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RESEARCH ARTICLE

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Mangrove diversity enhances plant biomass production and carbon storage in Hainan island, China

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Abstract

1. Mangrove forests, one of the highest carbon density ecosystems, are very different from other forests as they occupy saline and tidal habitats. Although previous studies in forests, shrublands and grasslands have shown a positive effect of biodiversity on plant biomass and carbon storage, it remains unclear whether this relation to biodiversity also exists in mangrove forests.
2. Here, we evaluate the possible effects of mangrove species diversity, structural characteristics and environmental factors on mangrove biomass production and carbon storage, using survey data from 234 field plots of 30 transects in the mangrove forests along the coastlines of Hainan Island, China, during 2017 and 2018.
3. We found that mangrove species diversity had a positive effect, not only on mangrove biomass production but also on soil carbon storage. This positive effect was more strongly evident in the forest communities than in either the shrub communities or forest-shrub mixed communities, with the forest type having the biggest mangrove biodiversity and carbon storage. Besides, the diversity effect was affected by structural characteristics, namely, mangrove biomass increased exponentially with tree stem diameter and decreased with tree density. Furthermore, we observed a resource-dependent mediation of the mangrove ecosystem when linking diversity to biomass. The areas with high soil Nitrogen content and Mean annual precipitation (MAP) showed higher mangrove biomass and carbon storage. This suggests that the spatial pattern of mangrove carbon storage and diversity was driven by both climate factors (MAP) and soil fertility (soil N).
4. To our knowledge, this is the first study based on an intensive field survey that has verified the positive effect of biodiversity on mangrove biomass and carbon storage. Our findings suggest that mangrove forests with greater diversity also have higher carbon storage capacities and conservation potential. Thus, biodiversity conservation is crucial for mangroves to mitigate the greenhouse effect.

Our findings strengthen the understanding of the diversity effects on mangrove ecosystem services and have important implications for mangrove restoration and conservation.

KEYWORDS

biodiversity, biomass, carbon storage, environmental factor, Hainan Island, mangrove forest, restoration, structural factor

1 | INTRODUCTION

Mangrove forests consist of unique bionetworks of halophytic trees, shrubs and other woody plants growing in the tidal zone of tropical and subtropical coastlines. Mangrove forests are one of the most carbon-dense density forest ecosystems, due to the mangrove's high biomass and slow decomposition rate in the anaerobic environment. They are thus considered to be one of the most important blue carbon ecosystems (Alongi, 2014; Donato et al., 2011). Generally, the carbon storage in mangrove forests (often over 1,000 Mg C/ha) is several times that of other tropical forests (about 300 Mg C/ha on average; Alongi, 2012; Kauffman & Donato, 2012). Furthermore, mangrove wetlands provide numerous ecological services and functions (e.g. marine animal breeding habitats, water purification, harvestable forest products, coastal protection, etc.) that amount to billions of dollars (Duke et al., 2007; Lee et al., 2014; Lovelock & Duarte, 2019). Because of their high carbon sequestration capacity, studies of mangrove ecosystems have increased rapidly world-wide in the last two decades, most of which have focused on assessments of mangrove biomass carbon storage, soil carbon storage and dynamic changes in mangrove area and carbon storage (Atwood et al., 2017; Doughty et al., 2016; Hutchison et al., 2014; Rovai et al., 2018). Nevertheless, the factors related to carbon storage in mangrove forests are still poorly understood. In particular, we have a poor understanding of the relationships between mangrove diversity, environmental factors and mangrove biomass, which has severely limited our ability to assess the values of both mangrove forest carbon storage and biodiversity for conservation.

Biodiversity plays an important role in maintaining function and service within ecosystems and high diversity has been well-documented to accelerate plant growth, thereby enhancing carbon sequestration (Duffy, 2009; Isbell et al., 2015). The mechanisms by which plant diversity regulates plant productivity have been much debated. Studies of diversity–productivity relationships (DPRs) have been conducted in various ecosystems over the last two decades, including tropical forests (Poorter et al., 2015), temperate forests (Chisholm et al., 2013) and grasslands (Fraser et al., 2015). These studies found that species richness has a consistently positive effect on plant productivity. Chen, et al., synthesized data from 6,098 field sites (including forest, shrubland and grassland), and analysed the effects of diversity on above-ground biomass (AB), below-ground biomass (BB) and soil organic carbon (SOC) storage. They found that higher species richness resulted in higher AB and BB, which then enhanced below-ground carbon input and SOC storage (Chen et al., 2018). The enhancement of productivity caused by species richness might result from the niche complementary effect, where species have specific niches, which allow plants to more efficiently use resources, thereby enhancing the biomass production and carbon storage (Turnbull et al., 2013; Yachi & Loreau, 2007). Furthermore, enhanced productivity might also result from the selection effect, wherein the dominant species are selected by chance and contribute to the highest productivity in a community (Loreau & Hector, 2001; Zuppinger-Dingley et al., 2014). It has been shown that plant facilitation depends on plant assemblage and environmental factors, which significantly influence the effect of diversity on productivity (Fichtner et al., 2018; Forrester & Bauhus, 2016).

Although most studies have shown positive effects of biodiversity on productivity, the negative diversity effect on productivity can also be found in some studies (Gherardi & Sala, 2015; Rose & Leuschner, 2012; Wu et al., 2018), especially after disturbance (precipitation, human influences, plant invasion) or under a different time-spatial scale. We questioned what kind of diversity effect was applicable to mangrove ecosystems. Few studies have been conducted to assess the species diversity, biomass and carbon sequestration of mangrove forests (Abino et al., 2014; Joshi & Ghose, 2014; Kristiningrum et al., 2019). However, those studies mainly focused on the species occurrence and carbon storage of mangroves, the interactions among the mangrove diversity, environmental factors, and mangrove carbon storage were still not to estimate. Besides, the soil carbon pool of mangroves was also not to assess in those studies. The soil carbon pool contributes the biggest carbon pool for mangrove forests (60%–90%; Donato et al., 2011; Sasmito et al., 2020), which constitute an essential part to assess the mangrove carbon storage. Furthermore, Mangroves are the only species of tree that can adaptively flourish in highly saline environments (Alongi, 2009); These adaptive mechanisms result in special growth patterns in mangroves that are completely different from other tropical or subtropical forests. We wonder whether a special diversity effect that is different from inland forests exists for mangrove forests.

In this study, we evaluated the possible effects of mangrove diversity, structural characteristics and environmental factors on mangrove biomass production and carbon storage, utilizing data from 234 mangrove forest survey plots established in 30 transects across the coastline of Hainan island, which is the second largest island in China and has the highest mangrove plant biodiversity (26 out of 27 true mangrove species) and carbon storage capacity in China (Li &

Lee, 1997). We also collected data on climate, soil properties and water properties to test the interrelationships among those factors. Our study was designed to address two questions: (a) what are the effects of mangrove diversity on mangrove biomass production and carbon storage and (b) how do the structural variables and the environmental factors affect mangrove biomass production and carbon storage?

2 | MATERIALS AND METHODS

2.1 | Field survey and sampling design

This study was conducted on Hainan Island (Figure 1), which has 4,891 ha of mangrove habitat and represents nearly 20% of the mangrove forest area of China (24,578 ha; Wu et al., 2013). The first National Mangrove Nature Reserve of China, Dongzhai Harbor Mangrove Reserve, was established in Hainan in 1986, and was listed as one of the International Important Wetlands in 1992 (Qiu et al., 2011). Among a total of 27 true mangrove species in China, 26 have been documented in Hainan Island (Li & Lee, 1997). Hainan Island is therefore considered a hotspot for mangrove research and conservation since it has the highest biodiversity and the highest carbon storage capacity of all mangrove forests in China (Liu et al., 2014).

An intensive field survey of mangrove biodiversity and carbon pools was carried out along the entire coastline of Hainan Island in 2017–2018. Before the field survey, all measurement plans, mangrove boundaries and survey area size were defined based on previous field investigations and information in the literature (Dan et al., 2016; Liao & Zhang, 2014; Wu et al., 2013). A total of 234 plots were chosen along 30 transects and in seven study sites out of the four main mangrove regions of Hainan Island (Figure 1). The details of sites and transects are described in Table 1. In each transect, the number of survey plots was determined according to the distance from the seaward edge or the area size of the mangrove forest at each site. For sites with smaller patches of mangrove forests (e.g. distance from seaward to land edge was 60–90 m or the area was 60–120 ha) we selected six plots with three plots each for low and high sections of the transect perpendicular to the coastline. Only three plots parallel to the shoreline were selected for sites where a distance from seaward to land edge was <60 m

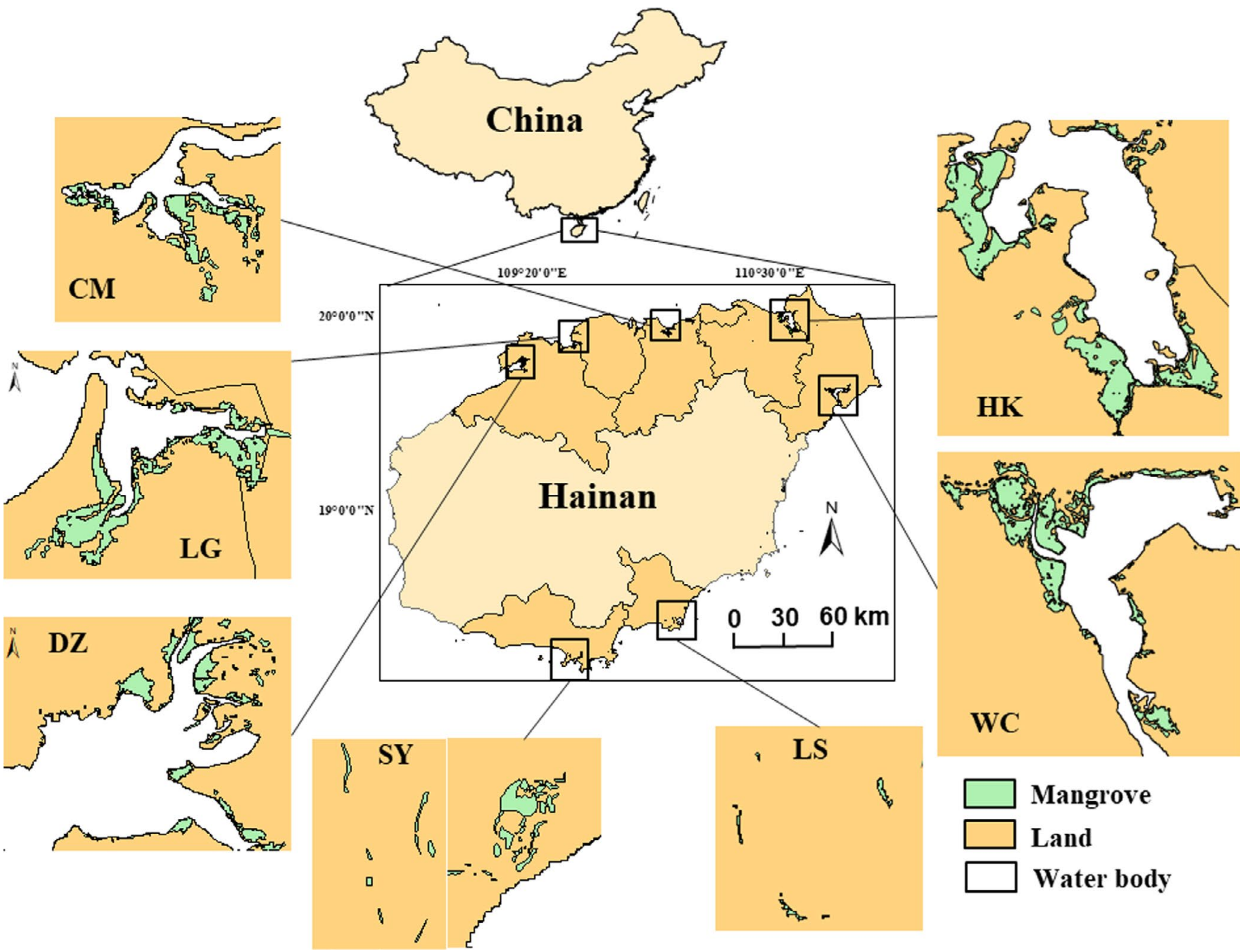

FIGURE 1 Map of mangrove distribution and sampling sites in Hainan Island, China (CM, Chengmai; DZ, Danzhou; HK, Haikou; LG, Lingao; LS, Lingshui; SY, Sanya; WC, Wenchang

TABLE 1 Detailed descriptions of the field survey and sampling locations

Region	Site	Transect	Longitude (E)	Latitude (N)	Number of plots	Geomorphic Setting	Number of species
East	WC (Wenchang)	PG	110°50′17.78″	19°37′37.43″	9	Open Coast	13
		DCA	110°48′46.33″	19°37′07.99″	3	Open Coast	11
		XC	110°47′38.84″	19°37′28.02″	9	Estuary	10
		TY	110°47′28.98″	19°37′39.28″	9	Estuary	15
		XCN	110°47′47.37″	19°36′28.63″	9	Estuary	10
		BK	110°47′26.84″	19°36′55.44″	9	Estuary	13
		HW	110°47′30.27″	19°36′48.40″	9	Estuary	11
		HT	110°47′54.50″	19°35′59.74″	9	Estuary	10
		DJ	110°50′20.79″	19°33′31.70″	9	Estuary	9
North	HK (Haikou)	QS	110°32′36.47″	19°58′28.90″	6	Estuary	8
		WL	110°32′21.45″	20°00′06.13″	3	Estuary	6
		MS	110°32′32.70″	19°59′45.20″	9	Estuary	6
		LL	110°34′53.04″	19°56′23.91″	8	Estuary	8
		DCU	110°33′09.49″	19°58′18.37″	9	Estuary	9
		JW	110°34′59.02″	19°56′16.97″	9	Estuary	4
		HG	110°35′24.37″	19°55′47.41″	9	Estuary	7
		BJ	110°35′40.12″	19°55′10.08″	9	Estuary	9
		NJ	110°32′46.51″	19°58′07.53″	9	Estuary	8
		WLI	110°36′52.55″	19°55′27.10″	9	Estuary	9
		KS	110°37′03.53″	19°55′34.61″	9	Estuary	11
		CW	110°37′53.09″	19°55′43.18″	9	Open Coast	8
South	SY (Sanya)	SYH	109°42′08.22″	18°15′46.77″	3	Estuary	8
		QMG	109°36′59.91″	18°13′21.20″	9	Lagoon	8
		TLG	109°30′16.88″	18°15′32.92″	3	Lagoon	7
	LS (Lingshui)	LS	109°58′55.72″	18°25′48.09″	9	Lagoon	3
Northwest	CM (Chengmai)	FLW	109°59′13.18″	19°54′32.23″	9	Estuary	9
	DZ (Danzhou)	DOC	109°32′57.73″	19°51′20.60″	9	Open Coast	1
		BC	109°32′06.83″	19°51′09.83″	3	Open Coast	4
		HC	109°15′20.75″	19°46′02.97″	9	Lagoon	6
	LG (Lingao)	CQ	109°34′00.27″	19°51′23.27″	7	Estuary	6

or area was <60 ha. All plots were spaced at least 20-m intervals along each transect, and the plot sizes for forest plots were 10 m × 10 m for trees with DBH > 5 cm and Height > 2 m and for shrub plots, they were 2 m × 2 m for mangrove saplings and seedlings with DBH < 5 cm and height < 2 m. The DBH and height of each tree in the plot were measured to determine plot size.

2.2 | Biomass and carbon stock assessment

In each plot, we measured all the diameters of all trees at breast height (DBH), which was generally 130 cm above-ground level for trees and 30 cm above-ground level for shrubs (Kauffman & Donato, 2012). The species, basal diameter, height and live/dead status were recorded at the same time. In the case of many small trees (<5 cm DBH) or shrubs growing together, we set up subplots of 2 m × 2 m to count all plants in the plot. Furthermore, tree density (trees/m^2) also was calculated using survey data from each plot. Both the above-ground and below-ground biomass values of the mangrove forests were estimated based on individual DBH data by species-specific allometric equations (Chave et al., 2005; Kauffman & Cole, 2010; Komiyama et al., 2008; Saenger, 2002; Smith & Whelan, 2006) (see Table S1). If there was no specific allometric equation available for a given species, a common allometric equation (Komiyama et al., 2005) was used to estimate the above- and below-ground biomass.

Biomass carbon storage was calculated using the species-specific carbon concentration (Kauffman et al., 2011). If local or specific values were not available, the standard carbon contents of 47% and 39% were used to assess the above-ground and below-ground biomass carbon storage, respectively, as described by Kauffman and Donato (2012). We also recorded the dead tree basal diameter, height and DBH. Dead status was subcategorized into three classes (fine, medium, rotten) based on the state of decomposition (Solochin et al., 2019). The carbon stock of the dead tree was estimated with the planar intercept method, according to the subcategory (Harmon, 1996).

2.3 | Soil property and carbon pool assessment

Soil samples were collected from all 30 transects using a 5-cm diameter PVC pipe. Due to the heavy manpower requirements for digging soil cores by hand, only 30 soil cores were extracted with one core in the middle portion of all survey plots (3–9 plots) and divided into four layers of the following depth range: 0–20 cm, 20–40 cm, 40–60 cm and >60 cm respectively. If the soil cores were longer than 100 cm, the values of 60–100 cm were applied to the deeper layer (>100 cm). After collection, each soil sample was placed in an oven at 60°C and dried for 48 hr till constant weight; the bulk density was then calculated. Next, soil samples were ground with a mortar and passed through a 2-mm sieve to remove large plant debris. The carbon and nitrogen contents of soil samples were measured using the combustion method (Schumacher, 2002) using a MACRO Cube Elemental Analyzer (Elementar, Germany) in the Stable Isotope Laboratory of Tsinghua Shenzhen International Graduate School. Soil carbon storage was calculated by multiplying the C content with the bulk density. The environmental parameters, including the pH and salinity of both soil and water, were also measured in the field. The pH was measured with a Thermo Scientific A321 pH Portable Meter (Thermo Fisher, USA), whereas water and soil salinity were measured by using the YSI Pro30 Salinity Instrument (YSI Inc, USA) and HM-TY soil salinity instrument (HM Inc, CHN) respectively.

2.4 | Biodiversity index calculations

We calculated multiple indices representing mangrove plant diversity in this study. For each plot and each transect, the number of species and trees was recorded to calculate the Shannon diversity index (Shannon & Weaver, 1998), Simpson diversity index (Simpson, 1949) and species richness (Margalef, 1957).

$$H' = -\sum_{i=1}^{s} p_i \ln(p_i) \quad (1)$$

$$D = 1 - \sum_{i=1}^{s} p_i^2 \quad (2)$$

H' = Shannon diversity, D = Simpson diversity, s = number of species, p_i = proportion of the i species ($p_i = N_i/N$, N_i = amount of i species, N = Total amount of all species). The tree density (trees/m^2) was also computed.

2.5 | Statistical analyses

Plant diversity indices were statistically calculated using the 'VEGAN' package in R. A linear regression model was used to analyse the relationship between mangrove diversity, plant biomass and carbon storage. One-way analysis of variance (ANOVA) was used to evaluate the statistical significance of different plant communities. Mangrove diversity, biomass and carbon stock differences between group means were evaluated with Tukey's honestly significant difference multiple comparison test, where $\alpha = 0.05$ (Murtaugh, 2009). The relationships between plant productivity, plant diversity and environmental parameters were analysed with redundancy analysis (RDA) using CANOCO 4.5 software (ter Braak & Smilauer, 2002). Pearson's correlation analysis was also performed to determine the correlation between carbon storage and soil and plant properties by using the 'CORRPLOT' package in R. The statistical analyses were performed in R 3.6.2 and and graphs were plotted in OriginLab 2018 (OriginLab Corporation).

3 | RESULTS

3.1 | Relationship between mangrove diversity and biomass

Within all plots, the mangrove biomass tended to increase significantly ($p < 0.001$) with the Shannon diversity increasing (Figure 2A).

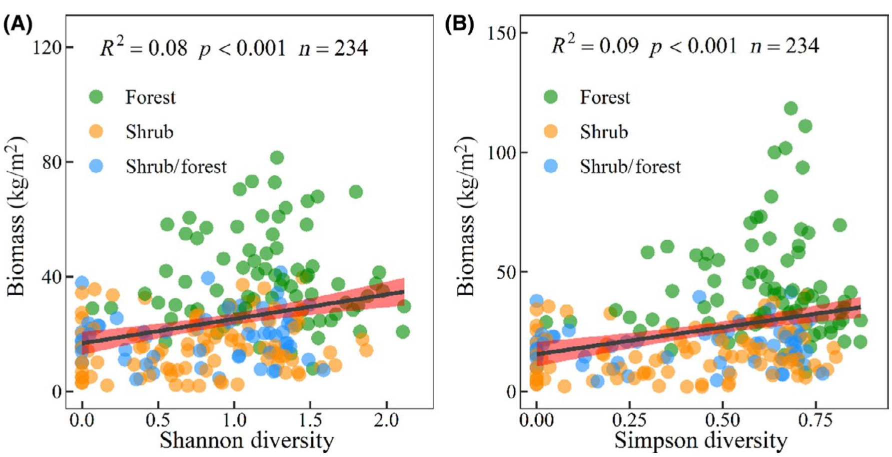

FIGURE 2 Relationship between biomass and Shannon diversity (A) and Simpson diversity (B) for mangrove plants. While the red shadow areas indicate the 95% confidence interval for the fitted line

This trend also existed in the relationship between Simpson diversity and mangrove biomass (Figure 2B). Mangroves in the forest plots had the highest total biomass, which was significantly different ($p < 0.001$) from that of the shrub plots and the forest-shrub mixed plots. There was no significant difference between the shrub plot and the forest-shrub mixed plot (Figure 3A). The forest plots also showed higher plant diversity (1.23 ± 0.43) than the shrub plots (0.77 ± 0.51) or the forest-shrub mixed plots (0.79 ± 0.53; Figure 3B). The biomass of mangroves at the East site was significantly greater (40.84 ± 24.43 kg/m^2, $p < 0.001$) than those of the other three sites (Figure 3C). The lowest biomass (17.67 ± 9.57 kg/m^2) was observed at the South site. Similar to the plant biomass measures, the plant diversity index was also significantly different among sampling sites ($p < 0.001$, Figure 3D). The sites with the highest Shannon diversity index, in descending order were the East (1.37 ± 0.35), North (0.89 ± 0.0.41), South (0.51 ± 0.46) and Northwest sites (0.48 ± 0.54). Within all plots, the mangrove biomass of Estuary (ES) plots was significantly higher than those of Lagoon (LG) and open coast (OP) plots. The mangrove diversity of Estuary plots was also higher than Lagoon plots but not significantly higher than open coast plots. It is worthy pointing out that the significant differences between the east region (where Wenchang site was located) and other three regions were due to the significant difference between Wenchang and other six sites (Figure 3).

3.2 | Relationship between mangrove biomass and structural variables

The total biomass tended to decline sharply with increasing tree density, which was estimated ($R^2 = 0.31$, $p < 0.001$) using an exponential equation (Figure 4A). This kind of trend was also found in the relationship between mean biomass and tree density with a better regression coefficient ($R^2 = 0.66$, $p < 0.001$) than was found for the comparison between total biomass and tree density (Figure 4B). The relationship between mean DBH and total biomass showed a positive ($R^2 = 0.59$, $p < 0.001$) linear effect in all forest types (Figure 4C). However, this positive effect ($R^2 = 0.91$, $p < 0.001$) became nonlinear when comparing mean DBH and mean biomass (Figure 4D). The exponential model was fitted preferably ($R^2 = 0.50$, $p < 0.001$) for mean DBH and tree density (Figure S1). In general, the biomass was positively related to DBH and negatively related to tree density, which may have led to the much greater differences among the different forest types. Compared to shrub types, forest types had a lower tree density, but higher biomass.

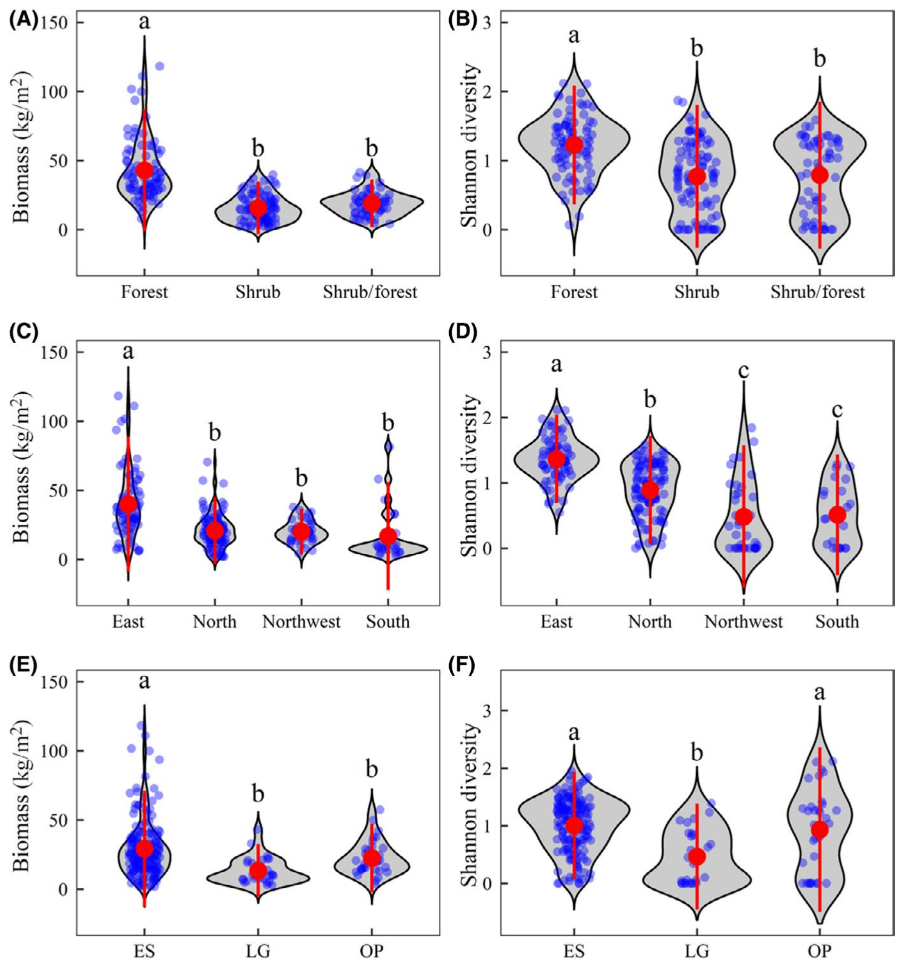

FIGURE 3 Comparisons of total biomass among different forest types (A), sampling sites (C) and hydro-geomorphic setting (E) and the comparisons of Shannon diversity index among plants in different forest types (B), sampling sites (D), and hydro-geomorphic setting (F). Different letters above the bar indicate significant differences ($p < 0.05$) among different sampling sites or forest types. Blue solid circles indicate the observed values, center red bars indicate mean ± *SE*. ES, Estuary; LG, Lagoon; OP; Open coast

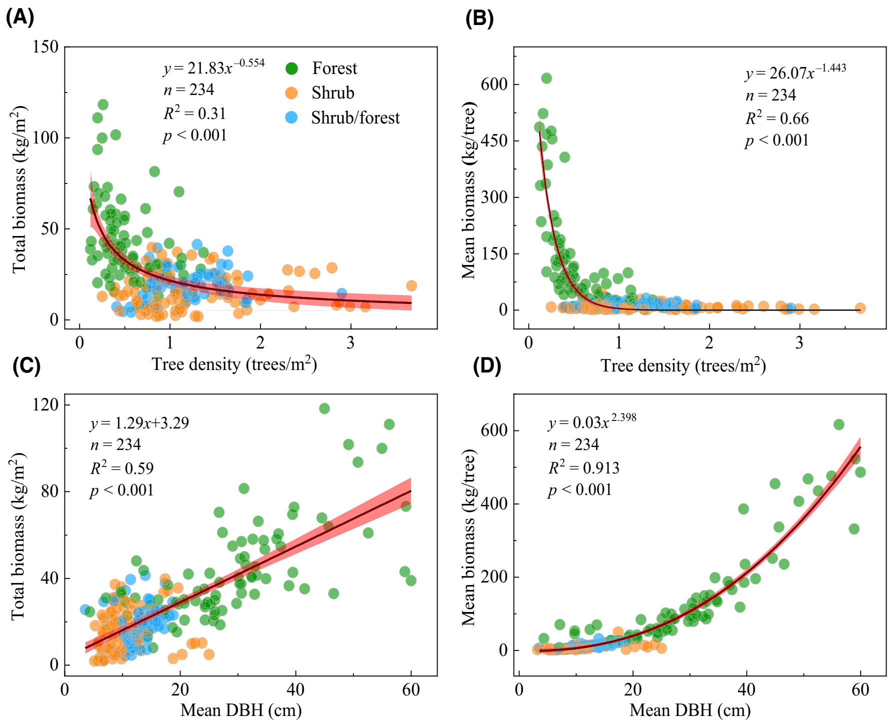

FIGURE 4 Relationship between biomass and mangrove structural variables: total biomass and tree density (A), mean tree biomass and tree density (B), total biomass and mean DBH (C). The solid colored circles indicate different mangrove types: green circles indicate Forest types, orange circles indicate Shrub types, and blue circles indicate Shrub-Forest mixed types. Red shadow areas indicate a 95% confidence interval for the fitted line

3.3 | Relationship between mangrove biomass and environmental variables

A similar distribution pattern was found among total biomass, soil N and soil C in all 30 transects (Figure 5A). Generally, the highest mangrove biomass (75.80 ± 19.74 kg/m^2), soil N content (4.85 ± 0.92 g/kg) and soil C content (126.50 ± 32.10 g/kg) were observed in the East region, while the lowest biomass (3.42 ± 2.83 kg/m^2) was found in the Northwest region. Soil carbon and nitrogen mainly contained in above 40 cm soil cores and above-ground biomass (AGB) constitute the major part of biomass carbon pool. Nevertheless, there were distinct differences among all transects due to the specifics of different mangrove communities. Therefore, a significantly positive linear correlation was fitted between soil N and soil C (R^2 = 0.79, $p < 0.001$) and the total biomass (R^2 = 0.52, $p < 0.001$) (Figure 5B,C).

A redundancy analysis (RDA) diagram was performed to illustrate the relationships between diversity indices, forest structure and other environmental factors (Figure 5D). As the figure shows, the two axes of the RDA totally explain 66.2% of the whole data variability. The first axis accounts for 54.8% of the total data variance. According to the Monte Carlo permutation tests ($p < 0.05$), the biomass of mangroves was positively correlated with soil C ($F = 17.40$, $p = 0.0020$), soil N ($F = 13.29$, $p = 0.0040$), MAP (mean annual precipitation, $F = 12.10$, $p = 0.0042$) and WC (water content, $F = 7.78$, $p = 0.0140$). The second axis (11.5% of data variance) was correlated with water salinity, soil pH, water pH and MAT (mean annual temperature). Positive relationships were observed among the total biomass, diversity and mean DBH, but a negative relationship was seen when factoring in tree density. Furthermore, the mangroves in the East site were the most productive, due to the highest Soil N content, diversity and MAP, while mangroves in the South were mainly influenced by the temperature, which contributed to higher water and soil salinity than at other sites. The mangroves of the North and Northwest sites were smaller and thinner than those at the East sites, which was highly related to the tree density.

The Pearson's correlation analysis indicated that mangrove productivity was positively correlated with diversity, soil N, soil C, water content and MAP, but was negatively correlated with tree density (Figure 6). MAT had a negative effect on water content and soil N content, but positively affected water salinity. The pH and salinity of both water and soil had no significant effect on mangrove biomass accumulation.

3.4 | Relationship between mangrove diversity and carbon storage

A positive diversity effect was observed on both mangrove biomass carbon storage (BC, R^2 = 0.28, $p = 0.002$) and soil carbon storage (SC, R^2 = 0.23, $p = 0.007$) (Figure 7A). A similar significant trend was found in Simpson diversity, but showed a weaker diversity effect on BC (R^2 = 0.20, $p = 0.014$) and SC (R^2 = 0.21, $p = 0.012$) (Figure 7B). Species richness, as a main taxonomic attribute, was shown to have a stronger effect on BC (R^2 = 0.31, $p = 0.001$) and a weaker effect on SC (R^2 = 0.19, $p = 0.015$; Figure 7C). The mangroves in the East (WC) showed the highest carbon storage (537 Mg C/ha) compared to the means of all sites (328 Mg C/ha) and the world mangrove mean value (386 Mg C/ha; Table 2). Despite the high carbon storage of mangroves at WC, the carbon stock was much lower than those of mangroves in equatorial areas (e.g. Indonesia, Malaysia and Brazil) and higher than those of mangroves in temperate areas (e.g. India, the USA and Australia; Table 2).

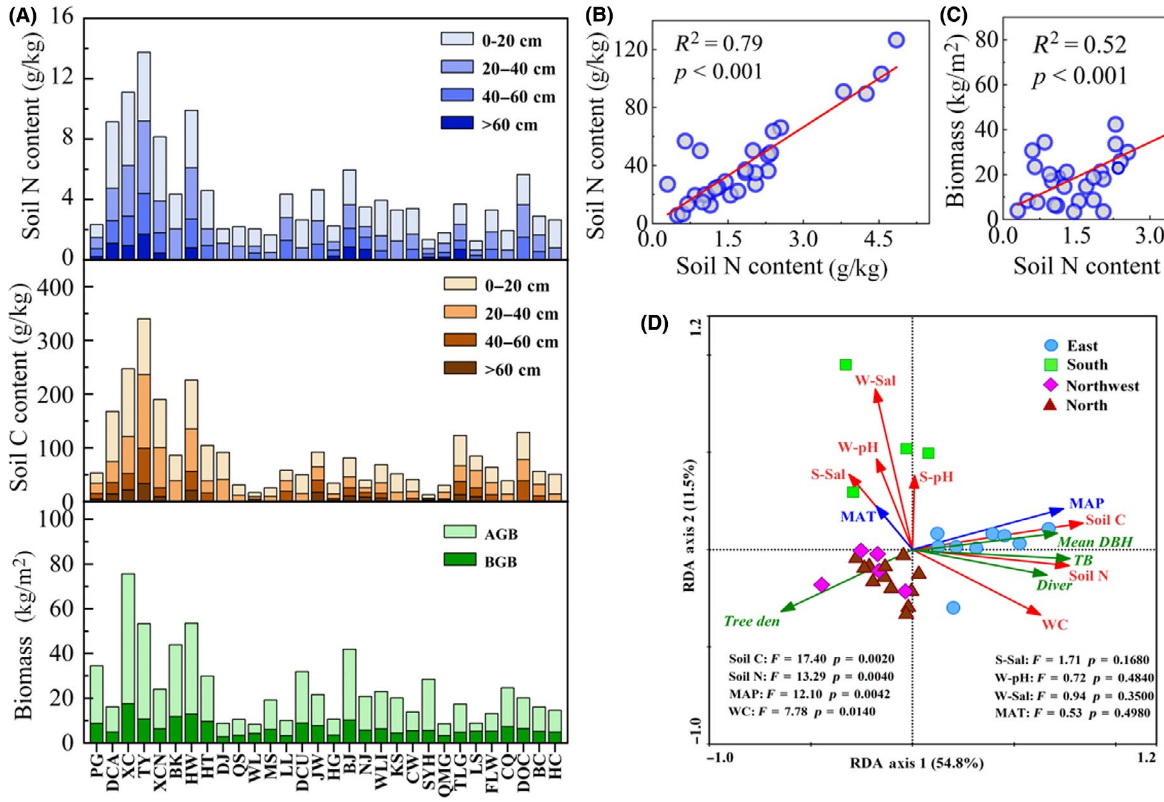

FIGURE 5 The distributions of the biomass, soil N, and soil C in all 30 transects (A), the relationship among soil N, soil C, and biomass (B, C), and the results from the redundancy analysis (RDA) diagram for correlation between total biomass, structural variables (green line), climatic factors (blue line), and ambient environmental variables (red line) (D). Note: AGB, aboveground biomass; BGB, belowground biomass; Diver, diversity index; MAP, mean annual precipitation; MAT, mean annual temperature; S-pH, soil pH; S-Sal, soil salinity; TB, total biomass; Tree den, tree density; WC, water content; W-pH, water pH; W-Sal, water salinity

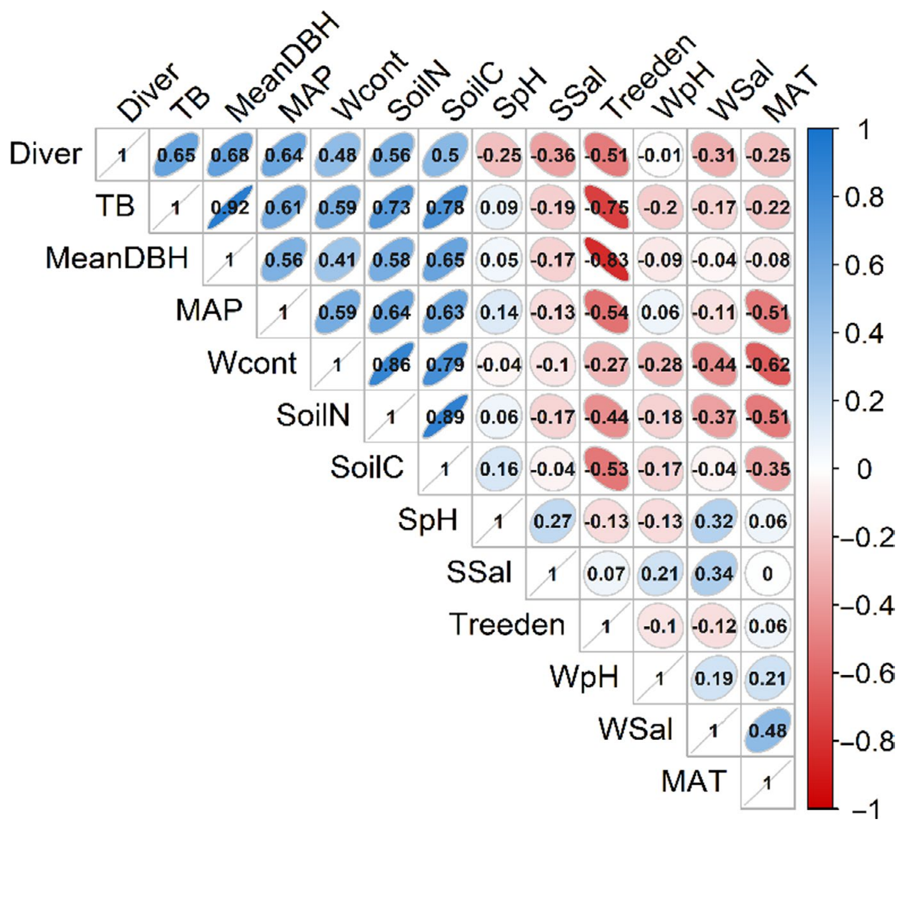

FIGURE 6 Correlation coefficients among soil properties, plant structure, and climatic factors. Circle size and label indicate the Pearson's correlation coefficients from a 2-tailed test of significance

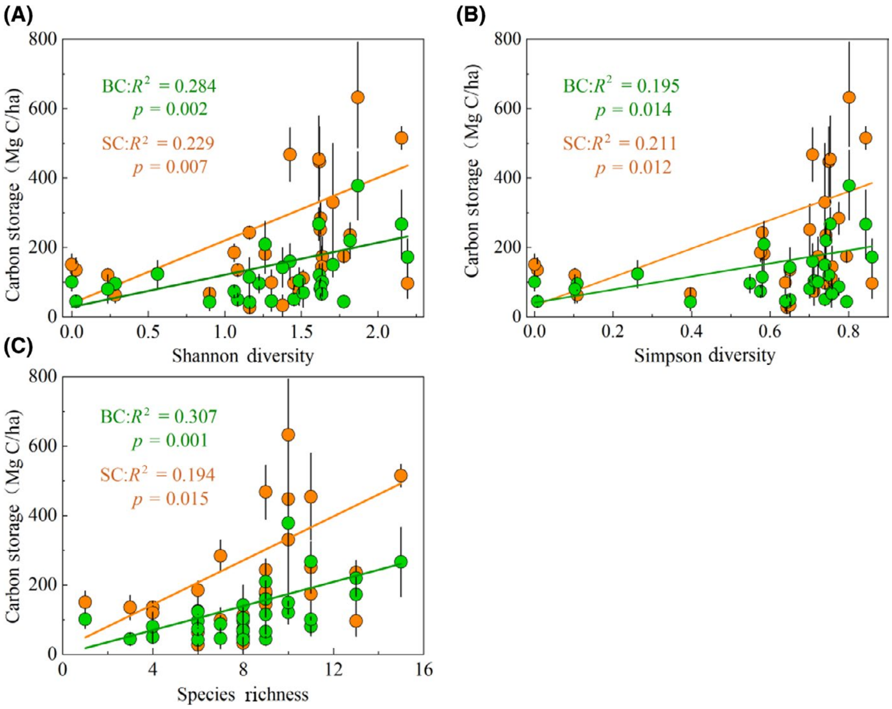

FIGURE 7 Relationship between mangrove carbon storage and mangrove Shannon Diversity (A), Simpson Diversity (B), and Species Richness (C). The solid orange circles and lines indicate soil carbon storage (SC) and fitting line, green indicates biomass carbon storage (BC) and fitting line, error bar (mean ± *SE*)

TABLE 2 Comparison of carbon storage among different mangrove forests in this study and studies from the literature (Mg C/ha). AGBC: Above-ground biomass carbon; BGBC: Below-ground biomass carbon

Site	Latitude	Longitude	Soil C	AGBC	BGBC	Total C	Reference
East, Hainan	110.4728	19.3739	348 ± 175	141 ± 83	47 ± 22	538 ± 261	This study
North, Hainan	110.3453	19.5623	147 ± 116	66 ± 39	28 ± 10	242 ± 152	This study
South, Hainan	109.3659	18.1321	129 ± 111	55 ± 43	23 ± 4	209 ± 113	This study
Northwest, Hainan	109.3206	19.5109	164 ± 54	59 ± 18	28 ± 5	254 ± 59	This study
Bhitankanika, India	20.6998	86.932	102 ± 42	73 ± 29	53 ± 26	229 ± 89	Bhomia et al. (2016)
Tiwoho, Indonesia	1.5864	124.8263	509 ± 70	182 ± 41	25 ± 8	717 ± 128	Cameron et al. (2019)
Matang, Malaysia	4.8383	100.6311	545 ± 277	224 ± 45	89 ± 18	858	Adame et al. (2018)
Florida, USA	25.162	−80.2523	276 ± 63	29 ± 11	16 ± 1	321 ± 73	Jerath et al. (2016)
Ceará, Brazil	−2.5099	−40.0188	603 ± 59	69 ± 2	14 ± 1	687	Kauffman et al. (2018)
New Zealand	−37.6219	176.1421	69 ± 1	20 ± 15	8 ± 6	98	Bulmer et al. (2015)
Pantanos, Mexico	18.353	−92.3411	355 ± 148	122 ± 34	74 ± 17	552	Kauffman et al. (2016)
Hinchinbrook, Australia	−18.2529	146.1131	296	123	52	471	Matsui (1998)
World Mangrove mean						386 (55 ~ 1,376)	IPCC (2014)
World Saltmarsh mean						255 (16 ~ 623)	IPCC (2014)
World Seagrass mean						108 (10 ~ 829)	IPCC (2014)

4 | DISCUSSION

4.1 | Diversity enhances mangrove biomass and carbon storage

Our question was whether or not mangrove plant diversity is related to carbon stock. The field survey data reported here provide direct evidence to support our hypothesis that mangrove biomass is positively related to mangrove plant diversity and species richness, based on theoretical and experiment studies. The positive relationship is observed in both the mangrove biomass carbon pool and the soil carbon pool. Our results are consistent with similar observations in tropical forests (Poorter et al., 2015; Potvin & Gotelli, 2008), grasslands (Fraser et al., 2015; Wang et al., 2019) and shrublands (Chen et al., 2018). Higher diversity results in a more complicated niche composition in the community (complementary effect), therefore providing increased access to available resources (e.g., water, light, nitrogen), thus leading to a more rapid accumulation of mangrove biomass (Forrester & Bauhus, 2016; Turnbull et al., 2013). The positive effects of diversity may also result from selection effect, namely that the highly productive or dominant species contribute the most biomass in a community (Fargione et al., 2007; Loreau & Hector, 2001).

4.2 | Distribution patterns of mangrove carbon storage and diversity

Across the sites, both the highest carbon storage and highest diversity were observed in mangroves of the East region. This was further evidence that mangrove carbon stock is related to mangrove biodiversity in spatial scales. The carbon storage of mangroves at the Wenchang site was much lower than that of mangroves in the tropical zone and significantly higher than that of mangrove forests in the subtropical zone (Table 2). It is likely that carbon storage is closely related to environmental factors; this bio-geographical pattern may be due to the regions possessing higher MAP, and radiation to some degree, and therefore promoting mangrove growth (Osland et al., 2017; Simard et al., 2019). Furthermore, the mean value of Hainan island's C storage (328 Mg C/ha) is close to that of the world mangrove mean value (386 Mg C/ha), but higher than the world saltmarsh mean (255 Mg C/ha) and the world seagrass mean (108 Mg C/ha), which means that there is a huge carbon stock potential in Chinese mangroves.

4.3 | Structural and environmental factors affect mangrove biomass

We also found that mangrove carbon sequestration is strongly driven by other factors, such as plant structural attributes and environmental variables. Mangrove biomass exponentially increases with tree diameter and decreases with tree density, hence, the big trees (forest type) contribute the most significantly to total biomass. This phenomenon has been well demonstrated in a number of studies that demonstrate that tree carbon accumulation increases continuously with tree size; 70% of the variation in biomass was determined by tree size (Stephenson et al., 2014). Assuredly, the largest- and lowest-density trees were found in the East (e.g. WC site), which partially explains why the WC site had the highest carbon storage but the South (SY) had the lowest carbon storage (small trees with high tree density).

As predicted, a positive correlation was found among biomass, soil N and MAP in our results, which means that soil N (nutrient availability) and MAP (water availability) increase the biomass of mangrove on a spatial scale. Generally speaking, mangroves are regarded as a nitrogen-limiting plant community (Reef et al., 2010); nitrogen input provides more nutrients to facilitate mangrove growth. Indeed, we found that mangroves tend to have greater biomass in areas with intensive aquaculture, which is consistent with previous research (Hamilton & Friess, 2018; Sasmito et al., 2019). So, we conclude that the higher biomass may be caused by nitrogen input that come from anthropogenic activities such as aquaculture. Additionally, rainfall plays an important role in the facilitation of mangrove growth, although the magnitude of mangrove growth response to rainfall increase. For example, the addition of non-saline water can reduce salinity stress and increase nutrient availability, which then accelerates mangrove growth (Hayes et al., 2019). Another study by (Simard et al., 2019) showed that precipitation is one of the major factors influencing global mangrove canopy height and carbon stock. Hayes et al. (2019) also found that groundwater and rainfall, are important for the growth and productivity of mangrove forests. These results maybe provide major parameters with which to assess the mangrove carbon stock and diversity at a large spatial and long-term scale.

4.4 | Implications for mangrove restoration and carbon management

Firstly, we found that that mangrove biodiversity has a positive effect on biomass production, indicating that 'multiple-mixed' mangrove species should be planted in the same restoration area, instead of a single species. On one hand, higher diversity increases the amount of carbon storage. On the other, high diversity maintains the ecological function of mangrove communities. Mangrove diversity not only provides habitats for hundreds of species (fish, birds, benthos) but also maintains the stability of the mangrove ecosystem against other disturbing factors (biological invasion, climate change, extreme events; Isbell et al., 2011; Lee et al., 2014). Therefore, mangrove restoration projects should prioritize the co-benefit of mangrove diversity and ecological function.

Our results also indicated that mangrove biomass is not only related to structural factors (diameter, tree density) but is also affected by environmental factors (MAP, soil N). These findings provide major parameters with which to predict the mangrove carbon storage at a large spatial scale. Normally, the assessment of carbon storage is calculated by the allometric equation based on tree DBH. However, the tree DBH is hard to acquire efficiently at a large scale, whereas the MAP, tree density and tree canopy are relatively easily to acquire through remote sensing. Although this study focused only on Hainan island, we believe the relationship we found here should be applicable to other Asian country mangroves because of the similar mangrove species and growing habitats. These results perhaps provide a better assessment of mangrove carbon storage and a better understanding of the geo-distribution pattern of mangrove biomass at larger scales.

5 | CONCLUSIONS

To our knowledge, this is the first study that highlights the relationships between mangrove biomass, carbon storage and mangrove diversity, based on an intensive field survey. Mangrove biodiversity has a positive effect on biomass production and enhances the carbon storage in the mangrove forest. In addition, mangrove biomass is affected by mangrove structural and abiotic factors. These biotic and abiotic relationships can provide a better benchmark to assess and map spatial patterns of mangrove carbon storage over large areas. These results have important implications for mangrove restoration projects, underscoring the fact that restoring plant diversity is crucial for the preservation of ecological function.

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CONFLICTS OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

J.B., G.L. and X.Z. designed the research; J.B., Y.M., R.G., J.L. and Z.D. performed the field survey; and J.B. analysed the data and wrote the manuscript. All authors especially G.L., X.Z., X.D., H.Z. and Y.L. either supported the field surveys and/or contributed to the revisions of manuscript.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.c866t1g5s (Bai et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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