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Seasonal atmospheric and oceanographic factors influencing poleward mangrove expansion in the southeastern American coast

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A R T I C L E I N F O

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A B S T R A C T

Mangrove ecosystems are distributed worldwide, along tropical and subtropical coastlines. For a long time, mangrove biogeographers have been challenged by the question: why is mangrove distribution restricted to its current latitudinal limits? The Araranguá estuary in Brazil is located ~75 km beyond the eastern South America mangrove limit. Despite its geomorphology apparently being suitable for mangrove colonization, mangroves have been reported absent from this estuary. In this work, we analyze key environmental variables (such as the longest available observational *in-situ* records of air temperature) and provide an assessment of other environmental players (such as the adjacent ocean circulation and upwelling system) to better understand which factors could be determinant in the species range limits in eastern South America. Our results and assessment suggest that, depending on the season, multiple factors could combine to prevent a poleward dispersion of mangrove species. These are mainly the northward-directed longshore drift which dominates throughout the year and the high occurrence of chilling events during winter, although seasonal upwelling of cold waters in spring and summer could also influence the propagules' viability.

1. Introduction

The mangrove forest is an ecosystem with worldwide distribution in tropical and subtropical coastal environments (Spalding et al., 2010; Giri et al., 2011; Bunting et al., 2018). This ecosystem has a range restricted to latitudes around 30°, at the eastern sides of continents. This spurred the analysis of limiting factors that allow mangroves to expand or restrict their global distribution further north and south (Chapman, 1975; Barth, 1982; Duke, 1992; Quisthoudt et al., 2012; Osland et al., 2017b; Cavanaugh et al., 2018).

Low air temperature is considered an important limiting factor for mangrove expansion into higher latitudes at a global scale (Chapman, 1975; Woodroffe and Grindrod, 1991; Quisthoudt et al., 2012; Osland et al., 2017b; Wu et al., 2018). This is explained since the temperature can directly and/or indirectly affect the physiological and phenological processes of the plants (Chuine and Beaubien, 2001; Larcher, 2003). Laboratory experiments and empirical studies showed how temperature conditions, depending on their duration and intensity, can influence species distribution by inhibiting the metabolic activities of the plants and/or by damaging cell or tissues (Larcher, 2003; Kao et al., 2004; Krauss et al., 2008; Chen et al., 2017).

Explanations have been proposed for the absence of mangroves in Araranguá (Schaeffer-Novelli et al., 1990; Soares et al., 2012; Ximenes et al., 2018), an estuary geomorphologically suitable for this ecosystem, that is ~75 km south from the actual mangrove limits in Brazil. Schaeffer-Novelli et al. (1990) suggested that the chilling events of air temperature in this estuary is not suitable for mangroves. On the other hand, Soares et al. (2012) put forward multiple limiting factors for mangrove range limits dispersal in eastern South America, reflected by mean air temperature, annual mean Sea Surface Temperature (SST), the occurrence of frost events, upwelling, and the northward-directed longshore drift.

More recently, Ximenes et al. (2018) used daily Multi-scale Ultra-high Resolution Sea Surface Temperature (MUR-SST) data to analyze the frequency of chilling events of SST that could negatively affect the dispersal of (viable) propagules beyond their limits. While, *Rhizophora mangle* can float much longer than *Laguncularia racemosa* (Van der

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Stocken et al., 2017), it is probably less tolerant to cold SST (Ximenes et al., 2018). For this reason, Ximenes et al. (2018) suggested that chilling events of SST could explain why *R. mangle* is limited in Praia do Sonho (~27°S) and a higher abundance of *L. racemosa* is found in Laguna (28°30′S). However, the chilling events of SST cannot explain why mangroves are restricted to the region to the north of Laguna (Ximenes et al., 2018).

Predictions of mangrove range expansion can be improved since refined temperature thresholds for mangrove species frost damage, mortality, or recovery are somewhat better known nowadays (Quisthoudt et al., 2012; Cook-Patton et al., 2015; Osland et al., 2017b; Cavanaugh et al., 2018; Ximenes et al., 2018; Wu et al., 2018; Cavanaugh et al., 2019; Osland et al., 2020a,b; Devaney et al., 2020; Bardou et al., 2021; Chapman et al., 2021; Snyder et al., 2021). Moreover, Santos Borges et al. (2019) showed that the germination rate of *L. racemosa* propagules is below 50% at air temperatures of 10 °C and 15 °C. Reduction in seedling stem elongation rate, altered leaf gas exchange rates, and increased mortality were associated with chilling events at 10 °C especially under high salinity and low humidity conditions (Devaney et al., 2020).

Contrasting literature statements on the limiting factors reflect our lack of understanding as to why mangroves do not cross their current limit in eastern South America. Analysis of hourly and daily data of air temperature in terms of the frequency of freezing and chilling events, as it was done for the SST in Ximenes et al. (2018), could contribute to this understanding (Osland et al., 2013, 2017b; Cavanaugh et al., 2018, 2019). In addition, a state-of-the-art literature review with respect to oceanographic conditions could provide us with insights into other possible limiting factors playing a role in restricting mangroves within actual limits.

Despite not being located within the mangroves, the meteorological stations provide the closest available continuous *in situ* measurements of air temperature. Atmospheric and oceanographic factors will be viewed in the light of their seasonality, and compared to the period of propagules production. In this direction, we will analyze meteorological and oceanographic factors both at mangrove sites (including the mangrove's southernmost limit) and beyond it. To the best of our knowledge, this study is the first to follow this approach for studying the mangrove range limits in eastern South America and beyond it.

2. Material and methods

2.1. Study area

The study area encloses the region with the southernmost mangrove patches (Itajaı, Praia do Sonho and Laguna) in the southeastern American coast, as well as the Araranguá estuary, which is located at about 75 km beyond the mangrove limit (Fig. 1a). Both referred mangroves and estuary are located within Santa Catarina (SC) state, in South Brazil region (Fig. 1b).

In Praia Brava-Itajaı (26°56'S) three species are found: *Avicennia schaueriana*, *Laguncularia racemosa*, and *Rhizophora mangle* (Tognella and Oliveira, 2012). About 15 km southward of Itajaı, in Camboriú, mangroves were reported with a species composition of *Avicennia schaueriana* Stapf and Leechm. ex Moldenke (Acanthaceae) and *Laguncularia racemosa* (L.) C.F. Gaertn. (Combretaceae), but absence of *Rhizophora mangle* L (Rhizophoraceae) (Tognella and Oliveira, 2012). However, since these two mangrove forests are close to each other, we will treat them as a single patch, hereafter Itajaı mangroves. On the mainland and facing the southern tip of Santa Catarina island, the mangrove in Praia do Sonho (27°48'S) is composed of all three species. *Rhizophora mangle* reaches its geographical limit at 27°53'S, ~78 km north of Laguna, in the municipality of Palhoça (Fig. 1c).

The eastern South America mangrove limit (hence for all species), also recognized as the Brazilian southernmost mangrove limit, is located in the municipality of Laguna. This means that in Laguna (28°30'S) lies the geographical limit of *Avicennia schaueriana* Stapf and Leechm. ex Moldenke (Acanthaceae) and *Laguncularia racemosa* (L.) C.F. Gaertn. (Combretaceae) (Schaeffer-Novelli et al., 1990; Soares et al., 2012).

In turn, Araranguá is an estuary beyond the eastern South American mangrove limit (28°55'S) (Schaeffer-Novelli et al., 1990; Soares et al., 2012). It may be suitable in its geomorphological setting (Fig. 2), although saltmashes are present, mangroves are absent due to other environmental conditions and/or its difficult accessibility (Fig. 2b). In between Laguna and Araranguá, the orientation of the coastline changes sharply (Fig. 1c and 2a), which is potentially deflecting propagules offshore.

2.2. Data sets

2.2.1. Air temperature data

To assess the air temperature data at the southernmost mangrove patches in eastern South America and beyond the mangrove range limit, we used data from the closest meteorological stations (Fig. 1). It is worthwhile saying that often meteorological stations are not located within the mangrove forests. This is the case for our study since no long-term measurements of air temperature are available for the mangrove sites. Facing the same shortcomings, other mangrove-related studies used data from meteorological stations located nearest to studied mangrove areas (Schaeffer-Novelli et al., 1990; Soares et al., 2012; Osland et al., 2017a) or gridded climate data sets interpolated from several meteorological stations in order to study mangrove biogeography (Ximenes et al., 2016) or mangrove-saltmarsh interface dynamics (Osland et al., 2013, 2017a). The local conditions of an estuarine ecosystem are particularly shaped by soil, shallow and brackish water, and wind and wave exposure (Tomlinson, 2016). Even if these factors slightly affect the microclimate inside mangroves (Devaney et al., 2017), some of them are likely to have a correlation with chilling temperature events captured by the meteorological stations, which are good proxies of the conditions of the surrounding mangroves, though locally logged data may differ between weather stations (Seghers, 2014). While acknowledging the limitation of not having a meteorological station within the mangrove forest in the present study, we make an effort to incorporate this in the interpretation of our findings.

The available air temperature data was obtained from the Brazilian National Institute of Meteorology (INMET) (INMET, 2020). More precisely, we use data from four meteorological stations that are the nearest to the southernmost mangrove patches (Itajaı, Praia do Sonho, and Laguna), as well as near Araranguá estuary, beyond mangrove limits. As named by INMET, from north to south, the meteorological stations are: A868-Itajaı (SC), A806-Florianópolis (SC), A866-Santa Marta (SC), and A867-Araranguá (SC) (see Fig. 1c).

The observing periods for each station differ. Florianópolis station has the longest observations spanning from 01/Jan/2003 to 31/Dec/2019 (see Fig. 3b). However, since our main goal is to compare the conditions between stations, we selected an overlapping period spanning from 01/Jan/2011 to 31/Dec/2019. Within that period, Santa Marta and Araranguá stations have distinguishable gaps. The first between 27/Oct/2015 and 18/Feb/2015, and from 23/Jun/2018 to 27/Nov/2018 (see Fig. 3c), and the second between 09/Feb/2017 and 12/Jul/2017 (see Fig. 3d).

Whenever comparisons among stations are made, the common period (01/Jan/2003–31/Dec/2019) and the data gaps are considered for having paired data from all four stations. Comparisons are made in terms of air temperature metrics such as: mean annual air temperature, mean air temperature of the coldest month (July), absolute minimum daily air temperature, mean air temperature of the 10 coldest days and monthly mean thermal amplitude.

We also analyzed the different sites based on the cumulative occurrences of chilling events. Again, the same overlapping period and data gaps were considered. Since germination rate was reported to be

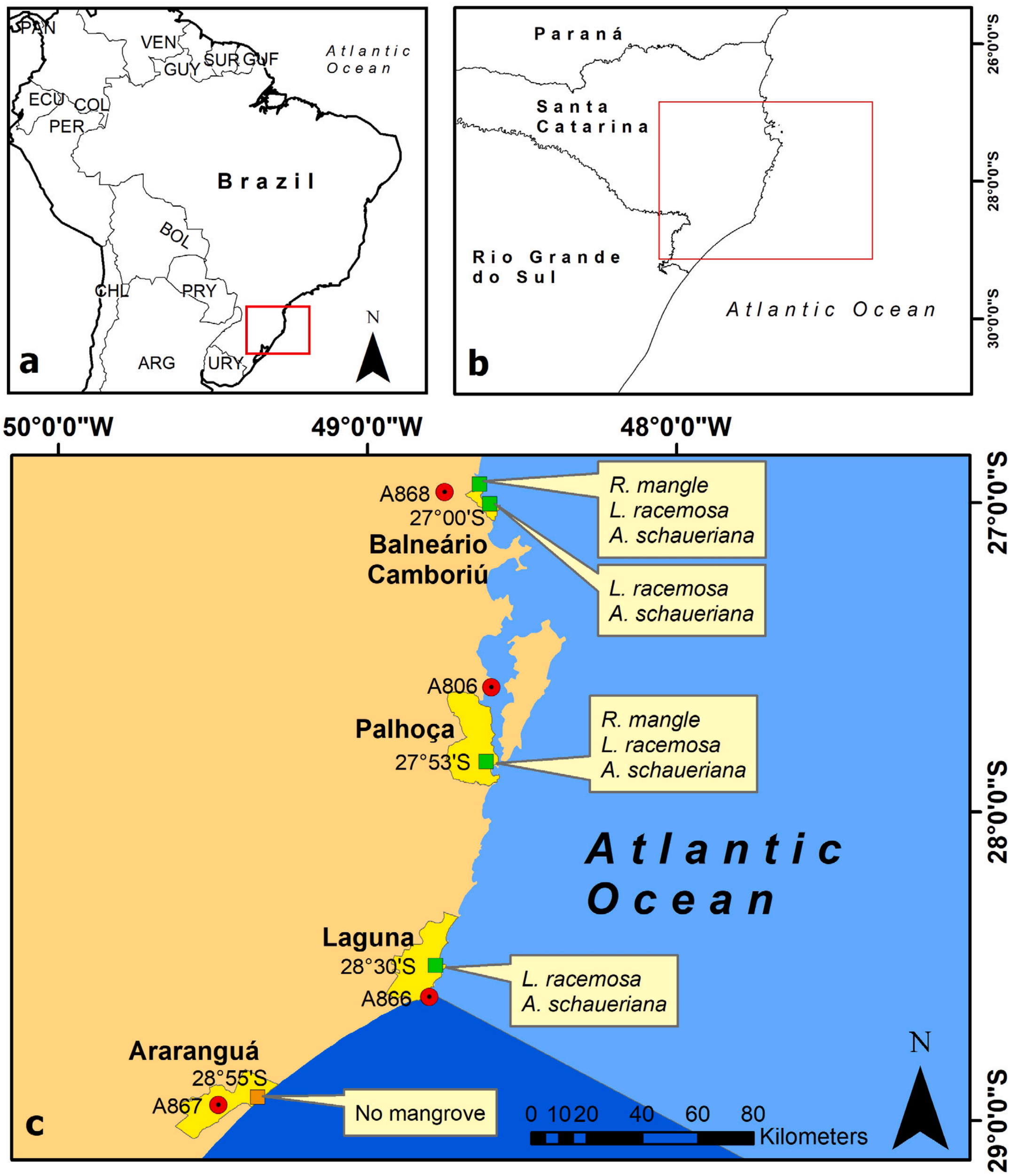

Fig. 1. (a) The geographical location of the study area in eastern South America (Brazil); (b) Santa Catarina State (SC) boundaries and the area within the red square shown in detail; (c) Detailed map of the eastern South America mangrove limit located in Laguna, Brazil. The green squares represent the southernmost mangrove stands in Itajaı (Balneário Camboriú municipality in yellow), Praia do Sonho (Palhoça's municipality in yellow) and Laguna (Laguna's municipality in yellow). The orange square represents Araranguá estuary (Araranguá's municipality in yellow), beyond the eastern South America mangrove limit. The red circles show the location of the meteorological stations in Itajaı (station code A868 - 26°57′S - 48°45′W) located about 12 km from Itajaı mangroves and 15 km from Camboriú mangroves; Florianópolis (station code A806 - 27°36′S - 48°36′W) located about 25 km from Praia do Sonho; Santa Marta station (station code A866 - 28°36′S - 48°48′W), about 12 km from Laguna estuary (mangrove limits); and Araranguá station (station code A867 - 28°57′S - 49°29′W), about 15 km beyond the southernmost mangrove limit. The light blue Atlantic Ocean is the Southeastern Brazil marine ecoregion and the dark blue is the Rio Grande marine ecoregion according to Spalding et al. (2007). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reduced below 50% in 10 °C and 15 °C for *L. racemosa* (Santos Borges et al., 2019), all temperature values below 15 °C for air temperature were classified as chilling events for mangrove plants. The hourly air temperature $\leqslant$ 5 °C, daily $\leqslant$ 10 °C, and daily $\leqslant$ 15 °C events are used as references. Moreover, based on the scientific literature (more detail in Section 3.1.3), these values were deemed to influence the physiology and metabolic activities of the mangrove plants.

Physiological stress responses were reported in the scientific literature for plants that were subjected to temperatures we consider herein as chilling events. This threshold allows us to investigate differences between the studied sites. After the chilling events (hourly and daily) for air temperature were defined, the cumulative occurrence of chilling events was determined by the number of occurrences of chilling events that happened over the studied years.

Besides the fact that chilling events expectantly occurred mostly during the winter, some low values were also found in other seasons, for example, in autumn. The intensity of such events is represented by the temperature values (chilling events), and the frequency by the number of occurrences of chilling events observed along the years. These two diagnostics (intensity and frequency) are also known to affect the geographical distribution of species (Larcher, 2003).

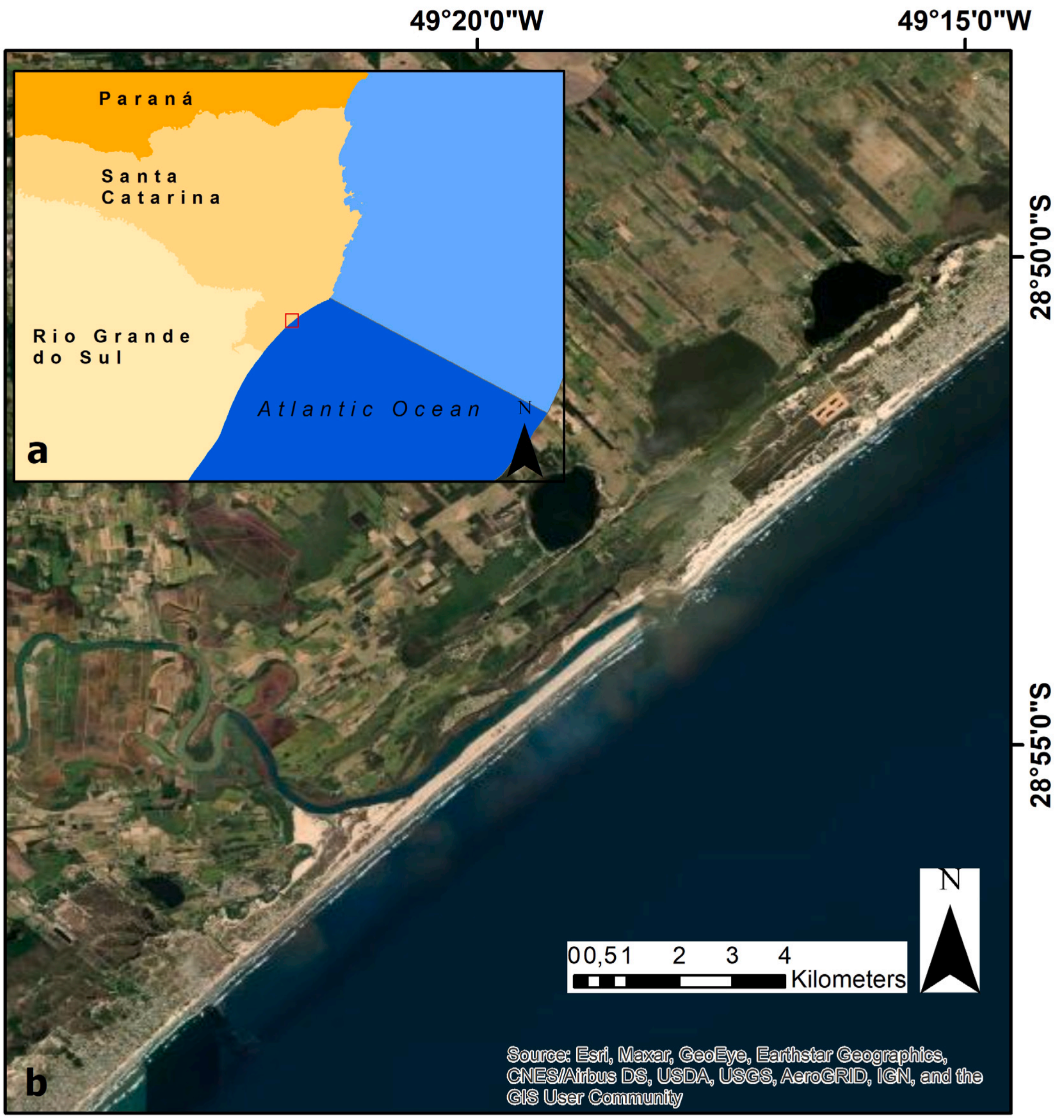

Fig. 2. (a) The geographical location of the study area in eastern South America (Brazil), Santa Catarina State (SC) boundaries and the area within the red square shown in detail. The light blue Atlantic Ocean is the Southeastern Brazil marine ecoregion and the dark blue is the Rio Grande marine ecoregion according to Spalding et al. (2007); (b) Detailed map of the eastern South America located in Araranguá estuary. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2.2. Precipitation data

Precipitation data is provided by INMET through the same meteorological stations: A868-Itajaı (SC), A806-Florianópolis(SC), A866-Santa Marta (SC), and A867-Araranguá (SC) (see Fig. 1c). Integrated seasonal means of precipitation (mm/season) are calculated based on daily hourly observations. As for the air temperature, for having paired data when comparing stations, the overlapping period and data gaps are considered.

2.2.3. Oceanographic data

The oceanographic (sea surface temperature) data used for representing the upwelling system off Cape Santa Marta (28°36′S) was sampled during the Plata Summer Cruise (2004) and is available in Möller and Piola (2004) (see their Table A.1; https://www.researchgate.net/publication/292331706_The_Plata_Summer_Cruise_2004). Information about the upwelling seasonality is provided by (Campos et al., 2013).

The seasonality of SST fields is estimated using the Operational Sea Surface Temperature and Sea Ice analysis (OSTIA) database (Donlon et al., 2012) for the period 2007–2015, while the patterns of longshore drift is inferred from Siegle and Asp (2007).

3. Results and discussion

3.1. Air temperature influencing mangrove expansion

3.1.1. Temporal series of air temperature, means and amplitude

Fig. 3 shows the hourly, daily, and monthly air temperature as provided by the meteorological stations and Table 1 summarizes the air temperature averages calculated in terms of annual, winter, individual winter months (July, August, and September), and 10 coldest days periods. These metrics are calculated over the defined common period (01/Jan/2011–31/Dec/2019). Table 1 also displays the mean air temperature amplitude and the absolute minimum value of daily temperatures for the reference period. For most of the metrics shown in Table 1, air temperature is warmer in Florianópolis. By comparing Laguna and Araranguá, mean annual air temperatures (19.77 and 19.86 °C) are higher in the second location so that air temperature is slightly higher beyond the mangrove limit.

Our results seem to corroborate those of Chapman (1977), Soares et al. (2012), where a mean air temperature of the coldest month (July) at ~16 °C isotherm coincides with the mangrove range limits in

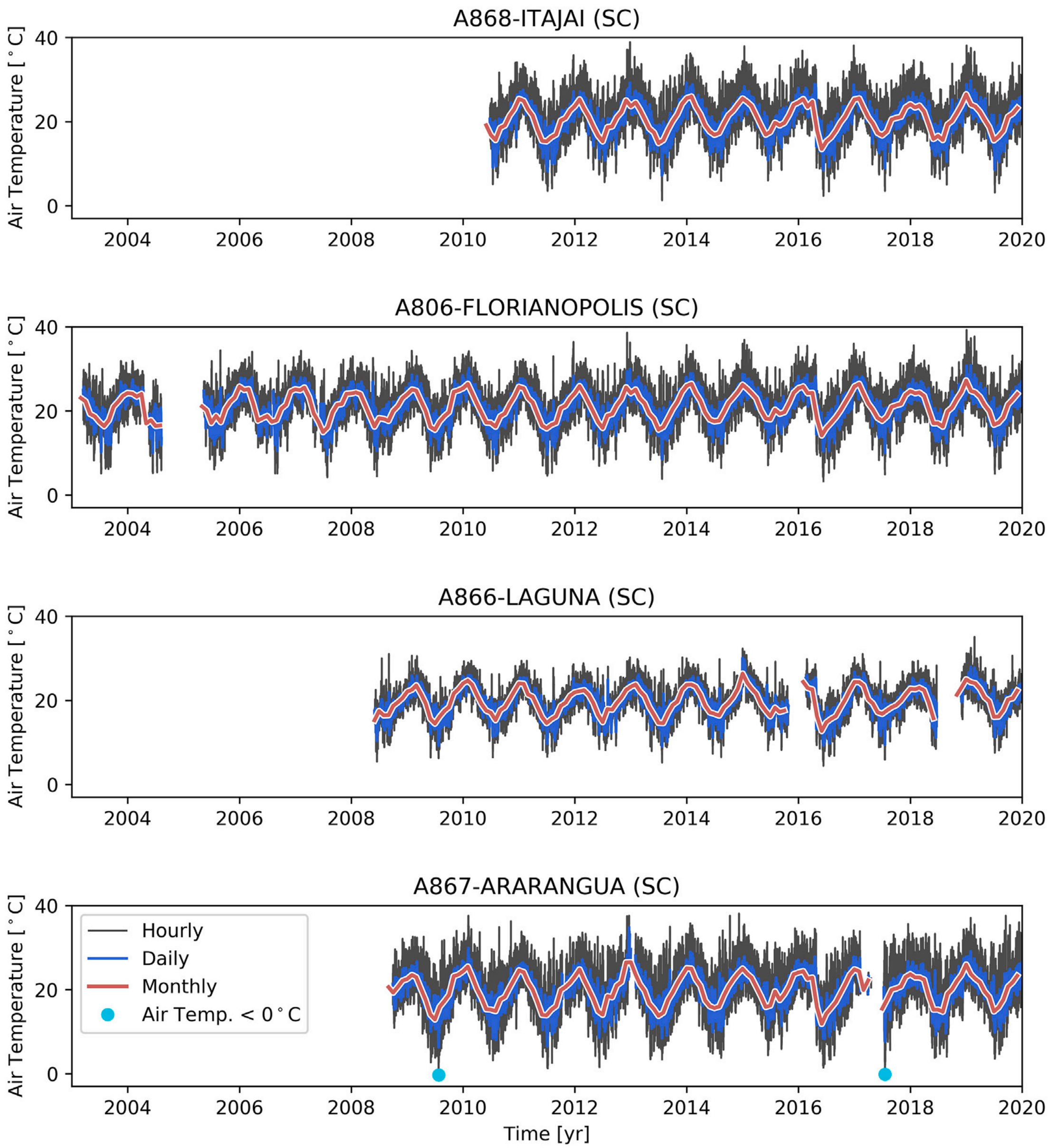

Fig. 3. Temporal series of air temperature measured in four different meteorological stations in the state of Santa Catarina, Brazil: (i) Itajaı (Station code A868), (ii) Florianópolis (Station code A806), (iii) Laguna (Station code A866) and (iv) Araranguá (Station code A867). Hourly, daily and monthly averages are represented by the black, blue, and red lines, respectively. The light blue point in the Araranguá panel represents the two occasions when the air temperature was negative. Data provided by the Brazilian National Institute of Meteorology (INMET, 2020). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Air temperature (°C) metrics over 8 years (2011–2019). All metrics are calculated from the data provided by the Brazilian National Institute of Meteorology (INMET, 2020).

Variables	Itajaí	Florianópolis	Laguna	Araranguá
Mean annual air temperature	20.64	21.26	19.77	19.86
Winter mean air temperature	17.24	17.82	16.46	16.40
Mean air temperature of July	15.89	16.6	15.52	14.74
Mean air temperature of August	17.25	17.86	16.49	16.60
Mean air temperature of September	18.58	18.97	17.35	17.83
Mean air temperature amplitude	7.53	6.64	4.28	8.19
Absolute minimum daily air temperature	7.17	8.54	9.03	6.51
Mean air temperature of the 10 coldest days	8.37	9.83	9.70	7.92

the Southern Atlantic. The mean air temperature of the coldest month reached 15.52 °C and 14.74 °C in Laguna and Araranguá, respectively. Even though the mean August and September air temperatures are slightly lower in Laguna, the mean for all winter months is 0.06 °C colder in Araranguá.

The mean annual air temperature has been considered a factor that represents a restrictive climate condition for mangroves expansion at higher latitudes in the eastern South American mangrove limit (Soares et al., 2012). However, this contrasts with our results which suggest that the mean annual temperature and the August–September mean

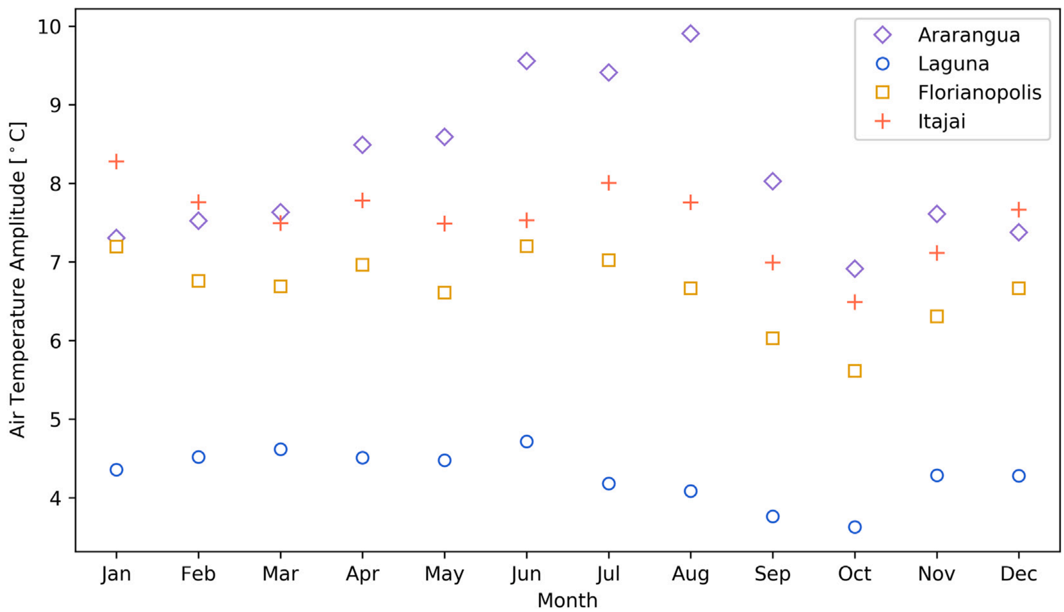

Fig. 4. Monthly mean thermal amplitudes calculated from daily air temperature amplitudes (°C) over 8 years (2011–2019) for each studied site.

do not seem to impose constraints on mangroves. In this direction, the discussed means do not support the mangrove distribution limit in Laguna, as they may present similar mean temperature values or, in this sense, could represent suitable conditions for mangrove growth in Araranguá.

In terms of air temperature amplitude, Walsh (1974) suggested that amplitudes should not exceed 5 °C, otherwise it may stress mangrove plants and impose difficulties to their establishment. As shown in Fig. 4 the mean monthly amplitude is higher in Araranguá (8.19 °C) compared to Itajaı (7.17 °C), Praia do Sonho (6.64 °C), and Laguna (4.28 °C) (Table 1).

Even though Laguna has been previously reported to present a mean annual thermal amplitude of 8.0 °C (Schaeffer-Novelli et al., 1990; Soares et al., 2012), our results reveal only about half of this value (4.28 °C). So, in that location, mangroves species are not expected to be negatively impacted by air temperature amplitude according to Walsh (1974). On the other hand, it is noticeable that higher thermal amplitudes take place in Araranguá, compared to the other three sites. In Araranguá, air temperature amplitudes are more pronounced during the colder months in autumn and winter (April–September), with a maximum amplitude of 9.7 °C in August. Therefore, high amplitudes of air temperature may stress mangrove plants and impose extra difficulties to their establishment in Araranguá.

3.1.2. Freezing events

From all stations and records, the hourly air temperature dropped only twice to temperatures below zero: on 25/07/2009 and 19/07/2017 in Araranguá (Fig. 3d). Frost events are of high importance since they can cause injury to tropical and subtropical plants (Pearce, 2001; Larcher, 2003; Krauss et al., 2008; Saintilan et al., 2014; Cook-Patton et al., 2015; Osland et al., 2017a, 2020a,b). They have already been reported to kill entire mangrove forests in Cedar Keys (29°08'N), Florida, in the 1980's, where they were replaced by saltmarshes in the intertidal zone. However, after mild winters, mangroves returned to this area (Saintilan et al., 2014). Stevens et al. (2006) predicted that after freezing events had killed the mangroves, it would take about 25–30 years for recolonization and increased seedling cover, as long as the area is not impacted by another frost. On the other hand, temporal series of satellite images available at Google Earth showed that the mangrove was naturally restored in this same area in less than half of the time predicted by Stevens et al. (2006).

At the northernmost mangrove limit in eastern North America (in Florida), an analysis indicated that air temperatures below a threshold zone of −6.3 to −7.6 °C were responsible for changing the mangrove coverage (Osland et al., 2017a). Cook-Patton et al. (2015) studied mangroves species in USA's eastern coast and they found that species and populations varied dramatically in freeze tolerance. Also in North America, a laboratory experiment of seedling sensitivity to freezing temperature showed that *Laguncularia racemosa* was more susceptible to freezing conditions than *R. mangle* and *Avicennia germinans* (Coldren and Proffitt, 2017). As opposed to what was found by Coldren and Proffitt (2017), *L. racemosa* and *A. schaueriana* seem to have more tolerance to low temperatures in eastern South America compared to *R. mangle* and *A. germinans*, since the two first reach higher latitudinal limits (Ximenes et al., 2016). Although, at the eastern North American mangrove limit temperatures reach lower values than in eastern South America (Osland et al., 2017b).

In 1988, a report to propose suitable zones for wood forest plantation and exploration reported freezing events in the cities of Florianópolis (close to Praia do Sonho), Laguna and Araranguá, which occurred on average about 0.5, 0.3 and 2 times per year, respectively (Carpanezzi et al., 1988). However, this report dates from more than 30 years ago and its data source was not specified. Our data showed that not a single freezing event took place in Laguna, Itajaı, or even in the ~17-year Florianópolis time series (Fig. 3a–c). In addition, Cohen et al. (2020) revealed a mangrove expansion of around 10 ha in Laguna (Eastern South America mangrove limits) between 2003 (96.1 ha) and 2019 (106.1 ha). The absence of freezing events is likely one of the conditions that allow for such an expansion (Fig. 3b).

In the northern Gulf of Mexico, Osland et al. (2020b) found strong negative relationships between the frequency of extreme freeze events and *A. germinans* abundance, height and coverage. In Araranguá, the two occurrences of negative air temperature took place about 8 years from each other (Fig. 3). Unfortunately, the available observations for that location span for a relatively short period (~11.5 years) so that we cannot reach further conclusions about the duration and frequency of freezing events.

3.1.3. Chilling events

Araranguá showed a higher occurrence of cumulative (Fig. 5 and Table 2) and yearly frequency (Fig. 6) of chilling events than the three mangrove sites investigated for air temperature over the 8-year

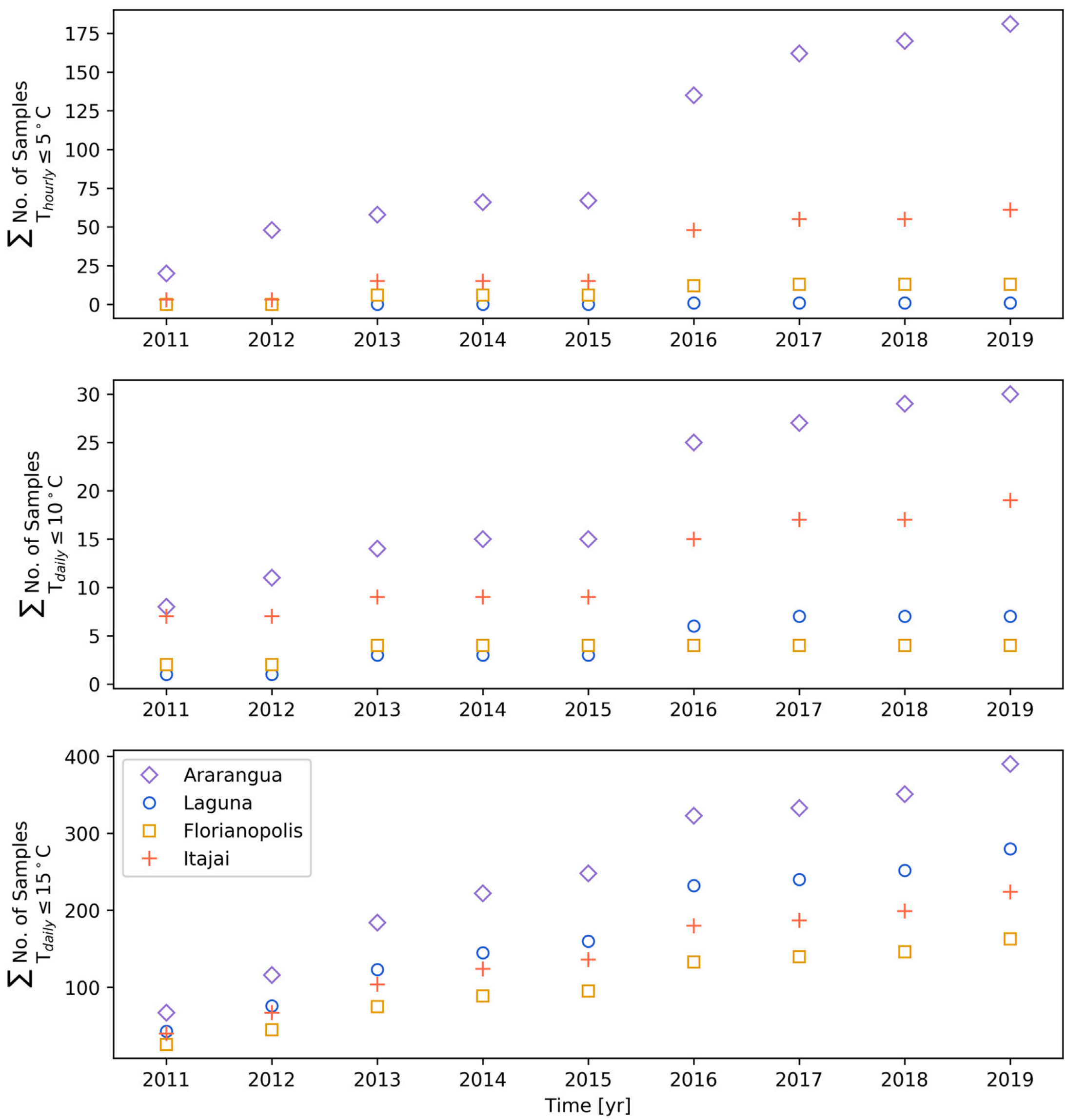

Fig. 5. The cumulative occurrence of hourly and daily air temperature events over 8 years (2011–2019). (a) Hourly air temperature ⩽5 °C; (b) Daily air temperature ⩽10 °C; (c) Daily air temperature ⩽15 °C.

common period (Table 2). This is true for the three chilling thresholds defined in Section 2.2.1: hourly air temperature ⩽ 5 °C, daily air temperature ⩽ 10 °C and ⩽ 15 °C. For instance, for the first defined chilling event, Araranguá registered a cumulative occurrence of 181 events, while Itajaı and Florianópolis registered 61 and 13, respectively. Surprisingly, in Laguna only once the air temperature dropped to below 5 °C (Table 2). For daily air temperature ⩽ 10 °C and ⩽ 15 °C, Araranguá experienced 30 and 390 events, while Itajaı, Florianópolis, and Laguna experienced 19 and 224, 4 and 163, and 7 and 280, respectively (Table 2). For all three thresholds, it is noticeable the differences between Laguna and Araranguá.

In the frequency space, chilling events with a daily air temperature ⩽10 °C occurred 1.5, 7.5 and 4.2 times more often in Araranguá than in Itajaı, Florianópolis, and Laguna. For the air temperature ⩽15 °C threshold, Araranguá presented 1.7, 2.4, and 1.4 times more events than the other three stations (same order). The higher frequency of chilling events in Araranguá is an overall rule for all analyzed years rather than a bias imposed by only a few years (Fig. 6).

Based on the results discussed above, chilling events are likely a limiting factor for mangrove colonization in Araranguá. It is worthwhile saying that the term “limiting factor” is not necessarily a lethal condition for the species, but can rather be seen as a factor that contributes to stress, which renders growth and reproduction difficult, or which leads the species to become less efficient physiologically, eventually affecting its survival capacity (Cox and Moore, 2000). According to Larcher (2003), low-temperature events negatively affect the photosynthetic performance of plants. Based on several studies of mangrove plants, Larcher (2003) reported that air temperatures between 0 and 5 °C limit the absorption of CO_2 and that temperatures between 25–30 °C are optimal for photosynthetic production in mangroves. A study with the leaves of *Avicennia marina* (Forssk.) Vierh. showed that those plants grown over 10 days at an air temperature of 15 °C had significantly lower rates of light-saturated photosynthesis,

Table 2
The cumulative occurrence (CO) of hours or days of chilling events for air temperature using a total of 8 years (2011–2019).

Variables	Itajaí	Florinópolis	Laguna	Araranguá
CO Hourly ⩽5 °C	61	13	1	181
CO Daily ⩽10 °C	19	4	7	30
CO Daily ⩽15 °C	224	163	280	390

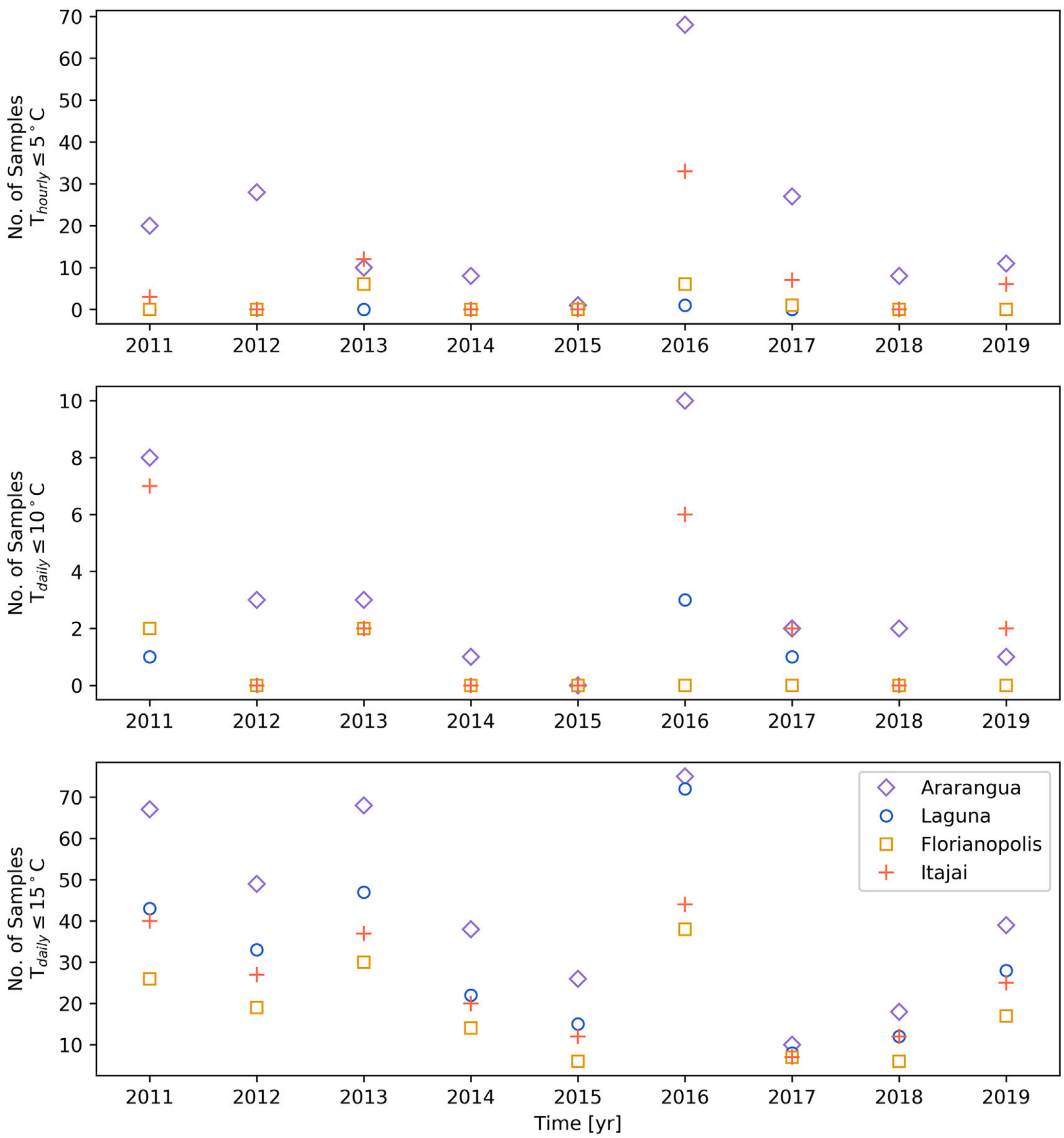

Fig. 6. The frequency of occurrence of daily air temperature events per year (2011–2019). (a) Hourly air temperature ⩽5 °C; (b) Daily air temperature ⩽10 °C; (c) Daily air temperature ⩽15 °C.

stomatal conductance, and electron transportation than plants grown at 30 °C (Kao et al., 2004).

3.2. Precipitation influencing mangrove expansion

It is well known that low precipitation rates and arid conditions harm the colonization of mangrove species (Saenger, 2002; Quisthoudt, 2013; Osland et al., 2017a). For instance, this is the case for the distribution of two *Rhizophora* in some arid regions of the northeastern Brazilian coast (Ximenes et al., 2016). However, because of the high precipitation rates at the eastern South America mangrove limits, previous studies have not considered precipitation as a limiting factor for the occurrence of mangrove in our region of study (Schaeffer-Novelli et al., 1990; Soares et al., 2012; Ximenes et al., 2016).

If precipitation is not a limiting factor, it is likely a condition that influences the production of propagules, although a detailed phenological study regarding the eastern South America mangrove limit is lacking. However, concerning the northeast of Brazil, Nadia et al. (2012) concluded that the production of propagules was seasonal, always peaking in the dry-to-wet season transition. The synchronism of the propagule peak with the rainy season was explained by Duke et al. (1984), who suggested that it could be a strategy of mangrove plants to disperse seedlings to distant sites. In our area of interest, the highest precipitation periods are in summer. There is no typical dry season, since the lowest precipitation rate, considering all sites, is >250 mm/season (Table 3). Therefore, if summer is the rainier then the transition between spring–summer or summer are periods for propagule dispersal. This assumption is reinforced by the observation that the peak of propagules' release happens in summer for the southern hemisphere (Van der Stocken et al., 2017).

Table 3
Mean precipitation (mm/season) calculated for the period January/2011–December/2019 for each season. Data source: INMET.

Sites/Season	Summer	Autumn	Winter	Spring
Itajaí	599.0	392.2	366.6	435.0
Florianópolis	617.8	334.3	382.0	392.6
Laguna	328.0	340.3	316.5	253.1
Ararangua	402.0	267.0	361.9	308.0

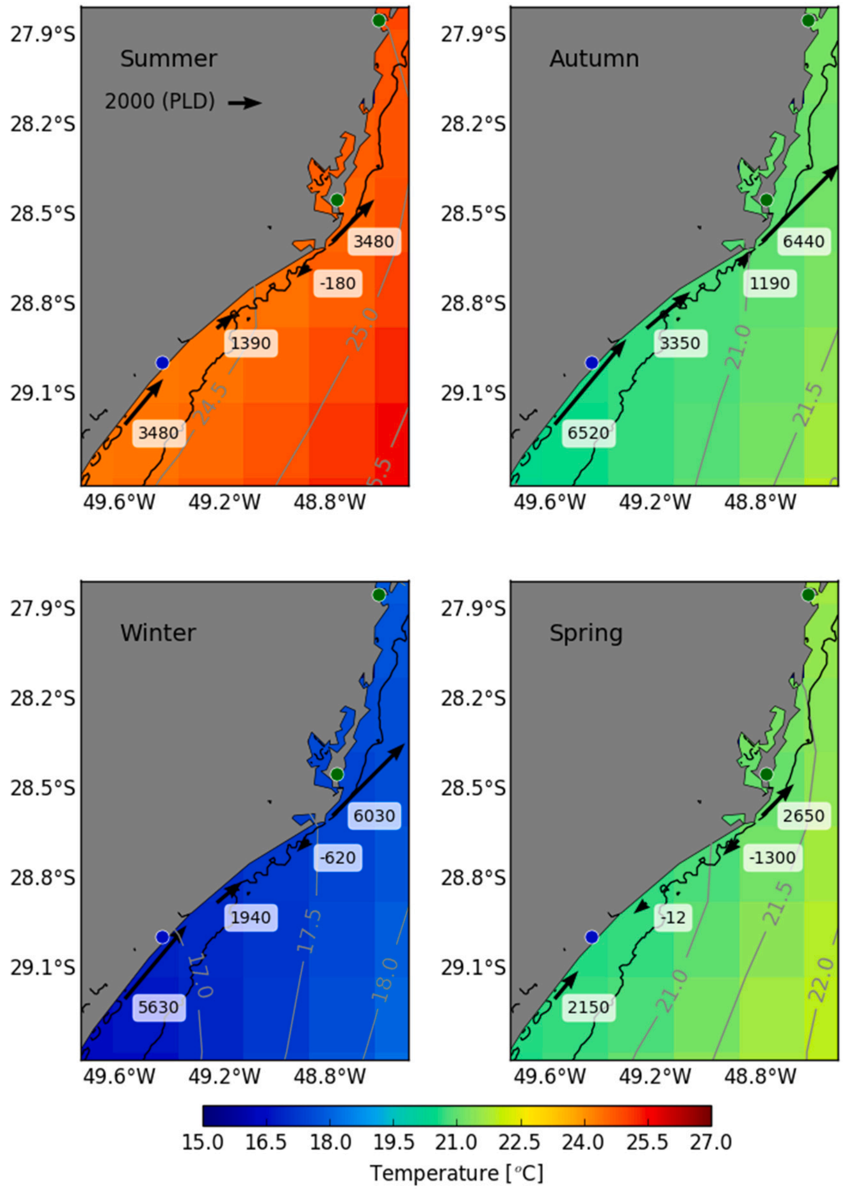

Fig. 7. The potential longshore drift estimated and the seasonal fields of SST along eastern South America mangrove range limits and beyond them. The black arrows indicate the direction of the longshore drift current and their respective numbers indicate the potential strength of the current in such direction. These longshore drifts were estimated using wave climate, at a depth of 6 m (Siegle and Asp, 2007). The green points indicate the location of Praia do Sonho (northernmost) and Laguna (southernmost), while the blue point shows the location of Ararangua estuary. The black line adjacent to the coast represents the 20-m isobath extracted from the General Bathymetric Chart of the Oceans (GEBCO) database (Sandwell et al., 2002). The figure also shows the seasonal SST fields (gray isoclines and colored contours) estimated from OSTIA database (Donlon et al., 2012) for the period 2007–2015. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Oceanographic features influencing mangrove expansion

Different oceanographic features can potentially play a role in mangrove expansion by allowing or preventing the transport of mangrove propagules and species settlement in higher latitude regions (i.e. beyond their actual limits). These are: (i) longshore drift, a mechanism which transports sediments (and potentially propagules) parallel to the shoreline, near the beach, and within the surf zone; (ii) circulation over the continental shelf, which is confined to the region inshore the shelf break; (iii) the mesoscale system of Western Boundary Currents (WBC), which takes place near the shelf break and slope, but often meanders over the continental shelf; and (iv) upwelling events, which raise cold deep waters towards the surface.

Siegle and Asp (2007) characterized the longshore drift in four cross-shore transects along the Santa Catarina state coast (Fig. 7). From the north to the south, the transects are located to the south of Praia do Sonho, near Laguna, nearly halfway between Laguna and Araranguá, and to the south Araranguá. Siegle and Asp (2007) showed that the longshore drift is predominantly northward directed in the region. However, due to seasonal variability, the flow is reversed to the south in Laguna during summer, winter, and spring. The same occurs in spring in the transect between Laguna and Araranguá. In all cases in which southward drift takes place, it is characterized by relatively weak transport. All the other transects and seasons are mainly marked by a considerably stronger northward flow. In this sense, a southward dispersal of propagules by longshore drift seems relatively difficult and if it occurs is most likely to happen in spring (Fig. 7).

Between the surf zone and the slope, the shelf circulation off the southern Santa Catarina coast is characterized by a complex pattern of circulation driven by different forces. According to Castro Filho et al. (2006), both the water mass properties and circulation patterns are influenced by meteorological conditions, by the offshore Western

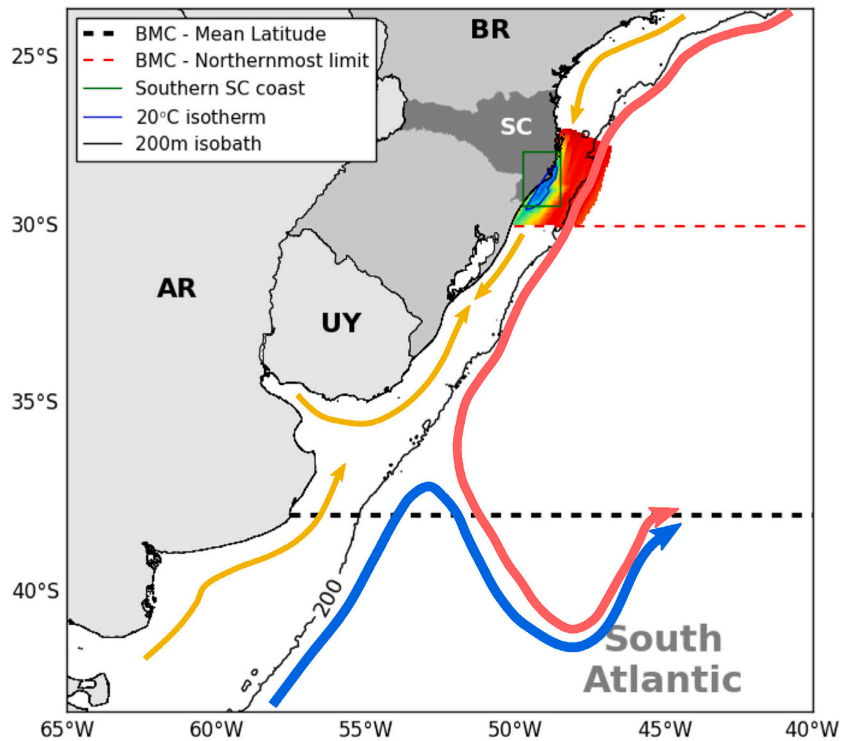

Fig. 8. Sketch of the continental shelf circulation (yellow arrows) and Western Boundary Current represented by the Brazil Current (red arrow) and Malvinas Current (blue arrow), adapted from Matano et al. (2010). The shelf circulation off Santa Catarina (SC) state should be interpreted with caution, since reversals in the flow have been reported to occur. The colored contours represent the SST field, while the blue line highlights the 20 °C isotherm observed during the Plata Summer Cruise 2004. The SST data is available in Table 1 A from Möller and Piola (2004) and it has been previously published by Campos et al. (2013). The black and red dashed lines indicate the approximate mean and northernmost latitude of the Brazil–Malvinas Confluence, respectively. The geostrophic currents, part of the Western Boundary Current systems, dominate the region near the shelf break and slope. The black line adjacent to the coast represents the 200-m isobath extracted from the General Bathymetric Chart of the Oceans (GEBCO) database (Sandwell et al., 2002). The green rectangle displays the region plotted in Fig. 7. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Boundary Currents (see below), by the freshwater discharged from La Plata River, and, on a smaller scale, from Patos and Mirim Lagoons. On average, the shelf circulation is southward-directed (yellow arrows in Fig. 8). Nevertheless, northward reversals were observed, mainly in winter, when intrusions of relatively colder and fresher water have been reported to occur (Piola et al., 2000; Palma et al., 2008). Due to the passage of cold fronts, short reversal events also occur in summer.

While northward longshore drift seems to prevent the expansion of mangroves to the south, the continental shelf circulation and the mesoscale Brazil Current are favorable to a southward transport. However, since propagules need to be somehow transported offshore in order to get embedded by one of these two current systems and, after being transported to the south, they need to again approach the coast, the links between continental shelf circulation and/or Brazil Current against propagules dispersal is not straightforward, but still possible. Even though the Malvinas Current and the Brazil–Malvinas confluence were already speculated as possible restricting factors to limit mangroves in Laguna (Soares et al., 2012), we did not find evidence to support such a connection. The Malvinas Current indeed migrates northward in winter to about 35°-30°S (Ciotti et al., 1995), but still 110 km away from Araranguá and far away from the coast. Nevertheless, Malvinas Current waters could be indirectly transported farther north, under influence of the shelf circulation (Piola et al., 2000; Palma et al., 2008).

Near the continental shelf break and slope, the ocean circulation is marked by the poleward Brazil Current, which flows until it encounters the equatorward Malvinas Current (Fig. 8). The Malvinas Current was pointed out as a possible factor that could restrict mangrove limits to Laguna (Soares et al., 2012). However, the location of this encounter, the so-called Brazil–Malvinas Confluence (BMC), takes place on average at ~38°S (Matano, 1993) far away from the mangrove limit. In summer, when the Brazil Current is relatively stronger (Wainer et al., 2000), the retroflection is observed farther south at ~40°-46°S (Legeckis and Gordon, 1982), while it migrates northward to about 35°- 30°S during winter (Ciotti et al., 1995). The BMC is not likely to reach the southernmost site of this study (Araranguá). However, it may have an indirect effect by feeding the continental shelf with relatively colder and fresher water, which could eventually be transported to the study area by the shelf circulation, as described above.

Lastly, another remarkable oceanographic phenomenon occurs near Santa Marta Cape, where the Brazilian coast changes orientation at ~28.6°S, immediately to the south of Laguna (Castello and Möller, 1977; Matsuura, 1986). The orientation of the coastline combined with certain wind characteristics (direction, intensity, and persistence) create the right conditions for the development of a phenomenon known as upwelling. In other words, a relatively strong and persistent wind from the northeast (parallel to the coast), balanced by the Earth′s rotation, generates an Ekman Transport perpendicular to the coastline, transporting waters from the first tens of meters of the water column towards the open ocean. Due to this coastal divergence at the near-surface layer, cold waters from deeper layers rise to the surface due to continuity, replacing the water transported offshore. Between Laguna and Araranguá, this sequence of events develops a coastal upwelling system, mainly observed during summer and spring (Campos et al., 2013).

The colored contours in Fig. 8 show the SST sampled at the exact moment when an upwelling event was taking place, surveyed by the Plata Summer Cruise 2004 (Möller and Piola, 2004). This event was studied in detail by Campos et al. (2013). Notice that the SST dropped to about 18 °C or less near the coast, which is significantly colder than the mean summer or spring conditions displayed in Fig. 7. According to Santos Borges et al. (2019) 18 °C do not affect the

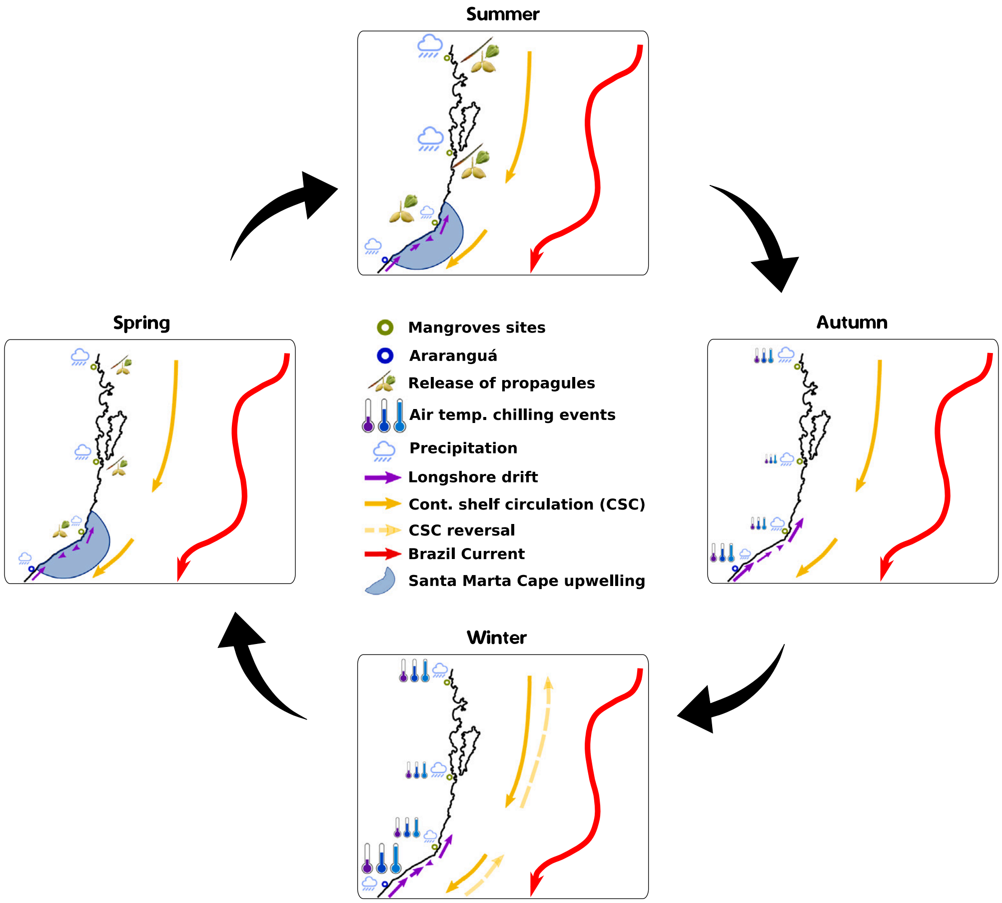

Fig. 9. Sketch of the meteorological (precipitation and air temperature) and oceanographic (currents and upwelling) factors influencing the mangrove southernmost limit in the southeastern American coast.

germination rate in *L. racemosa*. However, the other the two species *R. mangle* and *A. schaueriana* were not enough studied regarding their SST threshold. Ximenes et al. (2018) suggested that *R. mangle* is more sensitive to low SST than other species in eastern southernmost mangrove limits because their limit is in Praia do Sonho (27°48'S) instead of Laguna (28°30'S). When low SST conditions persist for days, it may decrease seedling viability and growth of certain propagules of mangrove species. Thus, upwelling events at Santa Marta Cape may represent a factor of stress for the propagules (Soares et al., 2012). Nevertheless, such interpretation must be taken with caution since each upwelling event lasts only for a few days or weeks, not the entire summer or spring.

4. Conclusions

We studied the seasonality of different meteo-oceanographic events and features at the mangrove range limits in southeastern South America. These factors are based on air temperature and precipitation metrics and diagnostics, as well as in patterns of ocean circulation and outcropping of deep and cold waters towards the surface – a phenomenon known as upwelling.

Globally, mangrove limits are commonly associated with the frequency of freezing events and intensity of aridity (Quisthoudt, 2013; Osland et al., 2017b; Wu et al., 2018; Cavanaugh et al., 2019; Bardou et al., 2021; Chapman et al., 2021; Snyder et al., 2021). In our case, aridity is not an issue restricting mangrove settlement since the region of study is marked by high precipitation rates throughout the entire year. However, because larger precipitations rates take place in summer and due to the fact that propagules production in the southern hemisphere seems to preferentially happen in summer and/or in the transition from the drier to rainier seasons (Nadia et al., 2012; Van der Stocken et al., 2017), it is expected that the peak of propagules production takes place in the transition spring–summer or summer.

The analyses of air temperature data suggest that freezing events are not a major restricting factor for mangrove expansion in the region. These events did not happen within the mangrove range, while only two one-hour-lasting events were registered in a decade (11 years) of analysis in Araranguá. On the opposite, chilling events occurring mainly in winter, but also autumn, are found to occur considerably more often in Araranguá than in Laguna (the actual mangrove southernmost limit). For this reason, punctual yet recurrent chilling events probably difficult mangrove colonization of new areas. In contrast, other average-based air temperature metrics should be interpreted with caution when used for identifying mangrove distribution. Averaged metrics might mask extremes events, such as low-temperature values, in the case of time series marked by high amplitudes. Our analyses show that this is the case for the higher annual, August, and September mean air temperature observed in Ararangua compared to Laguna. The higher averages in Araranguá are a consequence of the higher air temperature amplitude observed in this location. This reinforces the advantage of using hourly and daily observation directly provided by the meteorological stations, overcoming the limitation imposed by the fact that the stations are not exactly placed within the mangroves forests.

At times and places, the adjacent seas and ocean may also impose stress on the viability, dispersion, and settlement of mangrove species through different ways such as chilling events, circulation, and upwelling. Regarding the first aspect, Ximenes et al. (2018) have shown that chilling events are more intense and occur more frequently in Araranguá compared to sites covered by mangroves. These authors concluded that chilling events of sea surface temperature may play a role in reducing the viability of mangroves propagules, especially for *R. mangle*, but it is not a factor to restrain to their actual limits.

In terms of near-coastal and ocean circulation, three different systems could potentially transport or prevent that propagules reach new regions. These systems are marked by different forcings and spatio-temporal scales, although they are under constant interaction. From the coast to open ocean, the system of currents are classified as follows: longshore drift (parallel to the shoreline and within the surf zone), circulation over the continental shelf (confined to the region inshore the shelf break), and the mesoscale Western Boundary Currents represented by the Brazil Current. On average, this current flows near the shelf break and slope but often meanders over the continental shelf. Notice that apart from playing a role as a conveyor, the environmental state of the seawater (e.g., temperature and salinity) in which the propagules are embedded also influences their viability.

The literature suggests a northward-directed pattern of longshore drift prevailing during most of the year (Siegle and Asp, 2007). Since the longshore drift is the current system closest to the coast, this pattern might take a prominent role in preventing the southward transport of propagules to Araranguá, beyond the mangrove limit. If there is a chance of southward transport by the longshore drift occurs, it probably takes place in spring, when propagules production is not maximal. Also, upwelling could potentially impact the viability of some species in spring. During spring and summer, events of upwelling often occur near Santa Marta Cape, immediately to the south of Laguna. Forced by the wind, deep and cold waters are raised to the surface. This phenomenon forces a drop in the sea surface temperature to values colder than 18 °C (Campos et al., 2013). Experiments with *A. schaueriana* propagules revealed that no seedling germination occurred when propagules were exposed to a water temperature of 15 °C (Oliveira, 2005). In this sense, although *L. racemosa* probably is not affected by the SST found in the mangrove limits, other mangrove species can be affected by low SST values. According to Soares et al. (2012), the successful establishment of propagules is indeed prevented by the upwelling processes which occur at Santa Marta Cape.

In summary, atmospheric and oceanographic processes influence (positively or negatively) mangrove dispersion and colonization of new regions. As a well known limiting factor in other regions, aridity do not play a role in the mangroves limit in eastern South America since precipitation is abundant to sustain the species throughout the year. Precipitation is still important for determining the period in which propagules release reaches its maximum in the transition spring–summer or in summer. Chilling events of air temperature are considerable higher in Araranguá than in the other three studied sites. This is an indication that cumulative occurrence of low air temperature contributes negatively for species settlement mainly in winter, but also in autumn. In the ocean, the near-coastal circulation is dominated by a northward longshore drift which inhibits a southward transport of propagules the entire year but spring, when a weak mean southward flow could eventually contribute for the mangrove poleward expansion. Notwithstanding, this possibility could be counterpoised by upwelling events (Fig. 9).

Lastly, we have so far emphasized that in order to elucidate what is effectively impacting mangrove expansion in eastern South America, a broad environmental characterization combined with information on seasonal propagule production is required. In this sense, we have combined analyses of state-of-the-art atmospheric data and a literature review to identify possible unfavorable environmental events and features acting at the seasonal scale to prevent a poleward mangrove expansion. Nevertheless, mangrove dispersal and establishment can also depend on biotic factors (Cannicci et al., 2008; Dahdouh-Guebas et al., 2011; Langston et al., 2017; Langston and Kaplan, 2020). For instance, intensive propagule predation and herbivory have been reported to affect the development of a mangrove assemblage in absence of freezing events (Langston and Kaplan, 2020). In our study, biotic factors were not considered since they are not primarily linked to latitudinal positioning. Experimental approaches are required to assess unfavorable biotic conditions beyond the actual range limits.

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CRediT authorship contribution statement

Arimatéa C. Ximenes: Conceptualization, Methodology, Formal analysis, Visualization, Idealized all the figures, Prepared figures 1 and 2, Investigation, Project administration, Validation, Funding acquisition, Writing – original draft, Writing – review & editing. **Leandro Ponsoni:** Data curation, Formal analysis, Visualization, Prepared figures 3 to 9, Software, Validation, Writing – review & editing. **Catarina F. Lira:** Writing – review & editing. **Farid Dahdouh-Guebas:** Supervision, Funding acquisition, Writing – review & editing. **Nico Koedam:** Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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