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Inter- and intraspecific variation in mangrove carbon fraction and wood specific gravity in Gazi Bay, Kenya

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Abstract. The tropical mangrove ecosystem harbors great potential for carbon offsetting schemes because of their exceptionally high carbon sequestration potential. These cannot only generate an income for local communities by financially compensating for the non-exploitation of protected or replanted stands, but also simultaneously reduce emissions due to forest degradation and deforestation, thereby helping to counteract the global threat on these forests. As carbon is directly monetized through offsetting carbon emissions, accurate species-specific estimation of carbon content in trees is essential and reduces the propagation of errors generated by accounting uncertainties. Accordingly, this study assessed variation in both carbon fraction and wood specific gravity among and within the 10 mangrove species occurring in Gazi Bay, Kenya. Significant interspecific differences were found with values ranging from 45.8% (*Avicennia marina*) to 49.8% (*Ceriops tagal*) for carbon fraction and from 0.58 (*Sonneratia alba*) to 0.93 (*Pemphis acidula*) for wood specific gravity. The influence of environmental factors (soil salinity, stand density, and elevation a.s.l. as a proxy for multiple interrelated conditions) was investigated, but only elevation a.s.l. appeared to have a species-specific though moderate influence only on carbon fraction. Significant differences in carbon fraction and wood specific gravity were found between stem, aerial roots, and branches of *Rhizophora mucronata*. In contrast, no significant differences in carbon fraction were found among different stem tissues of *A. marina, C. tagal* and *R. mucronata*, the Bay's most abundant species. These results provide insight in carbon content variation, confirming the importance of considering species-specific or even site-specific values of carbon fraction and wood specific gravity, thereby rendering future carbon accounting more accurate.

Key words: blue carbon; carbon fraction; Gazi Bay; mangroves; wood specific gravity.

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INTRODUCTION

Mangrove forests are ecologically unique ecosystems that can be found in tropical and subtropical latitudes along the land–sea interface, bays, estuaries, lagoons, and backwaters (Mukherjee et al. 2014). They provide ecosystem services such as coastal protection, coastal fisheries, land-building, wood production, nutrient cycling, nursery and breeding protection to marine organisms, and opportunities for ecotourism (Lee et al. 2014, Murdiyarso et al. 2015). These directly or indirectly benefit local communities (Locatelli et al. 2014) as well as human society in its entirety through the global scale of such services (Lee et al. 2004, Jerath et al. 2016). An ecosystem service that has recently received increased scientific attention is the high carbon (C) sequestration capacity of mangroves (Kauffman and Donato 2012, Howard et al. 2014). Mangroves contain on average 1.023 Mg C/ha, predominantly due to belowground carbon storage, which makes them one of the most carbon-rich forest types (Komiyama et al. 2008, Donato et al. 2011). Mangroves can accumulate large amounts of peat (Ezcurra et al. 2016) and other forms of mangrove-derived carbon (Bouillon et al. 2008), making them very efficient coastal carbon sinks. They bury carbon at a rate up to 50 times higher than tropical rainforests because they not only trap their own organic material, but also litter from rivers and adjacent seagrass meadows (Bouillon 2011). Despite their role as important carbon sinks and the worldwide efforts to reduce carbon emissions, mangroves are threatened globally by deforestation resulting mainly from aquaculture and agriculture, but also by deforestation's indirect consequences which include drainage and high nutrient levels (Mukherjee et al. 2014, Atwood et al. 2017). This leads to an estimated annual loss of 0.16–0.39% globally but up to a staggering 8.08% in South-East Asia (Hamilton and Casey 2016). This is especially alarming since mangrove forests present high attractivity for carbon offsetting schemes, making their protection a cost-efficient strategy for climate change mitigation (Siikamäki et al. 2012, Sitoe et al. 2014, Murdiyarso et al. 2015) while at the same time providing local communities with numerous additional ecosystem services (Locatelli et al. 2004).

Carbon stocks can be directly monetized through carbon offsetting schemes (Jerath et al. 2016), which stresses the need for an accurate carbon stock assessment (Sitoe et al. 2014). However, several errors are generated by each level of the assessment: (1) field measurements, (2) choice of allometric equation for biomass estimation, (3) choice of standard wood specific gravity value, and (4) choice of standard carbon fraction value (Feldpausch et al. 2010, Thomas and Martin 2012, Chave et al. 2014, Hiraishi et al. 2014, Njana et al. 2016). The carbon fraction is represented as a mass/mass ratio and used as a conversion factor to determine the amount of carbon for a given amount of dry biomass (Hiraishi et al. 2014). Although the largest error is caused by the choice of the allometric model (Bastin et al. 2015), variation in wood specific gravity (Chave et al. 2009) and carbon fraction (Thomas and Martin 2012, Rodrigues et al. 2014) can also propagate important deviations. Even small differences among these parameter values can have important consequences, as, for example, an increase of the mean carbon fraction of all trees from 50% to 51% would result in a 7×10^9 tons overestimate of carbon globally (calculated for an estimated forest area of 4.1×10^9 ha; Dixon et al. 1994, Jones and O'Hara 2016).

Until now, research mainly focused on variation in wood density in tropical terrestrial forests (Muller-Landau 2004, Chave et al. 2005, Slik et al. 2008, Bastin et al. 2015). Much less is however known on the variation in mangrove wood density (Santini et al. 2012, Njana et al. 2016), whereas the mangrove carbon fraction in particular has been understudied (Jones and O'Hara 2016). The Intergovernmental Panel on Climate Change (IPCC) provides a standard value for mangroves of 45.1% carbon on a mass basis (Hiraishi et al. 2014), but previous research has demonstrated that values can vary among species, within species, and even among tree tissues (Lamlom and Savidge 2003, Negi et al. 2003, Khan et al. 2007, Kauffman et al. 2011, Jones and O'Hara 2016). Furthermore, a positive relationship between wood specific gravity and carbon fraction is expected due to the high carbon content of wood chemical components (i.e., lignin) which are commonly more important in denser wood, but this has not yet been demonstrated (Lamlom and Savidge 2006, Thomas and Malczewski 2007).

Out of the 10 mangrove species reported for Kenya, where the present study took place, only two species-specific carbon fractions have been established (Kauffman et al. 2011). Furthermore, the effect of prevailing environmental conditions in mangrove ecosystems, such as salinity and tidal regime, is not taken into account when determining carbon parameters (Rodrigues et al. 2014). E. Vlaminck (*unpublished results*) for example indicates influences of forest structure on the carbon content of *Rhizophora mucronata* but found no significant effect of salinity on three mangrove species in Gazi Bay, Kenya. Although their precise effect on carbon fraction remains as yet unidentified, environmental conditions have—at a larger scale—been shown to be important factors to consider when estimating carbon stocks with high accuracy (Rovai et al. 2016).

The aim of the study was to accurately estimate and compare potential sources of variation in carbon fraction and wood specific gravity in mangrove trees at species, tree organ, and tissue level while determining the species-specific effect of environmental conditions. Two main hypotheses were formulated: (1) Carbon content is equal for all species, and (2) carbon content is equal within a species and under all environmental conditions. Additionally, we compared two different methods for carbon fraction measurement: loss-on-ignition (LOI) and elemental analysis (EA), as well as two methods for salinity measurement.

The research was performed in a tropical bay in Kenya where a community-involving project called Mikoko Pamoja sells carbon offsetting credits to generate income for its members and the inhabitants (Huxham 2013). Community members gather in village meetings and designate projects to invest profits in, such as the improvement of the education system and the water and sanitation quality of the village (Abdalla et al. 2016). In return, the community protects and replants mangrove forest, enhancing biodiversity, carbon storage but also the inhabitants' livelihoods. Plan Vivo, the organization providing the legal framework, endows certificates after thorough controlling of, among others, carbon stocks. Because part of the community's income depends on sequestered carbon, it is crucial to find accurate estimations of specific carbon fraction and wood densities and to assess main sources of variation herein. We intended to identify patterns and processes of general interest regarding carbon fraction and wood specific gravity in mangroves, in this case specifically in a region where a carbon offsetting project has already been initiated.

MATERIALS AND METHODS

Study area

Gazi Bay (4°22′ S, 39°30′ E), located approximately 50 km south of Mombasa (Kenya), is a shallow coastal water system of approximately 15 km^2 (including the mangrove forest) with a tidal range of around slightly more than 4.0 m (Kitheka 1996). Two tidal creeks, Kinondo and Kidogoweni, drain into the northern area of the bay while the Mkurumuji river, the estuary of which is lined by the southern part of Gazi Bay's mangrove forest, is responsible for most of the freshwater inflow during the rainy season, together with the Kidogoweni river. Their peak discharge equals, respectively, 16.7 and 5.0 m^3/s during the long rainy season (Kitheka 1996). In Kenya, two rainy seasons occur annually; a long one from April to August and a short one between October and November (Bosire et al. 2003).

The Bay's coastline is vegetated by a rich assemblage of mangrove species (in reference to the Western Indian Ocean region), as Kenya's 10 species are found here (Kirui et al. 2008). These comprise *Avicennia marina* (Forsk.) Vierh., *Bruguiera gymnorrhiza* (L.) Lamk., *Ceriops tagal* (Perr.) C.B. Rob., *Heritiera littoralis* Dryand., *Lumnitzera racemosa* Willd., *Rhizophora mucronata* Lamk., *Sonneratia alba* J. Smith, *Xylocarpus granatum* Koen., *Xylocarpus moluccensis* (Lamk.) Roem, and, as a very rare occurrence, *Pemphis acidula* Forst. (nomenclature following Tomlinson 2016).

Sampling strategy

The sampling strategy in this study can be subdivided into different ecological levels, ranging from tree community to tree tissue. Carbon fraction and wood specific gravity were measured on a total of 93 wood samples.

Four major research objectives were put forward to assess the hypotheses on wood specific gravity and carbon fraction: (1) differences among the 10 mangrove species found in Gazi Bay; (2) the inter- and intraspecific effect of environmental gradients including forest structure, salinity, and elevation a.s.l. as a proxy for multiple interrelated environmental conditions (soil redox potential, soil type, and inundation regime); (3) differences between root, branch, and stem wood in *R. mucronata*; (4) differences within stem tissue types, from pith to bark, for *A. marina*, *C. tagal,* and *R. mucronata*. Additionally, determination of nitrogen (N) content in wood allowed for C/N estimation and determination of carbon stable isotope ratios allowed for additional information on environmental influence.

Sampling was conducted during the dry season between mid-February and mid-March 2017 at five different locations within the Bay with the aim of covering the largest possible range in measured environmental conditions (Fig. 1). A total of 73 trees were sampled within those five sites, where the number of replicates per species reflects their abundance in the Bay (Table 1). Sites varied in their topography (e.g., a basin) and hence their inundation frequency, but also in their species composition (i.e., monospecific, species-poor, and species-rich stands), tree density, and relative position compared to river mouths (see Appendix S1: Fig. S1 for detailed positions of species).

Trees were selected based on a specific set of criteria. Firstly, the maximal potential variation in environmental conditions was integrated in the sampling design by choosing the most seaward tree, the most landward tree, and trees in between for each species per specific location. We thereby maximized the range in elevation and salinity which could be expected to have an effect on the carbon content. Secondly, only trees within a certain D_{130} range (generally between 8 and 12 cm with differences according to species) were sampled to reduce any potential bias created by tree age (mangrove tree age cannot be estimated unequivocally). Subsequently, a wedge of the stem was taken at D_{130} using a handheld

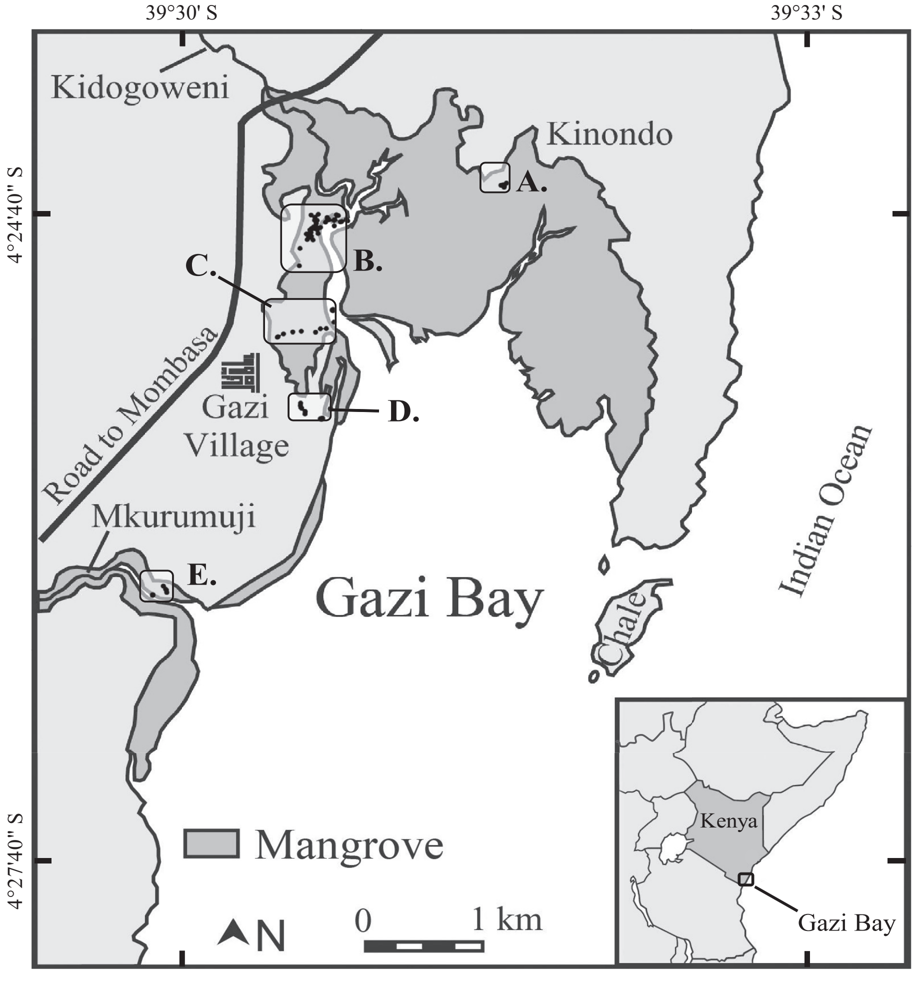

Fig. 1. Location the five sampling sites (translucent boxes, codes A–E) and each mangrove tree within those sites (black dots). See Appendix S1: Fig. S1 for detailed satellite images of all sampling sites and the exact position of each sampled mangrove tree. Adapted from Kitheka (1996).

Table 1. Carbon fraction and wood specific gravity values of all 10 mangrove species.

Species	N	Carbon fraction (%)	Standard error	Wood specific gravity	Standard error
Avicennia marina	20	45.82	0.28	0.76	0.02
Bruguiera gymnorrhiza	5	49.01	0.49	0.84	0.01
Ceriops tagal	10	49.82	0.25	0.85	0.01
Heritiera littoralis	5	48.07	0.11	0.84	0.01
Lumnitzera racemosa	6	47.43	0.42	0.82	0.03
Pemphis acidula	1	48.60		0.93	
Rhizophora mucronata					
Stem	10	47.35	0.20	0.88	0.01
Branch	10	45.82	0.21	0.83	0.01
Root	10	45.45	0.43	0.78	0.01
Sonneratia alba	5	48.47	0.03	0.58	0.03
Xylocarpus granatum	5	47.77	0.41	0.71	0.02
Xylocarpus moluccensis	6	48.83	0.71	0.82	0.04
Mean stem	73	47.23	1.78	0.80	0.09

Notes: Mean values of carbon fraction and wood densities and their standard error of the mean for all sampled species. Site-specific values for wood specific gravity are provided and can be incorporated in allometric equations, while the carbon fractions serve as biomass conversion factors. *Pemphis acidula* was only sampled once due to insufficient suitable individuals (site rarity) and shrub-like physiognomy.

saw in such way that every tissue type, from pith to bark, was sampled without making the tree-fall. Prior to sampling any tree, permission by the Kenya Marine and Fisheries Research Institute (KMFRI, Gazi station), as well as a research permit, was asked and paid. Mangroves in Gazi Bay represent the local community's natural capital because wood carbon is monetized directly through carbon offsetting schemes. For this reason, we minimized the impact on the trees as much as possible and maximized the usage of every single sample in laboratory observations. Wedges of the stem were preferred over increment wood cores as this proved to be the most efficient and feasible method for all wood types, especially for very dense woods like *R. mucronata*. To determine differences among tree components, wood disks of both aerial roots and branches were obtained for 10 sampled *R. mucronata* trees. Root samples were taken from the fifth highest root, 30 cm away from the main stem. Branch samples consisted of the lowest branch exceeding 3 cm in diameter, again 30 cm from the main stem.

For each selected tree, the environmental conditions that could potentially explain variation in wood specific gravity or carbon fraction were measured. Tree height was obtained using a scale hypsometer (0.1 m precision). Stand density and species composition in the direct vicinity of each sampled individual were assessed according to the Point-Center Quarter Method as in Mitchell (2010). Tree positions were obtained using a handheld GPS (Garmin, Schaffhausen, Switzerland). Salinity was measured with a handheld refractometer (VWR, Leuven, Belgium) on interstitial water samples at three points around the tree, about 50 cm from the stem and at a depth of 20 cm. This was done per location within a two-hour time window after a single spring tide to maximally standardize measurements. However, because salinity measurements were highly variable around a single tree (differences up to 20‰ for distances <2 m), we decided to apply an additional method that is less dependent on the moment of soil water extraction and could serve as a comparison for the direct extraction method. Around each tree, three holes of 20 cm depth were dug, after which a small soil sample was extracted and placed in a coded plastic bag. These samples were dried for 48 h at 70°C, after which they were weighed, ground using a mortar and pestle and suspended in an equal weight of freshwater (50:50 W : W). Once homogenized, the salinity was again obtained on the clear supernatant with the refractometer. To obtain elevation above sea level, strips of masking tape coated with water-soluble iodopovidone, turning the strip sections reddish, were applied to the stem right before high tide. When the tide retreated, the exact elevation of an individual could be calculated by subtracting the height of that particular tidal phase (using the tides table for Kilindini harbor in Mombasa, the nearest site with such data) with the observed water limit on the stem (D. Di Nitto, *personal communication*). Elevation a.s.l. is believed to provide the most robust method as it does not fluctuate between tides or among seasons, but it comprises many interrelated variables that cannot be distinguished.

Determination of wood specific gravity

Before carbon content analysis, whole wedges—including bark—were submerged in water for wood specific gravity measurements according to the water displacement method described in Chave (2005). The displaced water mass, weighed with a 0.01 g precision balance, corresponds to the volume of the sample, taking into account water salinity and temperature as well as the volume of the pincer used to submerge the sample. Wedges were subsequently oven-dried at 65°C until they reached a stable weight. Wood specific gravity was then calculated by dividing green sample volume (i.e., the volume before oven-drying) by dry weight and is in this case often also referred to as wood specific gravity in the literature.

Determination of carbon fraction

The carbon fraction was obtained using two different methods: EA and LOI, using the same subsamples of a single wedge. Each subsample was sawn off ensuring all tissue types, from pith to bark, were represented in the same proportions as they would occur in the stem because intra-stem variability in carbon fraction is a common feature in many species (Thomas and Martin 2012). For the within-stem study, every subsample was subdivided into three pieces, including the bark separately and two equally divided stem pieces (i.e., radially from pith to bark) for the most abundant species, being *A. marina, C. tagal,* and *R. mucronata*. Per species, five samples were radially subdivided, resulting in a total of 45 subsamples analyzed on carbon fraction. In the case of selected (tropical) species, there is no visible differentiation between heart- and sapwood, as used or referred to in Thomas and Martin (2012). Subsamples were ground to fine homogenous powder using a mixer mill (Retsch MM 400, Haan, Germany).

For the EA, 2–3 mg of homogenized sample material was placed in small tin foil recipients which were folded and placed in a CN analyzer (Flash Analyzer, Thermo Scientific, Waltham, Massachusetts, USA) which detects CO_2, N_2, ^{12}C, ^{13}C, ^{14}N, and ^{15}N content. The remaining wood powder samples were used for carbon fraction estimation using the LOI method adapted from Negi et al. (2003). Wood organic carbon was burnt using a muffle furnace at 500°C for 4 h after which the remaining ash weight can be used to extrapolate the carbon fraction.

Data analysis

All statistical analyses were performed using R statistical software (R Core Team 2016). We used the non-parametric Spearman rank test to test for correlation between LOI and EA for carbon content, and for correlation between directly extracted salinity and soil sample salinity.

An ANOVA was performed to test for differences in carbon content and wood specific gravity both between species and between *R. mucronata* components when assumptions of normality (using a Shapiro test) and homoscedasticity (using a Levene's test) were not violated. A non-parametric Kruskal–Wallis test was used when these assumptions were not met. Tukey honestly significant difference (HSD) tests were used to detect contrasts between species. For the within-stem carbon (and nitrogen) content, a two-way ANOVA including species, tissue type, and an interaction was used to test for species-specific differences among stem components.

When evaluating effects of environmental conditions on carbon content and wood specific gravity along the gradient, different strategies were applied. First, a principal component analysis (PCA; with the vegan package, Oksanen et al. 2016) was used to visualize relatedness of variables and to look for combinations of variables that could explain variation. Secondly, simple and polynomial regressions were used to detect trends in variation in wood carbon and wood specific gravity along elevation a.s.l. and directly extracted salinity values. Because the species variable was thought to cause most variation and thereby highly influence these regressions, general linear models including elevation or salinity, species, and an interaction term as predictors were made using the car package (Fox et al. 2016). A significant interaction could indicate species-specific effects. Only the most abundant and broad-ranging species were used for the latter analyses.

RESULTS

Comparison of methods for salinity and carbon fraction determination

A significant negative correlation ($n = 50$, Spearman $\rho = -0.34$, $P = 0.02$) was found between the directly extracted salinity and soil sample salinity methods. Both carbon fraction methods, EA and LOI, performed on 20 *Avicennia marina* samples were non-significantly positively correlated ($n = 20$, Spearman $\rho = 0.18$, $P = 0.48$).

Interspecific variation in studied wood characteristics

ANOVA tests showed highly significant interspecific differences in carbon fraction ($F = 14.176$, $P < 0.0001$), wood specific gravity ($F = 42.446$, $P < 0.0001$), and carbon stable isotope ratios ($\delta^{13}C$; $F = 4.84$, $P < 0.0001$; Fig. 2). Assumptions were met, except for one single group corresponding with carbon fractions of *A. marina* being not normally distributed (Shapiro test: $P = 0.02$). Appendix S2: Tables S1–S3 provide the output of the Tukey HSD test. Table 1 provides species-specific values of carbon fraction and wood specific gravity. Additionally, a significant correlation was found between: carbon fraction and wood specific gravity ($n = 72$, Spearman $\rho = 0.42$, $P = 0.0002$); directly extracted salinity and $\delta^{13}C$ ($n = 52$, Spearman $\rho = 0.49$, $P = 0.002$); and carbon fraction and $\delta^{13}C$ ($n = 72$, Pearson $\rho = 0.33$, $P = 0.004$; Appendix S1: Fig. S2).

Inter- and intraspecific effects of environmental conditions on studied wood characteristics

The PCA generated two first principal components explaining 42% of the total variation and no consistent trends were detected (Appendix S1: Fig. S3). We then focused on explaining variation in both carbon fraction and wood specific gravity using general linear models on the environmental variables used for the initial hypothesis: elevation a.s.l. and salinity, with a strong preference for elevation a.s.l. because of its robustness compared to salinity (*Discussion*).

General linear models included species, elevation (or salinity), and their interaction as predictors for carbon fraction and wood specific gravity. Only the most abundant and broad-ranging species (i.e., *A. marina*, *Ceriops tagal* and *Rhizophora mucronata*) were included because other species result in small scattered clusters due to their narrow elevational range, making their interpretation irrelevant (Fig. 3). The effect of the species factor on both response variables was highly significant ($P < 0.0001$), confirming the outcome of previous ANOVAs. The effect of the elevation (and salinity) factor was not significant ($P = 0.33$ for carbon fraction, $P = 0.17$ for wood specific gravity), indicating the absence of an overarching effect on mangrove species in general. The interaction term was only significant for the carbon fraction ($n = 28$, $F = 5.736$, $P = 0.009$), suggesting a species-specific effect of elevation. Interaction terms were not significant ($P = 0.12$ for carbon fraction, $P = 0.48$ for wood specific gravity) when substituting elevation with salinity.

Variation in studied wood characteristics among tree components in Rhizophora mucronata

Carbon fraction and wood specific gravity differed significantly among *R. mucronata* tree components (branch, root, stem; Fig. 4). For the carbon fraction, we used a Kruskal–Wallis test ($n = 30$, $\chi^2 = 18.263$, $P = 0.0001$) because the root replicates were not normally distributed (Shapiro $P = 0.02$). A pairwise *t* test comparison with Holm correction indicated contrasts between tree components while counteracting the problem of multiple comparisons. Significant differences in wood specific gravity were found between all components using an ANOVA followed by a Tukey HSD test ($n = 30$, $F = 26.570$, $P < 0.0001$).

Variation in studied wood characteristics among stem tissues from Avicennia marina, Ceriops tagal *and* Rhizophora mucronata

A two-way ANOVA indicated significant differences between species ($n = 45$, $F = 4.866$, $P = 0.013$; Fig. 5), but neither the tissue parameter ($P = 0.30$) nor the interaction ($P = 0.44$) were significant.

DISCUSSION

Comparison of methods for carbon and salinity measurements

The two different methods of carbon content determination which were tested, the LOI

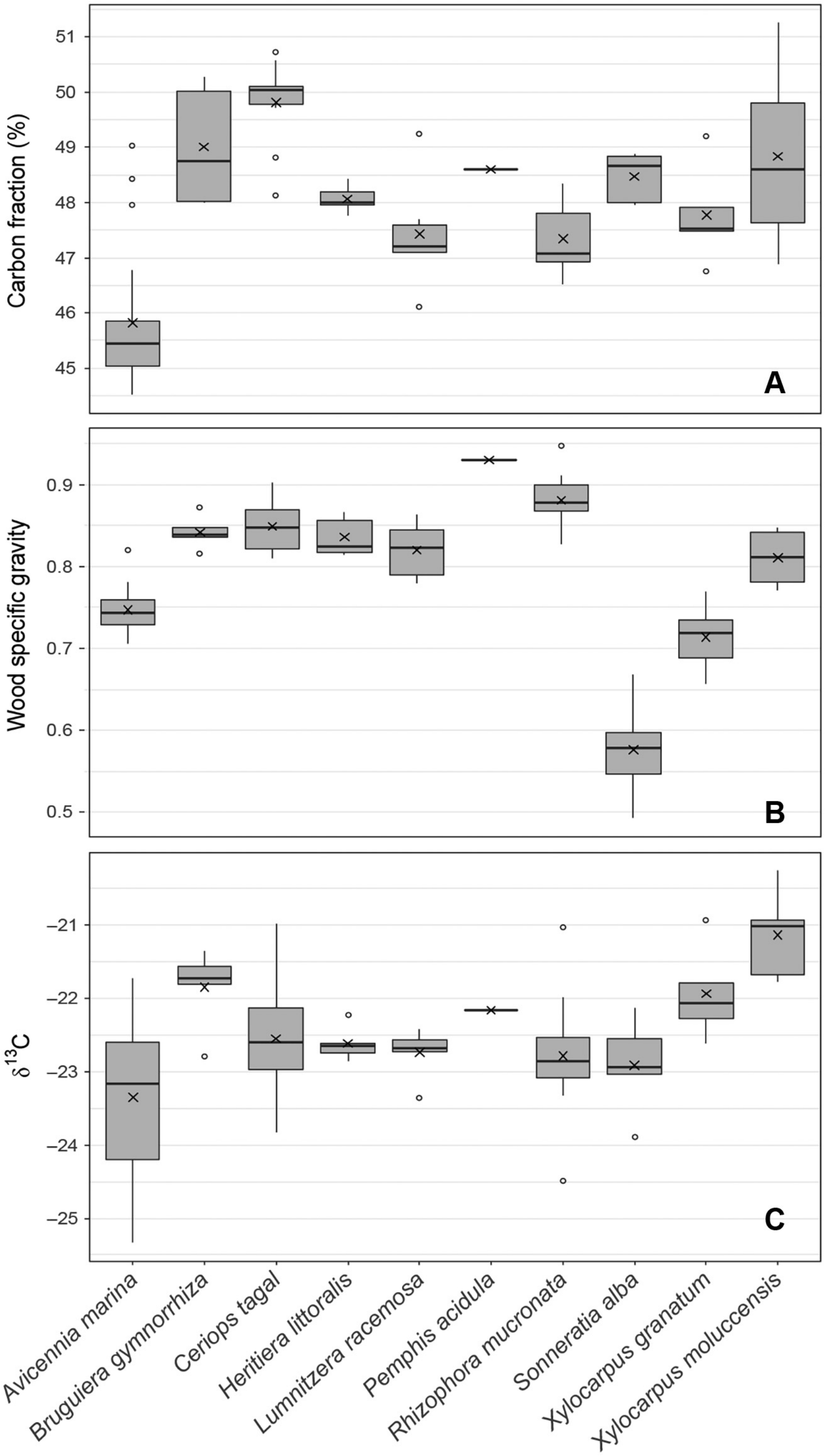

Fig. 2. Boxplots illustrating species-specific values in (A) carbon fraction (% of dry weight), (B) wood specific

(Fig. 2. *Continued*)
gravity, and (C) isotopic composition (δ^{13}C in ‰). Thick horizontal bars represent group medians, crosses represent means, and the whiskers extend until the lowest/highest value still within 1.5 IQR of the lower/upper quartile. ANOVA tests showed significant differences between species (see Appendix S2: Tables S1–S3 for Tukey HSD test outputs). The number of replicates per groups is as in Table 1.

method and EA, correlated very poorly ($\rho = 0.26$, $P = 0.29$). Furthermore, the LOI led to a much higher carbon content of *Avicennia marina* as compared to EA (resp. 50.82% and 45.82%). In contrast, E. Vlaminck (*unpublished results*) found a significant underestimation of LOI (44.99%) compared to EA (47.51%) for *A. marina*, *Rhizophora mucronata* and *Sonneratia alba* taken together, but also a similar weak positive correlation ($\rho = 0.48$, $P < 0.001$) for methods expected to yield identical results. Variation between methods could be explained by multiple factors related to the LOI procedure. It was shown that relative ash weight resulting from LOI is influenced by sample item size, exposure time, and the position of crucibles in the furnace (Heiri et al. 2001). Actual, albeit small, differences in carbon content could therefore be confounded because of the LOI procedure. Based on this study's data and the fact that EA is more commonly used in literature (Mitra et al. 2011, Thomas and Martin 2012, Jones and O'Hara 2016), EA should be strongly preferred for carbon content analysis. Although LOI is cheaper and easier to perform, which is especially important in countries with constraints as to equipment, it is also less reliable.

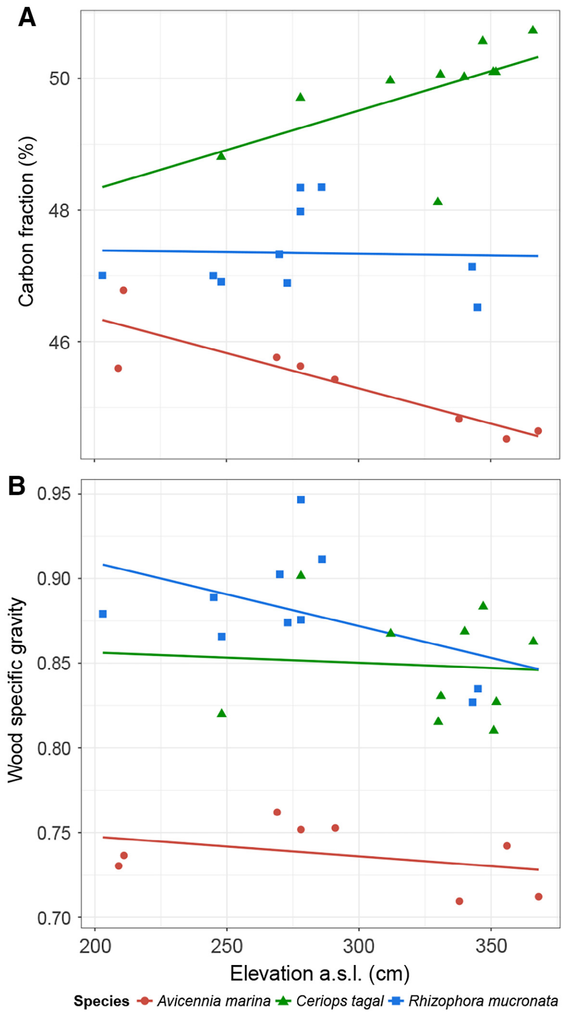

Fig. 3. The effect of elevation above sea level (a.s.l.) on (A) carbon fraction (% of dry weight) and (B) wood specific gravity for the species with the broadest elevational range; *Avicennia marina* (red dots), *Ceriops tagal* (green triangles), and *Rhizophora mucronata* (blue squares) with indication of the respective regression lines.

The two different salinity measurement methods, soil sample salinity and directly extracted salinity, are unexpectedly negatively correlated ($\rho = -0.34$, $P = 0.02$). However, soil sample salinity is suspected to be very dependent on soil type (i.e. organic or mineral/sandy) because organic soils proportionally hold more saltwater than mineral/salty substrates on a weight basis. Relatively more salt will thus remain in the organic soil after oven-drying. Therefore, we only used directly extracted salinity for further analysis, which is thought to directly reflect the interstitial water salinity available for a mangrove and is more frequently used in the literature (Matthijs et al. 1999, Santini et al. 2012). We found an increase in both salinity and variation in salinity around a single tree when proceeding to more landward trees, confirming previous results found in one of the same sites (Matthijs et al. 1999). Sampling in the dry season reflects the most demanding conditions as regards salinity,

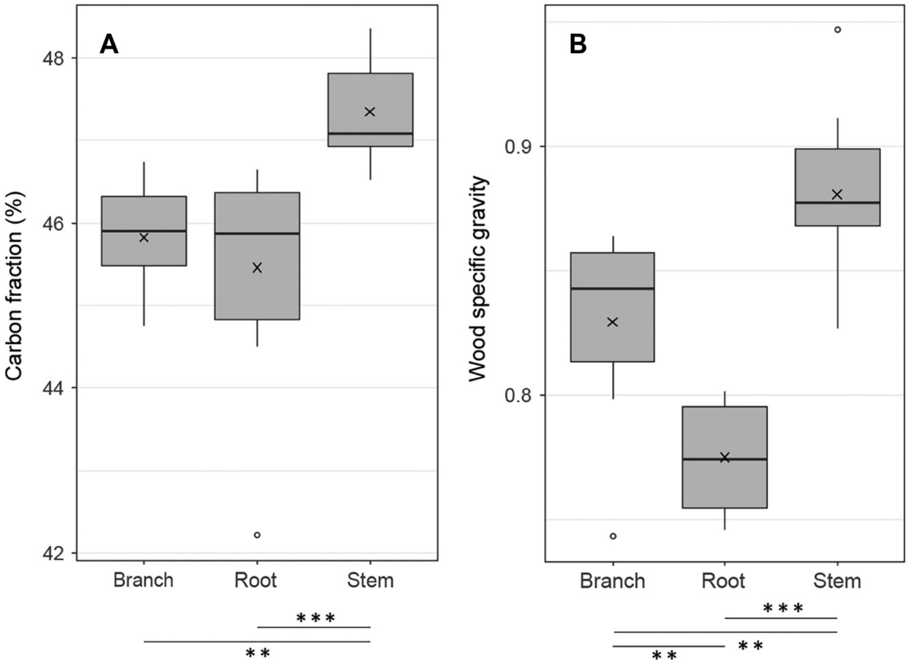

Fig. 4. Boxplots illustrating differences in (A) carbon fraction (% of dry weight) and (B) wood specific gravity among *Rhizophora mucronata* components (branches, roots, and stems). Thick horizontal bars represent group medians, crosses represent means, and the whiskers extend until the lowest/highest value still within 1.5 IQR of the lower/upper quartile. Significance levels are denoted as follows: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

the wood record of its effect covers however various seasons and integrates site conditions. Salinity is an important variable as it has been shown to cause stunted growth of mangroves, influencing the vessel density and leading to decreased biomass and carbon storage (Schmitz et al. 2006, Mitra et al. 2011). However, because salinity is a punctual measurement and thus dependent on the season and the moment of extraction between two tides (Schmitz et al. 2006), elevation a.s.l. was also included and preferred as a main predictor for analyses. Although both are indirectly related, elevation also contains more information as it can be considered a composite proxy for multiple interrelated environmental conditions including flooding regime, soil redox potential, and sulfide concentration (Matthijs et al. 1999).

Variation in carbon fraction and wood specific gravity

Interspecific variation.—We studied variation in carbon content of mangroves along environmental conditions and among species to determine the main factors influencing its sequestration. The species factor was shown to be the most important source of variation with substantial differences in carbon fraction (from 45.8% in *A. marina* to 49.8% in *Ceriops tagal*) and high differences in wood specific gravity (from 0.53 in *S. alba* to 0.93 in *Pemphis acidula*). Large differences in carbon fractions are not surprising, as a review from Thomas and Martin (2012) listed values ranging from 41.9% to 51.6% based on 134 tropical species, and values ranging from 44.4% (*Laguncularia racemosa*) to 47.1% (*S. alba*) were found in mangrove species specifically (Kauffman et al. 2011, Rodrigues et al. 2014). Thomas and Malczewski (2007) suggest species with high lignin content tend to have higher carbon fractions, which might partially explain found differences. Indeed, different proportions of carbon-containing chemical compounds between species, but also within species and between tissues, lead to varying carbon fractions because compounds themselves differ in carbon content. Lignin has a higher carbon content (63–72% on a mass/mass ratio) than cellulose (42%; Lamlom and Savidge 2006), explaining why lignin-rich trees like conifers tend to have higher carbon fractions (Lamlom and Savidge 2003, Thomas and Martin 2012). Moreover, high lignin content is often found in slow growing species which are, in turn, commonly also denser (Muller-Landau 2004). Thomas and Malczewski (2007) therefore suspected—but did not find—a correlation of carbon fraction with wood density. We however found a significant correlation suggesting denser mangrove wood indeed contains a higher carbon fraction, although no conclusions can be drawn regarding an effect of lignin content as yet.

The large interspecific differences in wood density are common (Chave et al. 2009, Howard et al. 2014, Njana et al. 2016) and are indicative of a species' life history strategy. Low wood densities are commonly associated with fast-growing, early-successional, light-demanding, and/or disturbance-tolerant species (Muller-Landau 2004, Slik et al. 2008, Bastin et al. 2015), which could partly explain patterns found. *S. alba*, for example, has the lightest wood, and is considered to be a pioneer species, colonizing mudflats at the seaward edge of mangrove forests (Friess et al. 2012, Tomlinson 2016). However, opposite patterns have been found in *A. marina*, also a typical pioneering species, where dense wood was found to be associated with fast growth and large tree size (Santini et al. 2012).

Inter- and intraspecific effects of environmental conditions.—Results suggest the existence of a species-specific effect of elevation a.s.l. (as a proxy for inundation regime, soil redox potential and related factors) on the carbon fraction of Gazi Bay's most abundant species (*A. marina, C. tagal,* and *R. mucronata*; Fig. 3). This species-specific effect is most clear in *A. marina*, which has a reduced carbon fraction at higher elevation a.s.l. (regression: $R^2 = 0.79$, $P = 0.003$) while, in contrast, *C. tagal* seems to increase its carbon fraction with elevation ($R^2 = 0.31$, $P > 0.05$). Literature to compare these results with is very scarce. Other studies found neither an effect of tidal frequency (Rodrigues et al. 2014) nor an effect of salinity (E. Vlaminck, *unpublished results*) on carbon fraction in different mangrove species in respectively Brazil and Gazi Bay. As for wood specific gravity, no significant influences of either elevation or salinity were found in this study. It has been shown that vessel density is higher in *R. mucronata* trees growing in saline conditions (Schmitz et al. 2006), but this does not directly determine wood specific gravity. Key factors are rather the total void proportion in wood tissue and especially the proportion of fiber cell walls (Beeckman 2016), indicating a gap in knowledge in explaining variation in mangrove wood density.

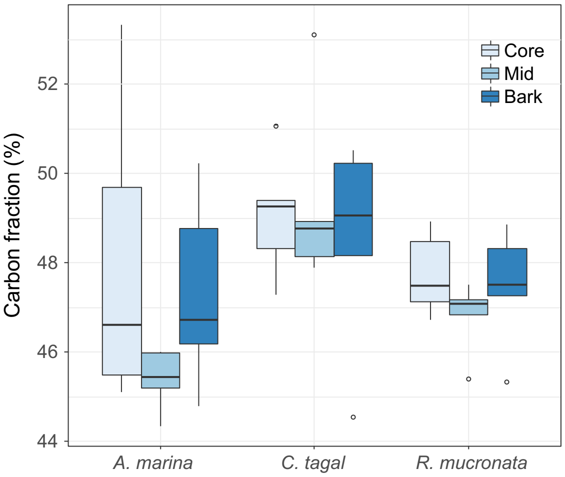

Fig. 5. Boxplot illustrating differences in carbon fraction between species and between tissue types (bark, core, mid). Thick horizontal bars represent group medians, and the whiskers extend until the lowest/highest value still within 1.5 IQR of the lower/upper quartile. The bark was put aside for each sample, after which the remaining wedge was radially divided in half, the core tissue corresponding with the pith of the tree and the mid-tissue corresponding with the wood situated between the core and bark samples. *A. marina*, *Avicennia marina*; *C. tagal*, *Ceriops tagal*; *R. mucronata*, *Rhizophora mucronata*.

Although our results suggest that there is an influence of factors related to elevation on the carbon fraction, the generally weak correlation to salinity and presumed species-specific responses which are dissimilar and contrasting for two widely occurring species *A. marina* and *C. tagal* should incite further research. Finally, it is important to note that small variations in carbon fraction caused by studied conditions are overshadowed by interspecific variation found in carbon fraction and especially wood specific gravity.

To further look into potential environmental influence, stable isotope ratios of carbon were used because they can be considered as a proxy for water use efficiency or, in other words, soil water availability to the growing tree. An increased $\delta^{13}C$ corresponds with less discrimination against heavy ^{13}C isotopes, which can occur when stomata close as a response to limited water availability (Farquhar et al. 1989, Galle et al. 2012) or increased salinity stress (Ball and Farquhar 1984, Verheyden et al. 2004). The present study's results indicate not only significant differences in $\delta^{13}C$ between species, but also a significant correlation between salinity and $\delta^{13}C$, supporting aforementioned studies. Moreover, although a significant correlation between carbon fraction and $\delta^{13}C$ was also found, extensive analyses failed to show a consistent relationship between salinity and carbon fraction. Altogether, this could indicate that trees are indeed experiencing salinity stress, but that this does not have an effect on the carbon fraction.

Variation among tree components in Rhizophora mucronata.—Results show significant within species variation at the organ level in *R. mucronata*. Similar to variation among species, wood specific gravity again accounts for the largest variation in carbon per biomass volume (relative differences up to 16% between root and stem). In accordance with the literature, we found both wood specific gravity and carbon fraction to be higher in the stem as compared to branches (Swenson and Enquist 2008) and roots (Chave et al. 2009, Rodrigues et al. 2014). But because the proportion of root biomass can be particularly high in mangroves (Komiyama et al. 2008), a lower wood specific gravity and carbon fraction could lead to biased figures if stem values are used for the whole tree volume-to-carbon conversion. A study in Gazi Bay even suggests that root biomass (38.64%) can surpass stem biomass (36.13%) in *R. mucronata* (Kirui et al. 2006). Because this prominent root proportion has been shown to vary significantly with environmental conditions like salinity and stand density (Adame et al. 2017), an error is generated even when using species-specific allometric equations. Equations that have been developed using mangrove trees growing under a wide array of conditions might minimize the bias because wood specific gravity is indirectly included through weighing of dry wood mass when developing equations. Differences in carbon fraction among tree components are however usually not accounted for but, ideally, they should be included in calculations as a conversion factor for obtained component-specific biomass (Rodrigues et al. 2014).

Variation among stem tissues in Avicennia marina, Ceriops tagal, *and* Rhizophora mucronata.—Carbon fractions do not differ significantly within the stem of *A. marina*, *C. tagal,* and *R. mucronata*, the Bay's most abundant species. This is fortunate regarding the complexity of carbon stock calculations. Negi et al. (2003) however found consistently lower carbon fractions in bark tissue of eudicotyledonous evergreen eudicots compared to inner stem wood (resp. 38.35% ± 5.82% and 44.91% ± 0.89% for 13 species). Hossain et al. (2016) found a similar trend in the mangrove species *Kandelia candel*. However, opposite results have also been found; a lower carbon fraction in stem wood compared to stem bark in the mangrove *Kandelia obovata* (Khan et al. 2007) and an increasing carbon fraction from pith to bark in the sugar maple (*Acer saccharum*; Lamlom and Savidge 2006). This indicates that inconsistencies in intra-stem variability could be species-specific (Thomas and Martin 2012), although bark is nonetheless expected to have a higher carbon fraction because of its higher lignin content (Jones and O'Hara 2016).

Subsamples were too small for reliable density calculations, so the magnitude of variation in wood specific gravity within the stem remains unknown. Yet, it is known that species-specific trends in wood density from pith-to-bark exist in tropical (Bastin et al. 2015) as well as temperate species (Woodcock and Shier 2002) and are related to the tree life strategy (shade-bearing vs. light-demanding). Fortunately, intra-stem variation only accounts for minor differences that do not introduce a significant bias in carbon accounting (Bastin et al. 2015).

Implications for carbon stock assessments

Carbon stock assessments suffer from multiple sources of error generated by different accounting levels; from assessing stand density, to tree biomass calculation and the considered wood specific gravity and carbon fraction. Although the largest error is caused by uncertainties related to the selection of allometric models (Chave et al. 2014, Bastin et al. 2015), nonspecific carbon fractions (Thomas and Martin 2012, Rodrigues et al. 2014) and wood densities in particular (Komiyama et al. 2005, Feldpausch et al. 2012, Bastin et al. 2015) represent a source of error which may be propagated throughout consecutive calculations. More accurate carbon fractions (which serve as conversion factors in biomass-to-carbon calculations) could become increasingly important in the near future as better volumetric biomass assessments are developing. As an example, recent remote sensing techniques like airborne laser scanning are evolving and can provide accurate wood volume estimations (Dalponte and Coomes 2016, Lee et al. 2017). In mangroves specifically, canopy height, $D_{130,}$ and above-ground biomass were predicted using remote sensing, which could represent great opportunities to estimate biomass in a non-destructive way (Fatoyinbo and Simard 2013, Cougo et al. 2015).

A standard carbon fraction value (45.1%) for carbon stock assessments is provided by the IPCC for mangrove above-ground biomass (Hiraishi et al. 2014). Thomas and Martin (2012) however show that a large variation exists in carbon fractions among tree species globally, that they have been understudied, and that the incorporation of species-specific fractions could reduce the error associated with biomass-to-carbon conversions by 2.5–3.7%. The potential importance of volatile carbon components in avoiding carbon stock underestimation has also been stressed (Lamlom and Savidge 2003, Thomas and Martin 2012, Jones and O'Hara 2016). A small-scale experiment on these volatile components was set up according to Thomas and Martin (2012), but differences appeared erratic and unreliable. Similar to global depositories for wood densities like the Global Wood Density database (Zanne et al. 2009), Thomas and Martin (2012) advocate the creation of a carbon fraction database. While a database has been created based on their literature review, it does not yet include any of this study's mangrove species, which are very wide ranging and abundant. Carbon fractions have only been determined for *Bruguiera gymnorrhiza* (46.3%) and *S. alba* (47.1%) in Micronesian mangrove forests (Kauffman et al. 2011). They do not correspond with this study's findings (resp. 49.0% and 48.5%), suggesting an important site-specific influence on carbon fractions.

In Gazi Bay, carbon stocks are currently calculated using general allometric equations created based on 6 out of 10 mangrove species occurring in Kenya (Komiyama et al. 2005). The equations include D_{130}, tree height (H), and wood density (ρ) as parameters. General wood density values for 7 out of 10 species are provided by the guidelines for coastal blue carbon assessments by Howard et al. (2014). However, it has repeatedly been shown that not incorporating site-specific wood densities, from, for example, global depositories, can lead to significant errors in carbon accounting (Muller-Landau 2004, Komiyama et al. 2005, Kairo et al. 2009, Njana et al. 2016). As an example, Santini et al. (2012) found a higher average wood density in Western Australia than in New Zealand for *A. marina* and even differences between the seaward fringing forests compared to landward stands. Likewise, values provided by Howard et al. (2014) differ considerably from our results, possibly because of site dependency. We therefore suggest using this study's values for both wood specific gravity and carbon fraction for Gazi Bay (provided in Table 1), since trees from all 10 mangrove species occurring in Kenya were sampled there at five different spread-out locations and should thus represent reliable values for the whole forest (Fig. 1). When looking within the site, the elevation of a tree above sea level was found to cause variation in carbon fraction. However, because the largest differences never exceeded 2% and because effects appear species-specific, we suggest to not take these effects into account for the sake of reducing the complexity of calculations and not to include them in planting or reforestation guidelines. Furthermore, relative errors propagated through unspecific allometric equations and unspecific wood densities are still of much greater magnitude and overshadow these small differences in carbon fraction caused by the environment. If future studies are considered to increase the precision of accounting even further, the emphasis should be placed on measuring wood densities values with more replicates over the whole Bay. Fortunately, Bastin et al. (2015) claim that taking small wood samples, 2 cm under the bark can provide accurate density values while avoiding the damage a tree suffers when extracting a full radial profile.

This study's results could benefit future management strategies in Gazi Bay as large differences in carbon densities (i.e., amount of carbon in a given volume of wood in tC/m^3) are apparent. For example, *S. alba* is the only species used for the present annual mangrove replantation in Gazi Bay (Huxham 2013) but appears to contain much less carbon (0.28 tC/m^3) than other abundant species like *R. mucronata* and *C. tagal* (respectively, 0.42 and 0.425 tC/m^3) for an equal volume of biomass. Focusing on *S. alba* replanting is therefore not necessarily the best management decision if only considering the purpose of carbon offsetting on a volume basis. This is however without including its growth rate, stand density, and other non-carbon benefits like coastal protection. Indeed, in the case of the carbon offsetting project Mikoko Pamoja, *S. alba* was chosen because of its tolerance to exposed conditions in order to prevent further erosion of an already degraded beach front (Huxham 2013, Tomlinson 2016). It is also a fast-growing species (Imai et al. 2009). Previous plantations in the context of Mikoko Pamoja include a monospecific *R. mucronata* stand and a young *A. marina* stand, which represent a better choice for management solely considering the amount of carbon per volume. To summarize, both non-carbon benefits and carbon sequestration potential should therefore be integrated in management decisions.

CONCLUSION

Significant sources of variation were found in carbon fraction and wood specific gravity, potentially having important influences on carbon accounting. Substantial interspecific differences in both carbon fraction and wood specific gravity were found and diverge from values found in databases, therefore suggesting the preferential usage of species and site-specific values for carbon accounting whenever possible. An effect of environmental conditions was found but shown to be species-specific and moderate. Furthermore, considerable differences in carbon density were found between stem, roots, and branches of *Rhizophora mucronata* but not within the stem of *Avicennia marina, Ceriops tagal,* and *R. mucronata*. The data gathered in this study could serve to increase carbon accounting accuracy in Gazi Bay and possibly in similar sites of the Western Indian Ocean, important in the sale of carbon credits which is a part of the local community's income. Besides their potential to increase carbon accounting accuracy, results could help to guide future management decisions with regard to the selection of the most carbon-rich mangrove species, balancing against all other aspects of system-wide C sequestration. It is therefore also an important factor for local incentive to safeguard and protect mangrove forests while serving as an important exemplary project for others to follow.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2306/full