ORIGINAL PAPER

Aboveground carbon stock in a restored neotropical mangrove: influence of management and brachyuran crab assemblage

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Abstract Mangrove forests are important sinks of atmospheric carbon, and the internal deposits and fluxes of organic matter can reflect how these ecosystems respond to disturbances and environmental changes. Data on carbon content of mangrove forests vary geographically due to differences in abiotic (climate, geomorphic settings, tides) and biotic (diversity, herbivory, bioturbation) conditions. Mangroves have been degraded worldwide and ecological restoration is an alternative to recover these ecosystems and their functionality. However, although growing and biomass after disturbances have been addressed, studies on the recovery of faunal groups are rare. The brachyuran crab assemblage is strongly integrated to carbon recycling and ecosystem functioning, since propagule consumption and fossorial activity can affect the diversity and biomass of mangroves. We assessed the aboveground biomass and carbon stock of differently managed mangrove areas in northeastern Brazil, after being deforested for shrimp culture and then abandoned, and compared data with other forests worldwide. After a decade, the area restored with *Rhizophora mangle* showed higher carbon stock than the self-recovered forest and similar amount as an older forest. We discuss the applied rehabilitation measures regarding the effects of management and brachyuran crabs on forest aboveground carbon storage. The effects of herbivory and bioturbation of brachyurans on the low recruitment of *Laguncularia racemosa* propagules, contributed to higher biomass levels in the restored forest through reinforcing the predominance of *R. mangle*, which stocks more aboveground carbon with respect to *Laguncularia.* This suggests that the particularities of target tree species and brachyuran assemblage need to be considered in mangrove restoration, since they are related to function recovering and carbon cycling in the ecosystem.

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Introduction

Mangrove forests cover around 170,600 km^2 of tropical and subtropical coasts worldwide (Lacerda 2002), representing around 0.5% of global coastal areas (Alongi 2014). These forests are significant sinks of atmospheric carbon since stock several times more carbon than the amount found in other terrestrial forests. Indeed, mangroves account for around 3% of carbon sequestering by tropical forests, although they only represent around 1% of them, so contributing significantly in counteract global warming (Donato et al. 2011; Alongi 2014; Bhomia et al. 2016).

Climate change and land-use disturbance can reduce goods and services of tropical mangroves in the next decades (Valiela et al. 2001; Alongi 2002; Twilley 2008). Changes in estuary hydrology and nutrient levels reflect in mangrove growth in terms of biomass, which represents carbon sequestered from the atmosphere. Mangroves are good indicators of these impacts, and as transitional sea-land forests can migrate inland and upper littoral in response to salinity intrusion from ocean level rise, and also from damming and water flux changes (Lacerda and Marins 2002; Lacerda et al. 2007). Aboveground forest biomass is used to assess growth, productivity and potential for the atmospheric carbon intake of mangroves (Ross et al. 2001; Juman 2005; Fonseca 2005; Soares and Schaeffer-Novelli 2005; Medeiros and Sampaio 2008; Camacho et al. 2011; Estrada et al. 2015). The accurate quantification of carbon stock is necessary not only as a baseline for improve knowledge on mangrove nutrient cycles, but also for their inclusion in national and international programs of climate change mitigation (i.e. Reduced Emissions from Deforestation and Degradation, REDD+) (Murdiyarso et al. 2012; Kauffman et al. 2014). However, regional data on biomass are highly variable (DelVecchia et al. 2014; Hutchison et al. 2014; Ferreira et al. 2015). This is result of different tree composition, variations in climate (temperature, rainfall) and geomorphic settings, soils and tides (Krauss et al. 2014; Alongi 2014; Bhomia et al. 2016), and also due to biotic factors like competition for light, tree structure, herbivory, and also macrobenthic diversity (Warren and Underwood 1986; Lee 1999; Cannicci et al. 2008; Ferreira et al. 2013).

Macrobenthic community structure, i.e. species richness and diversity, influences forest ecological

processes (Morrisey et al. 1999, Chapman and Tolhurst 2004; Smith et al. 1991; Kristensen and Alongi 2006). Brachyuran crabs from the superfamilies Ocypodoidea and Grapsoidea (Brachyura: Decapoda) (Ng et al. 2008), are extremely abundant in mangroves, and are 'ecosystem engineers' which play a significant role in topography and biogeochemistry of the sediment, and in plant diversity, structure and biomass (Warren and Underwood 1986; Robertson and Daniel 1989; Kristensen and Kostka 2005; Kristensen 2008). Brachyurans can influence type and structure of the mangrove forest by herbivory, such as consumption of specific propagule types (Smith et al. 1989; McKee 1995a; McGuiness 1997b; Sousa and Mitchell 1999; Bosire et al. 2005; Van Nedervelde et al. 2015). In East Africa, herbivorous crabs like Sesarmids (Grapsoidea) consume more *Ceriops tagal* and *Bruguiera gymnorhiza* propagules than *Rhizophora mucronata* (Bosire et al. 2004, 2005). In Neotropics, ecologically similar Grapsoids prefer to feed on propagules of *Avicennia schaueriana* and *Laguncularia racemosa* over *Rhizophora mangle*, oppositely to Ocypodoid *Ucides cordatus* (Smith et al. 1989; Delgado et al. 2001; Nordhaus 2003; Ferreira et al. 2013). On the other hand, large burrows and high crab populations can influence mangrove soils by burrowing activity and consequent sediment turnover (Warren and Underwood 1986). Some mangrove propagules like *Rhizophora mucronata, R. apiculata, Avicennia officinalis, A. germinans, A. schaueriana* and *L. racemosa,* can be affected by sediment burial (Terrados et al. 1997; Delgado et al. 2001; Thampanya et al. 2002; Ferreira et al. 2013). Smaller propagules like Neotropical *L. racemosa* and *A. germinans* cannot resist 2–3 cm of permanent burial (Delgado et al. 2001), so can be more affected by sediment extracted from crab burrowing. Considering different tree species stock different amounts of carbon (Ray et al. 2011; Rodrigues et al. 2014; Ferreira et al. 2015), herbivory and bioturbation behaviors of crabs could influence biomass stock at trees, and rates of atmospheric carbon intake of the forest could be in part a function of brachyuran assemblage composition and their effect on seedling recruitment aboveground.

Conversion into aquaculture ponds, overexploitation, human occupation through agriculture, salt production, and other factors, have destroyed at least 35% of mangroves worldwide, despite their important

ecological and social roles as fishing resources, biodiversity reservoirs, and in coastal protection (Barbier et al. 1997; Valiela et al. 2001; Alongi 2002; Lugo 2002; Manson et al. 2005; McLeod and Salm 2006). The ecological restoration is a powerful tool for reconstructing degraded mangroves worldwide (Hong, 1996; Macintosh et al. 2002; SER 2004; Ferreira et al. 2007; Lewis 2005, 2009). It can minimize greenhouse effect promoted by mangrove clearing (Alongi 2014; Bhomia et al. 2016). However, despite countless mangrove areas reforested worldwide, there are still few long-term data, in particular at Neotropics, on changes in tree biomass after disturbances, as well as on the relation of these changes with key faunal groups diversity and their life habits (Zimmer 2018; see Ferreira et al. 2015). These data are fundamental for the design of more specific and ecologically functional restoration measures.

In a long term reforestation program of a mangrove stand in northeastern Brazil, two deforested areas were managed and compared since 2006; one planted with *R. mangle* and the other left to recuperate by itself. Through periodic surveys, we assessed the influence of management (tree species, planted density) and brachyuran assemblage (species occurrence and number of individuals) on forest development and biomass stock in the areas. In this work, the aim was to (1) assess the aboveground standing biomass and carbon stocking of the different managed forest fragments in ten years and discuss the effectiveness of management measures applied since the intervention, and; (2) assess the effects of management factors and fossorial brachyuran crabs on aboveground carbon storage in a restored forest.

Methods

Study area

This long term study on restoration is being conducted in a mangrove area in Jaguaribe River (5°45′42″S/ 35°14′06″W), tributary of Potengi River in the city of Natal, Rio Grande do Norte State, Brazil (Fig. 1). The climate is tropical with air temperatures between 20 and 31 °C. The Potengi River runs through the northeastern semi-arid region, and have a catchment drainage of 3180 km², receiving wastewaters from Natal city and other towns along the river (Silva et al.

2007). Rainy season is between March and July, and annual precipitation averages reach around 1900 mm at coastal region; however, periodic rain shortages can occur, as in the decade 2006–2016, when most years showed rain levels below average (< 1600 mm), mainly since 2010 (Marengo et al. 2017). The estuary is covered by red mangrove *Rhizophora mangle* L. forests, but white mangrove *Laguncularia racemosa* Gaertn. and black mangrove *Avicennia schaueriana* Stapf. & Leech also occurring in lower abundance (Ferreira and Sankarankutty 2002). Many mangrove areas have been cleared and, although this economic activity has decreased in recent years, several enterprises continue in activity in the estuary.

The experimental areas are included in a mosaic of preserved mangrove fragments, shrimp ponds and secondary riparian forest (Ferreira et al. 2007). After being deforested at once for intensive exotic shrimp culture [*Litopenaeus vannamei* (Boone 1931)] in 2003, areas were abandoned without deploying the activity. During the tree clearing the soil was physically altered and populations of crabs greatly affected. Three years later, in 2006, experimental management was initiated. Sparse seedlings and small trees (0.3–0.7 m height) (< 0.004 individuals/m²) were established naturally after disturbance, although *Rhizophora mangle* and *Laguncularia racemosa* propagules (from now on called only by the genus) are carried to areas by tides from close mangroves (Ferreira et al. 2015).

Experimental setting

Rhizophora was chosen for reforestation because it was the predominant tree species in the deforested area. This tree develops fast and has high primary production, as well as resistance to management (Field 1996; Ross et al. 2001; Ferreira et al. 2007). Other mangrove species were expected to establish by themselves later. Prior to management application in the Jaguaribe areas, hydrological and edaphic conditions were assessed, and no further actions were performed, since these conditions were functional and waterborne propagules reach both areas (Lewis and Streever 2000; Lewis 2005; Lewis and Brown 2014). A smaller area (0.67 h), called "restored area" or RA (Fig. 1b), was chosen to reforest and planted in the rainy season of 2006 with propagules of *Rhizophora* at higher densities (4.14 individuals/m²) than
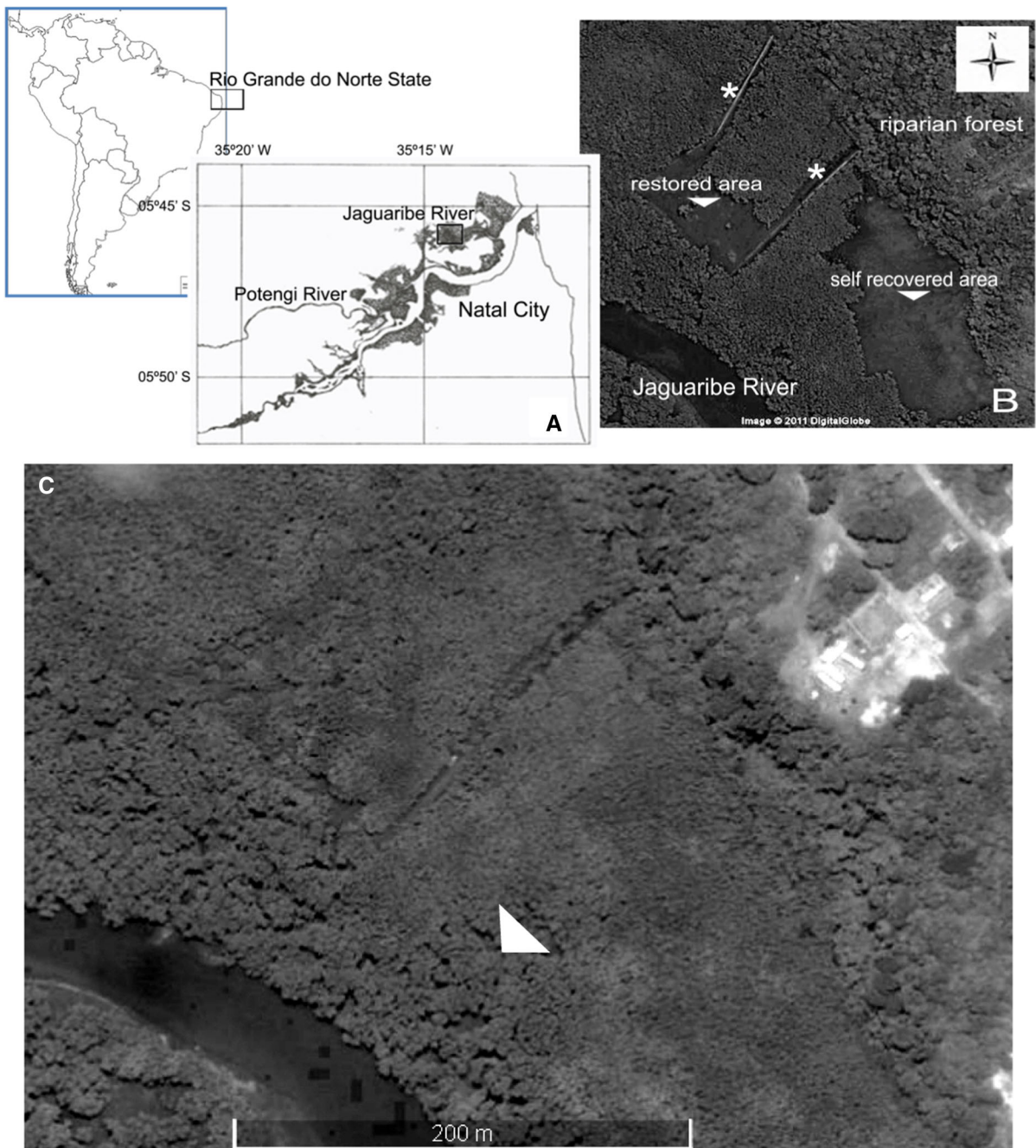
Fig. 1 Study area in the Potengi estuary, northeast Brazil. **a** Shaded areas indicate mangroves in the Potengi River estuary. **b** Satellite image of studied areas in Jaguaribe River in 2006, after deforestation, surrounded by native mangroves. Arrows show the restored and self-recovered experimental areas before the start of the experiment. Asterisks (*) show small creeks formed laterally to constructed dams. **c** The areas in 2016; top right corner, advance of human occupation in recent years (Images Google Earth). Arrow indicates preserved area surveyed at 10 years

surrounding preserved mangroves. A contiguous higher area, called "self-recovered area" or SRA (2.5 h) (Fig. 1b), suffered no manipulation and was used as the control of natural mangrove colonization. The absence of similar areas in the estuary to replicate the experimental setting, and operational restrictions

to apply both treatments (planting—self-recovering) in each area, lead to selection of the smaller area for planting and the larger area for self-recovery (see Methods in Ferreira et al. 2015).

Both areas were at the same shore level and have the same flooding regime of semidiurnal tides from the Jaguaribe river course (Fig. 1). Soil interstitial salinity at both areas was similar at management onset, but was more variable in the self-recovered due to influence of freshwater runoff from littoral riparian forest (Fig. 1c). Substrate softness ('penetrability') and percentage of clay and silt were also measured prior to the experiment, showing that the soil of the restored area was softer and slightly muddier, and contained denser fiddler crab populations than in the self-recovered area (Ferreira et al. 2015) (Table A, Supplementary material). From the start, the areas were managed through a social-environmental project, with the collaboration of the young sons and daughters of fishermen, who assisted plantings and monitored seedlings, and learned the necessary skills to further plant in their own degraded red mangrove areas along the river (Ferreira et al. 2007; Ferreira and Lacerda 2016). The project also targeted to raise awareness of conservation of the overfished crab *Ucides cordatus* (Ocypodoidea), a resource explored by fishermen.

Biomass and restoration assessment

Aboveground forest biomass is used to assess growth, productivity and atmospheric carbon intake of mangroves. Mangrove soils can stock a highly variable percentage of ecosystem carbon (from 10% to around 98%) (Matsui 1998; Kristensen et al. 2008; Donato et al. 2011; Bhomia et al. 2016). However, soil carbon was not included in the sampling since the aim was to estimate the specific contribution of trees to the sites' carbon stock. Surveys of biomass stock in trees were conducted in both areas 5 (2011) and 10 years (2016) after planting. Tree development was surveyed in each area in 10 squares of 5 × 5 m (Schaeffer-Novelli and Cintrón 1986) randomly selected from a grid superimposed over a satellite image of the areas (Ferreira et al. 2015). In each square, trees were counted and the diameter at breast height (dbh) and height of individuals higher than 1.8 m (called "mature" since they can start to produce propagules at around this average size) and trees lower than 1.8 m ("young") were measured.

In the first survey, young trees were considered post planting self-recruits for convenience.

Aboveground biomass was calculated using an allometric equation constructed by measuring weight, height and dbh of 20 sequential sized mature trees of *Rhizophora* and 20 of *Laguncularia*, between 1.3 and 6 m. The allometric equations that best fitted the data were polynomial and included only dbh (cm). For *Rhizophora* trees, biomass in grams was equal to $427.26(dbh^2) - 544.45(dbh) + 994.63$, and for *Laguncularia* biomass was equal to $299.43(dbh^2) - 486.06(dbh) + 393.04$ with R^2 coefficient of 0.85 and 0.99 respectively (Ferreira et al. 2015). Dead trees were included in biomass calculation. Carbon content was determined by multiplying aboveground biomass by the coefficient 0.44 (Rodrigues et al. 2014) for *Rhizophora* and *Laguncularia*. Equations were also used to calculate biomass at areas before managing, but since initial naturally established plants were mostly seedlings and saplings < 1.3 m, results are approximate. At 10 years, aboveground biomass of a contiguous preserved *Rhizophora* mangrove area close to 40 years old (Fig. 1) was also estimated, to compare their development with managed areas. Soil carbon was estimated using studies on similar mangroves in the Neotropics (DelVecchia et al. 2014; Kauffman et al. 2014; Bhomia et al. 2016).

Brachyuran surveys

Mid-littoral crab species have been surveyed extensively in sediment, tree canopies and roots in the study areas since 2004. Several species of Grapsidae and Sesarmidae burrowing crabs (Superfamily Grapsoidea) as well as Ocypodidae (Superfamily Ocypodoidea) occur in the Potengi mangroves (Ferreira and Sankarankutty 2002). Key brachyuran species populations were assessed before the experiment and 5 and 10 years after the beginning of the experiment. Grapsoid *Goniopsis cruentata* (from now on called by its genus) is a medium sized ($\leq$ 5.0 cm carapace width—c.w.) mobile and non-burrowing crab (Warner 1969) abundantly found in under mangroves. It is raptorial and propagule consumer under canopies and their vicinities (Burggren and McMahon 1988; Ferreira et al. 2013). The density of *Goniopsis* individuals $\geq$ 2.5 cm c.w. (sub-adults and adults) was estimated by visually counting individuals in 10 randomized quadrats of 5 × 5 m (Ferreira et al.

2013). The large burrower *Ucides cordatus* (Ocypodoidea) (from now on called by genus) is predominantly leaf eater but also consumes propagules (≤ 8.0 cm carapace width—c.w.). (McKee 1995a; Sousa and Mitchell 1999; Nordhaus et al. 2006). Their populations are decreasing in several Brazilian mangroves due to overfishing, diseases and habitat destruction (Goes et al. 2010; Maia et al. 2016).

The density of Ocypodids, such as several species of fiddler crabs "*Uca*" spp. (≤ 2.5 cm c.w.) and *Ucides* (≥ 4.5 cm c.w., i.e. sub-adults and adults), was performed by counting the burrows inside the same quadrats. Density was expressed as burrows/m^2, which is an estimation of individuals/m^2 (Branco 1993; Skov and Hartnoll 2002), significant by their direct relation with soil turnover intensity. Species of fiddler crabs present in Potengi are easily identified visually and by substrate where they occur (Bezerra et al. 2006). Plant density (prop roots in RA and stems in SRA) and also substrate coverage by *Bostrychia* sp. (Rhodophyta) in SRA, impaired accurate counts of fiddler crab burrows, which is a common methodological problem elsewhere (Ashton et al. 2003). At present, fiddler crabs of the genus "*Uca*" were split into several genus previously recognized as sub-genus (Shih et al. 2016): *Leptuca cumulanta* (Crane 1943) (around 1 cm c.w.), *Minuca thayeri* (Rathbun 1900) and *Minuca rapax* (Smith 1869) (around 2 cm c.w.), all occurring in the studied areas. Initial crab densities at contiguous mangrove areas were also included as reference (Ferreira et al. 2015).

Tests of Laguncularia development

Since *Laguncularia* seedlings recruits and develops in SRA, but not in RA, we performed at 5 and 10 years after planting, an experiment to investigate this. *Laguncularia* propagules were placed in closed cages of plastic mesh (1 cm—McGuiness 1997a, b) of 1 m^2 and 0.5 m in height (20 propagules/cage, total = 200 propagules) positioned between the roots in RA, with walls buried up to 20 cm in the mud, and was also covered at the top, to prevent entry of propagule consumers such as *Ucides* and *Goniopsis*. Propagule development was observed, and surveyed 3 weeks and 2 months after setting. The cages were frequently surveyed to prevent any invasion by *Ucides* through burrows under the fences. Stem and root density impaired similar tests in SRA where, oppositely to RA, *Laguncularia* seedlings were relatively abundant.

Statistical treatment

The correlation between the flora and fauna variables (Flora: Seedling, Young and Mature trees density, Tree diameter and Biomass; Fauna: *Goniopsis* density and *Ucides* density) was explored using principal component analysis (PCA, Rencher 2002) to detect trends in the RA and SRA in the 5 and 10 year surveys. PCA was performed with standardized data (Gotelli and Ellison 2004) and the principal components were inspected with cumulative proportion variation circa 70% (Pereira et al. 2014). Variable loadings were inspected for relative ecologic contribution (modular values higher than 0.4) in each component according to Rakocinski et al. (1996). Bootstrap permutations (n = 999) were performed to evaluate viability of the PCA inspection.

Multivariate normality (Doornik and Hansen 2008) and equivalence among covariance matrices (Box's M test, Anderson 1958) with Monte Carlo permutation were inspected. A permutational multivariate analysis of variance (PERMANOVA) using the Bray–Curtis similarity index with random permutations (n = 9999) (Anderson 2001) was performed to test hypothesis of significant differences between managed areas (RA *vs.* SRA) and their states after 5 and 10 years of monitoring. In addition, canonical variate analysis (CVA) (Rencher 2002) was performed to explore interrelation between variables and the prior classification of spatial (RA *vs.* SRA) and temporal (5 vs. 10 yrs) scales. CVA was evaluated for the canonical variables with more than 80% of cumulative variance.

Finally, to check more accurately the behavior of variables highlighted by the CVA according to the grouping results, data were tested independently. Means of two areas (RA *vs.* SRA) of each of the variables: (1) seedling, (2) young, (3) mature density, (4) diameter, (5) biomass, (6) *Goniopsis* and *Ucides* density and (7) enclosed *Laguncularia* propagules survival were compared. First, each variable was tested for normality (Shapiro–Wilk test, Shapiro and Wilk 1965) and homogeneity of variance (Levene test, Rencher 2002) assumptions, followed by a Student *t* test for normal variables and the Mann–Whitney test for the other variable (Zar 2010). Size effect was also calculated for variables.

All analyses were conducted using PAST Software (Hammer et al. 2001) considering a 5% significance probability (Zar 2010). Exploratory data and treatment for outliers presence, colinearity and temporal auto-correlation followed the protocol proposed by Zuur et al. (2010).

Results

Ten years after the start of management, the RA maintained itself as a monospecific *Rhizophora* forest with higher tree growing, while in SRA developed *Rhizophora* and *Laguncularia*. The first three principal component of PCA explained 69.84% of the total data variation, indicating a relevant association between tree and crab variables and managed areas (Fig. 2; Table B, Supplementary material). At 5 years in the temporal scale, density of mature trees was positively associated with RA status, while at 10 years, the main variables associated with this area were biomass, diameter and crab (*Ucides* and *Goniopsis*) density. The SRA status was negatively correlated with tree diameter, biomass and crabs density, and, while positively associated with seedling and young density at 5 years, this area was more related to mature density at 10 years (Fig. 2).

The PERMANOVA analysis revealed significant differences between areas and time for studied variables (Table 1). Canonical variate analysis (CVA) was similar to principal component analysis findings. In CVA, temporal scale is more evident for each managed area, with more dissimilarity for RA in comparison to SRA, and less between RA at 5 years and SRA at 10 years (Fig. 3). For RA, tree biomass was mainly discriminating at 10 years and secondarily diameter and crab density, while mature tree density was mainly discriminating at 5 years. Variations in the SRA were strongly associated with seedling and young plant density at 5 years but to mature density at 10 years. The first variable explained 83.55% of the variation (Table 2), associated positively mainly with tree diameter and biomass, and secondarily with *Goniopsis* density, all of which were strongly related to RA at 10 years. The second canonical axis, with 15.33%, show areas positioned contiguous along it. At

Fig. 2 Biplot of PCA of variables at restored area (RA) and self-recovered area (SRA). Variable vectors: M dens (mature tree density), Y Dens (young tree density), S Dens (seedling density), Diam (tree diameter), Biomass (tree biomass), Ucides Dens (*Ucides* density) and Gon Dens (*Goniopsis* density). Polygons are limits of point clouds. Symbols: filled circle, RA at 5 years; filled inverted triangle, RA at 10 years; open circle, SRA at 5 years; open inverted triangle, SRA at 10 years. (Eigenvalues and proportion of variance at Table B, Supplementary material)
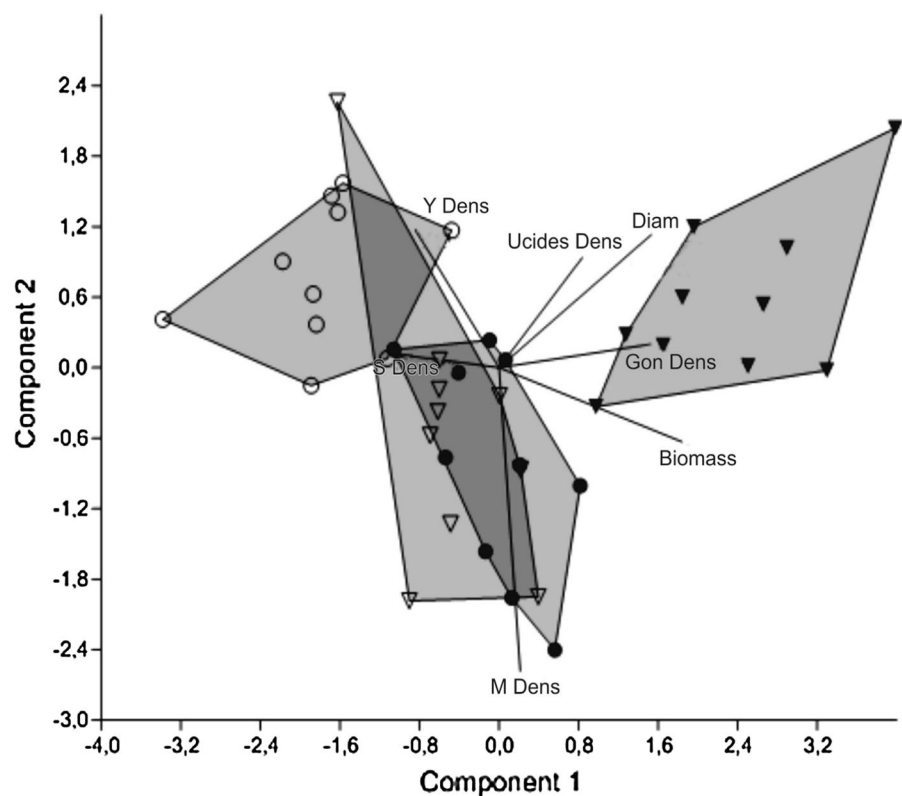
Table 1 PERMANOVA analysis on Bray–Curtis distance for tree and crab variables between managed areas (RA vs. SRA) and their states after 5 versus 10 years of monitoring (time) (permutations = 9999); values of $p < 0.01$ are statistically significant (in bold)

Source	Df	MS	F	p
Area	1	0.9051	18.724	**0.0001**
Time	1	0.5474	11.325	**0.0001**
Area x Time	1	0.2691	5.568	**0.0022**
Residual	36	0.0483		
Total	39			

5 years, the RA area appeared strongly related to mature tree density, whereas SRA was more associated to seedling density (Fig. 3). At 10 years, SRA was positively related to tree young density but negatively related to tree biomass and diameter and crab density.

Univariate comparison tests showed that while tree density decreased in RA in 10 years, it increased in SRA due to a proportionally higher (more than threefold) raise in *Laguncularia* density, despite a slight increase in *Rhizophora* numbers. Trends of tree species density in the areas observed 5 years before were inverted (Table C, Supplementary material). In SRA, the *Rhizophora/Laguncularia* density rate decreased from 0.96 to 0.38 in the last 5 years. *Rhizophora* young density decreased in both areas, but young *Laguncularia* in SRA did not change significantly in 10 years. The comparison showed that seedling density did not change significantly between the 5 and 10 years in the areas, but in the case of *Laguncularia*, size effect revealed a significant decrease. The diameter of *Rhizophora* trees increased significantly in both areas in 5 years, contrary to the self-recovered *Laguncularia*. Aboveground biomass and carbon stocking increased significantly in the last years, around 59% and 180% in RA and SRA, respectively (Table 3). In absolute terms, the aboveground biomass of *Rhizophora* in SRA continued higher than *Laguncularia,* since *Rhizophora* contains more biomass by unit (same size individual) than

Fig. 3 Biplot of CVA of variables at restored area (RA) and self-recovered area (SRA). Polygons are limits of point clouds. Symbols: filled circle, RA at 5 years; filled inverted triangle, RA at 10 years; open circle, SRA at 5 years; open inverted triangle, SRA at 10 years. Larger symbols are centroids of each polygon
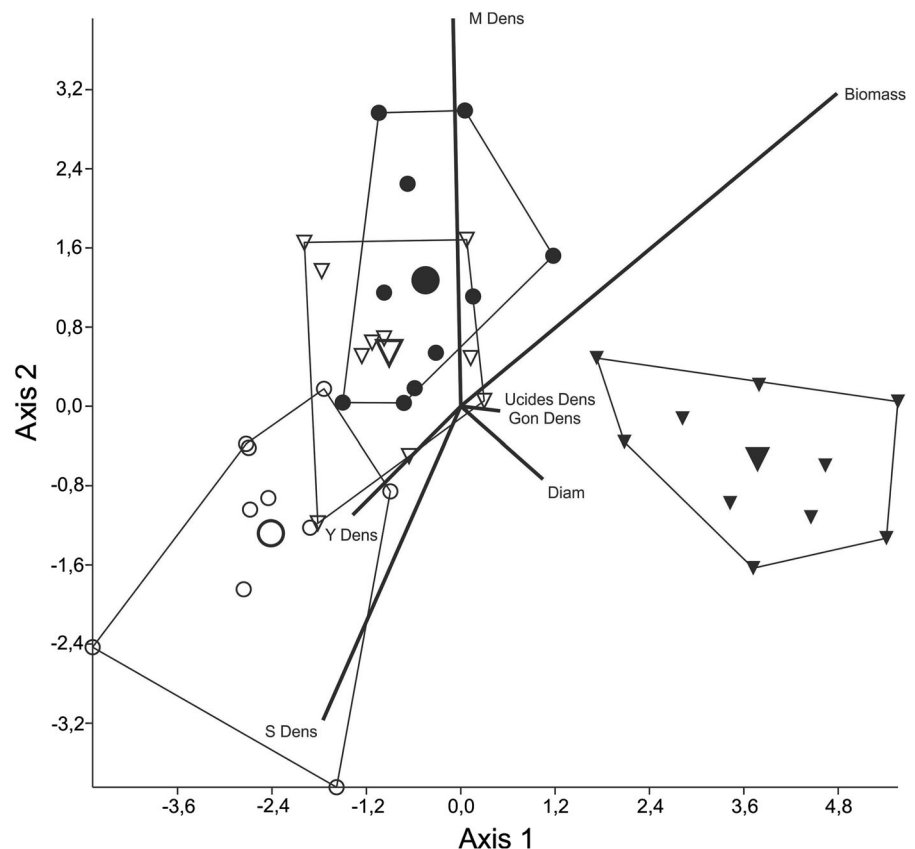
Table 2 Covariance analysis (CVA) of tree variables and crab densities in the restored area (RA) and self-recovered area (SRA)

	1	2
Proportion of variance		
Eigenvalue	5.833	1.07
% var	83.55	15.33
Loadings		
M Dens	− 0.2439	0.8578
Y Dens	− 0.2781	− 0.0840
S Dens	− 0.3666	− 0.6254
Diam	0.9214	− 0.6052
Biomass	0.9541	0.4319
Gon Dens	0.7418	− 0.1816
Ucides Dens	− 0.0072	− 0.1147

Eigenvalues and percentage of variance (%var) explained. M Dens (mature tree density), Y Dens (young tree density), S Dens (seedling density), Diam (tree diameter), Biomass (tree biomass), Gon Dens (*Goniopsis* density), Ucides Dens (*Ucides* density)

white mangrove, and this difference (i.e. *Rhizophora/Laguncularia* biomass rate) increases with tree growth (Ferreira et al. 2015) (Fig. A, Supplementary material). At 5 years, the biomass and carbon stock of RA increased more than threefold compared to SRA, but declined to about twofold in 10 years due to an increase in mature *Laguncularia* trees in the latter area. Estimated biomass of older, preserved adjacent *Rhizophora* area was similar to RA (Table 3).

Crab populations showed changes along time in studied areas (Table 4, Fig. 4). Covariance analysis showed a strongly positive association between crab density and the RA status at 10 years, but a less positive association in SRA (Fig. 3). Prior to the start of management (2006), propagule consumer crabs such as *Goniopsis* (together with other minor species like *Pachygrapsus gracilis*) were established in RA in low numbers, reestablishing in SRA 5 years after the onset of management (2011) (Fig. 4a). *Goniopsis* counting at 10 years showed close to a threefold increase of their populations in both areas, increasing significantly in RA (187.5%) while remained lower in SRA (Table 4). In 5 years *Ucides* were reestablished in both areas, but their populations recovered discretely (Fig. 4b). Although densities of *Ucides* in both areas and *Goniopsis* in SRA increased at 10 years, this trend was not significant due to high variability of data, and both crabs remained less abundant than in preserved area (Ferreira et al. 2015) (Table 4).

About half of the experimentally caged propagules and early seedlings of *Laguncularia* in RA were buried or downed by the increasing burrowing activity of fiddler crabs at 5 and 10 years (Table 5). Moreover, downed seedlings are more likely to be killed by other factors, including consumption (snails, small Grapsids, interstitial fauna) and shade intolerance, which operate less over erect seedlings. Mortality due to fiddler crabs was significantly higher than other mortality factors in both periods. Remaining erect seedlings also suffer herbivory or low growth and most subsequently wilted or disappeared. Surviving seedlings grew underdeveloped and only ≤ 5% survived 2 months. At present, none of these experimental propagules survived.

Table 3 Aboveground biomass and carbon (Mg/h) stock (mean ± SD) in restored (R), self-recovered (SR) and preserved (Pres.) areas before management (initial), 5 and 10 years after planting

| Area	Initial	5 years (2011)		10 years (2016)		% increase in last 5 years	p
	Biomass	Biomass	Carbon stock	Biomass	Carbon stock		
R Rh	8.77×10^{-4}	60.43 ± 20.94	26.59 ± 9.21	96.09 ± 22.71	42.28 ± 9.99	59	**0.001**
SR	2.46×10^{-4}	18.19 ± 6.89	8.00 ± 3.03	50.89 ± 15.24	22.39 ± 6.71	180	**< 0.001**
Rh		12.48 ± 4.68	5.49 ± 2.06	28.52 ± 11.09	12.56 ± 4.88	128	**< 0.001**
Lag		6.62 ± 3.94	2.91 ± 1.73	19.82 ± 11.61	8.73 ± 5.11	199	**0.009**
Pres. area Rh	–	–	–	99.25 ± 29.77	43.67 ± 13.10	–	–

Rh, *Rhizophora* trees; Lag, *Laguncularia* trees. **p**, significance of changes between 5 and 10 year surveys (t-test); values of $p < 0.01$ are statistically significant (in bold)

Table 4 Brachyuran density (mean $\pm$ SD) in restored (R) and self-recovered (SR) areas (individuals/m^2), before planting (Initial), 5 and 10 years after planting; densities in preserved area at experiment onset (initial) are included

	Area	Initial	5 years (2011)	10 years (2016)	p
G. cruentata	R	0.1 $\pm$ 0.08	0.32 $\pm$ 0.31	0.92 $\pm$ 0.25	**< 0.001**
density	SR	0.0	0.15 $\pm$ 0.17	0.42 $\pm$ 0.32	0.064
	Preserved[a]	2.2 $\pm$ 0.3	–	–	–
U. cordatus	R	0.0	0.07 $\pm$ 0.12	0.18 $\pm$ 0.35	0.216
density	SR	0.0	0.05 $\pm$ 0.10	0.05 $\pm$ 0.06	0.248
	Preserved[a]	4.0 $\pm$ 1.0	–	–	–

p, significance of change between 5 and 10 year surveys (t-test); values of $p < 0.01$ are statistically significant (in bold)

[a] Ferreira et al. (2015)

Fig. 4 Density of population (individuals/m^2) of *Goniopsis cruentata* (**a**) (error bars = standard deviation) and *Ucides cordatus* (**b**) (error bars = value range) in restored area (RA) and self-restored area (SRA)
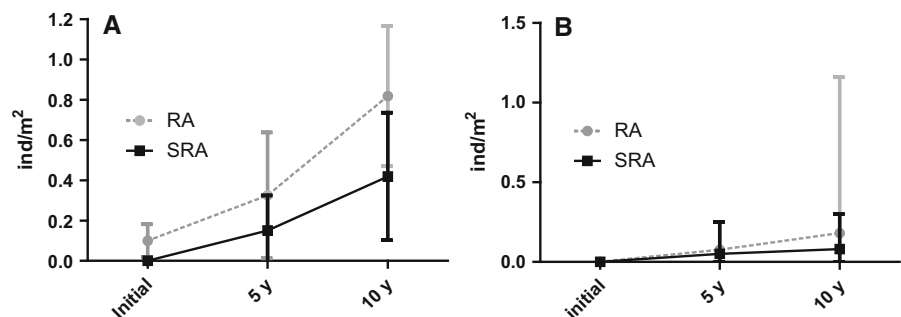
Table 5 Mean mortality of propagules of *Laguncularia* in 3 weeks and survival in 2 months at predator exclusion cages in restored area (RA), 5 and 10 years after planting

	3 weeks			2 months
	Mean propagules killed by fiddler crabs	Mean propagules killed by other factors	p	Mean of survivors
5 years	10.6 $\pm$ 2.67	6.5 $\pm$ 1.71	**< 0.001**	0.91 $\pm$ 1.28
	(53%)	(28.5%)		(4.5%)
10 years	9.6 $\pm$ 3.37	5.6 $\pm$ 1.64	**0.003**	1.0 $\pm$ 1.56
	(48%)	(28%)		(5%)

p, t-test significance of difference in number of propagules affected by fiddler crabs and by other mortality factors in 3 weeks; values of $p < 0.01$ are statistically significant (in bold)

Discussion

Biomass stock in worldwide mangroves

Several works on mangrove restoration at other regional realms assessed mangrove aboveground biomass and planted density, allowing comparisons (Table 6). Most species used for restoration are *Rhizophora* sp. due to lower cost/benefit issues, such as high biomass stocking and rapid growing (Field

1996; Ross et al. 2001). Levels of aboveground biomass reached by RA in Jaguaribe River (96.09 $\pm$ 22.71 Mg/h) were far higher than SRA (50.89 $\pm$ 15.24 Mg/h), already from the first 5 years after management start. Biomass stock of RA was higher in comparison to the same aged restored site by DelVecchia et al. (2014). Estrada et al. (2015) report higher biomass in southeastern Brazilian mangroves. Similar age and/or less densely planted *Rhizophora* forests in the Indo-West Pacific (IWP) tend to stock

similar or higher levels of carbon (Kairo et al. 2008; Camacho et al. 2011; Matsui et al. 2012; Putz and Chan 1986).

Natural forests of *Rhizophora* spp. in the IWP and Caribbean (Mexico, Tobago Is.) with comparable density or age to our surveyed preserved forest, are also able to stock higher levels of aboveground carbon (Juman 2005; Komiyama et al. 2008; Kauffman et al. 2015; Nam et al. 2016). In some places, biomass levels of restored and natural forests do not differ significantly (Lu et al. 2014; Nam et al. 2016), while in others the latter have higher biomass content (Thant et al. 2012; DelVecchia et al. 2014) (Table 6). To compare forest development in SRA with other mixed *Rhizophora + Laguncularia* stands, available data were taken from natural young mangroves (see Review in Fromard et al. 1998). Sites with dominance of *Laguncularia* over *Rhizophora* retain lower aboveground biomass than *Rhizophora* dominant sites (Soares and Schaeffer-Novelli 2005; Portillo et al. 2017). Mangroves in SRA of Jaguaribe River stocked lower biomass in initial 5 years than pioneer/young forests of predominant white mangrove stands in the Atlantic-Caribbean-East Pacific (ACEP) (Fromard et al. 1998; Kauffman et al. 2014; Bhomia et al. 2016), but values found at Central America Pacific coast where very similar (Bhomia et al. 2016). Self-recovered mixed forests (predominant *R. mangle*) in Florida and northeast Brazil had higher aboveground biomass levels than SRA at 5 years (Ross et al. 2001; Medeiros and Sampaio 2008) and probably also at 10 years (Table 6).

Mangrove soils can have high carbon content. Belowground carbon content of RA can be estimated using data from a similar Neotropical restored stand dominated by *Rhizophora* in Ecuador, where soil carbon represents between 94.07 and 97.19% of ecosystem (soil + trees) carbon, whereas these levels vary between 80.74 and 95.60% in a preserved mangrove (DelVecchia et al. 2014). Belowground carbon reaches around 88% of ecosystem stock in preserved mangroves of Central America (Kauffman et al. 2014; Bhomia et al. 2016). Using these data, we estimated that belowground carbon amount in RA could reach between 670.7 and 1462.35 Mg/h, and in the surveyed preserved forest between 183.07 and 948.83 Mg/h. For example, soils of young *Rhizophora* forests in the same Brazilian northeast region (Ceará

State) contained around 340 Mg/ha of carbon (Kauffman et al. 2018).

Biomass and carbon stock in managed areas

In forests, disturbances create patches in space and time and promote heterogeneity within them (Pickett and White 1985; Pickett and Cadenasso 2005). Considering deforestation as a disturbance, planted forests can be subjected to the same post disturbance factors that operates in natural forests (variation in nutrients, sedimentation, herbivory, self-thinning), allowing comparisons between these forest types. In restored mangroves, however, natural factors operate only after tree species have been chosen and the target area has been planted in a specific density, which are both controllable factors. Both managed areas in Jaguaribe showed significant growth and biomass rise in 10 years due to an increase in planted *Rhizophora* diameter, and in SRA mostly due to increase in *Laguncularia* density.

In 10 years, RA continues to be monospecific, and stocked close to twice more carbon than SRA. *Rhizophora* contains more aboveground biomass by individual of same size than *Laguncularia* (Ferreira et al. 2015), and this difference (i.e. *Rhizophora/Laguncularia* biomass rate in the case of SRA) increases with tree growing. The levels of carbon sequestered in *Rhizophora* forests tend to be initially high, and the bulk of the biomass is located mostly in the trunks, with less fixed in other parts, but with roots increasing their relative biomass with age (Clough 1992; Alongi 2009). As in other plantations, *Rhizophora* densities declined with forest age because some trees die and others become larger due to density-dependent self-thinning, notwithstanding increasing forest aboveground biomass (Clough et al. 1999; Hummel and O'Hara 2008). Data shows that in terms of forest recovery and carbon sequestering, management in RA was successful, since the biomass and carbon stock levels were extremely close to those found in a taller, 40-year-old, sparser and far thicker contiguous *Rhizophora* forest (Table 6). The SRA developed higher tree richness, but in 10 years it did not reach the status of RA at 5 years in terms of biomass and mature density, showing that the recuperation status of RA in 5 years was higher than the status reached by SRA in double the time.

Table 6 Biomass and C stock in Mega-grams by hectare (Mg/h) of some restored (Res.) and natural (Nat.) mangroves (including **pr**, preserved, and **sr**, self-recovered areas surveyed in this work) in different regions

Country-region/Reference	Res.	Nat.	Age (years)	Tree sp.	Tree dens. (ind/m or m²)	Aboveground biomass (Mg/h)	C stock (Mg/h)
Myanmar/Thant et al. (2012)	✓		6 years	S. apetala (*)	1.8 i/m (pl) 0.26 i/m² (pr)	69.3 ± 14.1	≅ 31.05
NE Brazil, This work	✓		**10 years**	**R. mangle**	**4.14 i/m² (pl) 2,27 ± 0,61 i/m² (pr)**	**96.09 ± 22.71**	**42.28 ± 9.99**
Ecuador, DelVecchia et al. (2014)	✓		10–12 years	+++ R. mangle + L. racemosa A. germinans	–	24 ± 5–46 ± 10	10.56 ± 2.2–20.24 ± 4.4
Thailand, Matsui et al. (2012)	✓		10 years	R. mucronata	1.5 i/m (pl)	98.7	46.39
Kenia, Kairo et al. (2008)	✓		12 years	R. mucronata	0.48 i/m² (pr)	106.7 ± 24.0	50.15 ± 11.28
Philippines, Camacho et al. (2011)	✓		15 years	R. stylosa	1.8–3.24 (pr)	312 ± 69.7	140.4 ± 31.4
Vietnam, Nam et al. (2016)	✓		30–40 years	R. apiculata	0.15–0.19 i/m² (pr)	100.6 ± 16.1–152.7 ± 10.2	47.28 ± 7.57–71.77 ± 4.79
Malaysia, Putz and Chan (1986)	✓		50 years	R. apiculata	–	409	192.23
SE China (**), Lu et al. (2014)		✓	12 years	Ae. corniculatum; S. apetala	0.18 i/m² (pr)	79.28 ± 21.39	≅ 158.56
NE Brazil, This work (sr)		✓	**10 years**	**++ L. racemosa + R. mangle**	**3.66 ± 1.87**	**50.89 ± 15.24**	**22.39 ± 6.71**
Florida, Ross et al. (2001) (**sr**)		✓	–	++ R. mangle L. racemosa	5.78 ± 0.9 i/m²	56.02 ± 11.96	28.01 ± 5.98
Mexico, Kauffman et al. (2015)		✓	–	R. mangle	0.11–0.51 i/m²	217 ± 58–223 ± 88	122 ± 27–141 ± 45
Rio de Janeiro, Estrada et al. (2015)		✓	–	+++R. mangle, +Av. schaueriana	0.59 ± 0.94 i/m²	≅ 210	92.56
Ecuador, DelVecchia et al. (2014)		✓	> 30 years	+++ R. mangle + L. racemosa Av. germinans	–	39 ± 11–193 ± 57	17.21 ± 4.84–84.92 ± 25.08
SW Brazil, Fonseca (2005)		✓	–	++ Av. schaueriana +L. racemosa	0.63 i/m²	152.19	76.09
Tobago II., Juman (2005)		✓	–	R. mangle	0.26 ± 0.12 i/m²	141 ± 81	62.04 ± 35.04

Table 6 continued

Country-region/Reference	Res.	Nat.	Age (years)	Tree sp.	Tree dens. (ind/m or m²)	Aboveground biomass (Mg/h)	C stock (Mg/h)
Honduras, Bhomia et al. (2016)		✓	–	+++ R. mangle, ++ Av. schaueriana + L. racemosa	0.06–0.23 i/m²	120 ± 26.66	54 ± 12
NE Brazil, Medeiros and Sampaio (2008)		✓	–	++ R. mangle ++ L. racemosa Av. germinans	0.35 i/m²	105	52.5
NE Brazil, This work (pr)		✓	**≅ 40 years**	**R. mangle**	**0.12 ± 0.03**	**99.25 ± 29.77**	**43.67 ± 13.10**
NE Brazil, Silva et al. (2007) (Potengi)		✓	–	+++ R. mangle + L. racemosa	0.32 i/m²	85.96	37.82
Guiana, Fromard et al. (1998)		✓	6 years	L. racemosa	1.2 i/m²	71.8 ± 17.7	≅ 35.9 ± 8.85
Dominican Rep., Kauffman et al. (2014)		✓	–	++ R. mangle L. racemosa	5.27 ± 1.14 i/m²	60.5 ± 4.6	29.04 ± 2.21
Philippines, Camacho et al. (2011)		✓	–	+ R. stylosa Av. marina	0.05–0.41 i/m²	236.3 ± 172.4	106.4 ± 77.6
Vietnam, Nam et al. (2016)		✓	–	R. apiculata	0.16 i/m²	158.9 ± 27.0	74.68 ± 12.69
SE China, Lu et al. (2014)		✓	60 years	Ae. corniculatum	6.32 ± 0.6 i/m²	83.17 ± 9.83	–
Myanmar, Thant et al. (2012)		✓	8 years	C. decandra; B. sexangula; Ae. corniculatum	2.9 i/m²	70 ± 18.4	≅ 35 ± 9.2

Only works with data on age, density and/or biomass were considered. Plant density expressed in individuals by meter of transects or by m^2 of area. Age in years. Positive signs of tree species indicate relative abundance in comparison to the other species present. Tree density: (pl), planted density, (pr), present density (i.e. at the time of cited article publishing). Chosen planted tree species was the species that stocked the highest biomass; (**) one mangrove species planted on a monospecific natural stand. Mangrove genera: Ae, Aegiceras; Av, Avicennia; B, Bruguiera; C, Ceriops; L, Laguncularia; R, Rhizophora; S, Sonneratia. Multiplication factor to transform biomass in carbon were 0.44 for R. mangle and L. racemosa, 0.47 for R. apiculata, and 0.45 for R. stylosa; for all the other species the factor was 0.5

Rows in bold are data obtained in this research

Disturbances, such as deforestation or changes in the hydrological cycling regime, increase the heterogeneity of mangrove soil conditions, thus affecting seed recruitment and other ecological relations like competition and herbivory (Ellison and Farnsworth 1993; Sherman et al. 2000; Rivera-Monroy et al. 2004). Although the density of both species of mature trees at SRA increased, *Laguncularia* largely predominated due to their ability to colonize disturbed areas like SRA (Soares 1999; Lacerda and Marins 2002) with variable salinity, penetrability, sulfides in waterlogged soil and in presence of patches of algae *Bostrychia* sp. exerting a nursing effect (Milbrandt and Tinsley 2006; Ferreira et al. 2015). Hence, initial conditions in SRA were more influenced by among-plant ecological processes such as pioneer colonization, facilitation and competition, and less influenced by herbivory and sediment disturbances by crabs, in contrast to RA, as shown below. High density of mature *Laguncularia* at SRA in 10 years also reflects the recruitment of locally produced propagules observed 5 years before, but increase in seedlings and young plants density expected from all these mature trees at 10 years was not significant.

Monospecific plantings have been questioned due to the possible trade-off between productivity and biodiversity (and the consequent functional diversity) since forests richness can be low in comparison to natural areas (Ellison 2000; Zhang and Stanturf 2008; Salmo III and Duke 2010; Rovai et al. 2012). However, since *R. mangle* was largely predominant in Potengi forests and in RA before deforestation, their planting has restored early some ecosystem traits and functions (Lewis 2005; Ferreira et al. 2015), such as carbon stocking and brachyuran crab assemblage, that fuel carbon cycling. For the regional poor tree species pool (3, rarely 4), planting *R. mangle* behaved like a shortcut for rapid recovery, and since the *Rhizophora* forests are a preferred habitat for *Ucides* (Nordhaus et al. 2006), promoted a faster return of their populations like observed at RA. Additionally, planting density can influence the trade-off between the growing of individual trees and the whole stand, and densely planted stands can produce more biomass (and more CO_2 fixation) through more wood (more branches) despite eventually growing to lower heights (Hummel and O'Hara 2008; Camacho et al. 2011).

Our findings show the biomass and carbon stock of dense planted mangrove forests in the Jaguaribe restored area can overcome the levels of natural stands and can, therefore, be used to capture high rates of atmospheric carbon to counteract releasing by mangrove deforestations, for example by aquaculture (Camacho et al. 2011; Thant et al. 2012; Alongi 2014; Kauffman et al., 2018). The emissions from mangrove conversion to shrimp ponds can represent losses of 58–82% of the ecosystem carbon to atmosphere, potentially reaching the largest emissions from land use in tropics (Kauffman et al. 2014, 2018). It needs to be noted that the magnitude of the carbon content of the 10 years old forest in SRA (22.39 ± 6.71 MgC/h) and of the 40 years old forest in preserved area (43.67 ± 13.10 MgC/h), can be used as an estimate of emissions from conversion, respectively, of a pioneer young forest and a 'climax' forests to shrimp ponds. Carbon content of planted forest in RA can be used as a similar estimate, applicable to deforestation of dense *Rhizophora* forests.

Effects of brachyuran assemblage

The return of faunal diversity, mainly key groups, can be an indicator of successful forest restoration (Macintosh et al. 2002; Ashton et al. 2003; Gorman and Turra 2016). Studied disturbed areas have shown the same brachyurans already at 5 years of management, despite in lower populations than natural forests. This suggests a significant recolonization, in terms of species richness, of this key faunal group (Macintosh et al. 2002; Bosire et al. 2005; Ferreira et al. 2015). Features of the areas was associated to the suffered disturbances over soil and crab populations (Ferreira et al. 2015).

Previous researchs showed that Grapsoids, mainly *Goniopsis*, but also others as *Sesarma rectum* and *Pachygrapsus gracilis*, together with Ocypodoid *Ucides*, can quickly consume nearly all ($\geq 92\%$) the propagules of three mangrove species experimentally placed under the canopy of *Rhizophora* contiguous forest (Ferreira et al., 2007, 2013). *Ucides* prefer *Rhizophora* propagules (and leaves—Nordhaus et al. 2006), but Grapsoids consumed in few days around 85% of propagules of *Laguncularia* (and 62% of *A. schaueriana*) experimentally placed in the RA. Thus, crabs are able to consume four times more *Laguncularia* propagules than *Rhizophora*. The exclusion experiments showed that enclosures increased *Laguncularia* survival under canopy respect to unprotected

propagules, by avoiding consumption by larger crabs. *Goniopsis* was more abundant in RA from the start and showed a significant increase in time, which agrees with the non-development of *Laguncularia* propagules in this area. This suggest that one important factor for the low recruitment of the higher nutritional *Laguncularia* propagules (Sousa and Mitchell 1999) at Jaguaribe River, is their consumption by populations of herbivorous crabs like *Goniopsis,* indicating that escape from predation is one primary window for recruitment of white mangrove (Ferreira et al. 2013).

From experiment onset, lower soil penetrability and the higher area of SRA (and, consequently, higher distance to preserved forest borders) represented high sun exposure for propagule consumer crabs, impairing early colonization and allowing white mangrove recruitment in the first 5 years, contrary to smaller RA. Before the end of this first period, mangrove development provided the ecological conditions for the brachyuran assemblage return at SRA (Ferreira et al. 2015), with an increase of *Ucides* and *Goniopsis* populations in several places of this area, which could explain the decrease of *Laguncularia* young/seedling stages at 10 years. Since *Goniopsis* do not excavate their own burrows (Warner, 1969), differently from *Ucide*s, low penetrability in some places of SRA probably affected the establishment of this latter species more significantly, contributing with their low populations. *Ucides* density rose in some parts of RA, but their increase was not significant due to high dispersion in numbers, remaining their populations less abundant in managed than in preserved areas.

Interestingly, cage experiments also revealed the exclusion of *Goniopsis* and *Ucides* allowed inside cages the increase of burrow density of two common *Goniopsis* preys, fiddler crabs *Minuca thayeri* and *Leptuca cumulanta* (Burggren and McMahon 1988). Both fiddler crab species feed on muddy sediment under roots and in vicinities (Ferreira 1998), and their burrowing can increase *Laguncularia* fragile propagules and seedlings (≤ 5 cm height) mortality by burying and downing (Delgado et al. 2001; Ferreira et al. 2013). Downed seedlings that escaped burial were attacked at substrate by small Grapsids (*Goniopsis* and *S. rectum* juveniles, and *P. gracilis*) and other small invertebrates like Gastropod snails, and microorganisms. In SRA, differently, burial and downing of *Laguncularia* propagules were prevented in clumps of *Bostrychia* sp. and *Eleocharis* sp., which

together with young stem density and cord roots development, constrained burrowing of fiddler crabs (Ferreira et al. 2015). Consequently, we observe that high concentrations of these crabs can decrease recruitment of *Laguncularia*, impairing their establishment and development, although fiddler crab sediment turnover has been considered beneficial for aeration of mangrove anoxic soils and tree growth elsewhere (Kristensen 2008; Smith et al. 2009; Mokhtari et al. 2016). Other factors could impair *Laguncularia* development, such as competition for light, physical and chemical properties of soil and features of microbiota (Rabinowitz 1978; López-Portillo and Ezcurra 1989; McKee 1993, 1995b; Chen and Twilley 1998; Sherman et al. 1998); however, these factors mostly operate after propagule germination.

Although several factors influence aboveground carbon stock in mangroves, our study reveals that this function is sensitive to the local diversity of crabs, which is one of the most important factors at Jaguaribe River and stress the role of Brachyurans in ecosystem engineering. The composition of brachyuran assemblage in terms of herbivorous and soil bioturbator species can affect processes that shapes the forest structure, such as tree recruitment and diversity, and hence influence mangrove structure and production (biomass and carbon stock) in managed but also in natural forests (Ferreira et al. 2013). These effects over energy flux can reflect in adjacent connected coastal ecosystems, such as coral reefs, seagrass beds, subtidal benthic habitats and upstream river environments (Koppel et al. 2015; Gillis et al. 2017), and should be considered when assessing the capacity of mangroves in carbon sequestering and climate change mitigation (Alongi 2012; Murdiyarso et al. 2012; Kauffman et al. 2014). Further studies can show whether the influence of specific Brachyurans in developing of *Rhizophora* dominant forests is extended worldwide, suggesting specific tree-crab coevolutionary patterns at mangrove community assemblages.

Conclusions

One decade after be cleared to shrimp culture, a restored forest of *R. mangle* at Northeast Brazil showed higher aboveground biomass and carbon stock than a mixed *R. mangle*/*L. racemosa* forest naturally

regenerated, which maintained relatively high recruitment levels but lower biomass in the same period. Restoration was successful in terms of native tree recovering and atmospheric warming mitigation, since carbon sequestering by higher density planted *R. mangle* allowed a significant aboveground biomass reservoir in the restored forest, similar to that of older preserved mangrove fragments around 40 years old. Carbon stock measured at aboveground compartment can be used as an estimate of emissions from conversion of these forests to shrimp ponds.

Specific key faunal groups, such as brachyuran crabs, can be significant ecosystem shapers, intermediating processes that shape forest structure and biomass stocking in mangrove stands, like herbivory and bioturbation. Larger populations of the propagule consumers *Goniopsis* and *Ucides*, together with soil turnover by fiddler crabs, can influence propagule recruitment and further vegetation structure in restored and natural mangrove areas. The predominance of *R. mangle* high biomass in the restored area can be reinforced due to the lower competition with *L. racemosa*, because of the consumption and burial of their propagules by crabs. This suggest that particularities of both target tree species and brachyuran crab assemblages need to be considered in mangrove restoration, management or to assess their influence on climate, given their relationship with ecosystem function recovery and the carbon cycle.

Compliance with ethical standards

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

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