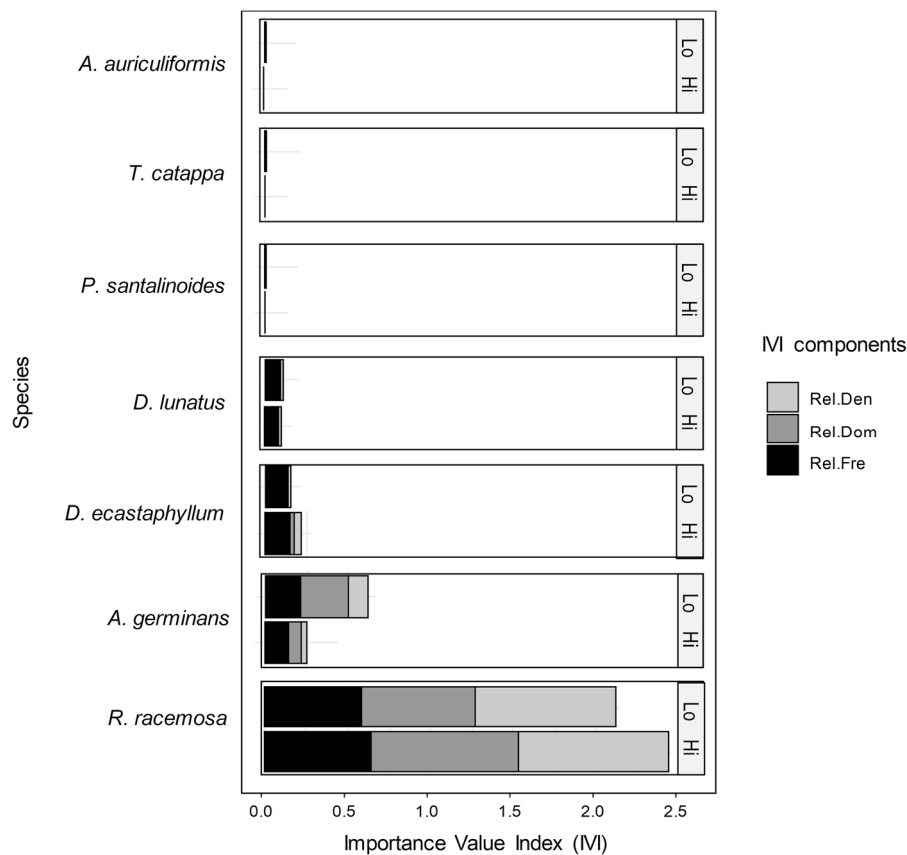
Fig. 3 Importance value index (IVI) of species in low- (Lo) *vs* high-harvesting (Hi) sites. Rel-Den, Rel-Dom, Rel-Fre are relative density, relative dominance, and relative frequency respectively

site. ICC$_{Site}$ is a measure of the proportion of the variation in a given structural parameter that is due to random variation among sites (see Pinheiro and Bates 2000).

Demographic structure and stand stability

Demographic structure was determined using the slope of the dbh size class distribution (SCD) (Martins and Shackleton 2017). SCD was established for the whole stand and each of the two most dominant species (i.e. species with the highest IVI). The SCD slope was estimated as the slope of the least squares regression of the tree density as a function of the centres of dbh classes on a log scale. A positive slope indicates poor recruitment with fewer small sized individuals and higher large sized individuals. A negative slope denotes the inverse J- shape SCD curve with good recruitment, higher densities of small sized

trees and low densities of large sized trees. However, because slope of SCD may not always be sufficient to better describe stand demography from snapshot data (Martins and Shackleton 2017), we additionally used Simpson index, permutation index, and quotients between consecutive size classes (Helm and Witkowski 2012; Botha et al. 2002). The formulas for the calculation of these indices are summarized in Table 1 and more details can be found in Shen et al. (2013), and Botha et al. (2002). A Simpson index less than 0.1 indicates uniform distribution in SCD, whereas values greater than 0.1 indicate that the frequency of size is steeper than what would have been expected from a stable population (Botha et al. 2002). A value of the permutation index close to zero suggests an undisturbed population while higher values indicate more disturbed population (Helm and Witkowski 2012). Fluctuating quotients between consecutive size-classes are indicative of unstable populations whereas

Table 4 Tree density, and growth patterns between low- and high-harvesting mangrove forests

Structural parameters		Low-harvesting	High-harvesting	p-value	ICC $_{Site}$
Density of individuals of dbh < 1 cm (individuals.ha^{-1})					
All species	m	9253.30	6942.87	0.028	30.78
	se	785.45	529.12		
A. germinans	m	3981.67	1851.57	0.048	52.67
	se	788.42	322.45		
R. racemosa	m	4823.70	4960.39	0.956	17.85
	se	495.79	499.51		
Density of individuals of dbh ≥ 1 cm (individuals.ha^{-1})					
All species	m	1229.10	884.20	< 0.001	50.00
	se	25.00	19.10		
A. germinans	m	145.80	29.33	0.028	43.79
	se	19.80	3.74		
R. racemosa	m	1043.80	807.60	0.038	19.84
	se	31.40	19.20		
DBH (cm)					
All species	m	11.10	7.61	< 0.001	52.05
	se	0. 23	0.18		
A. germinans	m	20.18	12.60	< 0.001	48.64
	se	1.44	0.81		
R. racemosa	m	10.24	7.51	< 0.001	38.44
	se	0.22	0.18		
Total height (m)					
All species	m	8.85	6.45	< 0.001	0.48
	se	0.10	0.10		
A. germinans	m	9.77	7.09	< 0.001	0.30
	se	0.23	0.33		
R. racemosa	m	8.50	6.62	0.033	0.48
	se	0.13	0.11		
Basal area (m^2.ha^{-1})					
All species	m	4.78	2.19	< 0.001	46.29
	se	0.04	0.02		
A. germinans	m	1.26	0.60	0.020	23.15
	se	0.40	0.18		
R. racemosa	m	3.61	1.49	< 0.001	51.57
	se	0.03	0.02		
Maximum dbh (cm)					
All species	m	19.73	12.82	< 0.001	–
	se	0.70	0.33		
A. germinans	m	26.10	14.09	< 0.001	–
	se	1.74	0.83		
R. racemosa	m	15.58	12.18	< 0.002	–
	se	0.40	0.32		
Maximum total height (m)					
All species	m	12.54	9.97	0.001	–
	se	0.14	0.17		

Table 4 continued

Structural parameters		Low-harvesting	High-harvesting	p-value	ICC $_{Site}$
A. germinans	m	11.13	7.66	0.002	–
	se	0.24	0.32		
R. racemosa	m	12.46	9.79	0.001	–
	se	0.16	0.17		

relatively constant quotients imply a stable population (Martins and Shackleton 2017). Statistical analyses were carried out with the R statistical software 3.3.0 (R Core Team 2015). The mixed models were implemented in packages lme4 (Bates et al. 2015) and lmertest (Kuznetsova et al. 2017).

Results

Patterns of tree harvesting across sites

Densities of logged, pruned and topped trees are direct indicators of wood harvesting for the diverse uses (Table 2). They were significantly higher on high-harvesting sites (2–4 times) than on low-harvesting sites for all species, and particularly for *Avicennia germinans* and *Rhizohpora racemosa* (the two dominant species, see Table 3). Furthermore, these densities were disproportionately higher for *R. racemosa* than for *A. germinans* (Table 2).

Impacts of harvesting on tree diversity and dominance patterns

Diversity patterns

In total, seven woody species were enumerated, of which two true mangrove (*R. racemosa* and *A. germinans*), two associate (*Dalbergia ecastaphyllum* and *Drepanocarpus lunatus*) and three non-mangrove (*Acacia auriculiformis*, *Pterocarpus santaniloides*, *Terminalia catappa*) species. All seven species were found on low-harvesting sites but only four were observed on the high-harvesting sites. Species diversity was generally low ($H_s < 1$, $E_s < 0.5$), irrespective of the harvesting intensity. Harvesting did not affect significantly average species richness, although slitghly higher richness was observed on the low-harvesting sites (4.30 ± 0.26 *vs* 3.90 ± 0.10) (Table 3). However, species Shannon diversity and evenness were significantly higher on high-harvesting sites (0.79 ± 0.06, 0.40 ± 0.02) than on low-harvesting sites (0.67 ± 0.08, 0.32 ± 0.04), respectively
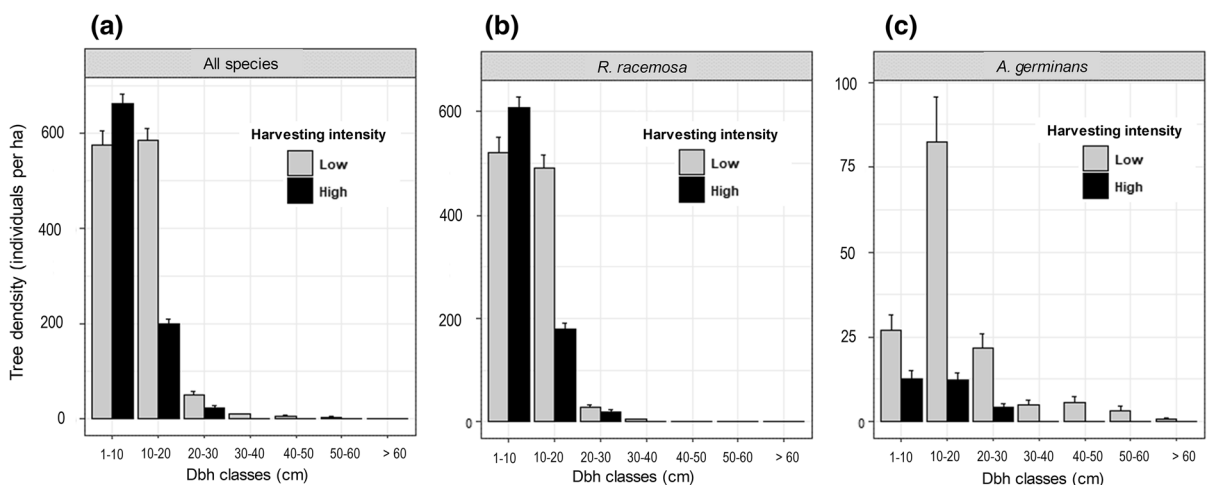

Fig. 4 Diameter size class distribution of mangrove forests in low- *vs.* high-harvesting sites

(Table 3). On the contrary, diameter-based Shannon diversity and Pielou evenness were significantly higher on low-harvesting sites, thus indicating higher structural diversity in low-harvesting sites (Table 3). Height-based diversity metrics were also slightly higher (although not significant; *p-value* = 0.528) on low-harvesting sites.

Dominance patterns

Across species and sites, *R. racemosa* had the highest values of IVI, irrespective of the harvesting intensity, and was followed by *A. germinans*, *D. ecastaphyllum* and *D. lunatus*. The remaining species had IVI less than 0.01 (Fig. 3). IVI of *R. racemosa* was 70.7% (2.12) of the total IVI on low-harvesting sites whereas it made 81.3% (2.44) of the total IVI on high-harvesting sites. *A. germinans* contributed 20.3% (0.61) of total IVI on low-harvesting sites whereas only 8.3% (0.25) on high-harvesting sites.

Impacts of harvesting on tree density, growth pattern and dbh size class distribution

Tree density and growth patterns

The densities of individuals of dbh ≥ 1 cm for all species, *A. germinans* and *R. racemosa* were significantly higher on low-harvesting sites (Table 4). Total regeneration density (individuals/ha) was also significantly higher on low-harvesting sites (9253.3 ± 785.45) than on high-harvesting sites (6942.8 ± 529.12). Similar observation was made for *A. germinans* which had density of regenerations twice higher on low-harvesting sites. Conversely, the density of regenerations of *R. racemosa* was not significantly different between harvesting intensities (Table 4).

Growth parameters include mean diameter, tree total height, basal area, maximum dbh, and maxium height. Mean diameter was significantly 1.5, 1.6, and

Table 5 Slope of SCD and stability parameters between low and high harvesting sites

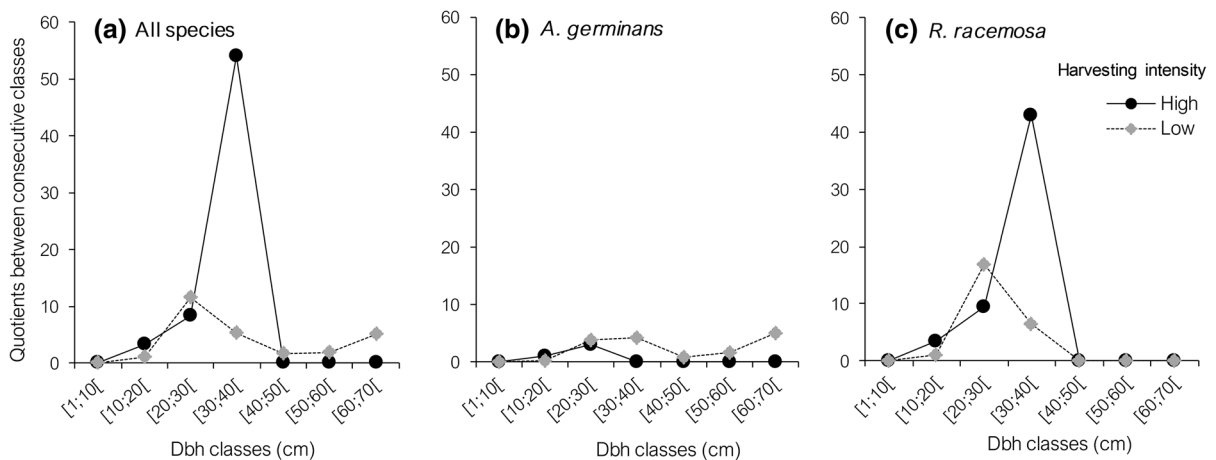| Parameters	Whole stand		A. germinans		R. racemosa	
	Low harvesting	High harvesting	Low harvesting	High harvesting	Low harvesting	High harvesting
SCD slope	− 0.11	− 0.13	− 0.08	− 0.09	− 0.14	− 0.13
p-value	< 0.001	< 0.001	0.007	0.014	< 0.001	< 0.001
R^2	94.82	88.44	73.19	66.4	91.52	86.87
Simpson index	0.55	0.38	0.62	0.62	0.53	0.38
Permutation index	2	0	4	0	0	0

Fig. 5 Quotients between successive size classes in low- *vs* high-harvesting sites for **a** the whole stand, **b** *A. germinans* and **c** *R. racemosa*

1.4 times higher on low-harvesting sites than on high-harvesting sites for all species, *A. germinans*, and *R. racemosa*, respectively, indicating negative impacts of harvesting on tree growth parameters. Similary, tree height was 1.3–1.4 times higher in low-harvesting sites (Table 4). Basal area, maximum dbh, and maxium height were also higher on low-harvesting sites for all species together, *A. germinans*, and *R. racemosa* (Table 4). Values of the ICC were relatively high (20–50%) for some parameters, namely density of individuals of dbh < 1 cm, density of individuals of dbh ≥ 1 cm, density of topped trees, dbh, and basal area, indicating large variations across sites for these parameters, after accounting for their harvesting intensity (Table 4).

Tree dbh size class distribution

Figure 4 shows the tree dbh-based size class distribution (SCD) of mangrove forests for low-harvesting sites and high- harvesting sites. Irrespective of the harvesting intensity, the SCD had an inverted J-shape distribution for all species together (Fig. 4a and b), *R. racemosa* (Fig. 4c and d), and *A. germinans* (Fig. 4e and f) as also indicated by the significant and negative values for the slopes of all SCD (Table 4). However, the SCD slopes were relatively less steep for *A. germinans* than for *R. racemosa* and were similar for low-harvesting and high-harvesting sites (Table 4).

Most trees were in the first two dbh classes: 96–97% for *R. racemosa*, 75–86% for *A. germinans* and 94–97% for all species together, respectively on low-harvesting and high-harvesting sites (Fig. 4). Trees of dbh larger than 30 cm were very rare in *R. racemosa* (0.44% and 0.05% on low-harvesting *vs.* high-harvesting sites, respectively) than in *A. germinans* (10.21% *vs* 0% on low-harvesting *vs.* high-harvesting sites, respectively) (Fig. 4,c–f). For the whole stand, 13.4% and 0.21% of trees had dbh larger than 30 cm on low-harvesting *vs* high-harvesting sites respectively (Fig. 4a, b). These statistics showed large reduction of trees in this dbh class from low-harvesting to high-harvesting sites. The density of trees in the 10–20 cm class on high-harvesting sites was approximately three and seven times lower than on low-harvesting sites for *R. racemosa* and *A. germinans*, respectively whereas approximatively 3 times lower for the whole stand on high-harvesting sites (Fig. 4). This ratio for the first class (i.e. 1–10 cm) remained relatively constant for the whole stand and *R. racemosa* but twice lower in *A. germinans*. Also, whereas the first two classes had similar densities on low-harvesting sites, the tree density in the second class was more than three time lower than that in the first class on high-harvesting sites for *R. racemosa* and the whole stand.

Mangrove forests' stability

Values of the Simpson index of the SCD were all higher than 0.1, indicating that the dbh classes are not evenly distributed and that the frequency of dbh classes is steeper than what would have been expected from a stable population at all scales (whole stand and each of the most two dominant species). The Simpson index was higher for *A. germinans* than *R. racemosa* (Table 5). The Simpson index did not differ between high-harvesting and low-harvesting sites for *A. germinans,* and was lower on high-harvesting sites than on low-harvesting sites for the whole stand and *R. racemosa* (Table 5). The whole stand and *R. racemosa* showed similar values for this parameter. The permutation index of the SCD of the the whole stand was higher on low-harvesting sites (P = 2), compared to high-harvesting sites (P = 0). Similarly, the permutation index indicates higher disturbances of the SCD on the low-harvesting sites (P = 4) while no SCD disturbance was observed for the high-harvesting sites (P = 0) for *A. germinans*. On the contrary, the permutation index was null and did not vary for either of the disturbance status for *R. racemosa*, indicating no disturbance of the SCD for this species. Figure 5 shows the variation of the quotients between successive dbh classes for the whole stand, *A. germinans*, and *R. racemosa*. For the whole stand, quotients fluctuated more in high-harvesting sites than in low-harvesting sites (Fig. 5a). For *A. germinans*, the fluctuation was more important in low-harvesting sites (Fig. 5b) whereas for *R. racemosa*, the fluctuation did not differ much between low-harvesting and high-harvesting sites (Fig. 5c).

Discussion

Small-scale wood harvesting from mangrove forests could vary considerably depending on national or local regulations in place (Walters 2005a). The

uncontrolled wood exploitation by local communities could thus dramatically alter mangrove forests (Walters 2005b). Therefore understanding how human activities through cutting intensity are affecting mangrove forests can help design specific actions that prevent their loss. Although several studies have been carried around the world on the impacts of human activities on mangrove forests, comparatively few examples are available from West African mangroves. Therefore, the information provided in this paper have potential to contribute to build a more complete understanding of how human activities, particularly wood harvesting globally affect mangrove forests. Our comparison focused on the differences in tree taxonomic diversity, structural diversity, dominance patterns, growth characteristics, dbh size class distribution, and stability between mangrove forests subject to low- vs high-harvesting sites.

Patterns of harvesting across sites

The classification of study sites into low or high harvesting categories was based on the intensity of harvesting in the study sites, considering the density of logged tree, pruned tree, and toped tree. Consistent to this, we found that densities of logged tree, pruned tree, and toped tree were respectively 4, 2, and 3.3 times higher on high-harvesting sites for the whole stand, 2.9, 1.6 and 7.1 times higher for *A. germinans*, and 3.4, 3.8, and 3.2 times higher for *R. racemosa*, thus confirming higher anthropogenic activities on these sites. Mangrove trees are harvested by local inhabitants who use them as wood for various purposes including local fish trap "Acadja" where young branches of *R. racemosa* and *A. germinans* are commonly used, fuelwood, salt production, and construction materials. The lack of alternative free sources of wood in their close environment added to the increasing human population are among others, reasons for the increasing harvesting of mangroves. Considering the actual density of trees logged, pruned, and toped, our results indicate that *R. racemosa* is the most collected species (see Table 2). This species is recognized by the local population in the study area as of high calorific value compared to *A. germinans*. *Rhizophora* spp. is also the most commonly harvested mangrove species elsewhere, e.g. in Central-America (Windevoxhel-Lora and Imbach 1999). It is also a major source of income in Cameroon where its local trade bring financial benefits of up to US$200 monthly to loggers (Feka and Manzano 2008).

Less impacts of harvesting on taxonomic diversity than on structural diversity and dominance patterns

Seven tree species were recorded in this study, with the red mangrove *R. racemosa* and the black mangrove *A. germinans* being the only two true mangrove tree species, i.e. characteristic of mangroves. These species are typical taxons of west African mangroves (Tomlinson 1986). The presence of species such as *A. auriculiformis* and *T. catappa* in the mangrove ecosystems is indicative of human activities near mangroves as these species are exotic introduced in Benin for reforestation programs (Akoegninou et al. 2006). It might also be linked to wind or animal dispersal activities. Folega et al. (2017) reported similar findings in Togo. The generally low tree species richness in these mangroves is not surprising, and is consistent with the view that very few plant species have morphologically, physiologically and reproductively adapted to the extreme environmental conditions in mangroves, primarily made of saline and anaerobic conditions (Kovacs et al. 2001; FAO 2007). The West Afrian region is also particularly known to have very low true mangrove plant diversity (Fernando 1998). The observed species richness is low compared to the ten species reported in Indonesia (Edi et al. 2017) but similar to that reported in a study by Azyleah et al. (2014) in Philippines.

There was not enough statistical evidence that harvesting intensity influences site-level species richness. This could be attributed to the naturally low diversity in the ecosystem such that despite the harversting activities, each taxon is still represented by some individuals, resulting in globally less differences. Surprisingly, we found that Shannon diversity and Pielou evenness were significantly higher on high-harvesting sites (0.79 ± 0.06, 0.40 ± 0.02) than on low-harvesting sites (0.67 ± 0.08, 0.32 ± 0.04). A reason for such results could be linked to a preference in cutting *R. racemosa* which was the super-dominant species (see Fig. 3). This preference probably contribute to reduce the dominance of *R. racemosa* and hence favours more even distribution of trees among species. While these results are similar to findings of Zhita et al. (2014) in Malaysia, they contrast with Ngole-jeme (2016) who found that tree harvesting in

mangroves has a significant negative effect on species diversity, richness, and evenness in Cameroon. Differences in both studies might be linked to differences in the intensity of wood harvesting and also the potential impacts on soil conditions which act as environmental filtering for species coexistence. In opposite, we observed significantly lower diameter-based structural diversity where wood harvesting was high. This suggests that tree harvesting might be specifically oriented towards some specific dbh classes, which removal from the stands, significantly reduce diameter diversity. Tree structural diversity is indicative of forest stability and such lower structural diversity due to harvesting might be prejudiciable to the mangrove forests.

The two most dominant species were *R. racemosa* and *A. germinans*, which is consistent with several previous studies in Benin (Ajonina et al. 2014) and in the region including Nigeria (Asuk et al. 2018), and Togo (Fousseni et al. 2017), and this trend was not affected by harvesting intensity.

Tree density, growth characteristics, and regeneration as affected by harvesting

As expected, high harvesting reduced tree density (individuals.ha^{-1}) by a factor of 1.4 at the whole stand level (from 1229.1 to 884.2), 5.0 at *A. germinans* level (from 145.8 to 29.3) and 1.3 at *R. racemosa* level (from 1043.8 to 807.6). These values suggest negative impact of harvesting on tree stock in mangrove forests. Anthropogenic activities such as cutting, and lopping, which occur in the study area have been identified as main drivers of reduction in tree density in mangroves in many sites elsewhere (Ayyappan 2009; Hoffman et al. 2006; Blanco et al. 2012). Our results also support the expectation that high harvesting has a negative impact on stand tree growth characteristics such as dbh, maximum dbh, height, and maximum height. For instance, trees were smaller and shorter both for the whole stand and each of the two dominant species. Other studies reported similar results, e.g. Ngole-Jeme et al. (2016) in Cameroon and Zhila et al. (2014) in Malaysia. Recurrent pruning and topping of trees are actually limiting factor of horizontal and vertical growth of trees (Fini et al. 2015). Removal of large-sized trees added to this recurrent pruning and topping of trees are likely to result in small sized trees

and explain why trees are smaller and shorter where harvesting is high.

We found a reduction of regeneration (from 9253.30 individuals.ha^{-1} to 6942.87 individuals.ha^{-1}) possibly as a consequence of high harvesting intensity at the whole stand level, similar to several previous studies; for e.g. Ngole-Jeme et al. (2016) in Cameroon and Zhila et al. (2014) in Malaysia. A similar observation was made for *A. germinans*. However, high harvesting has no effect on the renegeration density of *R. racemosa*; on the contrary high harvesting seems to be associated to increased regeneration density for this species; highlighting that trend at community level does not necessaritly apply at species levels. The results for *R. racemosa* could be explained by the fact that light conditions might be favorable factor for *R. racemosa* regeneration as was reported for other mangrove species (Ellison and Farnsworth 1993; Duke 2001). It is possible that tree cutting enhances light availability in the understorey, which might favor emergence of regenerations of *R. racemosa*. Harvesting large individuals of this species seems to be beneficial for its regenerations; however more detailed investigations are needed to confirm such hypothesis. Some studies have shown that moderate harvesting of old or large individuals might not affect the long term population dynamics of *Rhizophora* spp species (see Gaoue and Kowiyou 2019). Additional role of soil substrate might also be plausible as suggested by Sherman et al. (2000). Similar results were reported by Ajonina et al. (2014) in Benin and Kihia (2014) in Kenya. Further assessment of the impacts of harvesting on soil conditions will allow a better understanding of the impacts of anthropogenic activities on mangroves functioning. Nevertheless, relatively large values were observed for ICC, which is indicative of large variations across sites in structural parameters, after accounting for their harvesting status. This suggests that site specific initial and environmental conditions play an important role in the variation of structural parameters. Habitat heterogeneity (e.g. topography, soil conditions, etc.) and intensity of harvesting intensity might vary among sites, even within a specific harvesting category (Walters 2005a), and this is likely the main reason for relatively large ICC values in some cases.

Impacts of harvesting intensity on tree dbh size class distribution and stability

All SCD had an inverse J-shape distribution, irrespective of the harvesting intensity and the scale of analysis (whole stand or dominant species). No actual differences were observed based on the SCD slope, thus suggesting less impacts of harvesting on SCD. However, it has been argued that stability parameters such as Simpson index, permutation index and quotients between successive classes can provide additional useful information to the general trend as measured by the SCD slope on snapshot data (Martins and Shackleton 2017). This proved true in our study. Indeed, the Simpson index indicated no effect of harvesting on *A. germinans* but differences were noted for *R. racemosa* and the whole stand: trees were more evenly distributed in high-harvesting sites as a consequence of the selective harvesting. Permutation index was not different between low- and high-harvesting sites for *R. racemosa* and to some extent the whole stand, which suggests that despite the high harvesting, the resulting stand structure did not differ much from that of low-harvesting sites, possibly because of the initial conditions. But this was not true for *A. germinans*. Furthermore, there was relatively high fluctuations on high-harvesting sites at the whole stand level, and on low-harvesting sites for *A. germinans*. This indicates a certain level of instability in population through growth between successive size classes which might not necessarily result from higher harvesting. Together, these results suggest that impacts of harvesting on stand structure are unpredictable, and patterns at stand level may not necessarily be true for particular species in the community. This further highlights the importance of using multiple structural indices to better understand impacts of anthropogenic activities on tree SCD.

SCD can also help identifying which size classes are probably most affected by wood harvesting (Venter and Witkowski 2010; Traoré et al. 2013). In this line, our findings showed that individuals of dbh larger than 30 cm and comprised between 10 and 20 cm have sharply declined. We conclude that individuals of these classes are probably the most harvested, the first likely for construction and the second for firewood, acadja, and to a lesser extent construction.

Conclusions and implications for sustainable management

In this study we showed that harvesting intensity has less impacts on tree taxonomic diversity than structural diversity, growth characteristics (namely dbh and height), size class distribution and stability in mangrove forests in a coastal region of West Africa. We also found that low-harvesting sites, most of which host the local divinity "Zangbeto" showed higher tree density, structural diversity, and growth characteristics. Therefore, this traditional conservation system has prevented mangroves' destruction and might be formally included in sustainable conservation and management planning as long as this tradition is rooted in community culture. Their integration in national regulations for mangrove conservation will also be a plus. In addition, despite the several measures taken to ban or control the proscribed cutting of mangrove trees using a strict protection model, local people have continuously harvested mangrove trees, as also reported in China (Wang et al. 2020). This is mainly because of the lack of alternative free sources of wood in their environment and the rising human population. In addition, there is an acute lack of land which might allow local people to establish plantations of fast growing tree species (e.g. *A. auriculiformis*) which have been promoted in the region. Also, there are some uses of mangrove trees (e.g. the use of mangroves' wood for traditional salt preparation) which are rooted in traditions of local people and they might always refer to mangroves; as such, a participatory community-based management may offer a better alternative (Rakotomahazo et al. 2019). Using the framework of Biosphere reserve, some mangrove areas can be identified and subject to integral protection with the aid of "Zangbeto" while other mangrove sites could be assigned to controlled sustainable exploitation with a clear defined rotation and regulations in the exploitation. Such management could take advantage of the good natural regeneration of the *R. racemosa*, the most dominant species of the studied mangroves. Such strategy has been suggested by Rakotomahazo et al. (2019) and proved successful, for e.g. in Tanzania (Wells et al. 2010) and worth to also be tested in the study area. Nevertheless, additional studies on population dynamics of mangroves and wood productivity in low- and high-harvesting sites are necessary to better understand transition between

successive dbh classes, and wood productivity; this would aid to better define exploitation regime. Furthermore, mangroves are in the densely populated areas in Benin and also subject to impacts of urbanization. Conversion of mangrove forests to other land use has been observed to occur more quickly around some of the largest cities in the world (Branoff 2017). For e.g. development of road network is an important driver of mangrove forests degradation (Mulyadi and Amin 2016). In the study area, there are also some prospective projects, e.g. la "route des pêches" which aims at constructing a transnational road along the coast and bordering mangrove ecosystems. Such a road will undoubtedly increase urbanization and made mangroves more vulnerable. Important measures should therefore be taken to prevent further degradation of mangroves. Lastly, our findings showed that density of adults and regenerations of *A. germinans* were more affected than those of *R. racemosa*. Actually, mangrove species do not have the same resilience to wood harvesting. For example, Gaoue and Yessoufou (2019) found that *Rhizophora mucronata* was more resilient to harvesting than *Bruguiera gymnorrhiza* and *Avicennia marina* in South African mangroves. Yet, most restoration projects have so far mainly used *R. racemosa* as also observed elsewhere (López-Portillo et al. 2017). Therefore, more attention should be given to *A. germinans* in restoration projects. In synthesis, the following actions are suggested to the different stakeholders for the sustainable management of mangroves in the study area:

- Formal integration of "Zangbeto" in national regulations for mangrove conservation;
- Use of the framework of "Biosphere reserve" to manage and conserve mangroves. In this case, mangrove sites assigned to controlled exploitation will then be subject to participatory community-based management;
- Promote sustainable alternative sources to mangroves' wood for domestic uses (e.g. fast growing trees such as *A. auriculiformis*) to reduce harvesting pressure on mangroves;
- Take necessary measures to prevent further pressures on mangroves that could result from development projects such as "la route des pêches";

- Grant more attention to *A. germinans* in restoration projects, since it has been shown to be less resilient to harvesting compared to *R. racemosa*.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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