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Original Article

Recruitment and mortality of *Rhizophora mangle* L. seedlings in the Tropical Southwestern Atlantic mangrove

Recrutamento e mortalidade de plântulas de *Rhizophora mangle* L. no manguezal do Atlântico Sudoeste Tropical

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Abstract

Studies in the long-term recruitment and mortality of mangrove seedlings can help to understand mangrove demography and its relationship with climatic variables, environmental restoration and advances in the ecology of this ecosystem. A seven-year population dynamics study of seedling recruitment and mortality in cohorts of *Rhizophora mangle* L. was carried out to identify expansion processes and patterns of survival in the understory of mangrove forests on the Atlantic coast of Brazil. The present study aimed to evaluate the relationship between recruitment and mortality *R. mangle* seedlings at the population level, salinity, and climatic variables (precipitation, temperature and humidity). On an annual scale, seedling recruitment was positively correlated with mean temperature. Seedling density was negatively correlated with the number of recruits and positively with the number of deaths. The number of recruits was associated with dead seedlings, temperature and precipitation considering a population scale, without grouping the data. The seedling density in the stands increased with the number of dead seedlings. Our findings described the relationship between climate variability (durability and magnitude of the dry/rainy season) and the long-term population dynamics of *R. mangle* seedlings in a poorly studied region and from what moment, on a monthly and annual time scale, did this relationship become significant and changes occur. The findings of this study provide information on the population dynamics of the species that will help in understanding mangrove demography. These results have important implications for projections about the recruitment and survival of the species thinking about to long-term climate change that will modify current weather patterns and mangrove conservation efforts.

Keywords: mangroves, climate variables, plants, field data, cross-correlation.

Resumo

Estudos sobre o recrutamento e mortalidade de plântulas de mangue em longo prazo podem ajudar a compreender a demografia dos manguezais e sua relação com variáveis climáticas, restauração ambiental e avanços na ecologia deste ecossistema. Um estudo de dinâmica populacional de sete anos sobre recrutamento e mortalidade de plântulas em coortes de *Rhizophora mangle* L. foi realizado para identificar processos de expansão e padrões de sobrevivência no sub-bosque de manguezais na costa atlântica do Brasil. O presente estudo teve como objetivo avaliar a relação entre recrutamento e mortalidade de plântulas de *R. mangle* em nível populacional, salinidade e variáveis climáticas (precipitação, temperatura e umidade). Em escala anual, o recrutamento de plântulas correlacionou-se positivamente com a temperatura média. A densidade de plântulas correlacionou-se negativamente com o número de recrutas e positivamente com o número de mortes. O número de recrutas foi associado a plântulas mortas, temperatura e precipitação considerando escala uma populacional, sem agrupamento dos dados. A densidade de plântulas nos bosques aumentou com o número de plântulas mortas. Nossos resultados descreveram a relação entre a variabilidade climática (durabilidade e magnitude da estação seca/chuvosa) e a dinâmica populacional em longo prazo de plântulas de *R. mangle* em uma região pouco estudada e a partir de qual momento, em uma escala de tempo mensal e annual, essa relação tornou-se significativa e as mudanças ocorrem. As descobertas deste estudo fornecem informações sobre a dinâmica populacional da espécie que ajudarão na compreensão da demografia dos manguezais. Estes resultados tem implicações importantes para as projeções sobre o recrutamento e sobrevivência da espécie, considerando as alterações climáticas em longo prazo que modificarão os atuais padrões climáticos, e os esforços de conservação dos manguezais.

Palavras-chave: manguezais, variáveis climáticas, plantas, dados de campo, correlação cruzada.

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1. Introduction

Rhizophora mangle L. (Rhizophoraceae) is the species dominant in many mangroves' forests, and is ecologically and economically important throughout the tropics, with a broad distribution along the Atlantic coasts of the Americas and West Africa (Schaeffer-Novelli et al., 1990; Spalding et al., 2010; Deyoe et al., 2020). This species, among other mangrove species, has some particularities as greater longevity in the understory (Kock, 1997; Lima et al., 2018), reproductive characteristics (*e.g.* viviparity) (Tomlinson, 1986; Vannucci, 2001), unique life story strategies and recruitment (Kibler et al., 2022), physiological mechanisms under fluctuating salinity conditions, high carbon stocking, among others (Pascoalini et al., 2022; Silva et al., 2023), and is susceptible to climate change (Agraz-Hernández et al., 2015; Irizarry and Andreu, 2023) that became it an interesting research subject.

Studies of seedling population dynamics are fundamental for understanding the ecological processes in mangroves colonized by this species, and can be applied globally, given the ecological and genetic proximity between the species (Tomlinson, 1986; Francisco et al., 2018). New-individual recruitment and mortality rates in *R. mangle* are widely variable across ontogeneticstages (Ellison and Farnsworth, 1993; Kock, 1997; Padilla et al., 2004; Proffitt and Travis, 2010; Goldberg and Heine, 2017; Simpson et al., 2017) and the early mangrove seedling establishment and development are regulated by intrinsic characteristics and environmental variables (He et al., 2022). Sloey et al. (2022) highlight the importance of recognizing that the causes of mortality vary according to the ontogenetic stages depending on species, geographic location, and interactions between species, and the relative influence of environmental drivers may shift throughout a species' ontogeny. In mangrove's ecosystem, survival is relatively low during the early stages (Rabinowitz, 1978; McKee, 1995; Lamb and Cahill, 2006), and demographic variations are linked to both biotic and abiotic selection pressures. The structure of the forest depends on the survival of seedlings to expand and maintain the ecosystem (Gillis et al., 2019).

The study of mangrove seedling demography is fruitful in interpreting mangrove demography, longevity dynamics and is of great importance to the restoration and conservation of the mangrove forests in response to global climatic change. In Brazil, population studies of mangroves are generally restricted to descriptive analyses of biometric measurements and structural characterization of forests as a function of environmental variables (e.g., Zamprogno et al., 2016; Pascoalini et al., 2019) or biomass-based measurements of diameter at breast height (DBH) (Soares and Schaeffer-Novelli, 2005; Zhila et al., 2014; Estrada and Soares, 2017). Different studies have evaluated the recruitment and mortality of *R. mangle* seedlings in natural forests (Baldwin et al., 1995; Padilla et al., 2004; López-Hoffman et al., 2007), the establishment, growth and survival in field (McKee, 1995; López-Hoffman et al., 2007; Proffitt and Travis, 2010; Goldberg and Heine, 2021; Kibler et al., 2022). These studies in mangroves were developed in different geographic locations and different time intervals. Those variables were also evaluated in studies with other mangrove species in controlled conditions (mesocosm experiments) (Balke et al., 2013; Gillis et al., 2019; Silva and Maia, 2019; van Hespen et al., 2022) and in field situations (Ewel and Baldwin, 2022; Sinsin et al., 2022; Sloey et al., 2022). Despite these studies, there are gaps in knowledge about the relationship between recruitment dynamics and seedling mortality. With regard to climatic variables, there is a gap in their association and demographic parameters and from what moment, on a monthly and annual time scale, these relationships become significant and changes occur. Furthermore, macroclimatic changes predicted by the Intergovernmental Panel on Climate Change (IPCC) are projected to alter coastal wetland ecosystems in the next century (Gabler et al., 2017), as a consequence of changes in the temperature and precipitation regimes and also in the amplitude and frequency of tidal flooding. These variables affect the most critical life stage of the mangrove forest – the seedling stage (Krauss et al., 2008; Riascos et al., 2018), and population dynamics. Seedlings are considered a critical period in the life cycle of the mangrove species because it presents physiological mechanisms and plant tissues that are still underdeveloped to tolerate the stress of the intertidal environment (Reyes-De la Cruz et al., 2002; Krauss et al., 2008). The seedling demography is one of the major drivers of the development of forest dynamics and structure in different phases of the ecosystem (McKee, 1995; Krauss et al., 2008), as well as for species mangrove establishment and distribution patterns (Devaney et al., 2021). Understanding the dynamics of seedling recruitment will help to comprehend the sustainability and longevity of species in the understory, which can inform in the conservation diagnosis. This knowledge will improve the stakeholders about the better decision in environmental policies related to climate change and the restoration process.

On a global scale, there is a demand for studies on the demographic variability of mangrove populations as a mechanism for understanding responses to global climate change (Gilman et al., 2008; Doney et al., 2012; Alongi, 2015; Asbridge et al., 2015; Schaeffer-Novelli et al., 2016; Feller et al., 2017; Riascos et al., 2018; Snyder et al., 2022). Experimental studies aiming to assess the response of mangrove seedlings to climate-related variables have been carried out in relatively short periods, ranging from six months to just over a year (Alvarenga et al., 2017; Riascos et al., 2018; Devaney et al., 2021). The ecological variability of recruitment and mortality in different environmental conditions is limited by the absence of *in situ* information at longer time scales. Long-term studies that can identify ecological variability, therefore, play a key role in understanding population dynamics and *in situ* understory responses.

We collected data over seven years to assess the population dynamics of *R. mangle* seedlings in humid tropical stands, fringe stands, dominated by *R. mangle* in southeastern Brazil, considered a novelty of a long longitudinal study, a set data collected over time in the same sampling unit, with seedlings of this species. This species is dominant in mangrove forests in Espírito Santo state (Tognella et al., 2020) and was the species chosen in this study for being the most representative of the area.

The present study had two main objectives: (i) to assess the recruitment and mortality of *R. mangle* seedlings as a function of time, and (ii) to understand the relationship between recruitment and mortality of *R. mangle* seedlings, salinity and climate variables (precipitation, temperature and humidity) to elucidate the variability of these parameters in the long-term with different monitoring time scales as they may have implications at the population level. The results obtained provide a better understanding of the ecological attributes of the species and the development processes in the mangrove forest understory. The data generated in this study allow comparisons with mangroves in other regions and enable predictions of understory dynamics.

2. Material and Methods

2.1. Study area

The present study was carried out with authorization from the State Institute for the Environment (IEMA - Instituto Estadual de Meio Ambiente *in portuguese*) of the state of Espírito Santo under the number GRN no. 013-2013 (Process no. 59484527). The sampled sites were in mangrove stands at the natural mouth of the Itaúnas river (18º33’38”S, 39º43’56”W), which is fully located within the conservation area (Law no. 9,985/2000) of the Itaúnas State Park (PEI), Conceição da Barra municipality, Espírito Santo, Brazil (Figure 1). Four common mangrove species occur in the area: *Avicennia schaueriana* Stapf & Leechm. Ex Moldenke, *Avicennia germinans* (L.) L., *Laguncularia racemosa* (L.) C.F. Gaertn, and *R. mangle*, with the latter species dominating (Tognella et al., 2007, 2020). The region’s climate is classified as tropical with dry winter (Aw) according to the Köppen climate classification, with two well-defined seasons (dry and rainy) and average annual precipitation between 1,000 mm and 1,400 mm (Alvares et al., 2013). Rainy season is between October and April (Passos et al., 2017). The tidal cycle in the study area is semidiurnal and all sampling stations were low intertidal areas subject to approximately the same inundation regime as observed visually.

2.2. Data collection

Data were collected in natural forests classified as fringe physiognomy (Schaeffer-Novelli et al., 2000) in three sampling stations named A, B, and C, with areas of 100, 176 and 200 m^2, respectively. *R. mangle* is the dominant species in the three sampling stations. The plot A is a monospecific forest of the species, and the other plots have representatives of *L. racemosa* and *A. schaueriana*. Fieldwork was carried out between January 2008 and December 2014. All individuals of *R. mangle* present in the three sampling stations with a height of less than 1 m were marked with numbered plastic tags and classified as seedlings (Lima et al., 2018). The first annual cohort evaluated was from 2008, and the final one was from 2014. In the specific case of the 2008 cohort, only individuals registered from March (at the begging of the experiment) onwards were considered for analysis, as the specimens registered at the outset of sampling (January and February) may have been recruited at different times, making it impossible to determine which actually belonged to that cohort. In this study, recruitment refers to individuals that have passed from the propagule to seedling stage at any time period.

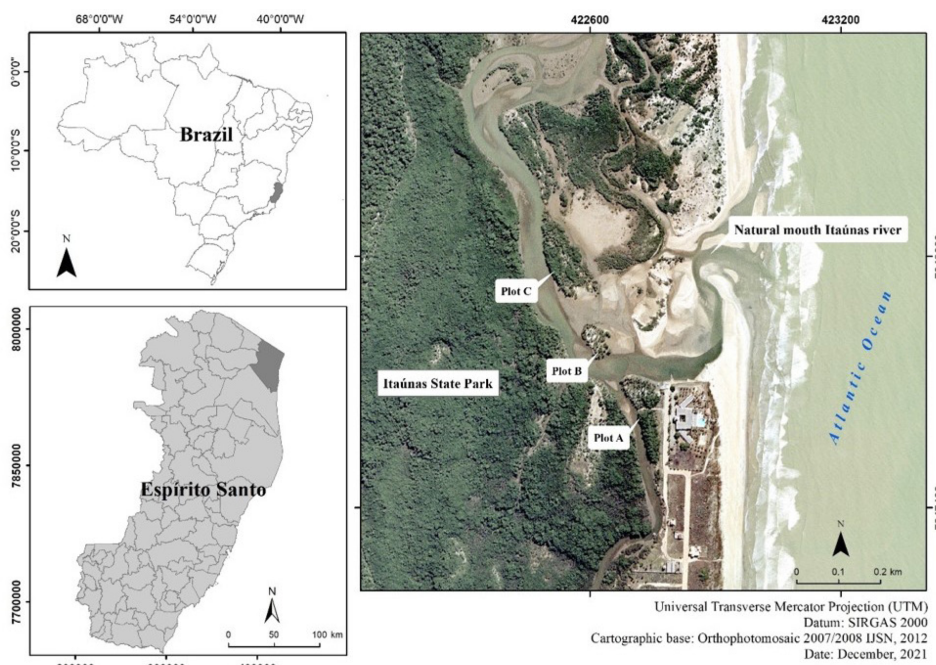

Figure 1. Location of the study area. Letters A, B, and C stand for the three collection stations in the mangrove swamp of the Itaúnas River estuary, Conceição da Barra, state of Espírito Santo, southeastern Brazil.

Between March 2008 and December 2013, the following variables were recorded on a monthly basis: 1) number of new seedlings (recruits), which were individually marked with a numbered plastic tag; 2) absent or dead seedlings that had been previously marked; 3) height (m) of each living individual; and 4) number and identification of alive specimens that advanced to the next ontogenetic stage (sapling). Here, we assumed that the cohorts are the sum of all seedlings established and sampled over a one-month period, and annual cohorts defined as the sum of seedlings recruited monthly within one year. Specimens with a height greater than 1 m were classified as sapling and those smaller than 1 m were considered as seedlings, following the specifications of Krauss et al. (2008). In 2014, sampling was carried out every two months according to the procedure described above, and, in 2015, occasional expeditions were carried out to count the number of marked live specimens.

Salinity (±1 psu) was measured in triplicate using a portable optical refractometer (model ITREF 10, Instrutemp, China) at each station from the water accumulated in galleries of "uçá"-crab, the swamp ghost crab (*Ucides cordatus* Linnaeus, 1763). Monthly meteorological data such as accumulated precipitation (mm), minimum, maximum and average temperature (°C), and average relative humidity (RH%) for the period between 2008 and 2014 were obtained from the records of meteorological station A616 (approximately 21 km distance from the study area) operated by the National Institute of Meteorology (INMET) located in São Mateus (Espírito Santo), the active station closest to the study area. These meteorological data were made available by the Capixaba Institute for Research, Technical Assistance, and Rural Extension (Incaper - Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural *in portuguese*) in 2014. Those environmental variables were selected for analysis, because there are available data and, for the reason that they influence the phenological patterns of the species (Van der Stocken et al., 2017; Chan-Keb et al., 2018) and, consequently, the release of propagules and the recruitment of seedlings, as well as they affect physiological process and survival of the seedlings (Ball and Farquhar, 1984; Krauss et al., 2008; Bompy et al., 2014).

2.3. Relationship between biotic and abiotic variables

Two statistical approaches were used to examine the relationships between biotic (mean density of adults and seedlings, seedling recruitment and number of dead individuals) and abiotic variables (namely mean salinity, precipitation, relative humidity, and mean temperature of the air). In the first approach we used canonical correlation analysis (CCorA) (Legendre and Legendre, 1998) and asymptotic tests (Wilks' Lambda) of the canonical dimensions (Wilks, 1935; Rao, 1973). In the second approach, cross-correlations were performed between the time series of the different biotic and abiotic variables (two by two) mentioned above. Whenever the assumptions of normality and homoscedasticity holds Pearson correlations were calculated. Spearman's ranks correlation (monotonic) was chosen when there was violation of normality. Different monitoring time scales were used in the cross-correlation analysis, namely data aggregated by year ("annual"), by month ("monthly") regardless of the year, or detailed "individual" measures obtained in the sampling across different months and years. Recruitment on an annual scale was calculated as the sum of all seedlings established in that year, which are defined as the annual cohort. Variations in monthly recruitment were analyzed to investigate if there are recruitment peaks during some specific period (*e.g.* rainy months). Cross-correlation was also used to assess the relationship between the mean density of adults and seedlings (individuals/m^2), the number of recruits, and dead seedlings. All statistical analyses were carried out in the R program (R Core Team, 2021) using *CCA* (González and Déjean, 2023), *CCP* (Menzel, 2022), *GGally* (Schloerke et al., 2021), *ggplot2* (Wickham, 2016), *MASS* (Venables and Ripley, 2002) and *vegan* (Oksanen et al., 2020) packages.

3. Results

The minimum, average and maximum values of temperature in different years oscillated around 20 °C, 25 °C and 30 °C, respectively (Figure 2a). Temperature variations showed seasonal pattern. High values occurred in austral summer (Jan-Mar), while temperature was low in the winter (Jul-Sep). Low salinities were close to 12 psu, but values close to 40 psu occurred in some months. Part of variability in salinity was due to time of collection, which occurred in different tidal stages (before or after the flood) and fluvial influence (high or low flow), as well as the interannual rainfall variability and river mouth migration. Precipitation was higher at the end of the year (Figure 2b), especially in the months of October and November, which coincides with the beginning of the rainy season in the region. The relative humidity of the air varied between 74.2% and 87.8% over the months from 2008 to 2014.

3.1. Recruitment, number of dead individuals, and density

The months with the greatest recruitment changed from year to year: recruitment peaked between January and April in 2010, May and November in 2011, and May and June in 2013 (Figure 3). In the first four years of monitoring, the annual number of recruits was greater than deaths in every cohort (Figure 4a). In contrast, the number of dead individuals has surpassed that of recruits in the later years of the study (Figure 4a). Overall, recruitment was higher on average during the dry season (April to September) (Figure 4b).

Similar temporal patterns were apparent in the density curves for the total number of individuals (adults + seedlings of all mangrove species in the study area) and the sum of only the seedlings of *R. mangle* (Figure 5), with no changes in the number of adult individuals over the study period. The numbers of seedlings and adults were stable throughout 2008 and 2009, with a sharp increase in April 2010 across all stages of development. These numbers remained stable until June 2011, when another increase occurred (December 2011), represented by the apex in terms of the density of individuals (individuals/m^2) recorded throughout the entire time series. This figure subsequently declined slowly until the end of monitoring, except for a slight increase between April and August 2013.

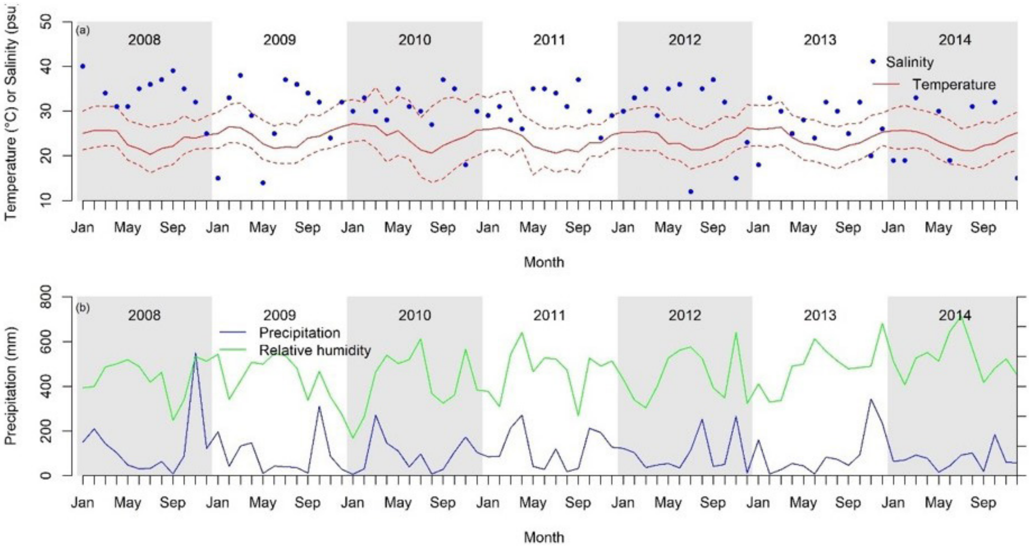

Figure 2. (a) Temperature (°C) and Salinity (psu); (b) Precipitation (mm) and Relative humidity (%) in the study area over the 7 years of monitoring. The dashed lines represent maximum and minimum temperature.

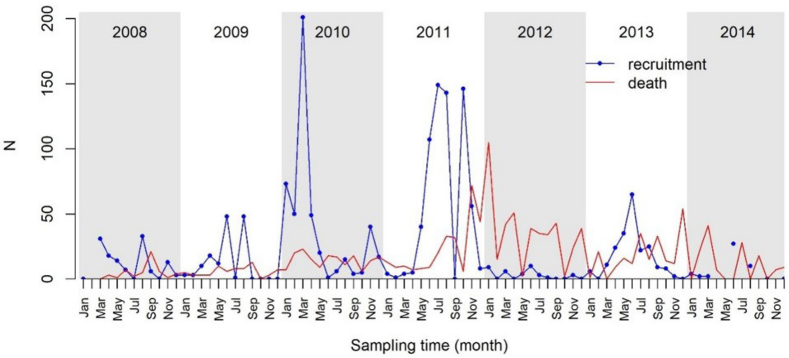

Figure 3. Variation in the number of recruited and dead seedlings of *Rhizophora mangle* in the cohorts month to month between 2008 and 2014 considering the three collection stations over the 7 years of monitoring.

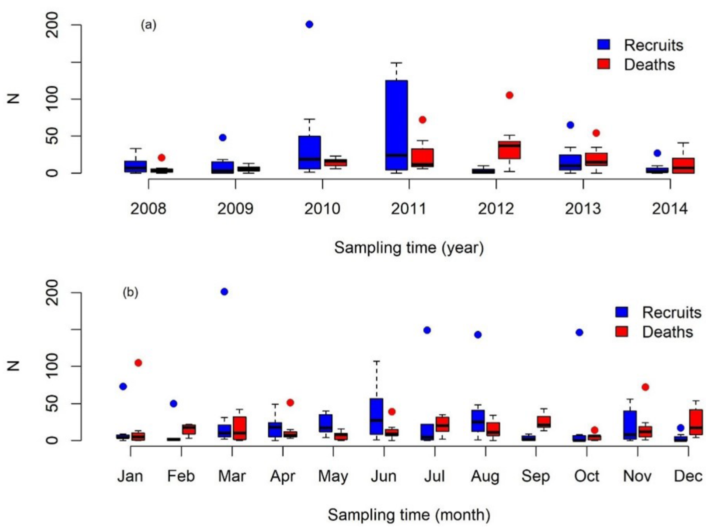

Figure 4. (a) Annual total number of recruited and dead individuals considering all the months of the year and the three collection stations; (b) monthly total of recruited and dead individuals, considering the same months regardless of the year.

3.2. Demographic and environmental variables

The CCorA results showed that the relationships between the number of recruits and dead seedlings, as well as with abiotic variables, were weak and non-significant (Table 1).

Cross correlation analyses are showed in Figure 6 and Figure 7. Significant correlations are indicated by vertical lines that crosses de dashed blue lines. X-axis stand for the time lags. On an annual scale, there was a significant positive correlation between temperature and recruitment, as shown by the cross-correlation analyses (Figure 6a) with a one-year lag period between the two variables. This implies that high mean temperature in a given year was associated with higher recruitment in the subsequent year, *i.e.*, past values of mean temperature influence future values in recruitment. On an annual scale, there was a significant negative correlation with a two-year lag between forest density and recruitment (Figure 6b). This implies that recruitment was lower two years after an increase in forest density. The highest number of dead individuals occurred in the years with the highest recruit density, as shown by the significant and positive correlation with no time lag between these variables (Figure 6c). On a monthly scale, the only significant correlation between biotic and abiotic variables was between relative humidity and recruitment, with no time lag (Figure 7a).

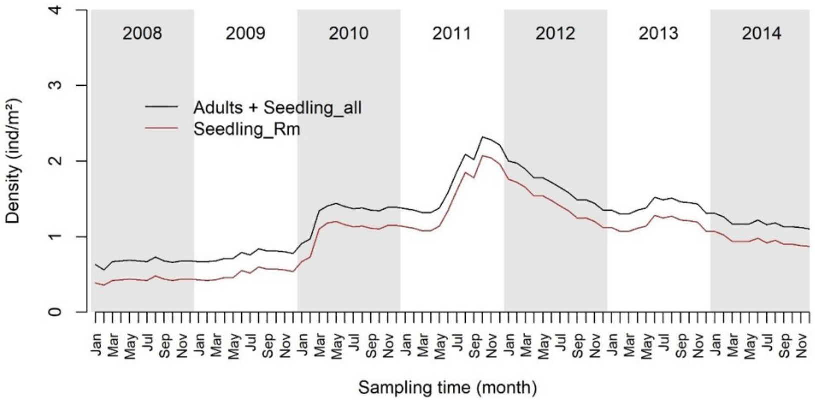

Figure 5. Monthly variation in the total density of adults and seedlings. Adults + Seedling_all: sum of adult individuals and seedlings of *Avicennia schaueriana, Laguncularia racemosa,* and *Rhizophora mangle*; Seedling_Rm: seedlings of *R. mangle*.

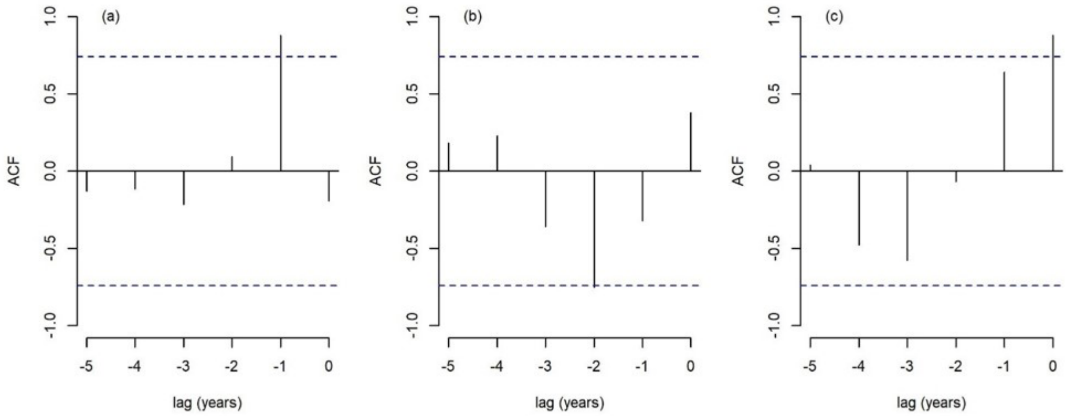

Figure 6. Cross autocorrelation function (ACF) on an annual time series between (a) mean temperature and annual number of recruits, (b) stand density and number of recruits, (c) stand density and number of dead seedlings of *Rhizophora mangle*. Dashed lines indicate 95% confidence interval.

Table 1. Tests of Canonical Dimensions.

Dimension	Canonical Correlation	F Approximation	Df1	Df2	p-value
1	0.169	0.425	8	156	0.905
2	0.118	0.374	3	79	0.772

F = This is the F statistic for the given multivariate test; Df = degrees of freedom used in determining the F statistic; p-value = p-value associated with the F statistic.

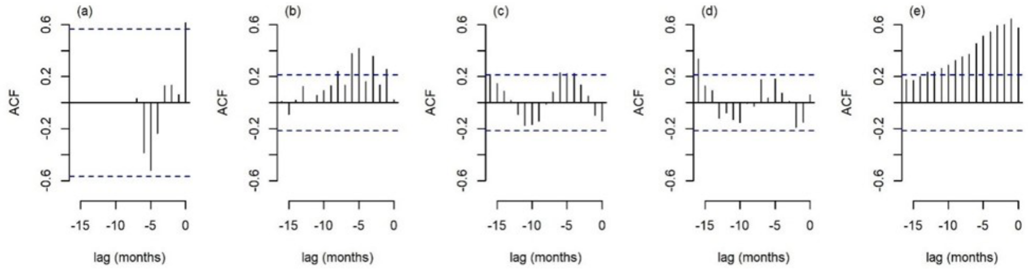

Figure 7. Cross autocorrelation function (ACF) for the monthly scale time series between (a) relative humidity and number of seedling recruits, and for individual-scale time series (b) number of recruits and dead seedlings, (c) mean temperature and number of recruits, (d) precipitation and the number of recruits, (e) stand density and dead seedlings of *Rhizophora mangle*. Dashed lines indicate 95% confidence interval.

Significant and positive correlations were observed between numbers of recruits and dead individuals, with monthly lags of one, three, five, six, and eight months (Figure 7b). Hence high number of recruits in the past are associated with high number of dead individuals in the near future. The positive correlation with a lag between four and six months (Figure 7c) between mean air temperature and the number of recruits indicated that high temperatures in the past led to greater recruitment later on. The correlation between precipitation and the number of recruits was also positive, with a lag of 16 months (Figure 7d). The positive correlation coefficient found between density and number of dead individuals described a lag between zero and 13 months. This variable result indicated that the fluctuations observed in the number of dead individuals might reflect the density of the stand, with seedling mortality increasing in denser stands (Figure 7e).

4. Discussion

Quantifying the mortality of seedlings in the first years after cohort recruitment provides a perspective on their potential for long-term establishment, clues about the quality of the environment, and allows an understanding of population dynamics in the understory of mangrove forests. Interannual differences were observed in terms of mortality and recruitment. In general, the recruitment of *R. mangle* seedlings in the population occurred throughout the study period but with different magnitudes in each generation (cohort). Similar to the findings of Proffitt et al. (2006), recruitment rates reflected the forest structure in which the seedlings settled, with more *R. mangle* recruits in forests where the species already dominated. In tropical mangroves, *R. mangle* produced propagules throughout the year (Fernandes, 1999; Peel et al., 2019), contributing to continuous recruitment, although not all seedlings establish successfully due to the different stresses involved in this process (Krauss et al., 2008; Simpson et al., 2017).

In addition to the variability in the number of recruits in the monthly and interannual analyses, there was an oscillation in the annual recruitment and the mortality of the cohorts. This variability was shown to be related to past environmental conditions like temperature and air humidity associated with the production of descendants by adults, higher humidity and temperatures results in higher recruitments, as observed by Alvarenga et al. (2017) and Chan-Keb et al. (2018). There is a tendency for recruitment to have reflected seasonal variation in air temperature and humidity, along with other environmental variables, not evaluated in this study. The results showed that relatively high temperature, considering the time series, is seasonal indicator of a favorable environment, but it is not an isolated regulator. Environmental conditions also affected the release of propagules (Van der Stocken et al., 2017), as well as, different phenophases and the health of the parent. The alternation between the periods of water deficit and surplus before and during the study period, may have influenced the production and phenology of *R. mangle* stands, and consequently the recruitment of seedlings. Variations in precipitation are associated with changes in salinity stress, litter production, and the species' phenology (Chan Keb et al., 2018), in addition to playing significant roles in these processes (Agraz-Hernández et al., 2015). Salinity is one of the most important factors in the mangrove environment that controls survival (Lugo and Snedaker, 1974), photosynthesis and growth of *R. mangle* seedlings (Krauss and Allen, 2003). The salinity variations in the present study did not reach values above 40, remaining within the physiological optimum for the species as reported by Bompy et al. (2014), not being significant for the recruitment of the species in the monitoring. The strong relationship between mean temperature and recruitment at annual and individual scales suggests that temperature is a good indicator of conditions that favor recruitment, especially between the dry season months of April to September. In contrast, higher temperatures favor the production of a greater number of descendants of the species, as long as precipitation remains high or stable. The photosynthesis of mangrove species is stimulated by temperature. Specifically, carbon assimilation increases with leaf temperature up to 35 °C (Ball, 1988; Clough, 1992). In the present study, the average air temperature did not exceed 26 °C. In general, the leaf temperature remains around 2 to 3 °C below the air temperature for *R. mangle* (Lugo et al., 2007), which remains within the optimal range for photosynthesis.

The detailed analysis of the time series allowed us to verify a correlation between recruitment and the number of dead individuals with lags of one, three, five, six, and eight months. This result means that the understory response to the entry of new individuals is not always instantaneous since it does not depend only on local conditions.

The variability observed between the months with higher mortality indicated the importance of factors related to the habitat, such as shading and density, and others linked to the stage of development of the recruits. The concentration of carbohydrates stored in the propagules can be a critical factor in the survival of seedlings like these at an early stage, depending on the reserves of the propagule (Dissanayake et al., 2014). After implantation, the individual starts to depend on the energy reserves of the hypocotyl of the seedlings. With declining reserves (Rabinowitz, 1978; Smith and Snedaker, 2000; Ball, 2002) and the rate of photosynthetic assimilation surpassed by respiration (Rabinowitz, 1978), the risk of death is high, making the individual more vulnerable to environmental fluctuations and reducing its probability of survival. This may explain the different time scales observed in this study.

Since new individuals increase competition for resources and space, the densification of the understory should act as the precursor of the first mortality in mangrove forests, as described by Jimenez et al. (1985). This behavior is typical of populations with self-thinning (Berger and Hildenbrandt, 2003). The increase in the number of dead individuals with higher forest density on different temporal scales, as indicated by the significant correlation between the two variables, corroborates these inferences. Thus, competition for conditions and resources associated with low photosynthetic biomass, production of conservative internodes for *Rhizophora* spp. (Padilla et al., 2004), and forest shading would amplify the mortality rate. Studies performed with seedlings of *Rhizophora* spp. analyzed over a year indicated that the complexity and development of the forest affected the mortality rate (Riascos et al., 2018). In the present study, preliminary field observations suggest that the complexity of the stand is a predictor of the mortality rate, with the number of dead individuals increasing as a function of stand density. The inverse relationship between stand density and recruitment suggests limited conditions and resources for the propagule-seedling stage transition.

The relationship between recruitment and precipitation was also evident in the detailed analysis of the time series, where higher seedling recruitment was recorded after periods of higher precipitation and showed that the seasonality of precipitation is also important in the recruitment process. These results suggest a delayed response in recruitment that is closely linked to the relationship between forest production and climatic variables since precipitation, temperature, and release of propagules are associated with the rainiest periods (Fernandes, 1999; Nadia et al., 2012; Van der Stocken et al., 2017). Precipitation is an important factor in flowering and propagule production in Rhizophoraceae. Water restriction reduces flower production and the development of propagules until they mature in below-average rainfall periods (Tyagi, 2004) and consequently influences the number of recruits for the seedling stage. High environmental temperature, low precipitation, and high relative humidity can reduce gas exchange at the stomatal level (Ball and Farquhar, 1984; Clough and Sim, 1989), decreasing primary productivity and consequently the acquisition of biomass, directly reflecting on the transition between stages of development. The significant relationship between climatic variables (precipitation, temperature, and humidity) and recruitment at different temporal scales showed importance in developing the mangrove understory. This relationship is essential for understanding how the population dynamics of *R. mangle* will behave in the face of long-term variations in mean temperature and precipitation since changes in the patterns of these variables can modify the period of propagule release (Van der Stocken et al., 2017). Changes in temperature patterns, rainfall, and relative sea level caused by climate change can impact coastal ecosystems such as mangroves (Doney et al., 2012; Riascos et al., 2018; Alongi, 2021), since precipitation and temperature are important seasonal indicators for plant growth and development (Van der Stocken et al., 2017). Changes in seasonal rainfall patterns may lead to faster and deeper salt fluctuations in the top layer of soil, with the potential to affect the physiology of trees, saplings and seedlings in tropical rain forest (Stahl et al., 2013) interfering in carbon assimilation (*in preparation*) and long-term population dynamics. Temperature, as well as the intensity and frequency of storms, can affect population dynamics, changing the productivity and reproductive success of these forests, as well as the recruitment dynamics of *R. mangle* (Peel et al., 2019).

Assessing whether a population of *R. mangle* seedlings is self-sustaining over the long-term or whether mortality is greater than recruitment is crucial for estimating and understanding the population-level response to climate variability. Since mortality exceeded recruitment in this study between 2012 and 2014, the ability to develop the understory and its re-establishment in the face of future impacts, such as prolonged drought and/or reduced rainfall, may become compromised and require long periods for impacted areas to recover.

Our results showed that the method of analysis presented was effective at assessing population dynamics of *R. mangle* seedlings and determining their relationship with climatic variables (precipitation, temperature and humidity), which are likely similar in other mangroves in the South Atlantic or other tropical countries with the same climate regime. Climate variability implies the relationships between variables and seedling population parameters and can explain differences in results evaluated at different time scales. The present evidence can be used as preliminary indications of the population dynamics of an entire mangrove forest, with an analysis of understory dynamics in different environmental settings. We suggest that further research should verify the potential of these long-term climatic variables *in situ* seedling recruitment and mortality. Future studies should take place in distinct regions with different stressors and geomorphological and oceanographic configurations to jointly assess the species' ability to change its population dynamics in the understory. In temporal observations, it is important to observe oceanographic conditions and climate since climatic events and their amplification over the coastal system produce different responses in individuals belonging to different cohorts.

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