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RELAÇÕES ECOLOGICAS ENTRE CARANGUEJOS E COMPOSIÇÃO ARBÓREA EM BOSQUES DE MANGUE NATURAIS E RESTAURADOS NO NORDESTE BRASILEIRO

Alexander Cesar Ferreira Román

NATAL, RN
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Tese apresentada ao Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio Grande do Norte, como parte dos pré-requisitos para a obtenção do título de Doutor em Ecologia.

Orientador: Prof. Dr.
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SUMÁRIO

RESUMO

O presente estudo teve como objetivo comparar o desenvolvimento das comunidades de árvores e caranguejos de duas áreas de mangue restauradas, uma plantada com *Rhizophora mangle* e outra naturalmente recuperada, além de comparar a magnitude da predação do Grapsídeo *Goniopsis cruentata* e do Ocypodídeo *Ucides cordatus* sobre os propágulos de três espécies de mangue: *Rhizophora mangle*, *Avicennia schaueriana* e *Laguncularia racemosa*. Em particular, foi testada a hipótese de que a predação de *Goniopsis* é mais importante que a predação por *Ucides* e que esses consumidores possuem efeitos antagônicos sobre a predação de propágulos. Em cada área, 10 quadrantes foram aleatoriamente selecionados para analisar a riqueza arbórea, diâmetro, altura, biomassa arbórea e riqueza e densidade de caranguejos cinco anos após o início do experimento de restauração. Os resultados mostraram que tanto a altura e biomassa arbóreas quanto a densidade de caranguejos foram significativamente maiores na área artificialmente restaurada. Não foram observadas diferenças significativas na riqueza de espécies de caranguejos entre as áreas, mas houve uma maior riqueza de espécies de árvores na área auto-recuperada. Estes resultados sugerem que o plantio de propágulos de *Rhizophora* pode aumentar significativamente a recuperação da cobertura vegetal, se o objetivo for elevar a biomassa arbórea e a densidade de caranguejos, o qual pode acelerar o retorno da funcionalidade ecossistêmica. *Goniopsis* foi um predador de propágulos mais importante que *Ucides* tanto em áreas naturais quanto restauradas. Os efeitos de *Goniopsis* foram maiores na ausência de *Ucides* devido a interações negativas entre estas espécies de predador. A preferência de *Goniopsis* por *Avicennia* e *Laguncularia* pode favorecer a dominância de *Rhizophora* observada nos mangues Neotropicais. Este estudo sugere que a predação de propágulos por *Goniopsis* em programas de restauração de mangue deveria ser controlada se a dominância de *Rhizophora* é indesejável em relação a comunidades com mais espécies de árvore.

Palavras chave: caranguejos de mangue; predação de propágulos de mangue; predadores múltiplos; restauração de manguezais; engenheiros do ecossistema; resiliência.

ABSTRACT

This study aimed to compare the development of crab and tree communities of two restored mangrove areas, one planted with *Rhizophora mangle* and the other naturally recovered, and also to compare the predation of Grapsid crab *Goniopsis cruentata* and the Ocypodid *Ucides cordatus* over the propagules of three mangrove trees: *Rhizophora mangle*, *Avicennia schaueriana* e *Laguncularia racemosa*. Specifically, we tested the hypothesis that *Goniopsis* predation is more important that *Ucides* predation, and that these consumers have antagonist effects over propagule consumption. In each area, 10 quadrates were selected at random to analyze tree richness, diameter, height, tree biomass and crab richness and density five years after restoration experiment start. Results show that tree height, biomass and crab density were significantly higher in artificially restored area. No significant differences were observed in crab species richness between areas, but higher tree richness was observed in self-recovered area. Results suggest that planting propagules of *Rhizophora* can significantly increase tree recovering if the aim was increase tree biomass and crab density, which can accelerate return of ecological functionality. *Goniopsis* is a more important propagule predator than *Ucides* both in natural and restored areas. The effects of *Goniopis* were higher in absence of *Ucides*, due to negative interactions among these two predator species. The preference of *Goniopsis* by *Avicennia* and *Laguncularia* can favor the dominance of *Rhizophora* observed in Neotropical mangroves. This study suggests that propagule predation by *Goniopsis* should be controlled in restoration programs, if dominance of *Rhizophora* is undesirable respect to more rich tree communities.

Key words: mangrove crabs; mangrove propagule predation; multiple predators; mangrove restoration; ecosystem engineers; resilience.

INTRODUÇÃO

Os manguezais são compostos por comunidades biológicas altamente dinâmicas e produtivas, e representam um dos ecossistemas costeiros mais afetados pelas populações humanas (Thom, 1967; Ferreira, 1998; Diegues, 1999; Alongi, 2002; Lugo, 2002). Ocupam entre 137.760 (Giri, 2011) e 152.310 km^2 (FAO, 2007) das costas tropicais e subtropicais do Planeta e desempenham um importante papel sócio-econômico e ecológico (Alongi et al., 1989; Barbier et al., 1997; Manson et al., 2005a,b; McLeod & Salm, 2006; Gowing et al., 2006; Donato et al, 2011). Porém, cerca de 35 % das florestas de mangue foram destruídas nas últimas décadas para o estabelecimento humano, a extração de madeira e o cultivo de camarões (Valiela et al., 2001), deixando abandonadas muitas áreas desmatadas passíveis de reflorestamento.

O reconhecimento da importância sócio-econômica e ecológica dos manguezais tem levado a um aumento nos programas de restauração na Ásia, América e África. Em geral, a restauração de manguezais é custosa e consiste na maioria dos casos no plantio de poucas ou uma única espécie de árvore nativa (Ellison, 2000). Porém, há controvérsias se o esses plantios mono-especificos podem recuperar a diversidade e a funcionalidade ecológica das áreas de mangue desmatadas, considerando que a maioria dos bosques plantados apresentam uma baixa riqueza de espécies de árvores em comparação com áreas recuperadas naturalmente (Ellison 2000; Walters, 2000; Lewis 2005; Salmo & Duke 2010; Rovai et al. 2012). Por outro lado, alguns bosques de mangue naturalmente recuperados se desenvolvem melhor do que bosques plantados, apresentando não apenas uma maior diversidade de espécies como também uma maior cobertura vegetal (Ruiz-Jaen & Aide 2005; Shafer & Roberts 2008; Martinuzzi et al, 2009; Luo et al 2010). No entanto, ainda são raros os estudos sobre os atributos da fauna de manguezais em áreas restauradas.

Os caranguejos das famílias Grapsidae e Ocypodidae (Crustacea: Decapoda: Brachyura) são animais extremamente importantes para os manguezais, desempenhando um importante papel na estrutura e biogeoquímica dos sedimentos, na reciclagem de nutrientes, na estrutura das comunidades biológicas e na produção de biomassa (Warren e Underwood, 1986; Smith, 1987a,b; Macintosh, 1988; Robertson e Daniel, 1989; Lee, 1999; Minchinton, 2001; Koch e Wolff, 2002; Cannicci et al, 2008; Kristensen, 2008). Nos manguezais dos oceanos Índico e Pacífico, estes animais podem ser indicadores do estado de conservação de bosques naturais e manejados (Tan and Ng, 1994; Ruwa, 1997; Macintosh et al., 2002; Ashton et al., 2003), mas este papel dos caranguejos têm sido pouco abordado na região Neotropical (porém, ver Ferreira et al, 2013). Desta maneira, as relações ecológicas entre o desenvolvimento do mangue e a comunidade de caranguejos são aspectos funcionais relevantes a serem monitorados em bosques naturais e artificialmente restaurados da região Neotropical.

A predação de sementes por caranguejos pode exercer uma forte influência no recrutamento das árvores e na dinâmica da floresta (Lindquist et al, 2009) determinando padrões de diversidade e distribuição arbórea (Wang e Smith, 2002) ou alterando as relações competitivas entre espécies (Hulme, 1996). Os efeitos são mais significativos quando a perda de sementes e plântulas por predação é alta (Smith III et al., 1989; Asquith et al., 1997; Ferreira et al., 2007). Vários estudos têm investigado o impacto dos herbívoros na estrutura da vegetação e a funcionalidade do ecossistema nas florestas de mangue (ver revisão de Cannicci et al., 1998). O caranguejo Ocypodídeo Neotropical *Ucides cordatus* (Linnaeus, 1763) é mencionado como um importante consumidor de propágulos nos manguezais do Mar Caribe (McKee, 1995; Sousa e Mitchell, 1999) e no Brasil (Branco, 1993; Paludo e Klonowsky, 1999; Koch e Wolff, 2002; Schories et al., 2003; Nordhaus et al., 2006). Porém, o ativo Grapsídeo predador *Goniopsis cruentata* (Latreille, 1803)(Warner, 1969) é outro consumidor muito comum (Smith III et al., 1989; McKee, 1995; Sousa e Mitchell, 1999; Ferreira et al., 2007), que tem sido frequentemente esquecido, embora possa diminuir fortemente as taxas de sobrevivência de propágulos de mangue plantados (Ferreira et al., 2007).

Vários fatores podem influenciar a magnitude da predação dos propágulos pelos caranguejos, como a espécie de árvore (Smith III, 1987b; McKee, 1995; McGuiness, 1997a,b; Sousa e Mitchell, 1999; Souza e Sampaio, 2011), posição em que a semente é deixada no solo pelas correntes (Dahdouh-Guebas et al., 1998; Clarke e Kerrigan, 2002; Bosire et al., 2005), distância da margem (Smith III, 1987a; Sousa e Mitchell, 1999; Krauss e Allen, 2003) e interferência entre predadores. A interferência entre caranguejos predadores tem sido relatada em outros ecossistemas por Jensen et al. (2002), DeGraaf e Tyrrell (2004), Quijón e Snelgrove (2005), Griffen (2006), Griffen e Byers (2006a,b) e Griffen e Williamson (2008). Porém, ainda não existem estudos sobre como múltiplos caranguejos predadores interagem e influenciam a magnitude do consumo de propágulos em bosques de mangue naturais e restaurados.

Este estudo tem como objetivo avaliar o desenvolvimento das comunidades de árvores e caranguejos de duas áreas de mangue restauradas, uma plantada e outra naturalmente recuperada, e discutir quais resultados poderiam suportar o uso de técnicas de restauração. Ao mesmo tempo, o estudo objetiva comparar a magnitude da predação do Grapsídeo *Goniopsis cruentata* e o Ocypodídeo *Ucides cordatus* sobre os propágulos das três espécies de mangue: *Rhizophora mangle* L., *Avicennia schaueriana* Stapf. & Leech. e *Laguncularia racemosa* Gaertn. Nós testamos a hipótese de que a predação de *G. cruentata* é mais importante que a predação por *U. cordatus*, e que esses consumidores possuem efeitos antagônicos sobre a predação de propágulos. Estes aspectos ecológicos foram estudados em áreas naturais e restauradas com o objetivo de aumentar o nosso conhecimento sobre a ecologia, manejo e restauração e dos mangues Neotropicais.

No primeiro artigo, uma área restaurada artificialmente foi comparada com outra área auto-recuperada, para testar a hipótese nula de que as áreas não diferem significativamente em riqueza de espécies e biomassa arbórea e em riqueza e densidade de caranguejos. Na área restaurada, plantamos *Rhizophora mangle*, enquanto na área auto-recuperada o mangue se recuperou sem intervenção humana. Em cada área, 10 quadrantes foram aleatoriamente selecionados para analisar a riqueza arbórea, diâmetro, altura, biomassa arbórea e riqueza e densidade de caranguejos 5 anos após o início do experimento de restauração. Os resultados mostraram que tanto a altura e biomassa arbóreas quanto a densidade de caranguejos foram significativamente maiores na área artificialmente restaurada que na área auto-recuperada. Não se encontraram diferenças significativas na riqueza de espécies de caranguejos entre as áreas, mas houve um aumento na riqueza de espécies de árvores na área auto-recuperada. Estes resultados sugerem que o plantio de propágulos de *R. mangle* pode aumentar significativamente a recuperação da cobertura vegetal, se o objetivo é elevar a biomassa arbórea e a densidade de caranguejos, o qual pode acelerar o retorno da funcionalidade ecossistêmica. Se o objetivo, porém, é aumentar a riqueza de espécies de árvores e caranguejos, a recuperação pode ser satisfatoriamente atingida sem intervenção humana.

No segundo artigo, encontramos que *Goniopsis cruentata* é um predador de propágulos mais importante que *Ucides cordatus* tanto em áreas naturais quanto restauradas. Nós testamos a hipótese de que *Ucides* e *Goniopsis* possuem efeitos antagônicos sobre a predação de propágulos usando um experimento com gaiolas aonde a presença/ausência destas espécies foi manipulada num desenho experimental fatorial 2 x 2. Os efeitos de *Goniopsis* foram maiores na ausência de *Ucides* devido a interações negativas entre estas espécies de predador. Além disso, encontramos que a preferência de *Goniopsis* por *Avicennia schaueriana* e *Laguncularia racemosa* pode favorecer a dominância de *Rhizophora mangle* observada nos mangues Neotropicais. Este estudo sugere que a predação de propágulos por *Goniopsis* em programas de restauração de mangue deveria ser controlada se a dominância de *R. mangle* é indesejável em relação a comunidades com várias espécies de árvore.

CAPITULO 1

PROPAGULE PREDATION IN A NEOTROPICAL MANGROVE: THE ROLE OF THE GRAPSID CRAB *GONIOPSIS CRUENTATA*

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PRIMARY RESEARCH PAPER

Propagule predation in a Neotropical mangrove: the role of the Grapsid crab *Goniopsis cruentata*

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Fúlvio A. Morais Freire · José Luiz Attayde**

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Abstract In Neotropical mangroves the crabs *Ucides cordatus* and *Goniopsis cruentata* have been considered the most significant propagule consumers, but their relative importance has not been investigated. The aim of this study was to compare the magnitude of predation by these crabs on three mangrove species propagules: *Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*. We found that *G. cruentata* is a more important predator than *U. cordatus* in both natural and restored areas. We also tested the hypothesis that *Ucides* and *Goniopsis* have antagonistic effects on propagules predation using a cage experiment where the presence/absence of these species was manipulated in a 2 × 2 factorial design. The effects of *Goniopsis* were stronger in the absence of *Ucides* due to negative interactions between these predator species. Moreover, we found that *Goniopsis* preference for *A. schaueriana* and *L. racemosa* can favor the dominance of *R. mangle* in Neotropical mangroves. This study suggests that propagule predation by *Goniopsis* should be controlled in mangrove restoration programs at abandoned shrimp farms and destroyed areas, if dominance by *R. mangle* is undesirable relative to mixed species communities.

Keywords Multiple predators · Prey preference · Higher-order interactions · Mangrove restoration · Exclusion experiment

Introduction

Mangroves are extremely productive and highly dynamic biological communities (Thom, 1967; Cintrón & Schaeffer-Novelli, 1983; Ferreira, 1998). They are subjected to great variation in edaphic (substrate composition, particle size, and topography) and hydrological (tidal flooding and salt levels) conditions. Changes in these conditions were viewed traditionally as establishing spatial gradients of mangroves in the littoral habitat (Davis, 1940; Chapman, 1944; Dansereau, 1947; Coelho, 1965; Warner, 1969; Lugo, 1980). However, frequent deviations of these patterns are observed (Snedaker, 1989; Ferreira, 1998; Bernini & Rezende, 2004; Clarke, 2004; Ferreira et al., 2007). Indeed, mangroves are constantly responding and adjusting to dynamic estuarine environment, where landforms are continuously being built, modified and eroded by abiotic (Thom, 1967; Cintrón & Schaeffer-Novelli, 1983; Woodroffe, 1983; Clarke & Allaway, 1993; Krauss et al., 2008) and also biotic forces (Warren & Underwood, 1986; Lee, 1999; Minchinton, 2001; Cannicci et al., 2008). Factors such as plant–soil

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interactions (McKee, 1993, 1995b; Lovelock et al., 2005), competition for light (Smith III, 1987a; Sousa & Mitchell, 1999; Clarke, 2004), differential seed dispersal (Rabinowitz, 1978; Sousa et al., 2007) and predation (Smith III, 1987a, b; Smith III et al., 1989; Sousa & Mitchell, 1999; Lindquist et al., 2009) are recognized as important forces controlling the distribution of mangrove tree species.

Seed predation can exert a strong influence on tree recruitment and forest dynamics (Lindquist et al., 2009) determining patterns of tree diversity and distribution (Wang & Smith, 2002) or altering competitive relationships among species (Hulme, 1996). Effects are more significant when seed and seedling loss to predators is high (Smith III et al., 1989; Asquith et al., 1997; Ferreira et al., 2007). Several studies have investigated the impact of herbivores on vegetation structure and ecosystem function in mangrove forests (Cannicci et al., 2008 for a review). Crabs of the families Ocypodidae and Grapsidae are among the most abundant and ecologically significant animals found in mangroves, playing a key role in food webs and energetic flux (Macintosh, 1988; Koch & Wolff, 2002; Cannicci et al., 2008; Kristensen, 2008). In particular, the Neotropical Ocypodid *Ucides cordatus* (Linnaeus, 1763) is mentioned as an important propagule consumer in Caribbean (McKee, 1995a, Sousa & Mitchell, 1999) and Brazilian mangroves (Branco, 1993; Paludo & Klonowsky, 1999; Koch & Wolff, 2002; Schories et al., 2003; Nordhaus et al., 2006). However, the active predator Grapsid *Goniopsis cruentata* (Latreille, 1803) (Warner, 1969) is another common consumer (Smith III et al., 1989; McKee, 1995a; Sousa & Mitchell, 1999; Ferreira et al., 2007) that has frequently been overlooked. It can heavily prey upon restored mangrove stands, decreasing survival rates of planted mangrove propagules (Ferreira et al., 2007).

Several factors may influence the magnitude of propagule predation by crabs including seed species (Smith III, 1987b; McKee, 1995a; McGuiness, 1997a, b; Sousa & Mitchell, 1999; Souza & Sampaio, 2011), stranding position (Dahdouh-Guebas et al., 1998; Clarke & Kerrigan, 2002; Bosire et al., 2005), shore level (Smith III, 1987a; Sousa & Mitchell, 1999; Krauss & Allen, 2003), and interference among predators. Interference among crab predators have been addressed in other ecosystems by Jensen et al. (2002), DeGraaf & Tyrrell (2004), Quijón & Snelgrove (2005), Griffen (2006), Griffen & Byers (2006a, b), and Griffen & Williamson (2008). However, to our knowledge, no previous studies have investigated how multiple crab predators interact to influence the magnitude of propagule consumption in both natural and restored mangrove stands.

Therefore, the aim of this study was to compare the magnitude of predation by the Grapsid *G. cruentata* and the Ocypodid *U. cordatus* on propagules of three mangrove tree species: *Avicennia schaueriana* Stapf. & Leech., *Laguncularia racemosa* Gaertn. and *Rhizophora mangle* L. We tested the hypothesis that predation by *G. cruentata* is more important than predation by *U. cordatus* and that these consumers have antagonistic effects on propagule predation. We investigate these ecological aspects in natural and restored areas with the aim of improving mangrove management and restoration in the Neotropics.

Materials and methods

Studied area

The studies were conducted in a mangrove area in Jaguaribe River (35°14′06″W/5°45′42″S), an affluent of the Potengi River estuary in the city of Natal, Rio Grande do Norte State, Northeastern Brazil (Fig. 1). The climate is warm and humid with average air temperatures between 20 and 31°C and annual average precipitation around 1,800 mm. Tides are semidiurnal and spring tides rarely reach more than 1.2 m above mean sea level. The littoral areas of Potengi estuary, including Jaguaribe River, are covered by mangrove trees of the species *R. mangle* (largely the most abundant), *L. racemosa* and *A. schaueriana* (Ferreira & Sankarankutty, 2002). Extensive mangrove areas have been cleared for shrimp breeding ponds in the past years, but the activity is falling today, leaving many abandoned and degraded areas in need for restoration programs.

Two mid-littoral areas were selected for this study (Fig. 1B): (1) an area reforested in 2005 and 2006 with *R. mangle*, called “restored area” (3.17–4.71 trees m^{-2}, average height = 1.5 m); and (2) a contiguous area with *R. mangle* forest (0.4–1.1 tree m^{-2}, average height = 5–8 m), called “mangrove area”. These sites (0.5 h each) are separated by a small creek, having freshwater influence in upper littoral zone and

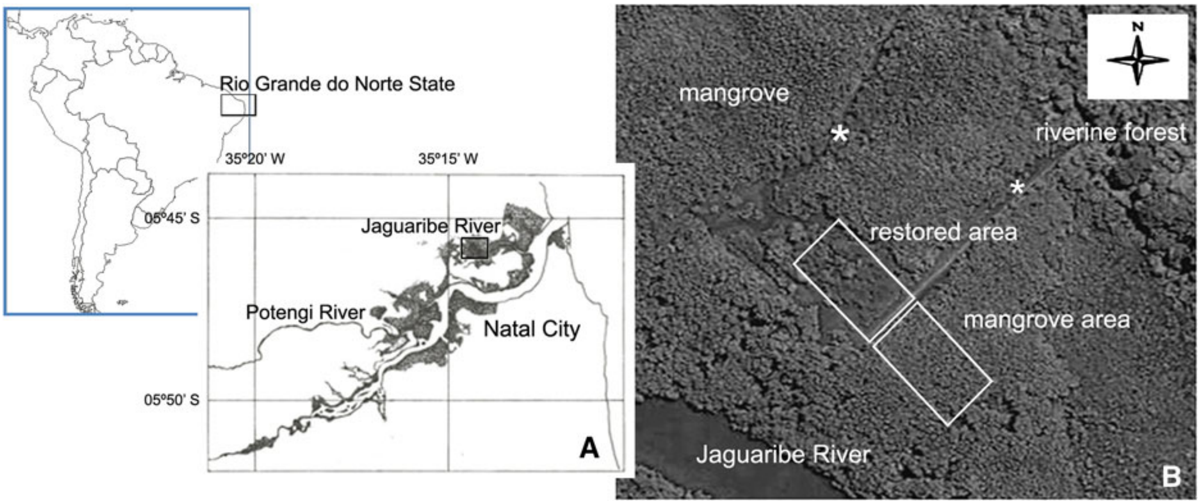

Fig. 1 Study area in Rio Grande do Norte State, Brazil. **A** Potengi River estuary: *shaded areas* represent mangroves. The study site in Jaguaribe River is located in the *black box*. **B** Mangrove and restored study sites; *asterisk* freshwater creeks

coverage by semidiurnal tide. Young trees of restored area form a patchy environment allowing light penetration on bare soil.

The sediment of both areas is wet and muddy, characterized as silty-sand (Shepard, 1954). Interstitial salinity was also similar in two areas, a pattern also showed by soil 'penetrability' (Botto & Iribarne, 2000) and percentages of Silt + Clay (Table 1). Only the organic matter content was markedly higher in mangrove area. Sediment grain size composition and organic matter content were determined at the laboratory of EMPARN (Rio Grande do Norte's Agriculture Company).

Previous work looking at the carcinofauna of the study area showed that Grapsids and Ocypodids are the most abundant and rich crab groups (Ferreira & Sankarankutty, 2002). Density of Ocypodids *Uca* spp. and *U. cordatus* were estimated by counting burrows in a square of 50 × 50 cm inside five replicated plots defined for experiments in each area, and transformed to express in burrows m^{-2}. This is equivalent to individuals m^{-2}, as burrow number is a good estimator of crab population (Branco, 1993; Skov & Hartnoll, 2001; Smith et al., 2009; Carmona-Suárez & Guerra-Castro, 2012). The restored area was more exposed to the sun and presented more *Uca cumulanta* burrows (Crane, 1975; Ferreira, 1998) than mangrove area, while the density of *G. cruentata* and *U. cordatus* showed an opposite trend (Table 1). Grapsid crab burrows were not counted because they are frequently small and constructed under roots, wood debris or litter. Because *G. cruentata* is a highly mobile and non-burrowing crab (Warner, 1969), its density was estimated by counting individuals in plots with ≥ 10 m distance during daytime before approaching the plots for counting the *Uca* burrows. *G. cruentata* is a medium-size crab (<50 mm carapace width), while *U. cordatus* can reach 90 mm carapace width. *Uca* and other Grapsid species present are small crabs (<25 mm carapace width).

Table 1 Sediment parameters and crab density (average individuals m^{-2}) measured in two studied areas

	Penetrability (cm)[a]	Salinity	% Clay + Silt	% OM	*Uca* species	*Uca* burrows	*Goniopsis cruentata*	*Ucides cordatus* burrows
Restored	18.1 ± 3.3	17.2 ± 2.6	33.6 ± 7.0	3.2 ± 1.5	*U. cumulanta*	$\cong$300	0.3 ± 0.3	0
Mangrove	16.2 ± 3.4	16.2 ± 3.6	34.8 ± 5.4	6.7 ± 2.0	*U. thayeri*	$\cong$100	2.2 ± 0.3	4.0 ± 1.0

Values ± SD. *OM* organic matter

[a] Measured in each plot using a graduated steel rod of 45 cm length, 1.3 cm diameter and 370 g weight, released from a height of 1.2 m (modified from Morrisey et al., 2002)

First experiment

The experiment was conducted at the beginning of the rainy season, when the propagules mature and drop from parent trees (February–March). Propagules of *R. mangle, L. racemosa*, and *A. schaueriana* (hereafter referred by genus) were collected at Jaguaribe River coasts, and only those not attacked by fungus or damaged by herbivores were selected. Twenty propagules of each mangrove species were placed in five replicated plots of 2 m × 2 m in both restored and mangrove areas (total propagules per plot = 60). Among the 20 propagules of each species per plot, 10 were placed partially buried and 10 laid over the sediment. The *Rhizophora* propagules are elongated (22–30 cm), and were implanted by burying 5–8 cm of their hypocotyl (or proximal portion) in mud. The small *Laguncularia* propagules (2–2.5 cm long) were similarly implanted, by burying 50% of its major axis in mud. The *Avicennia* propagules (around 3–3.5 cm long) are scarce in Potengi River, so were all collected from ocean coast with their radicle and two pairs of cotyledons partially expanded; the implanted ones had the radicle partially buried leaving the cotyledons out of mud.

Three categories of propagule consumers were defined: (1) the Grapsid crab *G. cruentata*, (2) the Ocypodid *U. cordatus* (both hereafter referred by genus); (3) a guild constituted by soil invertebrates of macro- and micro-fauna (Alongi & Christoffersen, 1992), which includes small (<25 mm c.w.) omnivorous Grapsid crabs of several species (*Pachygrapsus gracilis, Sesarma curacaoense*, *Sesarma rectum*, *Aratus pisonii*, *Armases angustipes* and juveniles of *Goniopsis*). This guild also includes Gastropod snails and other primary consumers like Nematodes, Polychaetes, small Crustaceans, and Turbellarians, among several others (Fauchald & Jumars, 1979; Alongi & Christoffersen, 1992; Camilleri, 1992; Yeates et al., 1993; Ruppert et al., 1996; Metcalfe & Glasby, 2008). The damage of crabs like *Goniopsis* and *Ucides* on propagules is recognizable by their magnitude, because in our study area they are the only seed predators that are able to remove large pieces or to carry the entire tethered propagule. *Ucides* carries rapidly their food to burrows (Ferreira, A.C., pers. obs.), while Goniopsis feed on the surface (McKee, 1995a). The effects of soil macro- and micro-fauna are associated with decomposer microorganisms, and were recognized through partial consumption of propagule tissues and burial in soil. Small Grapsids are unable to eat or completely extract the firmly tied propagules placed in the experiment allowing us to distinguish their damage from that of *Goniopsis* and *Ucides*. The resistant cuticle of *Rhizophora* propagules prevents rapid consumption by invertebrates and decomposers, oppositely to the other mangrove species that are smaller and lighter.

Propagules or cotyledons were tethered to 1-m-long nylon twines (Smith III, 1987b) and were tied to painted woody sticks fixed in the soil. A pair of propagules, one implanted and one laid, were tied by stick. The twine prevented the propagules to float away, and served as a "tracer" to recover it from predator crab burrows (Smith III, 1987b), allowing crab identification and predation effects to be assessed. Propagules were monitored and counted at low tides every 3 days during 2 weeks, and thereafter, in intervals of 5 days during 6 weeks. A propagule was considered consumed and nonviable when: (1) 50% of its mass had been consumed by predators, (2) it was entirely pulled down a crab burrow, or (3) their apical bud or cotyledons had been completely removed from propagule (Smith III, 1987b).

Second experiment

An exclusion experiment was performed in 2010 to discriminate the rates of propagule predation by *G. cruentata* and *U. cordatus* and to test for possible interference between the two crab species. The experiment had a 2 × 2 factorial design and manipulated by 2 weeks the presence/absence of the two crab species in four treatments: a control without crabs (C) and treatments with 3 *Ucides* (U), 3 *Goniopsis* (G) and with 3 *Ucides* and 3 *Goniopsis* (G + U). In this additive experimental design, both species composition and density are changing in the mixed crab treatment. The alternative would be to use a substitutive experimental design (total predator density constant) to address the effects of multiple crab predators. However, the appropriate design depends on the question of interest (Griffen, 2006) and the additive design is considered appropriate when the goal is to test simply whether interference among predators happens, as was the case in our study.

Crab densities were within the natural range of *Ucides* and *Goniopsis* densities in the mangrove area. Treatments were randomly allocated to four cages of

1 m^2 placed contiguously inside an experimental plot of 4 m^2 and were replicated 5 times in both the mangrove and restored area. The cages had 0.7 m height and the plastic mesh (1 cm—McGuiness, 1997a, b) walls were buried 20 cm in mud to prevent crab escape. The cage is expected to have low impact over sediment deposition rates (McGuiness, 1997a, b). Mesh walls surrounded trunks and roots, which were preserved inside the cages. The *Goniopsis* (35–45 mm c.w.) and *Ucides* (65–80 mm c.w.) specimens used were adults.

In each treatment, 5 propagules of *R. mangle* and 5 of *L. racemosa* (total of 40 per cage) were placed laid, as most in natural conditions. The propagules were tethered in twines with specific colors which were tied to roots or cage walls to serve as tracers. During 1 day prior to the beginning of the experiment crabs were allowed to excavate burrows and reduce capture stress. The cages were checked daily to assess escapes, and if escapes occurred, outlets were closed and new animals added. Litter fall over cages roof were introduced inside the cages to maintain natural litter input.

Statistical analyses

In the first experiment, a two-way Multivariate analysis of variance (MANOVA) was performed to test the effects of mangrove species and propagule position on predation during the experiment. Plots were considered as blocks. Mangrove species (*R. mangle*, *L. racemosa*, and *A. schaueriana*) and propagule position (implanted/laid) were the categorical variables, while the log-transformed numbers of propagules consumed at 11 different days were the dependent variables. We used time as a repeated factor and used MANOVA instead of repeated measures ANOVA to avoid the assumption of circularity (Gotelli & Ellison, 2004). In the second experiment, a two-way ANOVA was performed, using the presence/absence of *Goniopsis* and *Ucides* as categorical variables and the number of propagules consumed as the dependent variable. Statistica 7.1 (StatSoft Inc.) package was used to run the statistical analyses.

Results

Results of the first experiment show that most propagules (>97%) were quickly consumed at the mangrove area mainly by *Goniopsis* (Table 2). At the restored area, however, *Goniopsis* density and predation rates were much lower than at mangrove, and most *Rhizophora* propagules were left unconsumed (Table 1). *Ucides* is not present in restored area so consumed 0 propagule during the experiment, but small invertebrates were important predators consuming 66% of all *Laguncularia* propagules available (Table 2), with small Grapsids accounting for 25% of all *Laguncularia* consumption.

The two-way MANOVA results revealed a significant interaction between propagule species and position on consumption by crabs at both mangrove and restored areas (Table 3). Propagules were more quickly consumed at the mangrove than at the restored area (Fig. 2), but this difference was not statistically tested because there is only one site of each kind. In both areas, *Rhizophora* propagules were less consumed than *Avicennia* and *Laguncularia*, but this was more evident at the restored area (Fig. 2A). Position also affected the consumption of *Rhizophora* propagules which were less consumed when implanted than when laid on the sediment mainly at the restored area (Fig. 2A).

The second experiment results show (Fig. 3) a significant effect of *G. cruentata* on *Rhizophora* propagules in mangrove area but this effect was only evident in the absence of *U. cordatus* (Fig. 3C). The two-way ANOVA results revealed a significant antagonistic interaction between *Ucides* and *Goniopsis* (Table 4). The ANOVA results also show a reduction of *Laguncularia* propagules by *Goniopsis* predation at the restored area (Fig. 3B; Table 4). *Ucides* showed restricted activity in restored open area treatments, remaining buried in mud to avoid temperature stress.

Discussion

The above results show that *G. cruentata* had a much more important role as propagule predator than *U. cordatus* in our study area. The relative role of these species has not been investigated before and may change in different places, but in both Caribbean and Panamanian coasts *G. cruentata* seems to be an important propagule predator (Smith III et al., 1989; McKee, 1995a; Sousa & Mitchell, 1999). This suggests that most previous works in the Neotropics have overlooked the importance of *Goniopsis* on the

Table 2 Percentage of propagules of three mangrove species consumed by *Goniopsis cruentata*, *Ucides cordatus* and small invertebrates in the first experiment in 2 weeks

Area	Restored			Mangrove		
Mangrove species	*R. m.*	*A. s.*	*L. r.*	*R. m.*	*A. s.*	*L. r.*
Consumer						
Goniopsis	11 (2.2 ± 2.1)	41 (8.2 ± 2.7)	19 (3.8 ± 1.8)	87 (17.4 ± 2.8)	97 (19.4 ± 0.9)	95 (19 ± 1)
Ucides	0	0	0	5 (1 ± 1.4)	1 (0.2 ± 0.4)	0
Small invertebrates	0	21 (4.2 ± 3.0)	66 (13.2 ± 0.8)	0	2 (0.4 ± 0.9)	5 (1 ± 1)
Totals	11	62	85	92	100	100

Values between parentheses represent the mean number of propagules (± SD) consumed per plot

R. m., *R. mangle*; *A. s.*, *A. schaueriana*; *L. r.*, *L. racemosa*

Table 3 MANOVA for propagules consumed in restored and mangrove areas in 50 days in the first experiment

Effect	Restored				Mangrove			
	Wilk's value	df	*F*	*P*	Wilk's value	df	*F*	*P*
Blocks	0.385	11	1.88	0.13	0.647	6	1.6	0.19
Species	0.017	22	7.86	**<0.01**	0.060	12	9.2	**<0.01**
Position	0.121	11	8.54	**<0.01**	0.178	6	13.8	**<0.01**
Species × position	0.048	22	4.20	**<0.01**	0.079	12	7.6	**<0.01**

Species: *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia schaueriana*; Position: implanted/laid. Data of consumption were log-transformed. Significant values are in bold

mangrove food web. On the other hand, this study contradicts others emphasizing the role of *U. cordatus* (Schories et al., 2003; Glaser & Diele, 2004) as a propagule consumer in Brazilian mangroves (Branco, 1993; Wolff et al., 2000; Koch & Wolff, 2002; Nordhaus, 2003; Nordhaus et al., 2006). These contradictory results may be due to different population densities of the two species in different studies. However, results of our cage experiment with controlled densities of both species clearly demonstrate that *Goniopsis* is indeed more important than *Ucides* as a propagule consumer. Moreover, evidence from mangroves of Rio Grande do Norte State suggests that *Goniopsis* is a dominant species (McNaughton & Wolf, 1970) with an ample niche both in trophic (from detritus to small crabs) and spatial (burrows, substrate, and trees) dimensions (Burggren & McMahon, 1988; Ferreira & Sankarankutty, 2002).

Interestingly, we found a significant reduction on *Rhizophora* propagule consumption by *Goniopsis* in the presence of *Ucides*, suggesting some kind of interference of the latter species on *Goniopsis* foraging behavior at the mangrove area. Interactions among predators sharing the same prey can lead to effects that cannot be predicted by summing the effect of each predator separately (Sih et al., 1998; Griffen, 2006). If the effects of *Goniopsis* and *Ucides* were additive, the consumption of *Rhizophora* propagules in the mixed crab treatment would be much higher than was observed. Therefore, the magnitude of this non-additive effect was both statistically and biologically significant contributing to enhance recruitment of *Rhizophora* seedlings in our study area. Interference between crab predators were studied in rocky shores (Griffen, 2006; Griffen & Williamson, 2008; Griffen & Byers, 2006a, b), but never in mangroves. Although the mechanisms of interference among *Ucides* and *Goniopsis* are not clear, it may occur when territorial *Ucides* leave their burrows to search for food and encounter the more active *Goniopsis* feeding on the surface. However, we observed interference of *Ucides* on *Goniopsis* feeding on *Rhizophora* but not on *Laguncularia* propagules probably because its handling time is lower than that of *Rhizophora,* exposing *Goniopsis* less to agonistic interactions with *Ucides*.

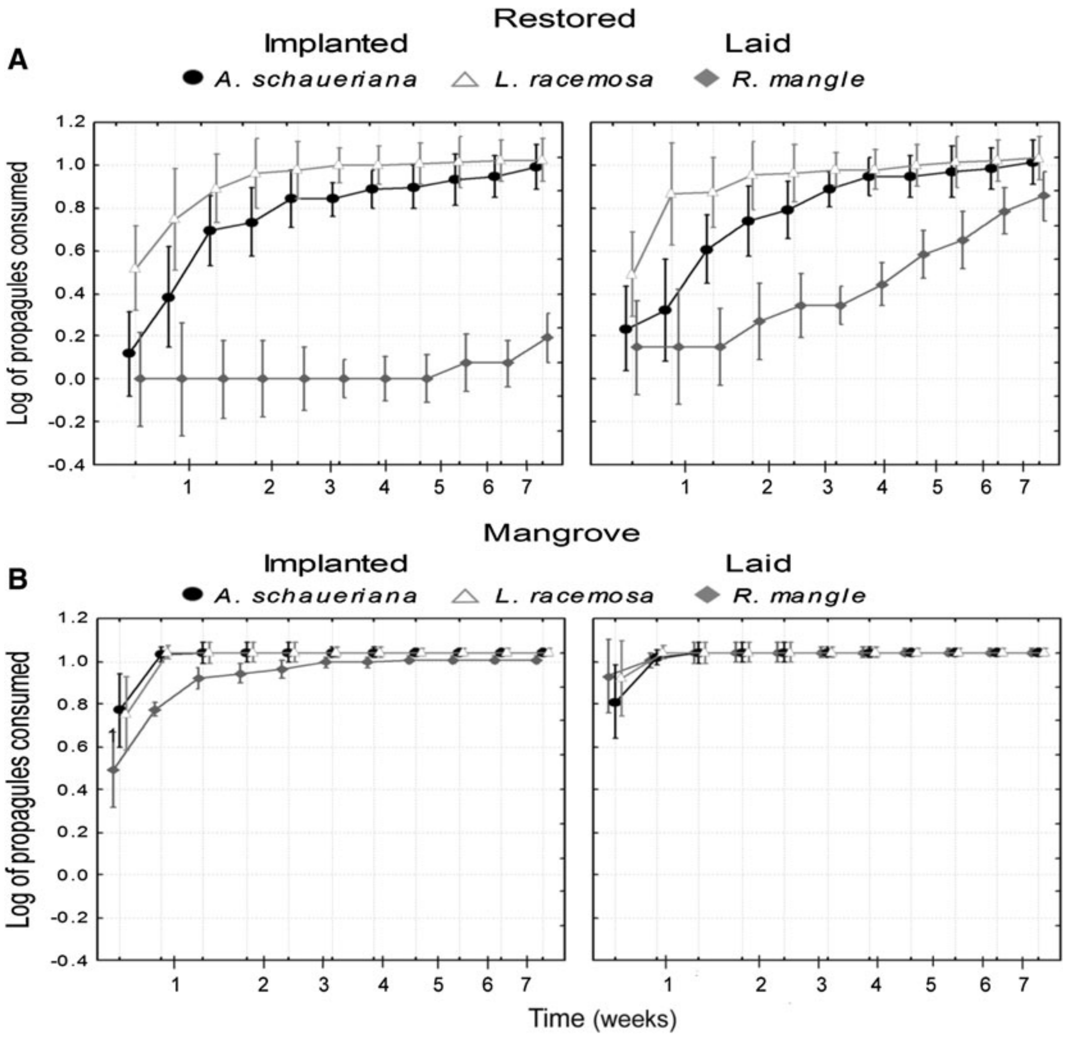

Fig. 2 Mean propagule consumption of *Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle* in restored (**A**) and mangrove (**B**) areas during 50 days. Data were log transformed. *Bars* represent 0.95 confidence intervals. *Horizontal axes* represent time (weeks)

We found that the increased mortality of *Avicennia* and *Laguncularia* propagules is due to the preference of *Goniopsis* by these species. Preference by *Avicennia* sp. was also found in East Atlantic (McKee, 1995a; Sousa & Mitchell, 1999; Souza & Sampaio, 2011) and Australian mangroves (Smith III, 1987b; McGuiness, 1997a, b; Clarke & Kerrigan, 2002; Clarke, 2004), while *Laguncularia* propagules were preferred along the Pacific coast of Central America (Delgado et al., 2001). Preference for smaller propagules by crab predators is due to its easier manipulation and burial in burrows; *Avicennia* seems preferred also by their higher nutritive value or lower concentration of inhibiting chemicals (Smith III, 1987b; McKee, 1995a; Sousa & Mitchell, 1999). The stranding position of *Avicennia* and *Laguncularia* propagules did not influence their rate of mortality, but *Rhizophora* suffer higher predation pressure when laid on the sediment than when vertically implanted. The vertical position for this large propagule may have influenced crab manipulation skills (Dahdouh-Guebas et al., 1998). These results have important implications for mangrove restoration programs as they suggest that the use of *Rhizophora* propagules would allow faster mangrove recovery (Ferreira et al., 2007) than *Avicennia* or *Laguncularia*. Additionally, *Rhizophora*

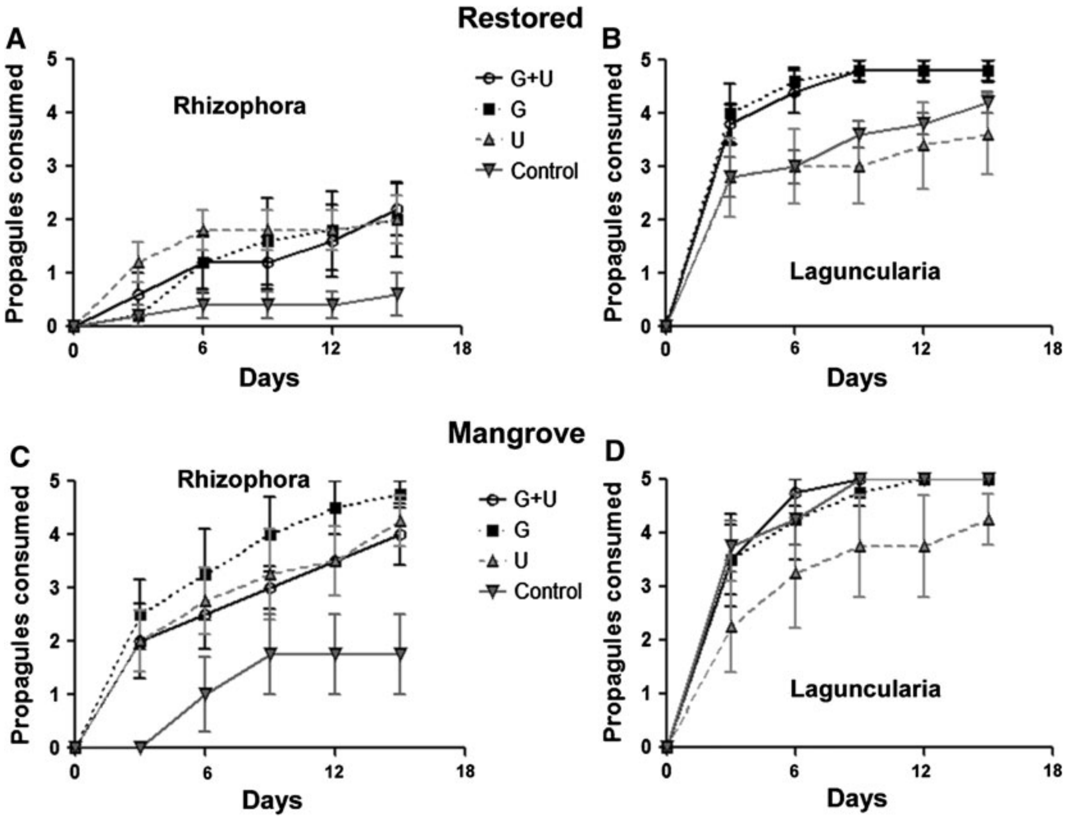

Fig. 3 Mean number of consumed propagules of *Rhizophora* mangle (**A**) and *Laguncularia racemosa* (**B**) in a restored area and *R. mangle* (**C**) and *L. racemosa* (**D**) in a mangrove area in 2 weeks. Propagule consumption was measured in four treatments: *Goniopsis* and *Ucides* (G + U), only *Goniopsis* (G), only *Ucides* (U) and a Control without these crabs. *Horizontal axes* represent time (days)

Table 4 Factorial Analysis of Variance (ANOVA) for predation by *Goniopsis cruentata* (G) and *Ucides cordatus* (U) on *Rhizophora mangle* and *Laguncularia racemosa* propagules in an enclosure experiment implemented in mangrove and restored areas

Effect	*Rhizophora* (mangrove)			*Rhizophora* (restored)			*Laguncularia* (mangrove)			*Laguncularia* (restored)		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
G. cruentata	1	**12.23**	**<0.01**	1	2.59	0.13	1	2.45	0.15	1	**7.71**	**0.01**
U. cordatus	1	4.95	0.05	1	2.59	0.13	1	2.45	0.15	1	0.85	0.37
Blocks	3	**4.68**	**0.03**	4	1.45	0.27	3	1.00	0.43	4	**3.47**	**0.04**
G × *U*	1	**17.09**	**<0.01**	1	1.45	0.25	1	2.45	0.15	1	0.85	0.37
Error	9	**–**	**–**	12	–	–	9	–	–	12	–	–

Significant values are in bold

propagules should be vertically implanted to reduce mortality by crab predation, and improve tree recruitment and recovery in restored areas (Dahdouh-Guebas et al., 1997, 1998; Bosire et al., 2005; Ferreira et al., 2007).

Differences in propagule predation between mangrove and restored areas seem to be strongly related to crab abundance. Higher crab densities exert predation pressure over seeds in coastal forests (Lindquist & Carroll, 2004; Lindquist et al., 2009). Propagule consumption was higher at the mangrove area where crabs are more abundant, showing that predation is more intense under closed canopies than in more open areas. This pattern was also found by Osborne & Smith

(1990), Clarke & Kerrigan (2002), and Clarke (2004), but is opposite to that found by Sousa & Mitchell (1999) and Souza & Sampaio (2011). Thermal and water stress limit crab populations in open areas (Warner, 1977), while food is more abundant in mangrove habitat (Ferreira, 1998). Small Grapsids (*Pachygrapsus gracilis* and *Goniopsis* juveniles) and Gastropods are more abundant under mangrove canopy (Ferreira & Sankarankutty, 2002; Maia & Tanaka, 2007), and could partially be responsible by a higher rate of burial/consumption of *Laguncularia* avoiding significant consumption by *Goniopsis* in treatments. Data suggest that rapid predation of propagules by high *Goniopsis* aggregation under canopy in the first experiment diminished propagule consumption by these small crabs. The lower rate of *Rhizophora* consumption by *Goniopsis* in restored area is also observed in the second experiment; probably territorial displays performed by *Uca cumulanta* in this open area could make it visually more conspicuous and nutritionally preferred item (Wolcott, 1988) than *Rhizophora* to *Goniopsis* (Ferreira, A.C., pers.obs.).

Several works have studied the effects of crabs on tree recruitment and community composition (Green et al., 1997; Sherman, 2002; Lindquist & Carroll, 2004; Lindquist et al., 2009), particularly in mangroves (Smith III, 1987a, b; McKee, 1995a; Osborne & Smith, 1990; Souza & Sampaio, 2011). Crab consumption of propagules is concentrated in the rainy season, when mangroves produce high amounts of tide-carrying propagules which strand in open and canopy areas. We observed that propagules of three mangrove species showed ability to grow in the same littoral areas along the Jaguaribe River, but need to survive from the predation by Grapsids and burial by fossorial crabs. In our study areas these biotic factors could limit the establishment and growth of propagules, especially *Avicennia* and *Laguncularia*. Therefore, the Grapsid crabs preference for these small propagules may explain in part the dominance of *Rhizophora* in our study area. Grapsid crabs have an important role in shaping mangrove community assemblage in the Indo-west Pacific (Smith III et al., 1989), and East Africa (Bosire et al., 2005; Dahdouh-Guebas et al., 1997, 1998). As expected, we found a similar ecological role (Smith III et al., 1991) of Grapsid crab *G. cruentata* in mangroves of Jaguaribe River. Dominance of *R. mangle*, due to higher tannins content (Alongi, 1987) and organic matter accumulation on soils (Lacerda et al., 1995), may lead to changes in the chemical characteristics and availability of organic matter to soil biota, affecting the distribution and abundance of meiobenthos in estuary (Alongi, 1987). Moreover, this may lead to higher nutrient retention in the estuary and lower nutrient release to adjacent ecosystems (Lacerda et al., 1995). Hence, *G. cruentata* may exert a significant effect in mangrove community structure.

Conclusion

Previous works in Neotropical mangroves have emphasized *U. cordatus*, but overlooked the importance of the predator *G. cruentata* on mangrove food webs. This generalist Grapsid species has an important role determining through propagule predation which mangrove species can establish in mangrove areas, influencing mangrove community structure. *Ucides* can interfere in *Goniopsis* foraging on *R. mangle*. Moreover, predation by *Goniopsis* is able to eliminate most propagules of *L. racemosa* and *A. schaueriana*, mainly under native mangrove, where this crab species is more abundant. Our results have important implications for mangrove restoration, suggesting that propagule predation by *Goniopsis* should be controlled in restoration areas if dominance by *R. mangle* is undesirable relative to mixed species communities. On the other hand, if restoration attempts to restore *R. mangle*, it is most effective to insert propagules vertically into the soil to avoid undue predation from crabs on that species.

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CAPITULO 2

PLANTING *RHIZOPHORA MANGLE* IN DEFORESTED MANGROVES INCREASES TREE BIOMASS AND CRAB DENSITY, BUT NOT TREE RICHNESS.

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PLANTING *RHIZOPHORA MANGLE* IN DEFORESTED MANGROVES INCREASES TREE BIOMASS AND CRAB DENSITY, BUT NOT TREE RICHNESS

Abstract: Mangrove deforestation has left many deforested areas in need for restoration in tropical estuaries worldwide. The intensity of degradation impacts would certainly influence mangrove resilience but few works have investigated how or if restoration intervention would differ from mangrove self-recover. Most restoration programs have planted few tree species, and have been questioned if such low tree richness can improve mangrove functionality and resilience, because are rare studies about relationships between animal functional groups and developing mangrove stands. We compared a restored area planted with *Rhizophora mangle* and a self-recovered area, to test the null hypothesis that the two areas do not differ significantly in plant richness and biomass as well as in crab richness and density. In each area, 10 plots were randomly sampled for tree richness, diameter, height and biomass, and for crab richness and density five years from the start of the restoration experiment. An allometric equation was constructed for estimate biomass of young mangroves showing that plant height and biomass, as well as crab density, were significantly higher in the restored than in the self-recovered area. However, no significant differences were found in crab richness between areas and there was an increase in tree richness in the self-recovered area. These results suggest that planting *R. mangle* propagules can significantly improve mangrove recovery if the restoration goal is to increase tree biomass and crab diversity. If the restoration goal, however, is to improve tree and crab richness mangrove recovery can be satisfactorily achieved without restoration intervention.

Key Words: Mangrove restoration; Mangrove self recovery; Crab richness; Plant Biomass production; Resilience

Introduction

Mangroves are highly productive biological communities and one of the most human-affected coastal ecosystems (Ferreira 1998; Diegues 1999; Alongi 2002; Lugo 2002). They occupy 137,760 km^2 of tropical and subtropical coasts in the world (Giri 2011) and play important social and ecological roles (Alongi et al. 1989; Barbier et al. 1997; Manson et al. 2005; McLeod & Salm 2006; Gowing et al. 2006; Donato et al. 2011). However, at least 35 % of their forest areas have been destroyed in the past decades due to human settlements, wood extraction and shrimp culture (Valiela et al. 2001) leaving many deforested and abandoned areas in need for restoration. Mangrove forests conservation and restoration are urgent coastal management activities (Alongi 2002).

Recognition of the ecological and social importance of mangroves has led to an increase in restoration programs in Asia, America and Africa. However, restoration programs are costly and most of them have planted only few species by planting facility (specific seed shape and abundance), resistance to management, specific goods and others (Saenger, 1996; Aksornkoae, 1996; Rosario & Bohorquez, 1996; Duke, 1996; Ellison 2000; Ferreira et al, 2007; Walton 2007). There have been questioned whether they can significantly improve species assemblage, ecological functioning and resilience of mangrove deforested areas, given that most planted stands sustain such low tree richness when compared to naturally recovered areas (Walters 2000; Ellison 2000; Lewis 2005; Salmo III & Duke 2010; Rovai et al. 2012). Indeed, some naturally recovered mangrove stands have achieved similar or better development than planted ones (Shafer & Roberts 2008; Martinuzzi et al. 2009; Luo et al. 2010). However, we ignore if this happens also for key invertebrate groups, because studies on fauna attributes are still rare in restored mangroves. There has been a debate on which attributes should be measured in order to identify whether artificially or naturally recovered areas reached ecological functionality (SER 2004; Ruiz-Jaen & Aide 2005; La Peyre et al. 2007), being vegetation structure, biomass and diversity the attributes most frequently measured.

Several Ocypodoid and Grapsoid (Brachyura; Decapoda)(Ng et al. 2008) crab species are an ecologically significant group of organisms living in mangrove communities, and play important roles on sediment topography and biogeochemistry, detritus recycling, plant structure and biomass production of coastal areas (Warren & Underwood 1986; Smith 1987a, b; Robertson & Daniel 1989; Lee 1999; Minchington 2001; Kristensen 2008). Mangrove crabs can have a role of ‘ecosystem engineers’ (Jones et al. 1994, 1997; Kristensen 2008) determining tree species that establish in littoral area through consumption of propagules in Indo-Pacific coasts and Neotropics (Smith 1987a,b; Osborne & Smith 1990; Robertson 1991; McKee 1995; Sousa & Mitchell 1999; Clarke & Kerrigan 2002; Souza & Sampaio 2011; Ferreira et al. 2013), but probably is a global phenomena, since it have been showed that propagule consumption can decrease mangrove recruitment in restoration projects in all continents (Aksornkoae 1996; Chan 1996; Hong 1996; Soemodihardjo et al. 1996; Dadouh-Guebas et al. 1997, 1998; Bosire et al. 2005 Paludo &

Klonowsky 1999; Ferreira et al. 2007). Grapsids and Sesarmids (Grapsoidea) crabs are the main responsible (Smith et al. 1991; Lee 1997; Dadouh-Guebas et al, 1998; Ferreira et al, 2013). On the other hand, the maintenance and improvement of some non-Grapsoid crabs colonization in restored mangroves can be associated to the return of soil and plant community features (Walton 2007; Middleton 2008). Hence, crabs can be an functional group related to community structure and indicators of natural and managed forests conservation status (Tan & Ng 1994, Ruwa 1997; Macintosh et al. 2002; Ashton et al. 2003), but these roles has been rarely assessed in Neotropical mangroves (but see Ferreira et al, 2007; 2013). Therefore, the study of relationships between mangrove development and crab assemblage is a relevant aspect that can reveal influence of crabs over Neotropical natural and restored stands ecological functionality.

The aim of this study was to assess the changes in tree and crab community of two mangrove areas, one planted and another naturally recovered, to identify the relationships between mangrove crabs functional group and tree assemblages in developing stands. Then, we discuss which results would support the use of restoration intervention techniques in regard to desired objectives.

Material and Methods

Study Area

The study was performed in a mangrove experimental area in Jaguaribe River (35°14’06” W / 5°45’42” S), an affluent of the Potengi River in the city of Natal, Rio Grande do Norte State, Brazil (Fig. 1A). The climate is tropical, hot and humid, with average air temperatures of 20-31° C and total precipitation around 1,900 mm. The tides are semidiurnal, and spring tides rarely reach more than 2.5 m (average level around 1.3 m). The Potengi River is a temporary river that receives freshwater discharge only in the rainy season (March to July), and also wastewaters from Natal and other smaller towns throughout the year. The Potengi estuary, including Jaguaribe River is covered by 15.61 km^2 (Maia et al. 2005) of mangrove forests dominated by the red mangrove tree *Rhizophora mangle* L., but white mangrove *Laguncularia racemosa* Gaertn. and black mangrove *Avicennia schaueriana* Stapf. & Leech. also occur in lower abundance (Ferreira & Sankarankutty 2002). Extensive mangrove areas have been cleared for intensive exotic shrimp culture (*Penaeus vannamei*), but this economic activity has decreased in the last decade. The experimental area

(Fig. 1B) encompasses a mosaic of preserved mangrove, cleared areas for shrimp culture and secondary riparian forest.

We selected two intertidal areas cleared in 2003 but abandoned before ponds were completely installed. During tree clearing process the soil was extensively degraded, and populations of fossorial crabs greatly affected. Areas were originally dominated by *R. mangle*, with lower abundance of *L. racemosa*. The areas differ in size, but both are mid-littoral and receive brackish water from high intertidal fringe and same semidiurnal tidal covering. In spite high numbers of *R. mangle* and *L. racemosa* propagules were brought by tides from surrounding mangroves, only very sparse seedlings and small trees (between 0.3 and 0.7 m in height) were observed established naturally before the starting of the experiment.

After mangrove clearing in 2003 and until reforestation in 2006, natural regeneration was negligible in the smaller area, called Restored Area (Fig. 1B), due to damages inflicted to propagules by fluctuating trunks and crab predation. Hydrology was modified by constructing dams and creeks, but they did not impair normal tidal coverage (Fig. 1B). Remaining of woods larger than 2 cm diameter were removed to prevent seedling damage, while small branches and leaves were left to decompose naturally. This Restored Area was reforested in the rainy season of 2006 by planting *R. mangle* due to its original predominance in the cleared sites. Propagules free from herbivore and fungal damage approximately 25 cm long, were collected at river coasts and planted by burying 5-8 cm of their proximal portion in mud, every 0.5 m in parallel transects that were 0.5 m apart. Propagules were planted in higher density (4.14 propagules/m^2) than natural mangroves to counteract crab predation (Ferreira et al. 2007). Special care was taken to preserve soft sediment and the populations of fossorial crabs.

The larger area, or Self-recovered Area (Fig. 1B), in its most landward fringe is waterlogged with brackish water, but salinity can reach seawater levels at places close to preserved mangroves in lower intertidal. Trunks of cut down trees were removed by shrimp breeders just after clearing, and no further manipulation was made, maintaining the area to natural colonization.

Parameters measures

Prior to planting, sediment of Restored and Self-recovered Areas was characterized by sampling 10 plots selected at random out of 100 equally spaced plots marked by dividing a satellite image of each area in a grid. Analysis of sediment texture was performed at the Sediment Laboratory of EMPARN, using the Gravimetric Method. Salinity was measured in water samples, extracted 15 cm deep in soil, using an Optical Refractometer (Schaeffer-Novelli & Cintrón 1986). We measured penetrability, which evaluates substrate softness by the amount of fine sediments found in the soil sample (a variation of "compaction" by Morrisey et al. 2002). Soil samples were collected by releasing a centimetre graduated steel rod of 45 cm length, 1.3 cm diameter and 370 g weight, from a height of 1,2 m (modified from Morrisey et al. 2002).

Five years after planting, trees were measured in both areas in 10 quadrats of 5 x 5 m (Schaeffer-Novelli & Cintrón 1986) selected at random using the same methodology described above. Trees higher than 1.8 m in height (hereafter called "mature" trees) were counted, and their diameter at breast height (DBH) and height (H) were measured using a Caliper and a Clinometer respectively (Schaeffer-Novelli & Cintrón 1996). Trees lower than 1,8 m (juvenile) were also counted. Density (trees/m^2) of both size categories was calculated. Dwarf mature trees present only in Self-recovered Area, although smaller than 1.8 m, had their diameter and height measures included in data bank. Basal area of mature trees was calculated using the formula $0,7854.DBH^2$ (Chave et al. 2005). One individual of mangrove *A. schaueriana* (h=3.35 m; DBH=12.73 cm) was found but was not included in the data. Above ground biomass was calculated using an allometric equation, constructed by plotting weight in function of height and DBH, after retiring 20 mature trees of *R. mangle* and 20 trees of *L. racemosa*, and weighed separately trunk, stems and leaves, and for *R. mangle* also above ground roots (Soares & Schaeffer-Novelli 2005; Medeiros & Sampaio 2008). Roots of *L. racemosa* were not measured due the impossibility to discriminate between different individuals. We compared the results of aboveground biomass obtained using our allometric equation with the results of input our data in the equations created by Medeiros & Sampaio (2008) based on measures of DBH and height for a similar species composition mangrove stand at Itamaracá, Pernambuco (Northeast Brazil).

Several crab species occur in the Potengi mangroves (Ferreira & Sankarankutty 2002), mainly territorial burrowing crabs of Families Grapsidae and Sesarmidae (Grapsoidea) and Ocypodidae and Ucididae (Ocypodoidea)(Ng et al. 2008). Mid-littoral crab species were surveyed extensively in the study areas from 2004, every 6 months, by searching at sediment, trees canopy and roots. The most conspicuous and abundant is the "mangrove red crab" Grapsid *Goniopsis cruentata*, which is more abundant under the mangrove forest canopy but consumes mangrove propagules both in open and structured forest areas (Ferreira et al. 2007; Ferreira et al. 2013). It is a medium sized (≤ 5.0 cm carapace width) mobile and non-burrowing crab (Warner 1969). Density of individuals ≥ 3 cm carapace width (sub-adults and adults) was estimated by counting individuals before the beginning of the experiment in 10 quadrants randomized with the same methodology described above. Counting was repeated 5 years later. Density of Ocypodoids *Uca* spp. and *Ucides cordatus* was estimated by counting burrows inside the same quadrates described above. Counts were averaged and expressed in burrows.m^{-2} which is equivalent to individuals.m^{-2} (Branco 1993; Skov & Hartnoll 2001; Smith et al. 2009). High density of *Uca* spp. is correlated with higher sediment bioturbation and increase in penetrability (Botto & Iribarne, 2000). *U. cordatus* is a large sized crab > 4,5 cm carapace width, therefore, individuals with carapace smaller than 4 cm width were considered juveniles; crabs smaller than 3 cm of carapace width are difficult to find and were not counted. Counts were also repeated 5 years later for *U. cordatus.*

Statistical analysis

Salinity and penetrability measures were compared between areas using a t-test. A PERMANOVA analysis using Bray-Curtis tests in 9999 random permutations (Anderson, 2001), was run to compare the following vegetation characteristics between Restored and Self-recovered areas: number of juveniles, number of adults, DBH, height and biomass. A Neuman-Keuls post-hoc test was performed to detect most significant effects. An ANOVA analysis was also used to compare crab densities between the two managed areas before the beginning of the experiment (2006) and five years after planting (2011).

Results

R. mangle was the only plant species registered in the Restored Area plots, either for adult or juvenile stages, and seedlings were found in this Restored Area. On the other hand, in the Self-recovered Area, *L. racemosa* was also present mixed with *R. mangle*, with higher total and juvenile density (63.35 %

for juveniles and 36,64 % for mature trees) than *R. mangle* (50.42 % for juveniles and 49.58 % for mature trees). Also, a single mature tree of *Avicennia schaueriana* was founded, which may have been present in the area before disturbance due to its dense crown and large DBH. Additionally, there was a higher seedling regeneration in the Self-recovered Area given that seedlings of *L. racemosa* were registered in seven out of ten plots surveyed and seedlings of *R. mangle*, were found in four of these same plots.

The allometric equations that best fitted the data were polynomial, and using the DBH. For *R. mangle* trees biomass in grams was $427{,}26(DBH^2)-544{,}45(DBH)+994{,}63$, and for *L. racemosa* $299{,}43(DBH^2)-486{,}06(DBH)+393{,}04$ with R^2 coefficient respectively of 0.85 and 0.99. Adjust was lower for *R. mangle* by the heterogeneous aerial roots proportion. PERMANOVA analysis revealed a significant difference between Restored and Self-recovered Areas for the vegetation variables measured ($F_{1,18}=17.86$; $p<0{,}001$). Post hoc test showed that after five years of restoration, the Restored Area had higher mature tree densities than Self-recovered Area (Fig. 2A), lower juvenile density (Fig. 2B) and similar mean DBH (Fig. 2C). Additionally, mean tree height (Fig. 2D) was higher in the Restored Area like total mature biomass for our equation (Fig 2E) and for the Medeiros & Sampaio (Fig. 2F). Aboveground biomass was sub estimated in Self-recovered Area, due to the predominance of *L. racemosa*, whose aerial roots were not possible to weight, and the existence of high number of seedlings and young plants (< 1.8 m) that were not included in biomass estimation.

Density of *G. cruentata* and *U. cordatus* increased in both managed areas five years after planting ($F_{1,39}=9.69$; $p<0.01$ and $F_{1,39}=6.08$; $p<0.05$ respectively; Fig. 3A, 3B). *G. cruentata* density was higher in Restored than in the Self-recovered Area ($F_{1,39}=5.21$; $p<0.05$; Fig. 3A) but *U. cordatus* was not significantly different between the two areas (Fig. 3B). Eight years after disturbance (2011), crab species composition of both managed areas reached the same characteristics of undisturbed areas (Table 3). Nearly all 9 crab species found in the undisturbed mangrove were also found in Restored and Self-recovered Areas (Table 3), considering that cryptic juveniles of *S. rectum* and *A. angustipes* were not collected but are actually common in mid-littoral areas. After clearing crab richness increased in the Restored Area, remaining high and constant before and 5 years after restoration, but increased slightly in the Self-recovered Area (Table 3). Additionally, *Uca (Minuca) rapax*, a species that is characteristic of open and sunny mangrove areas was registered only in this latter area before mangrove growing.

Discussion

Recovery of biodiversity, functionality, resilience and ecosystem services has been receiving an increasing demand when it comes to ecosystems restoration plans (SER 2004; Holl & Aide 2011). Depending on the frequency and intensity of disturbances (Holling 1973; Jones & Schmitz 2009; Biswas et al. 2012), some ecosystems may need human assistance for active restoration, in order to improve or accelerate the return of their ecological functions and self sustainability (SER 2004). However, in some conditions, ecosystems can recover without human intervention, and several examples rise from tropical forests (Finegan & Delgado 2000; Aide et al. 2000; Jones & Schmitz 2009), despite frequently with slower successional path (Rey Benayas et al. 2008). Many factors such as presence of key functional groups (La Peyre et al. 2007; Biederman et al. 2008; Menz et al. 2011; Critescu et al, 2012; Ortega–Alvarez et al. 2013), ecosystem resilience, its level of degradation and connectivity with pristine areas, and the aims of the restoration program, must be addressed in order to choose between “passive “or “active” restoration strategies (DellaSala et al. 2003; Rey Benayas et al. 2008; Holl & Aide 2010).

Present overall tree density in Restored area counteracted crab predation and yet increased by stranding of waterborne propagules. Restored Area showed higher average height and biomass but lower DBH than other restored mangroves of same age in the world, but data are scarce (Table 2). Mature tree biomass was lower than founded by Silva et al. (2006) in a developed *R. mangle* area close to Jaguaribe River (Table 2), showing the biomass levels that planted trees can reach in the estuary when grow. Self-recovered Area showed that in spite higher juvenile and seedling density, the mature tree density, average height, basal area and biomass values are lower, markedly when compared to others stands self recovered naturally or after disturbance (Table 2). Like Medeiros & Sampaio (2008) we found a best fit of DBH with biomass, and due to tight linear correlation between H-DBH (around $R^2=0,95$ for both tree species), we prefer the trunk diameter for construct the equation. Using our data of height and DBH in the allometric equation designed by Medeiros & Sampaio (2008) the biomass was super estimated in around 85 and 59.5 % for Restored and Self-restored Area respectively, showing that biomass allocation is specific of each mangrove stand restricting extrapolation of specific allometric equations (Komiyama et al. 2007). Despite Restored Area reach high growth, probably due to competition by light, neither area reached the expected DBH according to canopy height (Table 2), which is due probably to self-thinning (Shugart 1984).

The higher tree and crab richness in the Self-recovered Area studied shows that just leaving the area to recover by itself is a good alternative for Neotropical mangrove restoration, since hydrological and soil conditions were preserved (Lewis III 2005) and were not propagule predator crabs. However, lower soil penetrability could have impaired mangrove establishment and development in this area, like other stressing conditions such as accumulation of sulfides of waterlogged soils (McKee 1993b). On the other hand, clumps of red alga *Bostrychia* sp., an alga associated to mangroves in sites partially shaded and with wide salinity variations (Bouzon 1999; Cutrim et al. 2004) covered the soil of Self-recovered Area, contributing to lately seedling recruitment by creating hidden sites from propagule predators.

Tree richness in Restored Area was restricted to *R. mangle*, raising the question of what are the factors that maintain such low species colonization. Coastal gradients determined by physico-chemical factors have been appointed as main determinants of tree species zonation (Chapman 1944; Dansereau 1947; Coelho 1965; Warner 1969; Lugo 1980; Chen & Twilley 1998; Ball 2002). We have, however, frequently observed that all tree species seem able to establish in any littoral area including sites where their colonization is uncommon (Smith 1987a; Snedaker 1989; Ferreira 1998; Clarke 2004; Bernini & Rezende 2004; Ferreira et al. 2007; Fourqurean et al. 2009). Consumption of propagules by increasing populations of Grapsoid crabs, mainly *G. cruentata*, could explain the absence of *L. racemosa* and *A. schaueriana* in the Restored Area, since significant amounts of propagules of these tree species are consumed (Ferreira et al. 2007; 2013). Also, both tree species show some shade intolerance (Rabinowitz 1978; Smith 1987a; Sousa & Mitchell 1999; Clarke 2004), and competition for light with *R. mangle* may occur due to its fast development. Although *R. mangle* and *L. racemosa* are able to grow in the same littoral areas both species can compete, and in spite *L. racemosa* is able to dominate developing stands (Chen & Twilley 1998; Delgado et al. 2001; Souza & Sampaio 2001), generally *R. mangle* predominates later. Mangrove communities show a patch-dynamics structure, where forest gaps are occupied by a different set of species depending on size, climate, crab species present and species succession (Pickett & White 1985;

Ferreira 1998; Ferreira et al. 2013). This can enhance persistence and diversity of a community subjected to constant environmental changes, and a mosaic of successional stages can coexist within the same stand (Hutchinson 1961; Cintrón-Molero & Schaeffer-Novelli 1992; Alongi 2009). Successional trends, however, commonly lead to the development of a nearly pure stand of *R. mangle*, which seems to be stable and self-maintaining in Neotropics (Ball 1980; Duke et al. 1998).

Conservation of Grapsoid and increase in Ocypodoid richness, and increase in crab density in Restored Area after restoration may be due to several factors, such as proximity to surrounding preserved forests, early tree canopy development allowing shade and higher litter input, and resilience of crab assemblage. Also, the presence of anastomosing communal tunnels between *R. mangle* roots allows an early increase in crab richness under this species canopy (Warner 1969; Abele 1976; Ferreira & Sankarankutty 2002). These micro-habitats offer a refuge for juvenile stages of most crabs present in the Neotropical mangrove habitat, and also for all size stages of *Sesarma curacaoense* and *Pachygrapsus gracilis.* Forests restored with the same tree genera (*Rhizophora* spp.) in Indo-Pacific regions can support at least a crab density equivalent to undisturbed mangroves (Walton et al. 2007), but any study refers such micro-habitats out of Neotropics. Despite scattered under some *R. mangle* trees in Self-restored Area, these microhabitats are far rarely found under *L. racemosa* and *A. schaueriana* tree patches (Ferreira 1998), showing a connection between physical structure generated by monospecific *R. mangle* patches and earlier return of higher crab richness (Ferreira et al. 2007). Crab burrows are also richer in other functional groups of Polychaetes, Nematodes, Copepods and Platyhelminthes (Fauchald & Jumars 1979; Reise 1987; Dittmann 1996).

In spite of different successional paths determined by initial crab and tree richness, site size and propagule supply at planting, the studied carcinofauna reached in few years' similar species assemblage in assisted, naturally recovered and undisturbed areas, showing significant resilience. Resilience of a community is related and can be measured by the return of some functional groups (Lundberg & Moberg 2003; Nyström 2006; Fischer et al. 2007; Magalhães & Barros 2011), and faster colonization of crab assemblage in the Restored Area can allow an earlier return of the ecosystem ecological functionality (Peterson et al. 1998). Desiccation and thermal stress after deforestation, and probably also patches of less penetrable sediment, initially limited crab occurrence in the open and larger Self-recovered Area, as most of them (except *Uca (Leptuca) cumulanta* and *Uca (Minuca) rapax*) depend on vegetation cover (Ferreira 1998). Additionally, lower seed predation by crabs in larger gaps (Clarke & Kerrigan 2002) can explain the pattern of higher seedling survival in the Self-recovered Area (Osborne & Smith 1990; Clarke 2004). Despite carcinofauna returned to Self-recovered Area with young mangroves canopy, is far lower abundant.

Mangroves are high carbon stocking systems, reaching stocks of more than 1,000 T/ha in trees and soil (Donato et al. 2011). Additionally, mangroves can absorb high amounts of nutrients from sewages that flow into estuaries and coastal areas (Kathiresan et al. 1996; Feller et al. 2003; Souza & Silva 2011). There is a lacking of published data on biomass of restored stands as such as on same age natural stands to compare our Restored Area biomass production and stocking rates. However, Self-recovered Area biomass productivity was low compared with data of Fromard et al. (1998) on a young developing *L. racemosa* dominated stand. Beyond competition by light due to higher planted density, high development of Restored area is probably enhanced by nutrients from sewage disposed along Potengi estuary. In Jaguaribe River, nutrient discharge from shrimp ponds and urban wastes are relatively high, which explains such an increased tree growing rates, but only in restored area. Hence, if the aim of the restoration plan is to enhance plant biomass, carbon and nutrients stocking, abundance and speed of crab fauna colonization, active restoration with *R. mangle* is recommended. This not means that was not necessary promote the recover with the other mangrove species, instead, that is possible and recommendable to combine both managements (to plant and to promote self recover) to improve restoration of trees and invertebrate significant functional groups in Neotropical mangroves.

Conclusions

Restoration of an area with *Rhizophora mangle* can be justified in order to accelerate return of functional groups and recovery of ecosystem services, like high carbon capture, in spite low tree richness. To leave a cleared mangrove area for self-recovered can be a legitimate low cost alternative for mangrove restoration, but conditions like preserved hydrology and absence of populations of propagule predators are necessary. Crab assemblage need to be considered in Neotropical restoration plans, because in spite

Grapsoids can decrease desired tree richness through propagule predation, together with Ocypodoids can be indicators of return of functional tree canopy. Despite different successional paths (initial crab and tree richness and site size) the referred mangrove crabs reached in few years' similar species assemblage in assisted, naturally recovered and undisturbed areas, showing significant resilience in Potengi estuary.

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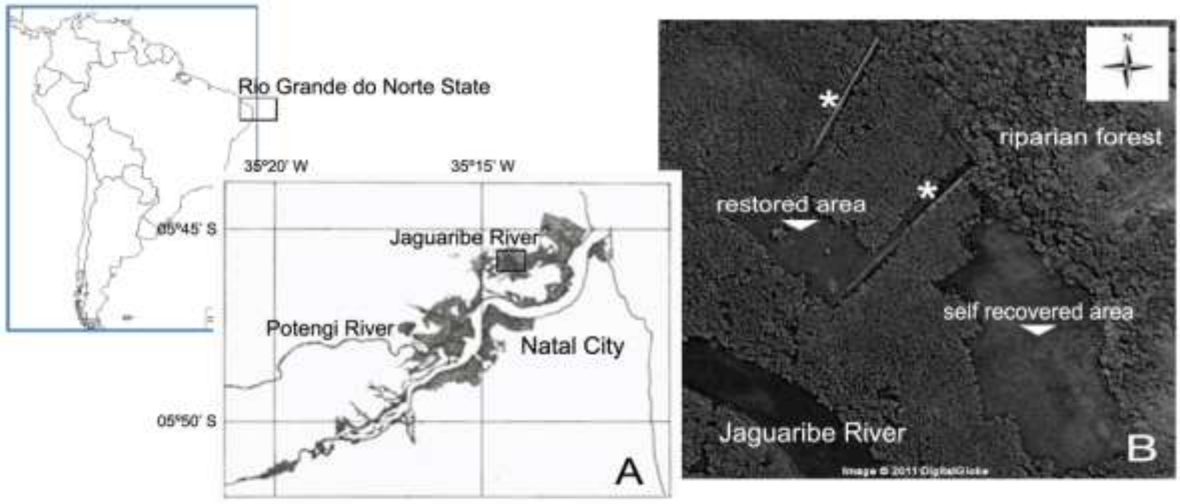

Figure 1 - Study area at Potengi estuary, northeast Brazil. A. Shaded areas indicate mangroves in Potengi River estuary. B. Satellite image of studied areas in Jaguaribe River. Arrows show the restored and self recovered experimental areas deforested, before experiment starting. Asterisks show small creeks (*) formed laterally to constructed dams.

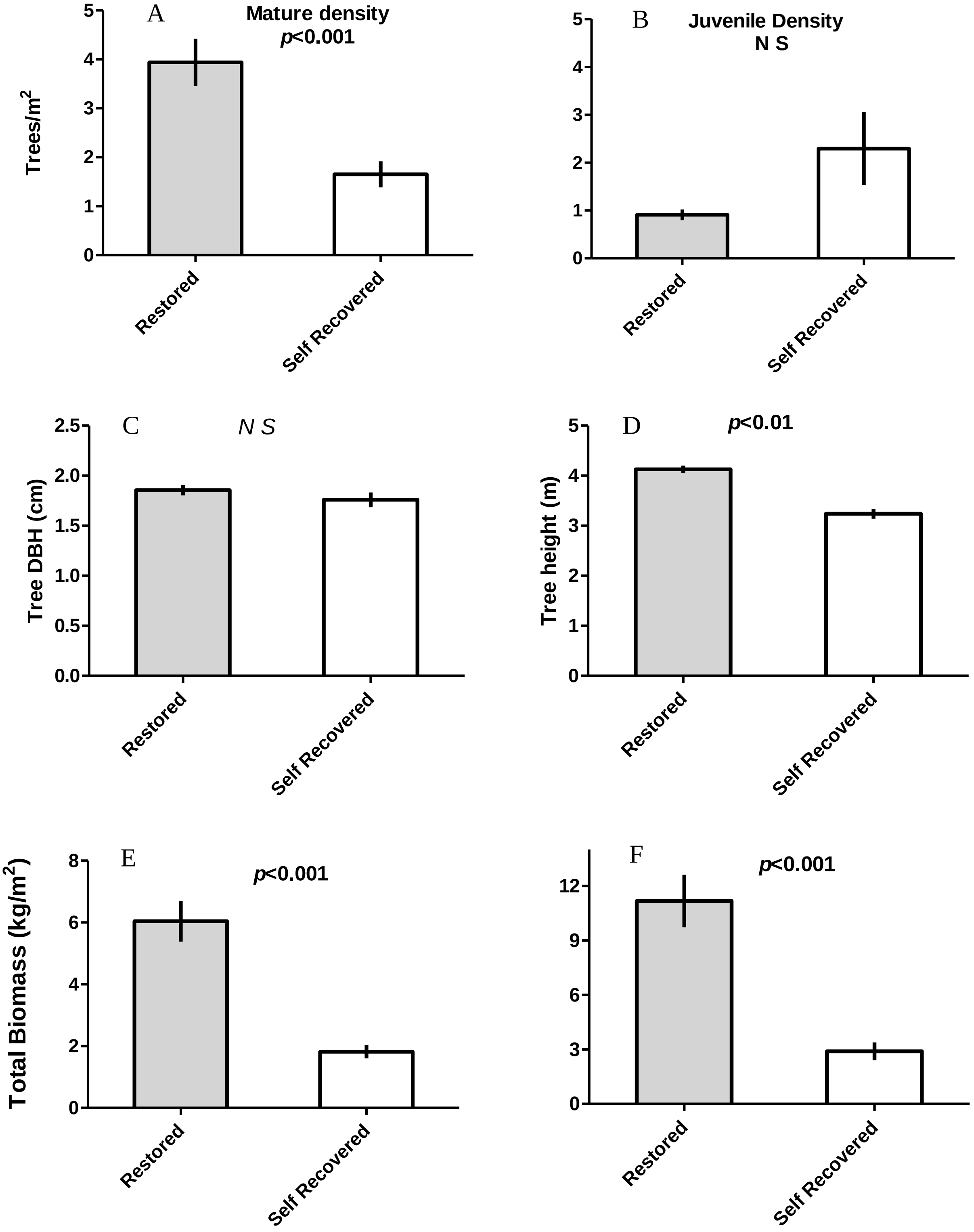

Figure 2 – Mangrove trees developing in Restored and Self Recovered mangrove areas in northeast Brazil 5 years after restoration (PERMANOVA $F_{1,18}$=17.86; p<0,001). Post-hoc test results are in graphics (NS– not significant). Juvenile (A) and mature (B) tree density; mean DBH (C) and mean height (D). Total **mature** tree biomass was calculated using our proper allometric equation (E) and using data on the equation of Medeiros & Sampaio (2008)(F) for *Rhizophora* mangle and *Laguncularia racemosa* in planted and self restored mangroves. Error bars represent standard error of mean.

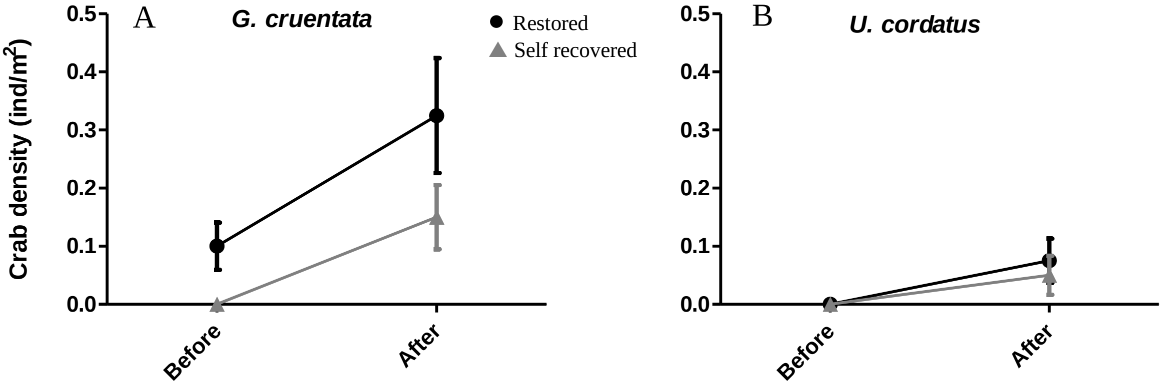

Figure 3 – Changes in density (individuals.m^2) of *Goniopsis cruentata* and *Ucides cordatus* before and five years after restoration ($F_{1,39} = 9.69$, $p < 0.01$; $F_{1,39} = 6.08$, $p < 0.05$ respectively) in Restored and Self Recovered mangrove areas. Density of *Goniopsis cruentata* is significantly different between areas ($F_{1,39} = 5.21$; $p < 0.05$) before and after restoration.

Table 1 – Sediment parameters measured at the two study sites previous to planting. Values of Penetrability and Salinity are means ± SD. Penetrability was significantly different between the two areas ($F_{1,18} = 7.7$; $p < 0.05$) but not salinity ($F_{1,13} = 0.005$; $p > 0.05$). Both areas were cleared in 2003.

	Penetra-bility (cm)	**Salinity (‰)**	**% Clay + Silt**	***Uca* species / burrow density (m^{-2})**	**Size (ha)**
Restored	14.23 ± 2.11	17.2 ± 2.58	Silty sand	*U. (Leptuca) cumulanta* / ≅ 300	0.67
Self recovered	10.67 ± 3.36	16.7 ± 15.86	Silty sand to sand	*U. (Leptuca) cumulanta,* *U. (Minuca) rapax* ≅ 80-100	2.30

Table 2. Data on mangrove trees in **Human Restored, Self Restored** after disturbances and **Natural** mangrove stands. *R.*, *Rhizophora*; *L.*, *Laguncularia; A.*, *Avicennia*. DBH and height values express means, except Medeiros & Sampaio (2008) which uses maximum heights. In **Human Restored** mangroves all data are propagule plantations, except Huber (2004) which planted 2 year old seedlings. In **Self Rcovered** and **Natural** mangroves all data are from Neotropical region, including solely forests with predominance of *R. mangle* and/or *L. racemosa*. **Natural** mangroves includes naturally developed stands that were not previously human cleared.

	Country	**Reference**	**Age of development (y)**	**Forest type / tree species**	**Height mean (m)**	**DBH (cm)**	**Biomass (T/h)**	**Basal area (m^2/h)**
Human Restored	Brazil	This work **P**	5	*R. mangle*	4.12	1.85	60.43	13.10
	Brazil	Huber 2004	5	*R. mangle*	1.23	--	--	--
	Brazil	Menezes et al. 2005	5	*R. mangle*	--	--	--	--
	Colombia	Elster 2000	5	*R. mangle*	--	--	--	--
	Cuba	Padrón 1996	5	*R. mangle*	1.78	1.85	--	--
	Mexico	Hernández et al. 2004	5	*R. mangle*	--	--	--	--
	USA	Goforth & Thomas 1979	5	*R. mangle*	--	--	--	--
	Kenya	Bosire et al. 2003	5	*R. mucronata*	2.90	--	--	3.0
	Thailand	Aksornkoae 1996	5	*R. apiculata*	3.56	2.64	22.81	--
	Vietnam	Hong 1996	5	*R. apiculata*	4.09	3.03	--	--
	Thailand	Macintosh et al. 2002	5	*R. mucronata*	3.82	3.37	--	--
			5	*R. apiculata*	3.73	2.73	--	--
Self Recovered	Brazil	This work **P**	5	Young *R.mangle* *L. racemosa.*	3.22	1.75	18.19	9.99
	USA	Ross et al. 2001	5	*R.mangle* *L.racemosa* *A. schaueriana.*	4.04	--	56.02	13.54
	Brazil	Silva et al. 2006 **P**	No data	*R.mangle* *L.racemosa* *A. schaueriana*	≤ 10	--	85.97	--
	Brazil	Medeiros & Sampaio 2008	No data	*R.mangle* *L.racemosa* *A. schaueriana*	*R.m* – 14 *L.r* - 18	--	105	14.1

Natural Mangroves	Brazil	Soares & Schaeffer-Novelli 2005	No data	*R.mangle* *A. schaueriana*	7.63	8,8	--	24.74
	Brazil	Soares 1999	No data	*R.mangle* *L.racemosa* *A. schaueriana*	6.32	--	--	14.81
	French Guiana	Fromard et al. 1998	No data	Young stage *L racemosa*	7.7	--	71.8	20.6
	French Guiana	Fromard et al. 1998	No data	Pioneer stage *L. racemosa*	3.5	--	31.5	13.70
	Puerto Rico	Golley et al 1962 **§**	No data	*R. mangle*	7,5	--	62.9	--
	USA	McKee & Faulkner 2000	> 60	*R.mangle* *L.racemosa* *A. schaueriana*	7.5	11.3	--	26.3
			> 50	*R.mangle* *L.racemosa* *A. schaueriana*	7.4	11.4	--	28.2
	USA	Coronado Molina et al 2004 **§**	No data	Dwarf / *R. mangle*	1.2	--	12.5	--
	USA	Ross et al. 2001	No data	Dwarf / *R.mangle* *L.racemosa* *A. schaueriana*	0.97	--	22.28	--

Biomass of “This work” were calculated using polynomial equations for Potengi mangroves, using DBH of **mature** trees in each area. **§-** data extracted from Komiyama (2008); -- no data; **P**- data of Potengi River.

Table 3. Size and occurrence of Brachyuran crab species of Superfamilies Grapsoidea and Ocypodoidea found in restored and self recovered areas before and 5 years after mangrove restoration. Crab size: S-small; M-medium; L-large. Occurrence information is represented by: --, absence; +, juveniles; ++, several age classes.

		Restored		**Self-recovered**		**Undisturbed mangrove**
Species	**Size**	**before**	**after**	**before**	**after**	
Grapsoids						
Goniopsis cruentata	M	++	++	--	++	++
Pachygrapsus gracilis	S	++	++	--	++	++
Sesarma rectum	S	+	--	+	+	+
Sesarma curacaoense	S	++	++	--	++	++
Armases angustipes	S	+	--	--	--	+
Aratus pisonii	S	+	++	--	++	++
Ocypodoids						
Ucides cordatus	L	--	+	--	+	++
Uca (Leptuca) cumulanta	S	++	++	++	++	++
Uca (Minuca) thayeri	S	--	++	--	++	++
Uca (Minuca) rapax	S	--	--	++	--	--
Grapsoids / Ocypodoids		6 / 1	4 / 3	1 / 2	5 / 3	6 / 3

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