Mangrove species range limits and species diversity: *A macroecological approach from regional to global scales*

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Mangrove species range limits and species diversity

A macroecological approach from regional to global scales

Thesis

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Figure cover page: Photo taken during a fieldwork expedition in Gazi Bay, Kenya in 2012.
Photo by Arimatéa C. Ximenes

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Table of contents

Abstract

The mangrove forest is an ecosystem distributed worldwide along tropical and subtropical coastlines. The environmental conditions are known to affect species distribution patterns, and to understand them is one of the main goals of biogeography. The association of environmental factors (e.g. temperature and precipitation) and species distribution patterns has challenged scientists since long. Species are distributed in a geographical space, however, why species are present in a certain location but absent in another is a fundamental question in biogeography. This PhD thesis aims at better understanding the most intriguing issues related to the role of environmental factors associated with mangrove distribution range limits and species richness from regional (Brazilian mangroves) to global scales.

For the Brazilian mangroves, two scales were used to comprehend the spatial ecological niche of mangrove tree species. First, the entire Brazilian mangrove-lined coast was considered, and several environmental variables were used to explain what is driving mangrove tree species distribution. Second, a detailed analysis of daily Sea Surface Temperature (SST) data for the Brazilian mangrove forest at the southernmost mangrove range limit was done, and compared with a site beyond the range limit. The chilling events of SST data, also considering ocean currents, show that *Laguncularia racemosa* is probably bounded by the southernmost Brazilian mangrove limit because of a dispersal constraint rather than by the frequency of chilling events. However, the abundance of *L. racemosa* in Laguna at the Southern mangrove range limit, compared with only a few individuals of *A. schaueriana,* is probably associated with the chilling events of SST constituting a constraint to the latter species. This proves that mangrove range limits are not explained by a single cause

This PhD thesis also has the objective to evaluate the influence of upwelling intensity on the distribution worldwide, which is its approach at a global scale. The sea surface temperature (SST) had been identified as one of the key drivers of global mangrove distribution, given the coincidence of isotherms with mangrove global limits. However, other factors play a role in the variability of SST. Cold waters from deep ocean layers rise to the surface (upwelling systems), which reduces SST values and can trigger aridity. Although previous research has confirmed that mangrove distribution is driven by a variety of factors, this PhD thesis additionally demonstrates a significant influence of upwelling intensity, and hence provides elements for a better understanding of the factors driving mangrove expansion/retraction at a global scale. In addition, this work emphasizes climate and oceanographic processes influencing mangrove range limits. While contributing to a better understanding of some of the most intriguing questions on the macroecology of mangrove, this PhD thesis also raises new questions that should be studied by future research.

Résumé

La forêt de mangrove est un écosystème présent dans le monde entier le long des côtes tropicales et subtropicales. Les conditions environnementales sont connues pour affecter la répartition des espèces; les comprendre est l'un des principaux objectifs de la biogéographie. Les associations entre les facteurs environnementaux (tels que température et précipitations) et la répartition des espèces intriguent les scientifiques depuis longtemps. Les espèces sont réparties géographiquement, et comprendre la répartition de leur diversité est une question fondamentale en biogéographie. Cette thèse vise à mieux comprendre les problématiques liées au rôle des facteurs environnementaux influençant la distribution spatiale et la richesse des espèces à l'échelle régionale (mangroves du Brésil) et globale.

Dans un premier temps, nous avons étudié les mangroves brésiliennes pour comprendre la biodiversité des espèces d'arbres et la niche spatiale et écologique de ces espèces. Une étude des mangroves le long de la côte brésilienne montre que plusieurs facteurs environnementaux expliquent la répartition de ces espèces d'arbres. En s'intéressant à une mangrove située à la limite australe de la forêt côtière des mangroves brésiliennes, ainsi qu'à un site situé légèrement au-delà de cette limite biogéographique, une analyse détaillée de la température de surface de la mer (*Sea Surface Temperature, SST*) a été faite. Les épisodes de froid (*chilling*) dans les données SST et les courants océaniques montrent que *Laguncularia racemosa*, est probablement plus limitée à la limite australe des mangroves brésiliennes par les contraintes de dispersion que par la fréquence d'épisodes de froid. Cependant, l'abondance de *L. racemosa* à Laguna à la limite australe de l'aire de distribution des mangroves, par rapport aux quelques individus d'*Avicennia schaueriana*, est probablement associée aux épisodes de froid des SST qui constituent une contrainte pour la dernière espèce. Ceci indique également qu'une seule cause ne peut pas expliquer les limites de distribution des mangroves.

A l'échelle globale, cette thèse avait l'objectif d'évaluer l'influence de l'intensité du phénomène de remontée d'eau (*upwelling*) sur la répartition mondiale de mangroves. Cependant, d'autres facteurs sont responsables de la variabilité de la température de surface. Le phénomène d'upwelling, la remontée des eaux froides des couches profondes de l'océan réduit la température de surface et peux occasionner l'aridité des zones côtières. Au-delà des études déjà publiées sur les facteurs influençant la croissance des mangroves, les résultats de cette thèse démontrent l'ampleur de l'influence de l'intensité de l'upwelling et permettent de mieux comprendre l'expansion/le recul des mangroves côtières au niveau global. Cette thèse souligne l'influence des facteurs climatiques et des processus océanographiques sur la répartition des mangroves, et permet de mieux comprendre la macroécologie des mangroves, tout en soulevant de nouvelles problématiques à étudier à l'avenir.

Samenvatting

Het mangrove-ecosysteem is wereldwijd verspreid langs tropische en subtropische kusten. Milieucondities maken deel uit van de factoren die de verspreiding van soorten kan beïnvloeden, en één van de voornaamste doeleinden van de biogeografie is het begrijpen hiervan. Wetenschappers werden reeds uitgedaagd door de associatie tussen milieufactoren zoals temperatuur en regenval enerzijds, en soortenverspreiding anderzijds. Soorten zijn op hun beurt verspreid in een geografische ruimte, maar waarom ze juist aan- of afwezig zijn op een bepaalde plaats is een fundamentele vraag in de biogeografie. Deze doctoraatsthesis doelt op een beter begrip van de meest intrigerende vragen rond de rol van milieufactoren, klimaat en oceanografische processen in het begrenzen van de verspreiding van mangroven en mangrovesoorten op regionale (Braziliaanse mangroven) tot globale schaal.

Voor wat betreft de Braziliaanse mangroven, werden twee verschillende schalen gebruikt om de ruimtelijke niche van mangroveboomsoorten te begrijpen. Eerst werd de volledige Braziliaanse mangrovekustlijn beschouwd en werden verschillende milieuvariabelen gebruikt om te verklaren wat de verspreiding van mangroveboomsoorten bepaalt. Vervolgens werd een gedetailleerde analyse op dagelijkse oppervlaktetemperatuur van het zeewater (*Sea Surface Temperature* of SST) vergeleken voor een Braziliaans mangrovewoud gelegen aan de meest zuidelijke areaalgrens van mangroven en een site buiten de areaalgrens. Episodes van koude in de SST gegevens toonden dat *Laguncularia racemosa* wellicht meer beperkt wordt aan de zuidelijke areaalgrens in Brazilië door een belemmering van verspreiding dan door de koude-episodes. Echter, de abundantie van *L. racemosa* in Laguna vergeleken met de weinige individuen van *Avicennia schaueriana* zijn wellicht wel geassocieerd met de episodes van koude.

Op wereldschaal had deze doctoraatsthesis de doelstelling om de invloed van de intensiteit van *upwelling* op de verspreiding en diversiteit van mangrovesoorten te onderzoeken. De SST werd eerder al geïdentificeerd als één van de voornaamste factoren van de wereldwijde verspreiding van mangroven omdat bepaalde isothermen overeenstemden met de areaalgrenzen van mangroven. Er zijn echter andere factoren die meespelen in de variabiliteit van SST. Koude wateren van de diepere oceaan migreren naar de oppervlakte (*upwelling*systemen), hetgeen op haar beurt de SST doet dalen en ariditeit veroorzaakt. Hoewel eerder onderzoek heeft bevestigd dat de verspreiding van mangrovesoorten wordt veroorzaakt door verschillende factoren, wordt met deze doctoraatsthesis aangetoond dat *upwelling*intensiteit een significante invloed heeft, en voorziet ze dus elementen voor een beter begrip van de factoren verantwoordelijk voor mangrove-uitbreiding of –inkrimping op wereldschaal. Daarnaast benadrukt dit werk de klimaatsgebonden en oceanografische processen die het mangroveareaal beïnvloedt.

Naast de bijdrage tot een beter begrip van enkele van de meest intrigerende vragen i.v.m. de macro-ecologie van mangroven, werpt deze doctoraatsthesis ook nieuwe vragen op waarop verder onderzoek zich kan toespitsen.

Acronyms and abbreviations

AEP Atlantic East Pacific

AVHRR Advanced Very High Resolution Radiometer

EBC East Boundary Current

EBUE Eastern Boundary Upwelling Ecosystems

ERS-1 European Remote Sensing Satellite

FAO Food and Agriculture Organization of the United Nations

GDD Growing-Degree Days

GHRSST Group for High Resolution Sea Surface Temperature

GIS Geographic Information System

IUCN International Union for Conservation of Nature (*officially* International Union for Conservation of Nature and Natural Resources)

IWP Indo-West Pacific

LANDSAT Land Remote Sensing Satellite Program

MODIS Moderate Resolution Imaging Spectrometer

MUR Multi-scale Ultra-high Resolution

SPOT Satellite Pour l'Observation de la Terre

SST Sea Surface Temperature

UNEP United Nations Environment Programme

USGS United States Geological Survey

WBC Western Boundary Current

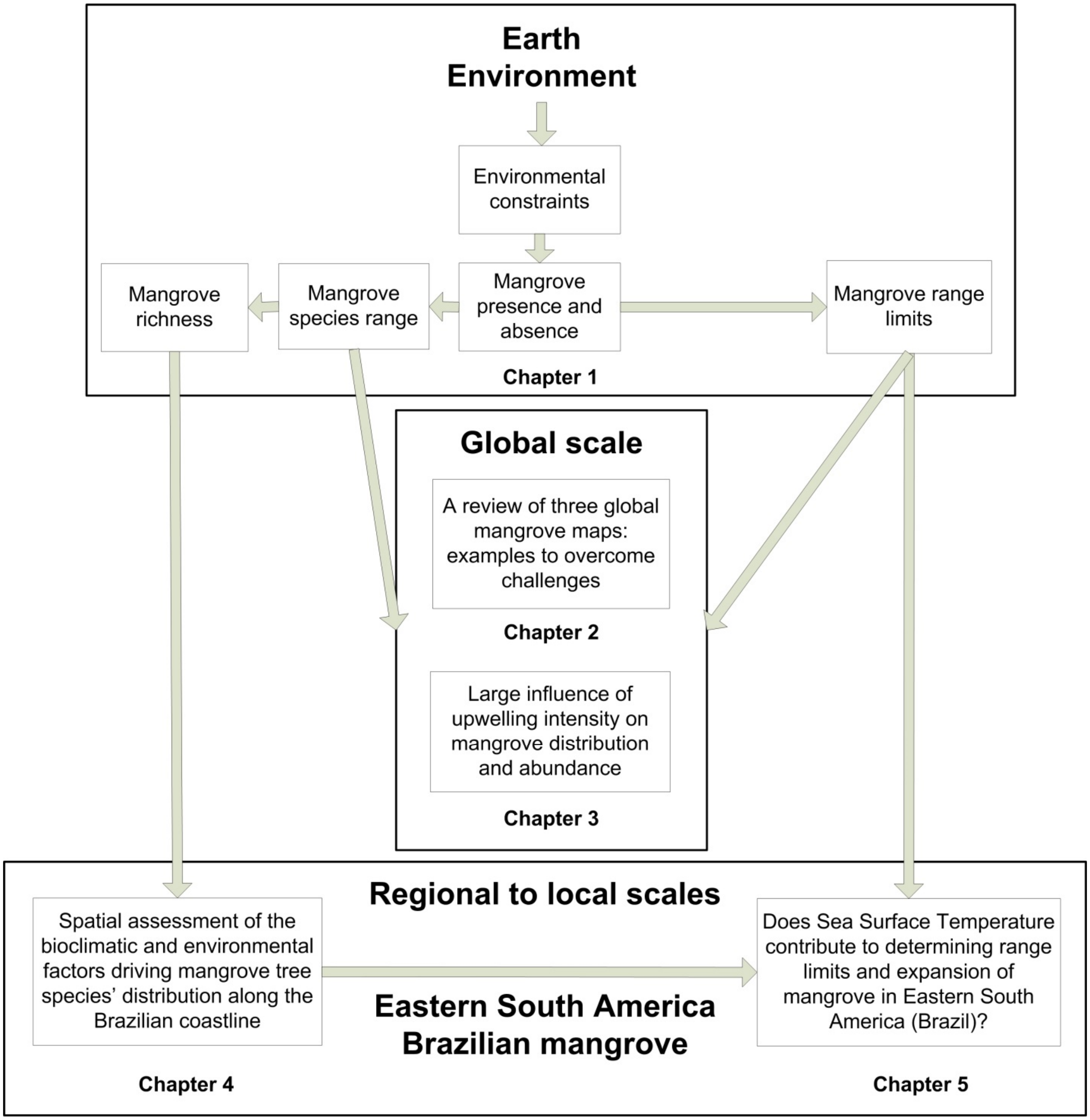
Thesis Outline

This PhD thesis aims at better understanding the association between mangrove species distribution and climate and oceanographic processes. **Chapter 1** is the introduction, where, basically I explain the distribution of mangrove plant species by constraining climate factors and oceanographic processes, and where the global mangrove species richness map made for this PhD thesis is introduced. In **Chapter 2**, I present the comparison of the three most recent global mangrove maps. This chapter is intended to draw the reader's attention to the importance of the global maps for conservation and environmental studies, especially for this PhD thesis. I highlight the differences between the three global mangrove maps, but I also explain why the oldest version of World Mangrove Atlas can still be used in conservation projects.

Chapter 3 is fully dedicated to better understand the influence of upwelling intensities on mangrove limits. In **Chapter 4**, I observe that two mangrove tree species have their limits in Rio de Janeiro state, which coincide with two upwelling zones in São Tomé Cape (22°S) and Cold Cape (23°S). When such coincidences repeat on a global scale, this is likely to be associated with mangrove distribution patterns.

To understand the relation between environmental variables and the spatial and climate niche of mangrove species, I decided to take into consideration the Brazilian mangroves, where I had previous fieldwork and survey experience. In this sense, in **Chapter 4**, I discuss what drives mangrove species distributions along the Brazilian mangrove coastline using a spatial assessment of the environmental factors and bioclimate variables. Although **Chapter 4** elucidates many issues, it also raises new questions. In continuity with **Chapter 4** a detailed study of eastern South American mangrove limits was necessary. For this reason, in **Chapter 5** I aimed at analysing in detail the daily Sea Surface Temperature (SST) data within and beyond the mangrove limits, in order to better understand what is limiting the latitudinal distribution of mangrove plants in eastern South America, localised in Paraná state, in Brazil.

Finally, **Chapter 6** is dedicated to the *general discussion & conclusion* giving a full overview of this thesis. The scheme below shows a framework that connects all chapters in a logical sense.



Logical framework underlying this PhD thesis, highlighting the links between chapters.

Figure: Surrounded by *Rhizophora mucronata*. Photo taken during the fieldwork in the mangroves of Gazi Bay, Kenya (2012). Photo by Arimatéa Ximenes

CHAPTER 1

General Introduction

Objectives

"An expert is a person who has made all the mistakes
that can be made in a very narrow field". **Niels Bohr**

Introduction

To understand the patterns of species distribution in space and time is a central interest for biogeographers (Brown & Lomolino 1998; Sexton *et al.*, 2009). A simple question such as 'Which factors are affecting species' range limits?' have challenged scientists over time (Gaston 2009). According to Sexton *et al.* (2009) a species' range limit is *'a point in a geographical space beyond which no living individual of certain species occurs*'. The species' range limits have dynamic movements, shifting through expansions and retractions in space and time, in which climate fluctuation and change, dispersal processes and stochastic events can be found (Gaston 2009; Sexton *et al.* 2009; Thomas 2010). The ecological niche (*sensu* Hutchinson 1957) is intrinsically related to the species' range limits because the realized niche is developed within the range of tolerance of a species to its environmental conditions (Holt & Keitt 2005; Sexton *et al.* 2009).

Since mangroves are widespread along tropical and subtropical coastlines, this ecosystem is distributed across diverse climate conditions, from humid to arid, and hot to relatively cold (Blasco 1983; Saenger 2002; Krauss *et al.* 2008; Tomlinson 2016; Osland *et al.* 2017b). Macroecology of mangrove forests is an intriguing research field. In several studies attempts were made to explain which barriers are driving the range limits of mangroves forests and their plant species. This question is challenging because what a geographical barrier is to one species can be a dispersal pathway to another. Most mangrove species are living in a relatively narrow geographical range of tolerance compared to one of the most widespread species such as *Avicennia marina* (Forssk.) Vierh.

Physical and environmental constraints are intrinsically related to the 'mangrove latitudinal range limits' (Figure 1). Recently, Osland *et al.* (2017b) reviewed the scientific hypotheses that have been used to explain the worldwide mangrove latitudinal range considering fourteen limits. In this review, factors acting alone or in combination were used to explain the causes of mangrove range limits, namely minimum temperature, rainfall, dispersal constraints and/or lack of potential habitat. In the next section, I will explain the constraining factors that can influence the mangrove range limits, based on the factors showed in figure 1.

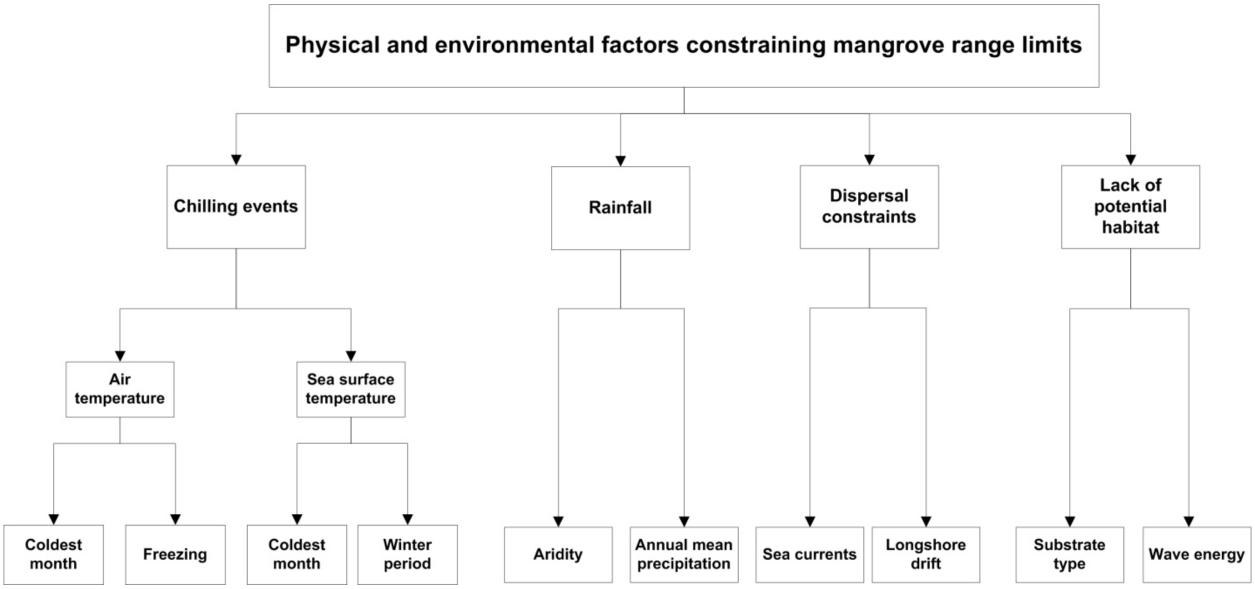


Figure 1: The main environmental drivers that explain the mangrove latitudinal range limits. Each mangrove limit can possess one or more of the above constrained factors (Barth 1982; Schaeffer-Novelli *et al.* 1990; Woodroffe & Grindrod 1991; Duke *et al.* 1998; Saenger 2002; Duke 2006; Soares *et al.* 2012; Quisthoudt *et al.* 2012; Osland *et al.* 2013, 2017b; Cavanaugh *et al.* 2014; Saintilan *et al.* 2014; Ximenes *et al.* 2016).

Mangrove dispersal and potential habitat

Mangrove propagules are dispersed by seawater (Rabinowitz 1978; Di Nitto *et al.* 2008; De Ryck *et al.* 2012; Van Der Stocken *et al.* 2017), making sea currents essential to comprehend the biogeography of mangroves. For mangrove plants, short or long-distance dispersal is possible through favourable ocean currents with suitable temperature promoting range expansion (Van der Stocken *et al.* 2019), and, eventually, genetic flow among populations (Triest 2008; Renner 2011; Lo *et al.* 2014). Otherwise, oceanographic processes can function as a barrier, for instance when unfavourable sea currents and (cold) seawater temperature exist (Duke *et al.* 1998).

The survival of propagules of *Avicennia marina* (Steinke & Naidoo 1991) and *A. schaueriana* Stapf & Leechman ex Moldenke (Oliveira 2005) are conclusive in reporting that low seawater temperature reduces and/or inhibits the germination and seedling development of mangrove propagules (McMillan 1971; Steinke & Naidoo 1991; Oliveira 2005). Moreover, long-distance dispersal of mangrove propagules depends on the duration of their viability, and ability to float for a long period of time (Duke *et al.* 1998; Lo *et al.* 2014; Ngeve *et al.* 2016, Van der Stocken *et al.* 2019). For example, *Laguncularia racemosa* (L.) Gaertn.f. has a much smaller floating time than other typical mangrove species in the Caribbean (Rabinowitz 1978). This fact explains the absence of *L. racemosa* in Bermuda (Ellison 1996). Potential dispersal of mangrove species through ocean current modelling and simulated floating times of 1, 6 and 12 months showed isolation and connectedness in the mangrove range and on the world's coasts.

For mangroves, a potential habitat can occur on various substrate types, although most mangrove trees grow particularly in muddy or mud soils (Hutchings & Saenger 1987). Moreover, mangrove forests need a site protected from wave actions to establish their seedlings (Chapman 1975, Hurst *et al.* 2015). Mangroves are found in habitats protected from wave exposure, such as bays, delta, estuaries and lagoons (Lugo & Snedaker 1974). Hence, with few exceptions, when propagules arrive on sandy beaches or other unsuitable sites they do not establish or survive.

Sea Surface Temperature isotherm in defining mangrove latitudinal range limits

Many researchers have assumed that the distribution of global mangrove latitudinal range limits is associated with Sea Surface Temperature (SST) (Chapman 1976; Barth 1982; Duke *et al.* 1998; Twilley *et al.* 1998), which is a parsimonious explanation in view of a fairly clear relationship of temperature conditions to latitude. This could be physiologically explained by the effects of low temperature on plant metabolism.

Sea surface temperature is an important factor for marine coastal organisms. The 20°C isocryme (average SST for the coldest month) is used to delimit the latitudinal distribution of tropical marine fauna (Briggs 1974); it is also used to delimit the Marine Tropical Zone (Briggs 2007). Moreover, several researchers assumed that the global distribution of mangrove latitudinal limits is associated with seawater temperature (Chapman 1976; Barth 1982;

Woodroffe & Grindrod 1991; Duke 1992; Duke *et al.* 1998). Over decades, mangrove specialists found coincidences between mangrove limits and specific SST isotherms for the winter period (Duke *et al.*, 1998), or mean SST for the coldest month (Woodroffe & Grindrod 1991), and the warmest month (Hutchings & Saenger 1987; Tomlinson 2016). Duke (1992) presented latitudinal mangrove range limits which are often uses. These indicate that mangroves are generally restricted to 20°C for the winter period (i.e. Marine Tropical Zone), highlighting, however, exceptions for Brazil, Australia and New Zealand (Duke 1992). Studying global mangrove latitudinal range limits, Quisthoudt *et al.* (2012) found variabilities on SST isotherm at each mangrove limit, concluding that mangroves at their limits have no common SST isotherm.

Upwelling versus mangrove distribution

Low SST can reduce the chances of mangrove propagules surviving (McMillan 1971; Steinke & Naidoo 1991; Oliveira 2005). For this reason, an oceanographic phenomenon known as upwelling can probably influence mangrove distribution due to its cold water (Chapman 1975). Upwelling occurs when deep cold water rises to the sea surface, although the mechanisms behind this event are more complex than they seem (Figure 2). There are many types of upwelling systems, though coastal upwelling is probably the one that affects mangrove distribution (Chapter 3). In this sense, coastline orientation together with winds parallel to the coast and balanced by the Earth's rotation generates an Ekman Transport (i.e. Smith 1968), in which cold water from deeper layers rises to the surface in continuity, replacing water that has been transported offshore (Figure 3).

Nowadays, satellite remote sensing data combined with weather buoys in oceans provide more detail on upwelling system patterns (Varela *et al.* 2015). Upwelling patterns show they are extremely dynamic in terms of strength and frequency in space and time (Varela *et al.* 2015; Wang *et al.* 2015).

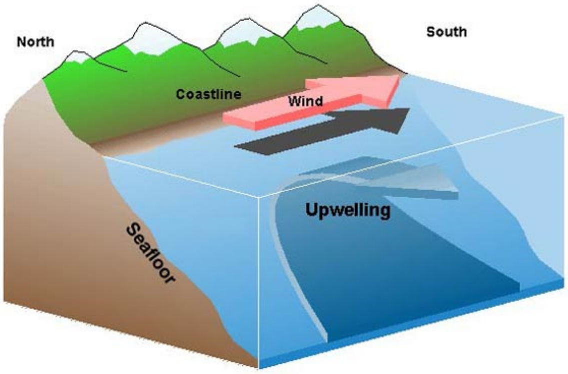


Figure 2: A sketch of the wind-driven upwelling due to a coastal divergence generated by an offshore Ekman Transport. Persistent winds parallel to the coast (red arrow) force an Ekman Transport perpendicular to the wind direction (to the right in the North Hemisphere, as shown in the sketch; to the left in the Southern Hemisphere). The offshore transport results in a region of coastal divergence. By continuity, the water transported offshore in the Ekman layer is replaced by cold waters from deeper regions.
Modified by D. Reed from image by J. Wallace and S. Vogel, El Niño and Climate Prediction. Image courtesy of Sanctuary Quest 2002, NOAA/OER.
Source: NOAA Office of Ocean Exploration and Research.
https://oceanexplorer.noaa.gov/explorations/02quest/background/upwelling/media/Fig1_cartoon.html

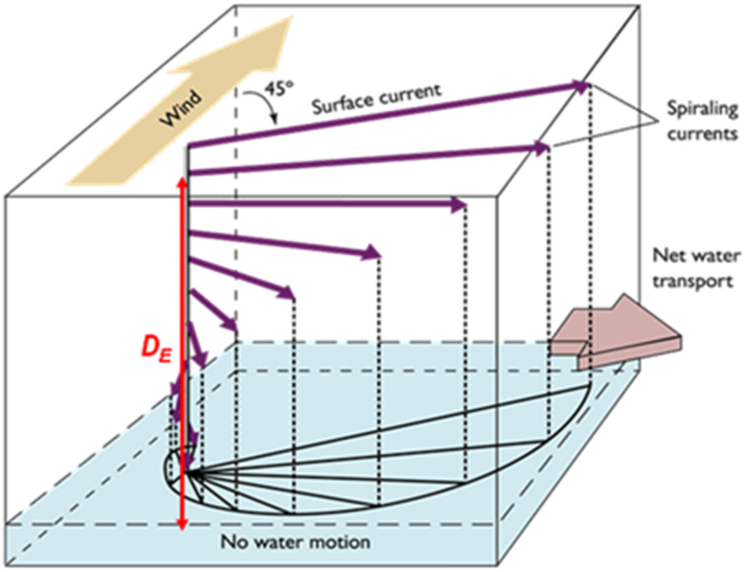


Figure 3: A sketch of the theoretical Ekman spiral for the North Hemisphere. At the surface, the Ekman velocities are directed 45 degrees to the right of the wind's direction. Nevertheless, the integrated horizontal water transport along the Ekman layer is directed 90 degrees to the right of the wind's direction.
Source:https://offshoreengineering.com/education/oceanography/114-education/ocean-environment/279-3-surface-currents-wind-driven

Chilling events due to air temperature

Experiments show that, depending on duration and intensity, low temperature conditions can inhibit and reduce the metabolic activity of plants, increasing rigidity and/or damaging biomembranes (Larcher 2003; Kao *et al.* 2004; Krauss *et al.* 2008; Chen *et al.* 2017a). Kao *et al.* (2004) concluded that low winter air temperatures (≤15˚C) explain the distribution of the grey mangrove *Avicennia marina* along the western coast of Taiwan. Physiological tolerance to chilling events vary by site in a same species. For instance, the Texas black mangrove *Avicennia germinans* (L.) Stearn is more tolerant to chilling events than the tropical populations of the Gulf/Caribbean region (McMillan & Sherrod 1986). According to Chapman (1977), the mean air temperature of the coldest month (at 16˚C isotherm) coincides with the mangrove range limits, and this also seems true for the eastern South America mangrove limits (Soares *et al.* 2012).

Freezing events

Mangrove plants are sensitive to freezing (Duke *et al.* 1998; Stevens *et al.* 2006; Krauss *et al.* 2008; Cavanaugh *et al.* 2014; Saintilan *et al.* 2014; Osland *et al.* 2017a, b), just as most tropical and subtropical plants (Pearce 2001; Larcher 2003). Freezing events can directly affect plant tissues, causing vascular embolism, dehydration, and cellular rupture because of ice crystal formation (Pearce 2001; Larcher 2003; Krauss *et al.* 2008). Freezing events have been pointed out as one of the main drivers for mangrove limits in Florida (Osland *et al.* 2013), where in the 1980’s freezing events killed entire mangrove forests in Cedar Keys (29º 08'N), temporarily substituting them by herbaceous saltmarshes (Stevens *et al.* 2006; Saintilan *et al.* 2014). Following mild winters, mangroves returned to this area (Saintilan *et al.* 2014) in a shorter time than predicted by Stevens *et al.* (2006). Another study found an ecological temperature threshold for mangroves on the east coast of Florida, where a reduction in the frequency of "extreme" cold events (frost days colder than -4 ˚C) is associated with mangrove expansion (Cavanaugh *et al.* 2014). In the southeastern United States, an ecological temperature threshold was empirically determined at -6.3 to -7.6°C, resulting in reduced mangrove cover area when this threshold is crossed (Osland *et al.* 2013). Even though freezing events are a constraining factor for mangroves in the United States, elsewhere worldwide, other constraints may play a role to restrict mangrove latitudinal range limits (Quisthoudt *et al.* 2012; Osland *et al.* 2017b).

Rainfall regimes

Precipitation is an important factor that reduces the salinity in an estuary and contributes to freshwater availability at the roots (Ball 1988). For this reason, precipitation has been recognized to influence mangrove distribution and species richness (Ball 1998; Duke *et al.* 1998; Saenger 2002; Spalding *et al.* 2010).

Several authors observed that the western sides of southern continents are generally more limited by aridity than by temperature (Saenger & Moverley 1985; Smith & Duke 1987; Saenger 2002). More recently, both annual precipitation and minimum air temperatures were reported to affect mangrove distribution, abundance and species richness (Osland *et al.* 2017b).

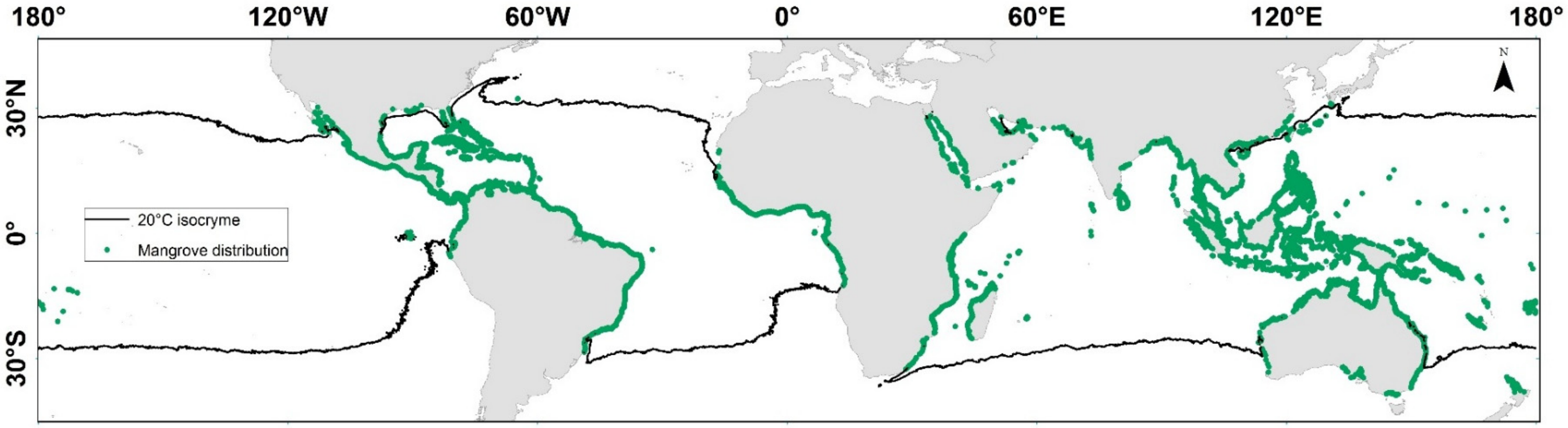


Figure 4: **The worldwide mangrove distribution (green points, n=6362 points) based on the three most recent mangrove global maps (Spalding *et al.* 1997, 2010; Giri *et al.* 2011)**. This mangrove distribution point map was generated for the objective of this PhD thesis. It was used in chapters 3 and 4 at different scales. See Chapter 4 for the methodology to generate this mangrove point map. The black lines represent the 20˚C isocryme of SST, which was obtained using the SST values from Bio-Oracle database (Tyberghein *et al.* 2012) and generated using ArcGIS 10.3 (ESRI 2011). The 20˚C isocryme coincides with mangrove range limits in Angola, South Africa and Peru. In Japan, the Gulf of Mexico and Florida-USA, the 20˚C isocryme is also near to the resp. mangrove latitudinal limits. For Australia, New Zealand, Brazil, Mauritania, China, and Pacific Mexico, however, there is no good correspondence.

Biogeography of mangroves

Biogeographic regions reflect spatial patterns of species' range limits and areas of endemism (Crisci *et al.* 2006), hence they are a useful tool to support strategies for species conservation action and to prioritize areas (Polidoro *et al.* 2010; Daru *et al.* 2013). Two mangrove biogeographic regions had been identified from early research: the Indo-West Pacific (IWP) and the Atlantic East Pacific (AEP) (Schimper 1891; Hadac 1976; Barth 1982; Saenger *et al.* 1983; Duke 1992). The two mangrove biogeographic regions are very different in terms of species, however, the AEP and IWP share many genera and families, with a few exceptions: e.g. Pellicieraceae and mangrove species within Fabaceae are endemic to the AEP and many families are endemic to the IWP, such as mangrove species from the large families, Lythraceae, Malvaceae, Euphorbiaceae, Meliaceae, Myrsinaceae, Plumbaginaceae, Arecaceae, Myrtaceae, Rubiaceae and Pteridaceae. The regions share four families, three typical mangrove families (Rhizophoraceae, Acanthaceae and Combretaceae) and one considered by some authors as containing associated mangrove species (Bignoniaceae).

Researchers assumed similar environmental conditions in the two biogeographic regions (i.e. AEP and IWP) (Chapman 1976; Duke 1992; Ricklefs *et al.* 2006), and their analysis focused on the historical biogeography of mangroves using fossil records to explain the large differences in biodiversity between bioregions called 'mangrove biodiversity anomaly' (Ricklefs & Latham 1993; Ellison *et al.* 1999; Ricklefs *et al.* 2006). Nowadays, a widely held explanation for the biodiversity anomaly of mangroves combines vicariance events (McCoy & Heck 1976; Ricklefs & Latham 1993; Ellison *et al.* 1999; Plaziat *et al.* 2001; Ricklefs *et al.* 2006) and long-distance ocean dispersal and its barriers (Lo *et al.* 2014, Van der Stocken *et al.* 2019)). The mangrove global distribution pattern is due to historical barriers identified by phylogenetic analysis (Triest 2008). Moreover, the general patterns of mangrove species richness have been explained by several physical, environmental and climate factors (Duke *et al.* 1998). In the next section, I will better explain the mangrove species diversity patterns.

Species diversity patterns

The number of mangrove plant species has always been debated depending on categorization put forward. A first distinction has been made regarding the categories of ''true' mangrove' vs. 'mangrove associates' (Dahdouh-Guebas *et al.* 2005b; Tomlinson 2016). These two terms are related to the spatial niche of species, in which the 'true' mangrove is exclusive to the mangrove biotope, and the 'mangrove associate' species may also be found beyond. Recently, a survey was done with mangrove experts to obtain a degree of concordance on which mangrove species are true or associates (Mukherjee *et al.* 2014).

The IWP region is about six times richer in mangrove plant species than the AEP (Duke 1992; Polidoro *et al.* 2010; Spalding *et al.* 2010), and this fact has intrigued scientists and led to hypotheses regarding both the longitudinal species richness gradient and the clear species richness break (Duke 1992; Ricklefs & Latham 1993; Duke *et al.* 1998; Ellison *et al.* 1999; Tomlinson 2016). The distinct species richness between the two regions has been called the 'mangrove biodiversity anomaly' (Ellison *et al.* 1999; Ricklefs *et al.* 2006).

Duke (1992) distinguished a total of 69 mangrove species belonging to 26 genera and 20 families, from which 58 species are found in the IWP and 12 in AEP regions (one being common to both regions). The Mangrove Reference Database and Herbarium is an effort to list mangrove plant distribution, and so far 73 mangrove species and hybrids were compiled (Massó i Alemán *et al.* 2010). The World Mangrove Atlas (Spalding *et al.* 2010) also considered a total of 73 species and hybrids of mangrove plants, where the IWP possess about 62 species, and the AEP only 12 species (one being common to both regions).

Species richness refers to the number of species in a defined area. Searching for the primary cause of species diversity, Rohde (2016) suggested that an increased temperature is the main cause for the diversification of species. The author claimed that higher temperatures can increase speciation rate of organisms (i.e. faster selection, faster mutation rate and shorter generation time); however, he alerted that local differences are likely related to multiple factors. On the other hand, Briggs (2007) pointed out that despite the fact that evolutionary speed seems a good explanation for species diversity, it still does not explain the longitudinal variation of species richness, especially for mangroves. This gradient parallels (with different total numbers of species for each group) species richness patterns in seagrasses and corals. Indeed, the longitudinal biodiversity gradient is also an important biogeographic pattern that has received less attention than the latitudinal gradients in ecology (Briggs 2007). Van der Stocken *et al.* (2019) by modelling actual connectedness through ocean currents indicated the isolation of the Atlantic when compared to the general Indian West Pacific regions.

The mangrove species richness patterns have been studied across several scales and multiple environmental factors are assessed to better explain it (Ball 1998; Duke *et al.* 1998; Osland *et al.* 2017a). At a local scale, salinity gradients also play a role in the zonation of species (Ball 1998). On regional and global scales, a quantitative study showed that low temperature and rainfall regimes, working in combination or alone, are influencing mangrove richness and distribution (Osland *et al.* 2017b). Global mangrove richness patterns show the highest values of biodiversity in the IWP region, mainly in Southeast Asia (Figure 5).

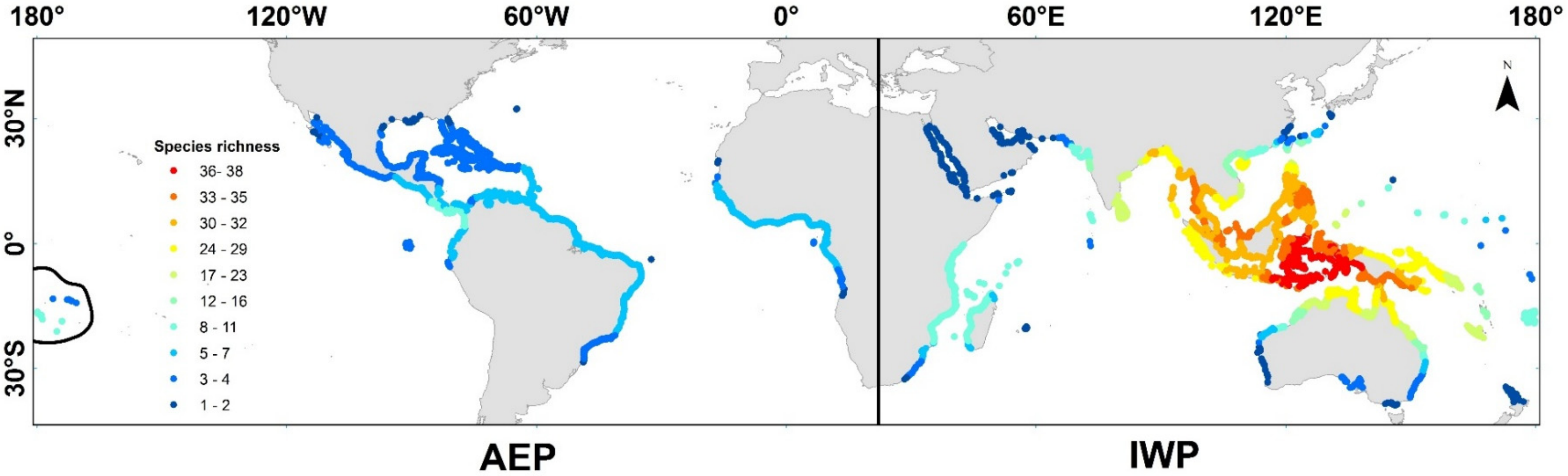


Figure 5. The global mangrove species richness map used in this PhD thesis was generated using the database of species distribution at IUCN (2016) and eight species based on literature information (Sheue *et al.* 2003, 2010; Duke 2006), resulting in 26 genera and 16 families with a total of 64 mangrove plant species and their hybrids worldwide, where 53 species are endemic for the Indo-West Pacific (IWP) and 10 species endemic from the Atlantic East Pacific (AEP), with one being present in both regions: *Rhizophora samoensis* (Hochr.) Salvoza (Polidoro *et al.* 2010; IUCN 2016). The two major biogeographic regions, the Atlantic East Pacific (AEP) and the Indo-West Pacific (IWP) are divided by the horizontal black line, and the black line surrounding islands in the left side of the figure are consider from IWP region. Further detail about the procedures used to build this map is in Chapter 4.

Justification: Why study mangroves?

Mangroves play an important socio-economical role on local, regional and global scales (Dahdouh-Guebas *et al.* 2000, 2005c, 2006; Barbier 2007; Walters *et al.* 2008; Biswas *et al.* 2009; Lee *et al.* 2014). For example, by protecting coastal areas, mangroves act as a buffer zone, potentially reducing strong effects from tsunamis, storms and other natural disasters (Dahdouh-Guebas *et al.* 2005c; Alongi 2008). Furthermore, mangrove plants possess medicinal properties that are used in the treatment of several diseases (Bandaranayake 1998; Walters *et al.* 2008). As an example, *Rhizophora mangle* L. is one of the most common species in the Atlantic East Pacific (AEP) biogeographic region, which includes the coastal areas in the western and eastern Americas and western Africa (Duke 1992). *R. mangle* has been reported in the treatment of malaria, dysentery, leprosy, tuberculosis, and other diseases (Bandaranayake 1998).

Mangroves form a habitat for diadromous species and a refuge for juvenile fish and crustaceans, and provide an ideal environment for the reproduction of many species (Primavera 1998; Cannicci *et al.* 2008). A new list of associated mangrove terrestrial fauna has been recently generated and 464 species were recorded globally, including mammalian, reptilian and amphibian species that use the mangrove habitat; this number is five times higher than previously reported (Rog *et al.* 2017). The authors concluded that our knowledge of the terrestrial mangrove fauna remains scarce for many locations.

The fauna comprises more than 40% of mangrove-endemic vertebrates that are globally threatened (Luther & Greenberg 2009). This high proportion of endangered species is mainly the result of habitat loss, explained by the rapid deforestation of at least 35% of the mangrove forest area during the 1980's and 1990's, exceeding the rate in tropical rainforests and coral reefs (Valiela *et al.* 2001). For example, due to the conversion of mangroves into other land uses, a species of frog that is restricted to mangroves and endemic in Haiti, called *Eleutherodactylus caribe* Hedges and Thomas, is threatened by habitat loss (IUCN 2016).

According to the International Union for Conservation of Nature (IUCN) Red List criteria categories of endangered species, up to 11 mangrove plants species are at elevated risk of extinction (Polidoro *et al.* 2010).

The greatest drivers for mangrove forest loss are direct conversion to aquaculture, agriculture, urban land uses (Spalding *et al.* 2010), and tourism infrastructure (FAO 2007). In addition, hydrological alterations, waste disposal, chemical spills (Blasco *et al.* 2001), oil spills (Duke 2016), oil palm and other plantations (Richards & Friess 2016) are pressuring the remaining forest. In addition, scenarios of climate change related to sea-level rise are presented as a great threat to mangroves (Gilman *et al.* 2008; Alongi 2015; Lovelock *et al.* 2015). In the past, due to sea level changes, mangroves have shifted in order to adapt and colonize new suitable areas (Woodroffe & Grindrod 1991). Nowadays, in many cases the areas surrounding mangroves are already occupied by cities, agriculture and other land uses. Since many mangroves have no natural areas to shift to, in case of sea-level rise, the impacts may be greater than expected.

Moreover, mangroves have been impacted by huge coastal projects. For instance, Meyer & Huete-Pérez (2016) have highlighted that the construction of a massive interoceanic channel in Nicaragua, connecting the Atlantic to the Pacific, will cause direct and indirect impacts in the region through deforestation and changes in its natural hydrodynamics. To date, hardly any research has been done to specifically evaluate the impact of this project on mangroves in Nicaragua.

A study suggested that, if deforestation continues at the same rate, functional mangrove systems could globally disappear in approximately 100 years (Duke *et al.* 2007). Unfortunately, mangroves are critically endangered in at least 26 countries (FAO 2003). This means that mangrove ecosystems are under threat in more than one fourth of the countries where they occur. Nowadays, the environmental impact is not only at the species level, but also at the level of ecosystems as a whole.

Given the remarkable importance of mangrove species to humanity, that species distribution should be better studied to help stakeholders and decision makers develop actions for conservation and prioritize areas for protection and sustainable uses of biodiversity.

Gaps in our knowledge

Global scale

For decades, the influence of upwelling events in driving mangrove distribution range limits has remained highly uncertain. Since Chapman's report (1975) recommending further analyses of the subject, little or no advances have been made in the field, partly due to the lack of global scientific databases on species distribution and lack of interest in studying the upwelling systems influencing mangrove range limits. In this sense, a manuscript exclusively dedicated to investigating the influence of upwelling systems in the mangrove species range limits is still lacking. This PhD thesis will address the important role of upwelling systems as a possibly important determinant of mangrove range limits.

We still lack a comprehensive understanding of the relationship between the sea currents and upwelling systems that are influencing mangrove distribution. Moreover, the Boundary Currents are poorly understood and have never been investigated in detail using scientific literature in respect to their association with mangrove and upwelling intensities. At a global scale, I want to better elucidate the influence of upwelling systems on mangrove species distribution.

Eastern South America mangrove limits and distribution

Brazil has a long coastline and mangroves are found along almost all of its extension. For this reason, a remarkable heterogeneity of environmental conditions is reported for the Brazilian mangroves (Schaeffer-Novelli *et al.* 1990). An update of the climate conditions along the Brazilian mangroves is needed, as the last comparable research was published >25 years ago (Schaeffer-Novelli *et al.*, 1990), in an era deprived of global scientific databases such as mapping distribution and climate databases.

The global mangrove map (Giri *et al.* 2011) fails to properly represent the mangrove latitudinal range limits, unlike that put forward by Quisthoudt (2013), for instance, in western Australia and South Africa.

In this PhD project, a detailed study of the southernmost Brazilian mangrove (or eastern South America mangrove limits) reveals that the range limits are not represented in Spalding *et al.* (2010) and Giri *et al.* (2011) (CHAPTERS 2 and 3). Because of the erroneous eastern South America mangrove range limit presented in Spalding *et al.* (2010) and Giri *et al.* (2011), subsequent studies using Giri's maps to study the range limits, such as Osland *et al.* (2017), retrieved information from a station ~92 km away from the actual mangrove limits in Laguna, Brazil.

In this sense, detailed climate research using the nearest station to the eastern South America mangrove limits has never been used to approach hourly and daily measurement of air temperature in order to better understand why mangrove species are restricted to Laguna-SC. Moreover, to our knowledge daily SST data have never been applied to explain the mangrove species distribution, only proxies of monthly means or annual means of SST. Studies have associated the low rate of success in mangrove seedling establishment to prolonged exposure to low SST (McMillan 1971; Steinke & Naidoo 1991).

In investigating mangrove distribution, especially at their range limits, the SST data has never been explored using daily data comparable to what is commonly used for air temperature data. In addition, authors have used proxies of extreme events through mean annual SST or minimum SST of the coldest month (Quisthoudt *et al.* 2012; Ximenes *et al.* 2016; Osland *et al.* 2017b). For this reason, we want to investigate the daily SST data in the eastern South America mangrove limits.

For this reason, in this PhD project I would like to answer the biogeographic questions with respect to the mangrove plant species, filling some of the important gaps in our knowledge expressed above.

2. General objectives

This PhD thesis addresses biogeographic questions which are related to species range limits and distribution associated with climate and oceanographic processes. The objectives are exposed below.

2.1. Global mangrove mapping

Global mangrove maps allow, upon access to spatially explicit information on environmental factors and oceanographic processes, such as climate, ocean currents and seawater salinity, to interpret possible causal factors of mangrove species distribution patterns. **Chapter 2** aims at comparing three recent global mangrove mappings and to generate a compiled map which will be used in subsequent analyses (Chapters 3 and 4). In Chapter 2 I also highlight opportunities and constraints to the use of distribution maps for mangrove conservation.

2.2. The association of upwelling intensity to mangrove distribution and abundance

Our objective is to unveil the influence of upwelling intensity zones on global mangrove latitudinal range limits. For this reason, our scientific question is: Are upwelling systems affecting mangrove latitudinal range limits and abundance at the global scale? Does the abundance of mangroves differ in different levels of upwelling intensity? and Are the two major mangrove biogeographic regions (Atlantic East Pacific and the Indo-West Pacific) environmentally similar with respect to the upwelling intensity? Our hypothesis is that upwelling affects geographical distribution limits and abundance of mangroves on a global scale.

2.3. What is driving mangrove species distribution along the Brazilian coastline?

Chapter 3 aims at a better understanding of latitudinal range limits of Brazilian mangrove trees species and their causality. For this objective, it was necessary to investigate and to update climate data along the Brazilian mangrove-covered coastline. An innovative method for assessing the environmental determinants of mangrove distribution was to apply a data-driven science approach using an artificial neural network of Self-Organizing Maps. This approach was used to verify correlations between 25 variables and geovisualise mangrove species distributions associated with environmental factors in neural maps. With a reduction to non-correlated environmental variables, descriptive statistics were extracted and resulted in a detailed analysis of mangrove species range limits and specific constrained factors, allowing a better understanding of the niche of mangrove plant species.

2.4. Does Sea Surface Temperature contribute in delimiting range limits and expansion of mangroves in Eastern South America (Brazil)?

Our objective was to analyse spatio-temporal daily SST data, which influence the mangrove expansion beyond their actual range limits, more specifically: to investigate the Brazilian southernmost limit, and to discuss causes of presence and absence. The frequency of chilling events of daily SST data playing a role to explain the mangrove latitudinal range limits in Eastern South America is an innovative interpretation for this topic.

CHAPTER 2

A review of three global mangrove maps: examples to overcome challenges

To be submitted for publication

Arimatéa C. Ximenes

"Destroying a tropical rainforest for profit is like burning all the paintings of the Louvre to cook dinner." **E. O Wilson**

Parts of the introduction were modified from the paper: Ximenes, A.C. (2015). Global mangrove mapping: a critical tool for conservation. *GLP news*, 12, 65–69.

Abstract

Mangrove forests are ecosystems that provide essential environmental services for the planet, but deforestation is still on the increase. Global mangrove maps have been used to estimate the area, biomass and geographical coordinates of mangroves. This work compares three global mangrove maps, 1) the World Atlas of Mangroves produced by Spalding *et al.* (1997), 2) the World Atlas of Mangroves produced by Spalding *et al.* (2010) and 3) Mangrove Forests of the World produced by Giri *et al.* (2011). This comparison was basically performed through visual interpretation and data from the literature. Although specific inaccuracies were detected on the maps, they can still be considered accurate on a global scale. The main results reveal that the limits of mangrove forests are mismatched on these global maps. For example, in eastern South America and western Australia mangrove limits differ among the three global mangrove forest maps. Certainly, new global maps will still appear in order to improve our knowledge in respect to the quantification of the remaining mangrove forests and the deforested areas or changes in land cover. Based on this, I believe that communicating specific discrepancies on the global maps can help to develop better maps in the future.

Keywords: mapping, mangrove, remote sensing, global maps, range limits.

1. Introduction

Maps are designed to help visualize and comprehend the landscape where a systematic planning of natural resources and area estimates of certain habitats is to be carried out (Turner *et al.* 2003). Mangroves are a type of ecosystem that has been under pressure for decades from human activities (Duke *et al.* 2007). Maps are essential to estimate the deforested areas (FAO 2003, 2007) and help design actions to protect and conserve these fragile ecosystems. Over recent decades, various techniques using satellite images, aerial photographs have been applied to identify and map mangrove forests (Dahdouh-Guebas 2002; Dahdouh-Guebas *et al.* 2005a; Dahdouh-Guebas & Koedam 2008; Heumann 2011; Kuenzer *et al.* 2011; Satyanarayana *et al.* 2011, Simard *et al.* 2019). Challenges to provide global maps are much higher than producing maps for specific areas, where a wide array of techniques and ground checks may be applied.

Global mangrove forest maps are crucial tools to understand the distribution patterns of these mangroves geographically. These geographical locations can be used to access information and to obtain environmental data *in situ* from each site or through spatial databases, such as WorldClim (Ximenes *et al.* 2016). For these reasons the worldwide mangrove maps are indispensable and there is also a need for more studies related to global distribution patterns of mangroves (Spalding *et al.* 1997, 2010; Giri *et al.* 2011). One practical example of the use of global mangrove maps is to estimate the carbon storage and biomass in neotropical regions (Rovai *et al.* 2015), as well as on a global scale (Hutchison *et al.* 2013).

In the late 90's, the first World Atlas of Mangroves (WAM-1) produced by Spalding *et al.* (1997) was launched by the World Conservation Monitoring Centre (WCMC). They found mangroves in more than one hundred countries and territories worldwide (Spalding *et al.* 1997). This is around twice the number of countries compared with the first mangrove map produced in the 80's (FAO 2003). One of the causes of this difference is due to new technologies and the popularization of remote sensing devices. As an example, WAM-1 (Spalding *et al.* 1997) used satellite images at high and low-resolution such as: National Oceanic and Atmospheric Administration/Advanced Very High Resolution Radiometer (NOAA-AVHRR), Land Remote

Sensing Satellite Program (LANDSAT), Satellite Pour l'Observation de la Terre (SPOT) and the European Remote Sensing Satellite (ERS-1) (Spalding *et al.* 1997). The WAM-1 map was hand-drawn by experts visually delineating mangroves forest areas from satellites images (Spalding *et al.* 1997).

The second World Atlas of Mangroves (WAM-2) map again produced by a team led by Spalding (Spalding *et al.* 2010) was generated using unsupervised digital image classification with an editing step of the results by experts (Spalding *et al.* 2010).

At the same time, another Mangrove Forests of the World (MFW) map was produced by Giri *et al.* (2011) for the United States Geological Survey (USGS); they used hybrid supervised and unsupervised digital image classification techniques (Giri *et al.* 2011). A global dataset of Landsat 30-m resolution satellite imagery (the Global Land Survey) acquired from 1997 to 2000, was used by Giri *et al.* (2011) to estimate the total area of mangrove forests. This most recent MFW map (Giri *et al.* 2011) estimates the total area of mangrove forests to be approximately 10% smaller than the other recent estimate reported in WAM-2 map by Spalding *et al.* (2010).

These three maps are still in use by the scientific community and stakeholders in conservation and ecological studies of mangrove ecosystems. Therefore, there is a need to identify some issues related to these maps in order to support future decisions and planning. Moreover, a better understanding of global patterns of mangrove ecosystems will improve our knowledge and will help studies related with biogeography and macroecology of mangroves. For this reason, the aim of this short chapter is to identify the main differences among these three global mangrove maps and point out some issues that should be improved in future maps.

2. Results and Discussion

The global maps in this study show the distribution of mangroves and some spatial inconsistencies regarding the limits of these mangroves (Figure 1). In order to fully appreciate the inconsistencies in these maps one should (i) analyze the scientific literature with fieldwork information; (ii) visually recognize the difference between the natural shapes of mangrove polygons from non-natural shapes (iii) misleading classification when it includes mangroves instead of another type of forest or the opposite.

The WAM-1 (Spalding *et al.* 1997) does not show mangroves in many oceanic islands, namely: Micronesia, Melanesia, Polynesia, Réunion, Mauritius, British Ocean Territory and Galapagos Islands. On the other hand, the WAM-2 (Spalding *et al.* 2010) shows the mangroves at these oceanic islands. Furthermore, in the MFW map by Giri *et al.* (2011) the mangrove areas are much more extensive in the oceanic islands compared to the other maps, as we can see in Figure 1. Moreover, in the WAM-1 (Spalding *et al.* 1997) the mangroves in the Gulf of Mexico are not shown; mainly in Texas and Louisiana. However, they were correctly marked on the two other maps with singular details in the MFW map (Giri *et al.* 2011) (Figure 1).

In respect to the mangrove limits in the South of China and western North America, the WAM-2 (Spalding *et al.* 2010) erroneously marked the limits more to the north than the real limits (Figure 1).

In some locations, mangroves have been introduced by humans. Some mappings may have the objective to map only the natural occurrences of mangroves, but others may include introduced mangrove areas as well as the natural occurrences of mangroves against a background of uncertainty. The MFW map by Giri *et al.* (2011) is more inclusive than the other maps, with at least two sites with introduced mangroves, such as in Morocco and Hawaii.

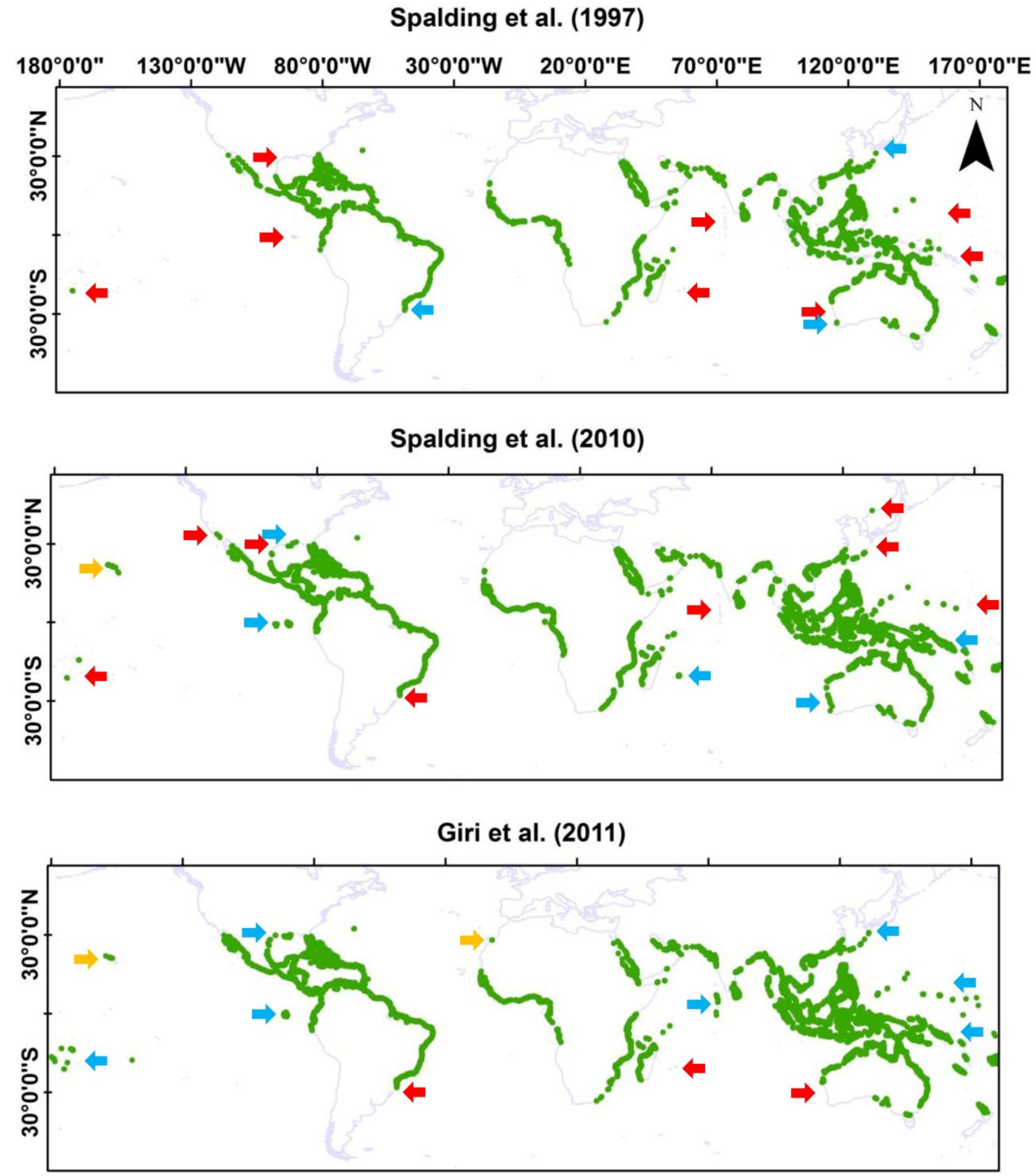


Figure 1: Comparison among the three global mangrove maps. The arrows help to highlight the geographic positions where mangroves were marked or not marked, or erroneous mapping, as well as correct locations and accurate mapping. The blue arrows demonstrate correct locations compared with the other mangrove maps. The orange arrows are the areas with mangrove sites that have been introduced, such as; Hawaii, USA (Allen 1998) and Morocco (Giri *et al.* 2011). The red arrows are the locations where we found incorrect mapping of mangrove forests (false positives).

In the WAM-1 and WAM-2 maps by Spalding *et al.* (1997, 2010) the limits of the mangroves in western Australia are shown to be up to ~33˚S (Figure 1 and 2). The WAM-2 map by Spalding *et al.* (2010) also shows many mangrove patches in the center of western Australian coast; this map is similar to the description made by Duke (2006) where mangroves are distributed throughout western Australia. Whereas the MFW map by Giri *et al.* (2011) shows the limits of the mangroves at around ~26°S in western Australia (Figure 2).

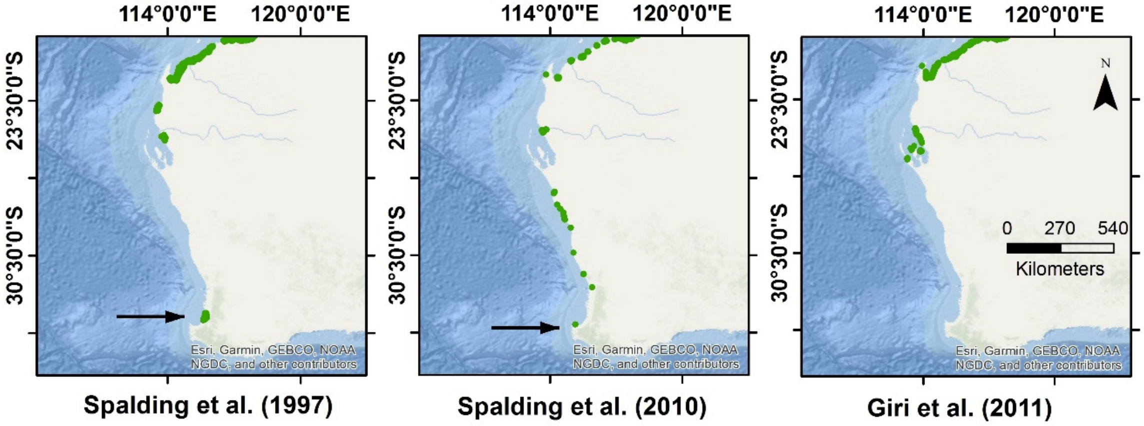


Figure 2. Example of omission of mangrove limits in west Australia. Mangroves are represented in green color where each polygon was enlarged for better visualization. The black arrows in the maps by Spalding *et al.* (Spalding *et al.* 1997, 2010) indicate the mangrove limits in western Australia, which have disappeared in the Giri *et al.* map (Giri *et al.* 2011).

The two most recent worldwide mangrove maps (Spalding *et al.* 2010; Giri *et al.* 2011) have mispositioned the Brazilian southernmost limits of mangroves and only the old version of the WAM-1 (Spalding *et al.* 1997) has properly mapped it (Ximenes *et al.* 2016) (Figure 3). The southernmost limit of mangroves in Brazil was identified by previous authors to be in Laguna, Santa Catarina state (Schaeffer-Novelli *et al.* 1990; Soares *et al.* 2012). These differences in the more recent maps are not due to recent changes in the locations of the mangroves because the latest publications and fieldwork in Laguna have affirmed that mangroves are still there (Soares *et al.* 2012). According to Ximenes *et al.* (2016) this mispositioning is probably because the mangroves are sparse at their extreme limits in eastern South America, and probably did not reach the minimum area size to be mapped by semi-automatic classification. Remembering that for the first World Mangrove Atlas (Spalding *et al.* 1997) manual delineation to map the mangrove forest was used, which depended on visual interpretation, with most likely also the use of reports from the scientific literature of the mangrove limits in Laguna in Santa Catarina state, Brazil.

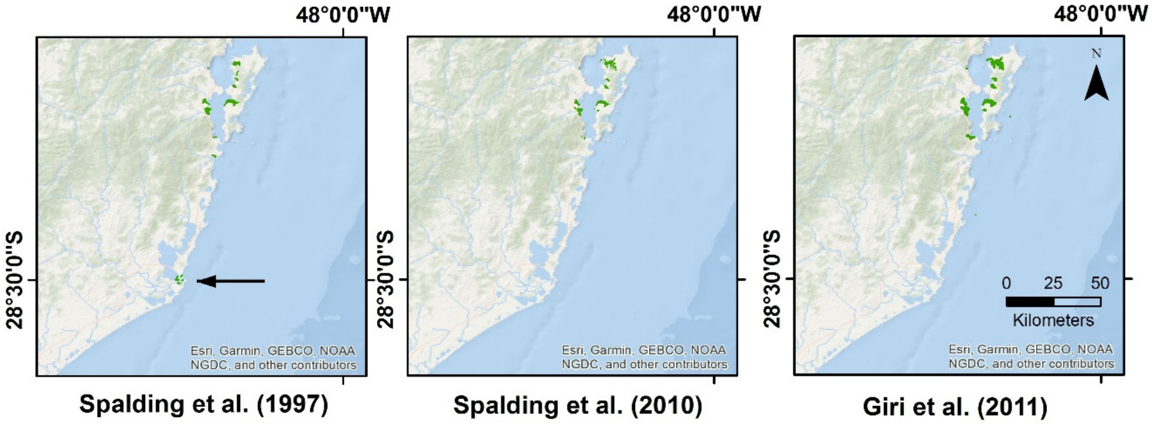


Figure 3. Example of erroneous mangrove limits in Brazil. Mangroves are represented in green color where each polygon was enlarged for better visualization. The southernmost Brazilian mangrove limits (or eastern South American mangrove limits) are indicated in the map by Spalding *et al.* (1997) by a black arrow pointing to Laguna (28°30'S) in the Santa Catarina state in Brazil. These mangrove limits disappeared in Spalding *et al.* (2010) and Giri *et al.* (2011), instead of Laguna, the limits are erroneously located near Florianópolis.

A recent study of the climate controlling the mangrove limits worldwide (Osland *et al.* 2017b) used the MFW map by Giri *et al.* (2011) as a base to localize the mangrove limits. For the eastern South America mangrove limits, Osland *et al.* (2017b) used a meteorological station from the Hercílio Luz International Airport in Florianópolis, Santa Catarina state. This airport is about 95 km north of the actual eastern South America mangrove limits, localized in Laguna (Figure 2). The MFW map (Giri *et al.* 2011) localized the eastern South America mangrove limits erroneously near the Hercílio Luz International Airport. Thus, we believe that these erroneous data are probably due to the inaccurate limits of mangroves in this region by recent mappings, as shown in Figure 3.

In the United Arab Emirates, an example of overestimation of mangrove areas in the MFW map (Giri *et al.* 2011) where the vegetation is localized inside the city of Abu Dhabi (Figure 4). Even that can be a mangrove trees inside of the city, this isolated trees do not play a role as an ecosystem integrated sheltering fish, crabs and other communities. For this reason, the mangrove maps should avoid to map the vegetation inside of the cities, which are using trees mostly with ornamental purpose. However, in the WAM-1 map by Spalding *et al.* (1997) mangroves are omitted in this country, while the WAM-2 map (Spalding *et al.* 2010) seems to represent the mangrove forests more restricted in this region than the other map (Figure 4). Moreover, the WAM-1 map (Spalding *et al.* 1997) covers 11 countries and territories less than the newest version of the WAM-2 (Table 1), however, there is also the possibility that new frontiers and new divisions between countries and territories have emerged, which can rise the number of them. In Figure 4 where we found the absence of mangroves in United Arab Emirates in the WAM-1 map (Spalding *et al.* 1997).

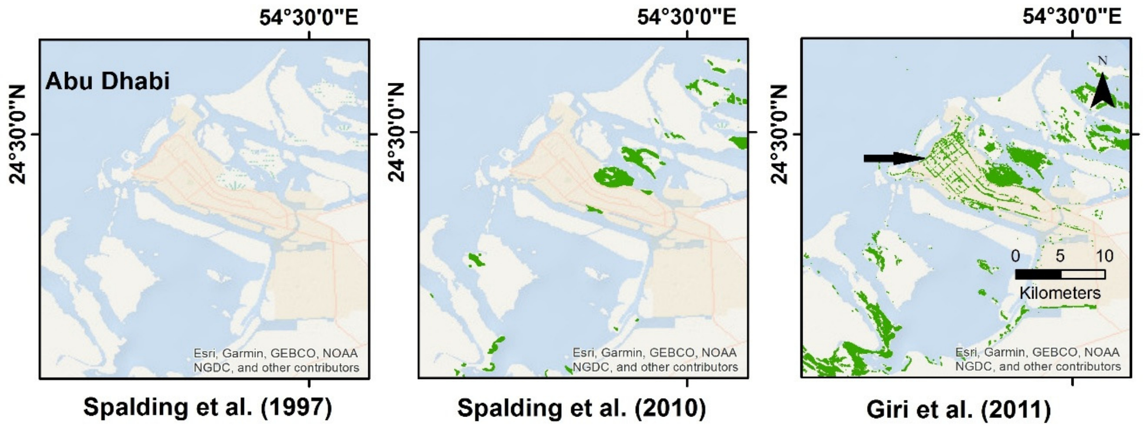


Figure 4. Example of over-estimation of mangrove forest areas in the city of Abu Dhabi (light red) in the United Arab Emirates indicated by the black arrow in the MFW map by Giri *et al.* (2011). Moreover, this figure indicates the absence of mangroves in WAM-1 by Spalding *et al.* (1997). In the WAM-2 map by Spalding *et al.* (2010), the mangrove forest areas are more restricted than in Giri *et al.* (2011). Mangroves are represented in green.

In the North of Brazil (part of the Brazilian Amazon) there is one of the longest continuous remaining forests (Lacerda 2002; Spalding *et al.* 2010; Giri *et al.* 2011) that are still well preserved from anthropogenic impacts. In the Brazilian Amazon mangroves, the WAM-1 map (Spalding *et al.* 1997) did not include all mangrove coverage (Figure 5). This is probably due to the intense cloud coverage in the Amazon region, a common issue when we use satellite images to map tropical forests in the north region of Brazil (INPE 2016). In the WAM-2 (Spalding *et al.*

2010) the empty gaps have been filled compared to the old version, although, they share almost the same delineation (Figure 5).

The World Atlas of Mangroves maps (Spalding *et al.* 1997, 2010) include the surrounding ecotones and it has less fragmented areas (i.e. the mangrove patches are more continuous than in the MFW map by Giri *et al.* (2011). The WAM-1 map by Spalding *et al.* (1997) has fewer polygons, but the total mangrove area is higher than in the other two, more recent maps (Figure 5; Table 1). This is mainly due to the inclusion of small water bodies and barren land ecotones when these were found inside the mangrove forests (Spalding *et al.* 1997). Such differences may in part be due to how a mangrove area is defined, i.e. including or excluding areas without mangrove canopy but possibly ecologically part of the system. On the other hand, in order to keep only the mangrove forests (i.e. 'canopy'), the MFW map by Giri *et al.* (2011) excluded water bodies and barren lands resulting in more fragmented mangrove patches (Figure 5; Table 1). In addition, the high resolution enabled the mapping of mangrove patches as small as 0.08 ha (Giri *et al.* 2011). The latter resulted from the high resolution for mapping, and not to scientific error. One benefit from this method according to Giri *et al.* (2011) is that it may improve the global carbon estimation, since only wooded forest areas have been mapped. Indeed, Rovai *et al.* (2015) preferred to use this map to estimate the carbon storage in mangrove forests.

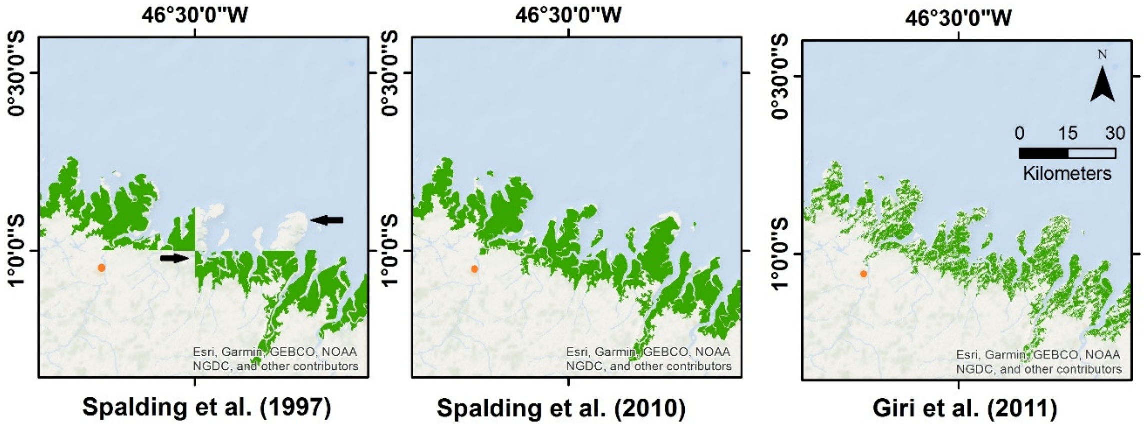


Figure 5. Example of 'lack of satellite image coverage' in WAM-1 (Spalding *et al.* 1997) indicated by black arrows and 'highly fragmented forests' in the MFW map by Giri *et al.* (2011). Mangroves are represented in green. The mangroves surrounding the town of Bragança (orange circle) in Pará state. Adapted from Ximenes (2015).

The number of polygons in the WAM-1 map (Spalding *et al.* 1997) is much lower than in other two more recent maps (Table 1). Although in the WAM-1 (Spalding *et al.* 1997) the number of polygons is substantially smaller than in the latest maps, the total area of mangrove is greater. Consequently, a smaller number of polygons in the WAM-1 map (Spalding *et al.* 1997) creates a lighter data file, which facilitates the geoprocessing analysis (Ximenes 2015; Ximenes *et al.* 2016). However, major revisions in the WAM-1 map using the other maps are necessary (Ximenes *et al.* 2016), as is shown in Figure 1.

Table 1 shows the number of polygons that are in each mapping, and the two most recent mappings increased dramatically the number of polygons as compared to the WAM-1.

Table 1: Comparison among the three global mappings, presenting the 'mean area of each polygon' (total area/nº polygons). The smaller the mean value is the more fragmented the mangroves in the map are.

	Spalding *et al.* 1997 WAM-1	Spalding *et al.* 2010 WAM-2	Giri *et al.* 2011 MFW
Area (km^2)	181,077	152,000	137,760
Nº of countries and territories	112	123	118
Nº of Polygons	34,315	1,115,610	1,397,008
Mean global area polygon (km^2)	5.28	0.14	0.10

The Global Database of Continuous Mangrove Forest Cover for the 21st Century (CGMFC-21) (Hamilton & Casey 2016) was not included in this paper because the CGMFC-21 map used the MFW map (Giri *et al.* 2011) as a reference of mangrove mapping. Therefore, the CGMFC-21 map and the MFW map (Giri *et al.* 2011) are spatially correlated sharing their distribution. However, the CGMFC-21 map is more restrictive in its definition of mangroves, and its total mangrove area is 39% smaller (Hamilton & Casey 2016) than in the MFW map (Giri *et al.* 2011).

3. Final considerations

Even nowadays with new technologies of remote sensing and complex algorithms for semi-automatic classification it is still a challenge for science to map mangroves on a global scale. Here, we showed that all the global mangrove maps need manual edition before their use on global scale studies, because they have some serious issues; such as erroneous location of mangrove range limits or wrong area estimation.

Our main focus was to draw attention to the mangroves at their range limits due to its important ecological and evolutionary aspects. The expansion and retraction of mangrove range limits have been studied in detail by many researchers (Quisthoudt *et al.* 2012; Cavanaugh *et al.* 2014; Osland *et al.* 2017a, b). Range limits are particularly valuable to understand causality of such ranges and must be preserved. For this reason, at the mangrove limits, these assemblages should maintain their potential of developing, also as sentinels of change.

Mangrove forests need a consistent policy-support classification within their geographical range boundaries in order to enable decision-makers to define policies to preserve and conserve them (Rog & Cook 2017). I call attention to the mangrove limits that have been ignored or mispositioned in global mappings, as observed in Spalding *et al.* (2010) and Giri *et al.* (2011) for the eastern South America and also the western Australia mangrove limits, in Giri *et al.* (2011).

The remaining mangrove forests are under threat by anthropogenic pressure, and consequently the irreplaceable environmental services provided by mangroves might be lost (Walters *et al.* 2008). For these reasons, more accurate maps of mangrove forests must be produced, since maps can help to design formally protected areas, hence remediate unsustainable actions, such as deforestation, chemical pollution, change in hydrography and catchment management. In this sense, knowing where mangroves are makes it possible to prioritize areas for conservation; however, local scale studies should be supported by more detailed maps.

In this sense, mangrove maps are crucial tools for conservation projects and scientific studies on a global scale (Spalding *et al.* 1997, 2010; Giri *et al.* 2011; Daru *et al.* 2013; Ximenes

2015) and to estimate carbon budgets at regional and global scales. Moreover, the demand for better and more accurate global mangrove maps is greater than ever before, due to the high rates of deforestation. In view of climate change and possible range shifts, maps of the current ranges can serve as a baseline as well as a tool in modelling such shifts. Therefore, my intention here was to show some inaccuracies in classifications of mangrove maps, since I believe that these can be overcome for future maps.

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CHAPTER 3

Large influence of upwelling systems on mangrove distribution and abundance

To be submitted for publication

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"Don't try to build everything you know into a model. Make it as simple as you can. Find the intensive variables – the ones that really make the system behave. Join them into the simplest of formal structures. Say only what you know about them. Then what you learn will be robust."

Advice of Robert MacArthur to Michael Rosenzweig

Abstract

Mangroves are tropical and subtropical coastal ecosystems that are distributed worldwide and often where river systems meet the sea. The sea surface temperature (SST) has been identified as one of the key drivers of the global mangrove distribution, considering the coincidences of isotherms and mangrove global limits. However, various factors play a role in the variability of SSTs, such as the cold waters from deeper layers moving upwards to the surface, typical of upwelling systems, which reduce the SST values that can trigger aridity conditions. Our objective is to evaluate the influence of upwelling systems on the distribution of mangrove limits worldwide. Although previous research has confirmed a variety of factors that drive mangrove species presence and ranges, we demonstrate that additionally upwelling systems may have a significant influence. Hence, our results provide further elements for a better understanding of the factors driving mangrove expansion/retraction on a global scale.

Key-words: Wetlands, upwelling, mangrove limits, species range, biogeography, sea surface temperature, geoprocessing, aridity, biodiversity, Boundary Current, latitudinal limits

1. Introduction

Mangrove ecosystems occur worldwide along tropical and subtropical coastlines. They are located at the land-sea interface and are influenced by both terrestrial and oceanographic abiotic factors (Tomlinson 2016). Multiple factors contribute to the range limits of mangroves and their species richness on a global scale. For instance, low air temperature events and precipitation are known to play a key role in defining mangrove limits (Cavanaugh *et al.* 2014; Osland *et al.* 2017b, a). Mangrove propagules require seawater as a vector for long distance dispersal.

However, in general, specific isotherms of sea surface temperature (SST) coincide with many mangrove limits, and this is the main reason why the SST is considered to play a key role in defining mangrove spatial distribution (Barth 1982; Hutchings & Saenger 1987; Woodroffe &

Grindrod 1991; Duke *et al.* 1998). Experiments have shown that when a physiological threshold value of low SST is crossed, the germination of the propagules or the rooting of seedlings can be affected directly, causing a significant reduction or a lack of development, and also there will be more susceptible to fungal infection (McMillan 1971; Steinke & Naidoo 1991; Oliveira 2005).

Though latitudinally a very wide ranging species, seedling growth of *Avicennia marina* (Forssk.) Vierh. propagules was strongly reduced at an SST of 17°C, in laboratory experiments (Steinke & Naidoo 1991) and for *Avicennia schaueriana* Stapf & Leechman ex Moldenke propagules, no seedlings germinated when they were exposed to a water temperature of 15°C (Oliveira 2005). Hence, cold water temperatures have been consistently shown to contribute to defining mangrove limits, mainly because they can affect the success rate of dispersed propagules (Duke *et al.* 1998).

In oceans worldwide, upwelling events are characterized by a vertical transport of cold and nutrient-rich deep waters towards the sea surface (Smith 1968). When the upwelling phenomenon occurs, the SST is reduced by 3°C to 8°C, compared to its surrounding waters, and its intensity depends on the site and season (Valentin 1984; Guimaraens & Coutinho 1996; Campos *et al.* 2013). Upwelling events have been reported to decrease the SST even from over 25°C to 14°C in ten days during July-August or during the summer along the coast of Florida (Pitts & Smith 1997).

Although studies have shown that many organisms can benefit from the upwelling nutrient-rich waters (Fréon *et al.* 2009), the cooling of surface water can prevent the growth of mangrove vegetation. Chapman (1975) highlighted that upwelling zones coincide with the mangrove limits on the southwestern coast of Africa (Benguela Upwelling), western coast of Australia and the western coast of South America (Humboldt Current). Woodroffe & Grindrod (1991), Lacerda & Schaeffer-Novelli (1999) indicated that the high intensity of upwelling events along the Peruvian coast (related to the Humboldt Current) may be an additional factor for the restriction of mangrove ecosystems, while Lacerda (2002) suggested the coincidence of the limits of mangroves in that region was dominated by the upwelling related to the California Current. The eastern South America mangrove limit is in Brazil (28°30'S latitude) (Schaeffer-

Novelli *et al.* 1990; Soares *et al.* 2012) where there is a summer and spring upwelling at the Cabo de Santa Marta (29°S latitude) (Campos *et al.* 2013) and possibly this could affect the survival of propagules eventually dispersed southward by the Brazil Current (Soares *et al.* 2012).

The upwelling phenomena can be triggered by different forces, such as Ekman Pumping (related to the wind stress curl), hurricanes and boundary currents. However, near the coast, upwelling cells are often triggered by coastal divergence, which is in turn mainly caused by a mechanism known as Ekman Transport (i.e. Smith 1968). In other words, the wind stress exerted on the sea surface, combined with Earth's rotation, transports surface waters 90° to the right of the wind direction in the northern hemisphere or to the left in the southern hemisphere. In addition, depending on wind conditions and coastal orientation, surface waters can be pushed away from the coast and, therefore, cold waters arise from deeper layers towards the surface. This phenomenon takes place in different areas around the world, varying in intensity, frequency and area of influence (Wang *et al.* 2015). On the other hand, the variability in upwelling events may also be related to global-scale phenomena, such as the major upwelling off the Peruvian coast, which vanishes during El Niño phases.

Globally, four major high-intensity coastal upwelling events are found, all of them associated with an Eastern Boundary Current (EBC), which in turn closes the subtropical gyres in the eastern part of the ocean basins, adjacent to the western coastal sides of continents. The association between EBCs and upwelling systems is also referred to as Eastern Boundary Upwelling Ecosystems (EBUEs), because the distribution of several marine organisms is influenced by these systems (Fréon *et al.* 2009). Moreover, in other parts of the globe, the upwelling events and their role in marine ecosystems explain the distribution of many marine species (Guimaraens & Coutinho 1996; Macpherson 2002; Fréon *et al.* 2009; Menge & Menge 2013; Armbrecht *et al.* 2014; Fenberg *et al.* 2015; Lourenço *et al.* 2016).

In addition, the upwelling cold waters reduce the evaporation, minimizing precipitation over the coastal zone, and thus increasing aridity, mainly in the regions of EBUEs (Shi *et al.* 2000a; Stuut *et al.* 2002; Houston & Hartley 2003). Thus, high upwelling intensities can be considered an environmental harshness for mangrove ecosystems (Jacobsen & Dangles 2012; Marks *et al.* 2016).

Our approach is supported by the spatial patterns agreement between the distribution limits of mangroves and the area of influence of upwelling systems at specific locations based on several scientific studies.

The aim of this work is to analyse the patterns of the mangrove distribution limits and their association with upwelling zones on a global scale. We propose to answer three questions: (i) Can spatial patterns of mangrove limits and discontinuities be explained by upwelling systems? (ii) Does the abundance of mangroves differ in areas with different levels of upwelling intensity? and (iii) are the two major mangrove biogeographic regions (Atlantic East Pacific and the Indo-West Pacific) environmentally similar with respect to the upwelling intensity? Our hypothesis is that upwelling affects geographical range limits and abundance of mangroves on a global scale.

2. **Methods**

The continuous and predictable/seasonal global upwelling importance/intensity was accessed using the DataBasin product provided by The Nature Conservancy (Hoekstra *et al.* 2010). To verify the upwelling intensities, we used a map indicating four levels of upwelling intensity, as defined by Hoekstra *et al.* (2010): 1 (present), 2 (significant), 3 (important) and 4 (very important). The four levels are also defined as a rank of upwelling intensity, level 1 and 2 are low; level 3 is intermediate; and level 4 is high.

The upwelling intensity map (Hoekstra *et al.* 2010) is indicated for each Marine Province *sensu* Spalding *et al.* (2007) to represent and estimate the area of upwelling influence. The influence of the upwelling systems is localised around specific coordinates along inshore waters, but the global upwelling database map uses the Marine Provinces to display data on upwelling intensity (see maps in results). For this study, these provinces were useful in order to select the mangrove point samples and give them their respective upwelling intensity value and to incorporate this into a geodatabase.

In spite of this reduction in resolution to visualise on a global scale, the upwelling patterns remain clearly visible (see the EBUEs) and the area of influence of the upwelling intensities are spatially heterogeneous. Although the upwelling intensity database seems well represented on a global scale, on a regional scale, some of the important upwelling zones are not represented on the map. The regional upwelling systems were assessed based on scientific literature and they were summarised in a map (Figures 1, 3 and 4) and table (Appendix S1) in order to show visually the spatial agreement among upwelling zones at mangrove limits, and mangrove discontinuities in distribution.

The mangrove ranges used were based on a combination of the maps by Spalding *et al.* (1997, 2010) and Giri *et al.* (2011), the methods to extract these data are better described in Ximenes *et al.* (2016). In short, the same methods as proposed by Ximenes *et al.* (2016) were applied on a global scale for mangrove distribution, following the sequence: (i) Conversion of the mangrove distribution map produced by Spalding *et al.* (1997) into points, (ii) data filtering to reduce redundant point locations, (iii) manual inclusion of mangrove location as observed from Giri *et al.* (2011) and Spalding *et al.* (2010) that were missing in Spalding *et al.* (1997). For instance, Spalding *et al.* (2010) mapped mangrove patches on the western coast of Australia that were not found on other maps and were included to complement the mangrove distribution. Moreover, to confirm the locations of the worldwide mangrove limits we used the study by Quisthoudt *et al.* (2012).

Although, the mangrove maps by Spalding *et al.* (2010) and Giri *et al.* (2011) are probably more accurate than the Spalding *et al.* (1997) map, Ximenes (2015) concluded that the oldest World Atlas of Mangrove version is lighter to manipulate and consequently facilitating computational analysis. Because in the oldest version, mangrove polygons are fewer in number and less fragmented than in other maps, reducing oversampling. However, oversampling persisted at determined locations and some point samples were excluded without losing the geographical representation of mangrove distribution (more detailed procedures are given in Ximenes *et al.* (2016). Although the point samples were reduced, the number of points at a certain location can still be used as a proxy for the abundance of mangrove patches, where places with a large abundance of mangroves have a higher number of points and places with a lower abundance of mangroves have fewer points.

The mangrove locations are spread worldwide with a total of 6362 points. However, many of the oceanic islands were marked as having no data in the upwelling database, because of a lack of information for specific regions (Hoekstra *et al.* 2010); in this sense, 600 points were localised in the Maldives islands while for many parts of Myanmar, Thailand, Indonesia, Melanesia, Micronesia and Polynesia there was no upwelling data. These point samples were excluded from the analysis. Finally, a total of 5762 points were used, with 3299 points from the Indo-West Pacific (IWP) and 2463 points from the Atlantic East Pacific (AEP).

ArcGIS desktop 10.3 (ESRI 2011) was used to manipulate the data collection. The statistical analyses were computed using RStudio 1.1.423 (R Core Team 2013).

3. Results

All the strongest EBUEs, the four major upwelling zones, are found in the AEP region, where they show a spatial agreement with the absence of mangrove and near to their limits in these regions (Figure 1, 3 and 4). Note that level 4 is present only in the EBUEs zones of the Pacific and Atlantic Oceans (Figure 1). Mangroves were more abundant in lower upwelling intensity regions than in higher intensities (Figure 2).

Few species localized in Mauritania, which is influenced by the Canary upwelling (high upwelling intensity level), could access this area, though this need not be the only cause of low species richness. Therefore, in general the limits of the mangrove range remained outside the boundary of the highest intensity of upwelling (Figure 3 and 4). The highest upwelling intensity cannot be observed in the IWP region (i.e. weaker than the four major EBUEs), but there are at least five important upwelling zones in this region that coincide with mangrove range limits (Figure 3) and mangrove discontinuities, such as; in the Somalia-Oman Complex, along the west coast of India, and along the south coast of Australia (Figure 4). In this context, the coastal distribution of SST is tightly influenced by upwelling cold waters that do not follow a specific SST isotherm.

Along the west coast of Australia there are minor upwelling intensities (Ningaloo, Capes Currents) due to the Leeuwin Current poleward warm water, which forms the only exception to the EBC main characteristics. The West Boundary Currents (WBC) are characterised by a strong flow (compared to the EBCs), narrow, deep and fast currents that inhibit the development of strong upwelling intensity, but the presence of upwelling zones in the WBC are relevant for mangroves due to their spatial coincidence of the phenomenon and the mangrove species range and limit. The WBC transports warm waters to high latitude regions at each subtropical gyre closing the gyre in the western part of the ocean basin (Eastern side of continents).

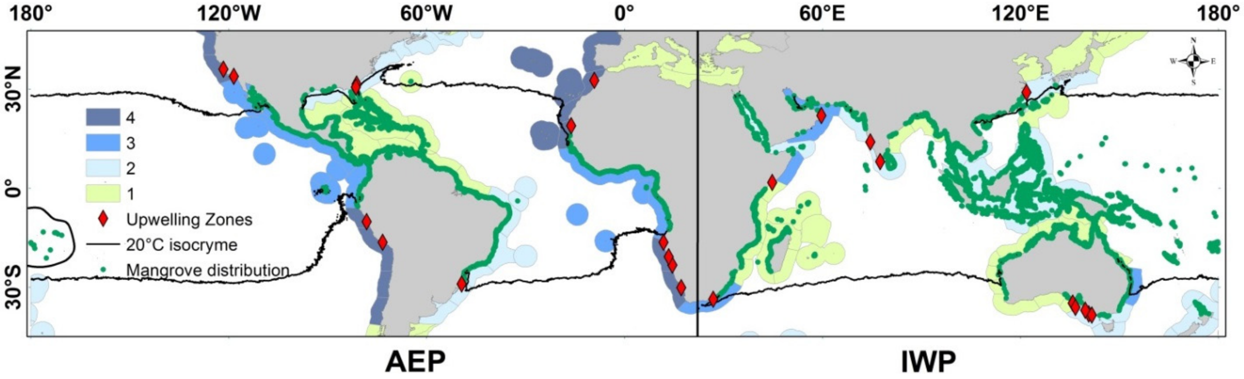

Figure 1: The upwelling intensity map (Hoekstra *et al.* 2010) is indicated for each marine province *sensu* Spalding et al. (2007). The red diamonds are the upwelling zones that were included based on scientific literature (Appendix S1). Specific buffer zones of the upwelling influence in adjacent red diamonds are more clearly detailed in Figures 3 and 4. The horizontal black line represents the 20°C isocryme of SST that was extracted from the BIO-Oracle database (Tyberghein *et al.* 2012) and generated in ArcGIS 10.3. The longitudinal black line is the division of the two major biogeographic regions; the Atlantic East Pacific (AEP) and the Indo West Pacific (IWP), and the black line surrounding the Pacific archipelagoes is part of IWP region (Saenger *et al.* 1983; Duke 1992).

We found much coincidence of upwelling zones and mangrove latitudinal range limits, with the exception of western Australia, south Australia, New Zealand and south Japan. These mangrove range limits are mainly restricted by minimum temperature and rainfall (Saenger 2002; Duke 2006; Semeniuk 2013; Osland *et al.* 2017b). Besides, in south Australia we found upwelling zones coinciding with absent of mangroves (e.g. Bonney upwelling) (Figure 4c).

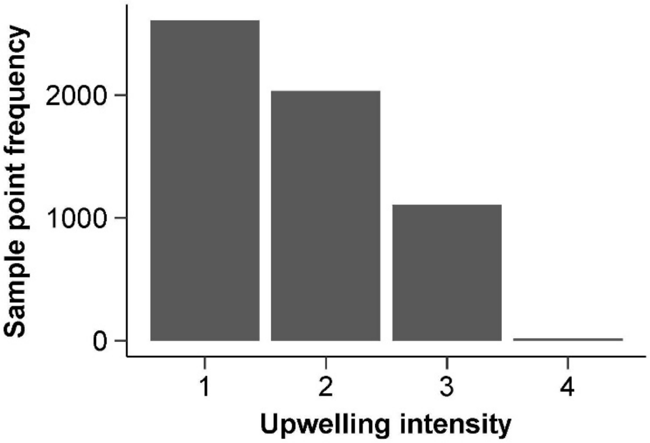

Figure 2: (a) Histogram of the frequency of mangrove point sample locations for each upwelling intensity value (n= 5762). Additional details on upwelling intensity are found in Figure 1.

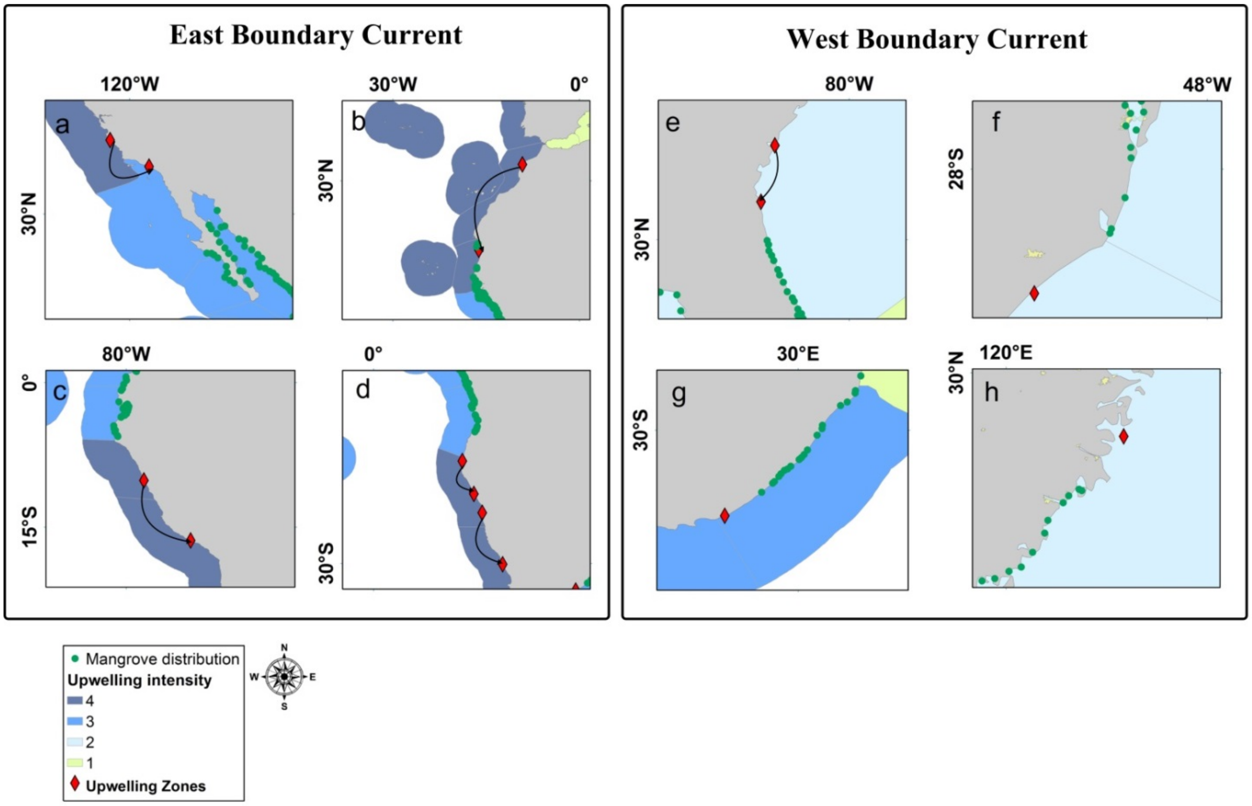

Figure 3. Detailed georeferenced upwelling zones (red diamonds, Appendix S1) and the upwelling intensity map (Hoekstra *et al.* 2010). The black lines connecting the red diamonds show an approximate upwelling zone of influence and when the red diamonds are alone it means that only the surrounding area is influenced by the upwelling. The East Boundary Currents (EBCs) are mainly characterised by weak flows (compared to the WBCs), shallow and broad currents that favour the development of the strongest upwelling intensities in the globe (a) California upwelling zone (b) Canary Upwelling along the west coast of Africa (c) Peruvian upwelling (related to the Humboldt Current) along the west coast of South America (d) Benguela Upwelling along the south west coast of Africa (e) the east coast of Florida (f) the upwelling in Cabo de Santa Marta near to the eastern South American mangrove limits. (g) Agulhas upwelling in South Africa (h) Yuedong upwelling in south China.

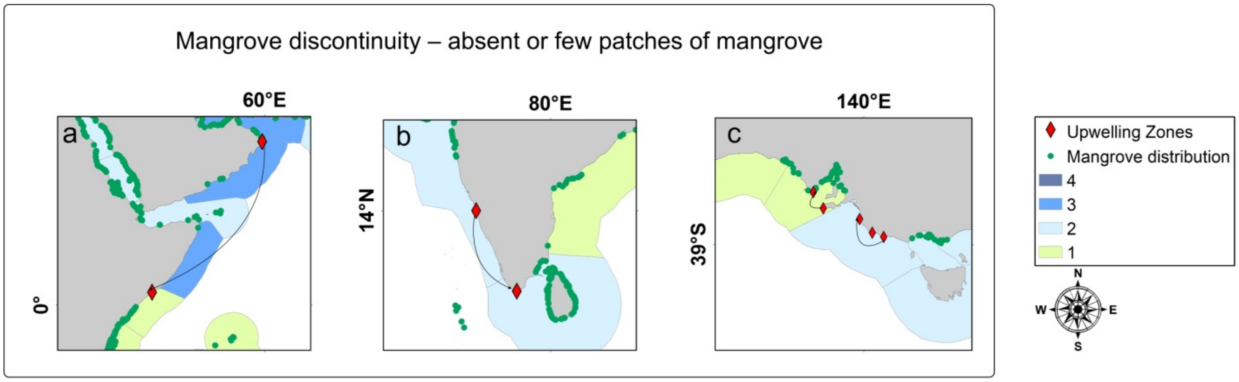

Figure 4: Detailed georeferenced upwelling zones (red diamonds, Appendix S1) and the upwelling intensity map (Hoekstra *et al.* 2010). The black lines are connecting the red diamonds with an approximate upwelling zone of influence and when the red diamonds are alone it means that only the surrounding area is influenced by the upwelling. (a) An upwelling zone in the Somalia-Oman Complex upwelling, resulting in few mangrove patches on the north coast of Somalia and Oman in the localities of upwelling zones, where the range abundance in the Red Sea further north but in the absence of upwelling, is higher again (b) The absence of mangroves along the west coast of India, coinciding with the Arabian upwelling zone. (c) Bonney upwelling along the south coast of Australia, coinciding with absence of mangroves.

4. Discussion and Conclusion

4.1. The weaker EBCs favour the upwelling phenomena and inhibit the expansion of mangroves into higher latitudes

Onshore waters from the relatively weaker EBCs, combined with the effect of upwelling-favourable alongshore winds, are easily deflected offshore, favouring the deep cold waters towards the surface due to coastal divergence driven by cross-shore Ekman transport. Hence, the most prominent upwelling systems that may act as barriers to the dispersal of mangrove propagules are at the EBCs in the AEP region, where we find the mangrove limits along the western coastlines of Africa and West-America. In this, we agree with other authors (Chapman 1975; Woodroffe & Grindrod 1991; Lacerda & Schaeffer-Novelli 1999; Lacerda 2002).

The cold waters and aridity are associated with upwelling zones directly or indirectly. Aridity is an important variable explaining mangrove limits in some parts of the world (Duke 1992; Saenger 2002; Quisthoudt *et al.* 2012; Osland *et al.* 2017b). Some studies suggested that the northernmost mangrove limit on the southwestern coast of Africa is more driven by aridity, rather than by temperature (Saenger & Bellan 1995). More recently, Osland *et al.* (2017b) suggested that the western sides of the continents (Peru, Mauritania and Namibia) are more likely to be affected by changes in precipitation rather than by temperature, with exception of the western coastline of Australian and California where both variables are associated.

Yet, it is well-established that upwelling events trigger arid conditions, as colder waters reduce evaporation and, consequently cause strong temperature inversions and minimize precipitation (Shi *et al.* 2000a; Adams 2007). Thus, the oceanographic conditions promoted by the strongest upwelling systems associated to EBCs (i.e. EBUEs) affect the adjacent terrestrial regions, where deserts are formed. The Atacama Desert (Peruvian upwelling) (Houston & Hartley 2003), Baja Californian and Sonoran Desert (Californian upwelling), Sahara Desert (Canary upwelling) and Namibia Desert (Benguela upwelling) are all associated with upwelling zones (Shi et al. 2000a; Adams 2007). In the northern part of the Arabian Sea, the seasonal upwelling events also contribute to the aridity of that coastal zone (Lacerda 2002). For this reason, since the intensification of upwelling events can also intensify aridity in certain regions, and together they affect the terrestrial vegetation patterns (Shi *et al.* 2000a).

In line with general EBC patterns elsewhere, the western coast of Australia should also have a strong upwelling zone. However, the Leeuwin Current inhibits high upwelling intensities in this region making the western coast of Australia an exception to these global EBC patterns (see next section).

4.3. The Leeuwin Current inhibits strong upwelling events and influences mangrove expansion along the western coast of Australia

We argue that the underlying causes of mangrove expansion along the western coast of Australia are linked to the inhibition of strong upwelling intensity. Hence, our results confirm that the occurrence of mangroves on the western coast of Australia is influenced by the anomalous coastal warm currents of the Leeuwin Current, as proposed by Semeniuk *et al.* (2000).

The association between Leeuwin Current and warm water marine species dispersed along the southwestern Australian coast was identified in earlier studies (Morgan & Wells 1991), and causes a discrepancy with the western coasts of South America and south western coasts of Africa, which are both influenced by the EBCs on the western sides of the continents and where strong upwelling intensities are found. The equatorward West Australian Current is shifted offshore by the poleward Leeuwin Current, which transports warm waters in winter from near equatorial regions along the west coast of Australia (Pearce 1991; Smith *et al.* 1991). The north-south thermohaline gradients between waters from the Indonesian Throughflow and the south western region of Australia are considered as the primary forcing to the poleward Leeuwin Current (Batteen *et al.* 2007). This current is also responsible for inhibiting the development of strong upwelling cells, despite the favourable winds (Hanson *et al.* 2005; Varela *et al.* 2015). Based on this, we suggest that the Leeuwin Current may permit mangroves to extend beyond 30°S on the western coast of Australia, given the low upwelling intensities in this region. Along the western coast of Australia, studies suggested that restricted mangrove expansion is due to the influence of upwelling systems (Chapman 1975; Woodroffe & Grindrod 1991). Although, large intensities of upwelling are incompatible on the western coast of Australia (Varela *et al.* 2015), variations in the Leeuwin Currents allow minor seasonal upwelling, particularly in Ningaloo (23–25°S) (Woo *et al.* 2006) and Cape Currents (26–28°S) (Gersbach *et al.* 1999). These two upwelling zones along the western coast of Australia are geographically near to a decrease of species richness; from six species and one hybrid (*Avicennia marina, A. marina* var. *marina, Aegiceras corniculatum* (L.) Blanco, *Aegialitis annulata* R. Brown, *Bruguiera exaristata* Ding Hou, *Ceriops australis* (C.T.White) Ballment, T.J.Sm. & J.A.Stoddart and *Rhizophora stylosa* Griff.) to just one species of *A. marina* and one hybrid *A. marina* var. *marina* that are distributed along the west coast of Australia (Duke 2006; Spalding *et al.* 2010).

Along the southern shelves of Australia, where the Leeuwin Current is less strong, there is the Bonney upwelling affecting the coast between Portland and Cape Jaffa (Rochford 1977; Kämpf 2015) and also off the southern tip of the Eyre Peninsula and off the southwestern coast of Kangaroo Island at the southern end of Gulf St. Vincent (Kämpf *et al.* 2004), which probably contributes to the absence of mangroves in these regions.

4.4. *WBCs enable mangroves to reach higher latitudes by inhibiting strong upwelling intensities, but minor upwelling still exists which influences mangrove limits*

The intensity of the upwelling phenomena is lower for WBCs, but they still exist with lower intensity than for EBCs. The expansion of mangroves towards higher latitudes in the two major biogeographic regions (AEP and IWP) can be explained by the fact that the WBCs are much stronger, warmer and faster currents than their eastern counterparts, the EBCs. These currents are unfavourable for upwelling resurgence and inhibit higher upwelling intensity when compared to EBC. For instance, the mangrove expansions in Bermuda (32°20'N) and Japan (32°22'N) are associated to the WBCs of the warm waters of the Gulf Stream and Kuroshio currents, respectively (Woodroffe & Grindrod 1991). These currents create suitable habitats favouring the flourishing of mangroves to higher latitudes (Woodroffe & Grindrod 1991). The WBCs are also found associated with high latitudinal mangrove limits, such as the Brazil Currents on the eastern coast of South America (28°55'S) (Soares *et al.* 2012), and the Agulhas Currents on the east coast of South Africa (32°36'S).

The presence of the upwelling cold waters along the east coast of Florida has been recorded for over 70 years (Green 1944; Taylor & Stewart 1959; Smith 1983; Pitts & Smith 1997). Other upwelling zones are found in lower latitudes on the east coast of Florida, from Daytona Beach to Fort Pierce inlet, and in these mangroves we observed a decrease of species richness and at the Fernandina Beach we found an upwelling just beyond the limits of the mangrove. Nevertheless, during winter the intensity and frequency of the extreme cold events are pointed out as the main reasons that cause the retraction and expansion of mangroves in the eastern North Atlantic, i.e. in Florida state (Osland *et al.* 2013; Cavanaugh *et al.* 2014). Although the decrease of mangrove cover using historical satellite images are significantly associated with extreme cold events of air temperature during winter (Cavanaugh *et al.* 2014), the upwelling phenomenon is seasonal and occurs mainly during summer in that region (Taylor & Stewart 1959; Smith 1983; Pitts & Smith 1997) from 29°N to 31.5°N (Aretxabaleta *et al.* 2007) which coincides with the limit of mangroves in and beyond that region.

Along the South African coast, mangroves can be observed above Port Alfred, but their limits are influenced by the cold inshore waters from the Agulhas upwelling at Port Alfred and Port Elizabeth (Lutjeharms *et al.* 2000) which coincides with an absence of mangroves.

4.5. *Red Sea - East Africa - Middle East and west India*

Along the east African coast, there is the Somalian upwelling (Izumo *et al.* 2008) which also coincides with the absence of mangroves. A few mangrove patches appear in northern Somalia, and between north Somalia and Oman, the Oman upwelling system (Elliott & Savidge 1990; Shi *et al.* 2000b; Izumo *et al.* 2008) causes a discontinuity distribution of the mangrove range or localised mangroves with few sites supported by a single species only (*Avicennia marina*). Along the western coast of India, the south-eastern Arabian Sea upwelling has an influence between 8° and 14°N (Smitha *et al.* 2014) coinciding with the absence of mangroves at those latitudes, while mangroves only occur on the west Indian coast up to 18°N (Figure 5).

5. Final Considerations

It is possible to conclude that depending on the intensity and frequency (of occurrence) level of the upwelling phenomenon, the response of mangrove ecosystems will probably be different. For instance, mangroves are usually distant from the strongest upwelling zones of EBCs, while mangroves are much closer to the upwelling zones of the WBCs, where there are more tolerant species, such as *Avicennia marina* in Australia. In addition, the upwelling phenomenon with minor intensities probably function as an additional factor although they are present only for a few weeks of the year, however, they are at an important time when there is a peak of propagules that occurs mainly in the spring-summer seasons, when for example the upwelling events occur in Brazil and Florida.

At the AEP regions, the EBCs' weaker currents can favour the development of strong upwelling intensities along the western coast of Africa and South America. Low temperatures and conditions of aridity have been used by other authors to explain mangrove limits, and the upwelling phenomenon is intrinsically associated with these constraining conditions of low sea temperatures and indirectly by aridity revealing environmental harshness factors that can help us elucidating important biogeographic questions on mangrove ecosystems. Thus, the restricted distribution of mangroves in EBCs is likely because of high upwelling intensity, rather than the effect of the sea current itself. The sea currents influence the entire coastlines, while the upwelling phenomena occur in specific zones, which coincide with a lack of mangroves and near their limits..

Detailed information about the differences of EBC and WBC and their association with upwelling and mangrove limits have been presented here. Also we consider that the EBCs are weaker than the WBCs which favour strong upwelling intensity zones, while the WBCs that are strong currents inhibit strong upwelling. Thus, we suggest that mangroves can reach higher latitudes in the IWP than in the AEP, due to the absence of strong upwelling intensities in the IWP region which is influenced by the WBCs and hence has a more suitable climate for mangroves.

The authors believe that these currents that can inhibit or favour the upwelling zones are associated with the retraction and expansion of the range of mangrove species. Thus, we believe that a better understanding of the effects of upwelling on mangroves will improve the scientific debate on mangrove species range retraction and/or expansion. Osland et al. (2016) highlighted the fact that climate change research of coastal wetlands currently focuses on one single driver; projections in the rise of the sea level, while other macro-ecological variables, such as sea surface temperature, air temperature and precipitation have received less attention. In this study, we draw attention to the importance of including upwelling intensification to assess mangrove ecosystems.

Future climate change scenarios of upwelling systems show an increase or decrease in their intensities for different parts of the world and these changes are expected to modify coastal winds and sea surface temperatures (Bakun 1990; Sydeman *et al.* 2014; Varela *et al.* 2015; Wang *et al.* 2015). This will most likely affect mangrove distribution. In addition, these scenarios of climate change may be intensified by the effects of a rise in sea levels (Lovelock *et al.* 2015). This study highlights the main upwelling regions and other minor systems which potentially affect mangrove distribution. Although satellite imagery has improved our scientific knowledge of intensity and spatial variability of upwelling systems, however, probably many of them still need to be identified.

We expect that these new findings will foster new perspectives on mangrove research, in which experts may take into account the upwelling systems besides other determinants to better understand the distribution of mangrove range limits.

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Appendix S1 – List of upwelling systems locations coinciding with mangrove range limits and mangrove species limits. These locations are shown in geographic maps in Figures 1, 3 and 4.

Country	Region	Upwelling or location	Mangrove reference	Upwelling Reference
Mauritania	North West Africa	Canary	(Chapman 1975)	(Sydeman *et al.* 2014; Wang *et al.* 2015)
Angola	South West Africa	Benguela	(Chapman 1975)	(Sydeman *et al.* 2014; Wang *et al.* 2015)
Peru	West South America	Humboldt or Peruvian	(Chapman 1975; Woodroffe & Grindrod 1991; Lacerda & Schaeffer-Novelli 1999)	(Sydeman *et al.* 2014; Wang *et al.* 2015)
United States of America	West North America	California	This study	(Sydeman *et al.* 2014; Varela *et al.* 2015; Wang *et al.* 2015)
	East North America	Florida (Bright South Atlantic)	This study	(Green 1944; Taylor & Stewart 1959; Smith 1983; Pitts & Smith 1997)
Brazil	South of Brazil	Santa Marta Cape	(Soares *et al.* 2012)	(Campos *et al.* 2013)
South Africa	South Africa	Agulhas	This study	(Lutjeharms *et al.* 2000)
Somalia	South Somalia	Somalian	This study	(Izumo *et al.* 2008; Varela *et al.* 2015)
Oman	Middle East	Oman	This study	(Savidge *et al.* 1990; Shi *et al.* 2000b)
India	West India	Southeastern Arabian	This study	(Smitha *et al.* 2014)
Australia	South Australia	Bonney	This study	(Rochford 1977; Kämpf 2015)
China	South China	Yuedong	This study	(Xie *et al.* 2003; Jing *et al.* 2009)

CHAPTER 4

Spatial Assessment of the Bioclimatic and Environmental Factors Driving Mangrove Tree Species' Distribution along the Brazilian Coastline

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"The rules of scientific investigation always require us, when we enter the domains of conjecture, to adopt that hypothesis by which the greatest number of known facts and phenomena may be reconciled."

Matthew Fontaine Maury

(The Pathfinder of the Seas)

remote sensing

Article

Spatial Assessment of the Bioclimatic and Environmental Factors Driving Mangrove Tree Species' Distribution along the Brazilian Coastline

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Abstract: Brazil has one of the largest mangrove surfaces worldwide. Due to a wide latitudinal distribution, Brazilian mangroves can be found within a large range of environmental conditions. However, little attention has been given to the description of environmental variables driving the distribution of mangrove species in Brazil. In this study, we present a novel and unprecedented description of environmental conditions for all mangroves along the Brazilian coast focusing on species limits. We apply a descriptive statistics and data-driven approach using Self-Organizing Maps and we combine data from terrestrial and marine environmental geodatabases in a Geographical Information System. We evaluate 25 environmental variables (21 bioclimatic variables, three sea surface temperature derivates, and salinity). The results reveal three groups of correlated variables: (i) air temperature derivates and sea surface temperature derivates; (ii) air temperature, potential evapotranspiration and precipitation derivates; and (iii) precipitation derivates, aridity and salinity. Our results unveil new locations of extreme values of temperature and precipitation. We conclude that *Rhizophora harrisonii* and *Rhizophora racemosa* are more limited by precipitation and aridity and that they do not necessarily follow a latitudinal gradient. Our data also reveal that the lowest air temperatures of the coldest month are not necessarily found at the southernmost limits of mangroves in Brazil; instead they are localized at the Mesoregion of Vale do Itajaí. However, the minimum sea surface temperature drops gradually with higher latitudes in the Brazilian southern hemisphere and is probably a better indicator for the decrease of species at the latitudinal limits of mangroves than the air temperature and precipitation.

Keywords: wetland; climate; conservation; remote sensing; data-driven; data intensive science; Rhizophoraceae; Acanthaceae

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1. Introduction

Understanding the influence of climate on the distribution of mangrove species is still a major challenge for science. Previous studies have shown that rainfall and temperature are commonly the main drivers of forest structure and species composition variability in the tropics [1]. However, in regions such as the Brazilian coast, where the latitudinal gradient is associated with a large climatic variability, the environmental conditions driving mangrove characteristics are still not fully understood [2,3].

Strikingly, only one study carried out by Schaeffer-Novelli *et al.* [2] has so far assessed the environmental factors on the coastline range of the Brazilian mangroves that was instrumental in improving our understanding of mangrove ecosystems. At the time of the study [2], several bottlenecks limited a more comprehensive and detailed assessment to understand the main climate pattern for Brazilian mangroves. However, the climatic database used by the previous study [2] is over 40 years old (Brazilian Ministry of Agriculture, 1972) with few climatic data samples coming mainly from states' capitals. Given these bottlenecks, the spatial variability of environmental conditions in the major Brazilian coastal mangroves is still unknown, considerably increasing uncertainties on the characterization of mangrove structure and species' composition.

Currently, the availability of satellite data for ocean, meteorological stations and spatially interpolated climate surfaces with high resolution have improved environmental information in sites where there is a lack of local data [4–6] and have integrated them in Geographical Information Systems (GIS). These remote sensing products and spatially interpolated surfaces enable us to obtain information that a few decades ago was not available. Thus far, the most recent environmental databases [4–6] and mangrove mappings [7–9], have not yet been used to update the environmental characterization of Brazilian mangroves. Therefore this large quantity of data creates an opportunity for scientists that requires new big data analysis techniques and tools [10–12]. Responding to this need, science that takes a "data-driven" approach is now emerging [10] in which the information is extrapolated from the data.

In this context, the Self-Organizing Maps (SOM) [13] provide a "data-driven" approach that it is supported by tools of data representation, mainly characteristic of data abstraction enhanced by visualization techniques [14–15]. The SOM have been used in several applications, such as mapping ecological and biogeographical features [16–20], determination of the most suitable sites for forest restoration [21] and selecting bioclimatic variables for species distribution modeling in the Brazilian north region [22]. The main advantage of the SOM algorithm as a data-driven approach is that it does not need to assume any *a priori* hypotheses [14,23]; it still has a robustness when data behavior is unknown and it shows the multivariate data cloud through visualization tools [14,23] or rather as geovisualization tools [14]. The SOM's ability to preserve the topological structure of the input data [14,23] provides a powerful advantage in studies with geospatial analysis [15]. Giraudel and Lek [24] compared the SOM with Principal Component Analysis (PCA) and Correspondence Analysis and they found similar results, with the latter two validating the SOM methods. Hence, SOM or a combination of SOM and ordination analysis seems to be a promising technique in ecological studies to explore multivariate data.

This study focuses on the ecological biogeography of finding patterns in the distribution of species that are constrained by bioclimatic and environmental variables [25], and due to the wide latitudinal and longitudinal range of the Brazilian mangroves, climate has a strong influence on the delimitation of species limits.

In short, we address the following questions: Which environmental variables influence the spatial distribution of mangrove species? Can the bioclimate and environmental data at higher temporal and spatial resolution improve the characterization of the Brazilian mangrove ecosystems? To answer these questions, we have set out four objectives: (i) to update the information on climatic and salinity conditions in Brazilian mangroves using the most recent environmental databases; (ii) to overcome data gaps found in the previous studies; (iii) to cluster relevant environmental variables according to their spatial dependence; and (iv) to provide a better understanding of the fundamental niche [26] of the mangrove plant species. With that in mind, we present an unprecedented data-intensive approach for the assessment of the environmental variables that drive species composition/distribution in mangroves along the entire Brazilian coastline.

2. Material and Methods

2.1. Study Area

Brazil has one of the largest areas and extension of mangroves found from the northern coast, starting at the Oiapoque River (04°30′N) in the state of Amapá, to the southern coast in the state of Santa Catarina (28°30′S) [2,7]. There is a minor discrepancy in its estimated size: it ranks third with a total of 7% of the global mangrove forests [9] while Spalding *et al.* [8] rank it second with a total of 8.5% of mangrove area worldwide. All in all, Brazil contains a huge area with approximately 50% of South America’s mangroves [27] stretching over a 6780 km coastline [28].

Figure 1. Mangrove species richness. The sample point distribution of Brazilian mangroves is colored by species richness (n = 390) and the species limits are shown by yellow circles (detailed information in Table 1). Brazil has 16 coastal states with mangroves. Two-letter codes represent States, whereas dots represent our samples, both of which are given below between parentheses. In the north, we have: Amapá (AP—34) and Pará (PA—64); in the northeast: Maranhão (MA—70), Piauí (PI—3), Ceará (CE—19), Rio Grande do Norte (RN—15), Paraíba (PB—10), Pernambuco (PE—10), Alagoas (AL—13), Sergipe (SE—11) and Bahia (BA—57); in the southeast: Espírito Santo (ES—15), Rio de Janeiro (RJ—25), São Paulo (SP—16); and in the south: Paraná (PR—11) and Santa Catarina (SC—17).

Brazil is politically divided in 26 states, among which 16 are lined with mangroves (Figure 1) and were represented in the neural map. We represent these 16 political divisions to be in the neural map, because they are commonly used to define public policy in Brazil. Furthermore, these political boundaries provide more coastal segments than the seven regions proposed by Schaeffer Novelli *et al.* [2]. However, because the political boundaries or states are not ecologically representative, we also used the latitudinal variation as an independent variable for the scatterplots.

Table 1. Brazilian mangroves species and their respective distribution limits from north to south (summary adapted from [29]).

SPECIES	SPECIES Abbreviation	FAMILY	LOCATION	LATITUDE		STATE
				Degrees	Decimal	
Rhizophora harrisonii Leechman	*R. harrisonii*	Rhizophoraceae	Preguiças River	2° 40'S	2.6° S	Maranhão, MA
Rhizophora racemosa G.F.W. Meyer	*R. racemosa*	Rhizophoraceae	Preguiças River	2° 40'S	2.6° S	Maranhão, MA
Avicennia germinans L.	*A. germinans*	Acanthaceae	Atafona	21° 37'S	21.6° S	Rio de Janeiro, RJ
Conocarpus erectus L.	*C. erectus*	Combretaceae	Araruama	22° 55'S	22.9° S	Rio de Janeiro, RJ
Rhizophora mangle L.	*R. mangle*	Rhizophoraceae	Praia do Sonho	27° 53'S	27.8° S	Santa Catarina, SC
Laguncularia racemosa Gaertn.	*L. racemosa*	Combretaceae	Laguna	28° 30'S	28.5° S	Santa Catarina, SC
Avicennia schaueriana Stapf. and Leech	*A. schaueriana*	Acanthaceae	Laguna	28° 30'S	28.5° S	Santa Catarina, SC

The term "species limits" is defined as the spatial boundaries beyond which no living individuals of a given species occur. In this study, we use this term to describe the latitudinal limits of mangrove species across the Brazilian coastline in a southerly direction to provide an overview of the effects of climate on the species distribution.

From the literature, we found the species limits of seven mangrove shrubs/trees occurring in Brazil (see in: Lacerda *et al*. [29]; Table 1). The mangrove plant species have their northernmost limit beyond the Brazilian border, so our attention will focus on the southernmost limits of the species. The mangrove plant species limits are localized in three states: in Maranhão (MA) for *Rhizophora racemosa* and *Rhizophora harrisonii* (northeast limit); in Rio de Janeiro (RJ) for *Avicennia germinans* and *Conocarpus erectus* (southeast limit); and in Santa Catarina (SC) for *Rhizophora mangle, Avicennia schaueriana* and *Laguncularia racemosa* (south limit), the latter of which is also the limit of Brazilian mangroves as a whole. Those with wider distribution, reaching the limit of the Brazilian mangroves, are *Avicennia schaueriana* and *Laguncularia racemosa*, whereas *Rhizophora mangle* occurs up to 75 km north of that limit (Table 1).

2.2. Environmental Geodatabase

There are different techniques for mangrove mapping [30,31]. For example, at local scale, a very high-resolution image of QuickBird was used to evaluate the extent of mangrove forest area and *in situ* measurement was used to calibrate and estimate the "leaf area index" that enable us to detect the mangrove forest condition [32]. Moreover, McCarthy *et al.* [33] who were studying the coastal wetlands in Tampa Bay, Florida, USA used very high-resolution of the WorldView-2 images providing a better accuracy than previous studies that used low spatial resolution images. However, the small area coverage offered by very high-resolution images is a limitation when there is a need for a regional or global mapping [30] and for this reason, until now there is no global or regional mapping using very high-resolution images for mapping.

Currently, there are three main data sources of worldwide mangrove mapping, developed by Spalding *et al.* [7]; Spalding *et al.* [8]; and Giri *et al.* [9]. These three maps were compared by Ximenes [34], concluding that the Spalding *et al.* [7] map can be useful for global conservation projects because of the lighter data files due to the lower number of mangrove patches compared with the newest maps that facilitate geoprocessing analysis. The Spalding *et al.* [7] maps were hand-drawn by experts visually delineating mangroves using satellite images (such as NOAA-AVHRR (National Oceanic and Atmospheric Administration / Advanced Very High Resolution Radiometer), LANDSAT (Land Remote Sensing Satellite Program), SPOT (Satellite Pour l'Observation de la Terre) and ERS-1 (European Remote Sensing Satellite)) and their methods included small water bodies and barren land ecotones found inside the mangrove forests. In contrast, Giri *et al.* [9] mapped mangroves excluding water bodies and barren lands in order to keep only the forest, creating a more fragmented mangrove.

Figure 2 describes the detailed methodological procedures that will be explained in the next chapter. However, our line of inquiry and scientific questions are outlined in the introduction of this study.

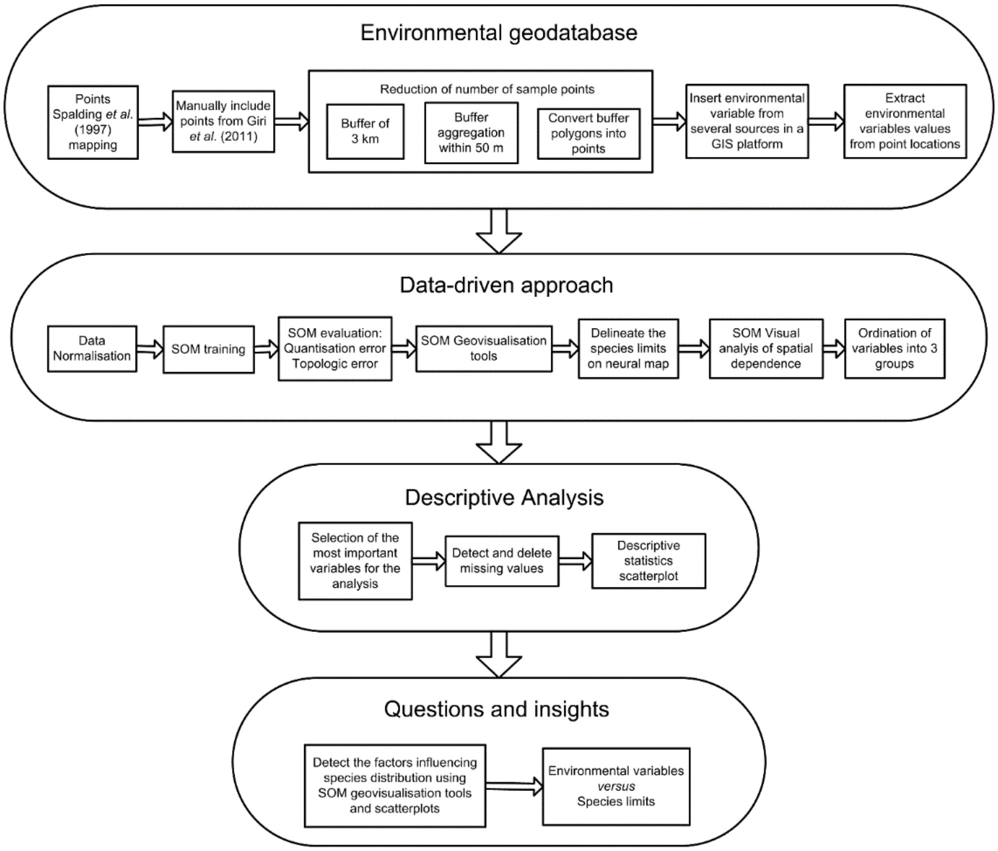

Figure 2. Methodological framework. Framework of the methodology applied in this study following four main steps. We refer to the text for methodological details.

For these reasons, the Spalding *et al.* [7] map was chosen to represent the location of mangrove forests, as in this study we needed to obtain at least one point for each mangrove location, rather than an accurate mangrove area. Furthermore, mangrove patches (=polygons) mapped by Spalding *et al.* [7] appear less fragmented, producing fewer cartographic point samples, which in turn correspond to the centroids of the mangrove patches, hence reducing redundant data. This fact can be explained by the low spatial resolution images used by Spalding *et al.* [7] that may exaggerate, exclude or reduce the mangrove areas, respectively by aggregating huge mangrove patches, or excluding small patches, that have a lower mangrove area size than the minimum area required for mapping. However, the Giri *et al.* [9] mangrove map was used to manually include mangroves that were not available in Spalding *et al.* [7].

Despite choosing a lower resolution mangrove map of Spalding *et al.* [7], the sample points were still numerous, and some redundant. The redundant sample points (*i.e.*, sample points located too close to each other) were deleted, given that they represented the same information in the environmental database (see below). To reduce the number of samples and eliminate redundant data, we applied a 3 km buffer around the center of each sample point and aggregated all buffers located within a distance of 50 m, creating a minimum distance between points of 6 km.

Once the data had been cleaned, an environmental geodatabase was assembled in a GIS platform with 25 environmental variables including bioclimatic variables, sea surface temperature and salinity

(Table 2) from several sources containing information from terrestrial and marine databases (see below). The bioclimatic variables were accessed from the Worldclim database and includes climate data for the 1950–2000 period, however, many records for the Brazilian Amazon are rather recent [4]. The 19 bioclimatic variables are monthly temperature and rainfall values from a historical climate database that represents annual trends, seasonality and extreme climate values, where the quarter is a period of three months in a year [4]. These bioclimate variables have a spatial resolution of *ca.* 5 km at the equator (2.5 arc-minutes) chosen to harmonize the scales of the variables from marine and terrestrial areas.

We highlight that Hijmans *et al.* [4] derived the "Min temperature of coldest month" or BIO6 from a multi-decade average of the minima of the coldest months, which is therefore comparable to the "mean temperature of the coldest month".

Table 2. List of variables used in this study composed of bioclimatic variables, sea surface temperature and sea salinity.

Code	Unit	Resolution	Variables
BIO1	°C	2.5 arc-min	Annual Mean Temperature
BIO2	°C		Mean Diurnal Range [Mean of monthly (max temp–min temp)]
BIO3	°C		Isothermality (BIO2/BIO7) (*100)
BIO4	-		Temperature Seasonality (standard deviation *100)
BIO5	°C		Max Temperature of Warmest Month
BIO6	°C		Min Temperature of Coldest Month
BIO7	°C		Temperature Annual Range (BIO5-BIO6)
BIO8	°C		Mean Temperature of Wettest Quarter
BIO9	°C		Mean Temperature of Driest Quarter
BIO10	°C		Mean Temperature of Warmest Quarter
BIO11	°C		Mean Temperature of Coldest Quarter
BIO12	mm		Annual Precipitation
BIO13	mm		Precipitation of Wettest Month
BIO14	mm		Precipitation of Driest Month
BIO15	-		Precipitation Seasonality (Coefficient of Variation)
BIO16	mm		Precipitation of Wettest Quarter
BIO17	mm		Precipitation of Driest Quarter
BIO18	mm		Precipitation of Warmest Quarter
BIO19	mm		Precipitation of Coldest Quarter
ARIDITY	-	30 arc-second	Aridity Index
PET	mm/day		Potential EvapoTranspiration
SSTMIN	°C	5 arc-min	Min Sea Surface Temperature
SSTMEAN	°C		Mean Sea Surface Temperature
SSTMAX	°C		Max Sea Surface Temperature
SALINITY	PSU		Sea salinity

N.B. min = minimum; max = maximum.

We also included two bioclimatic variables created by Zomer *et al.* [35] and Zomer *et al.* [36], the potential evapotranspiration (PET) and the aridity index, also using monthly climate data from the WorldClim database with a resolution of 1 km (30 arc-second). The PET is a measure of the ability of the atmosphere to remove water through evapotranspiration processes, whereas the aridity index can be used to quantify precipitation availability over atmospheric water demand [36,37]. In the Global-Aridity dataset, aridity index values increase with more humid conditions, and decrease with more arid conditions [37].

The sea surface temperature (SST) derivate and sea salinity were obtained from the BioOracle database, having a resolution of *ca.* 9.2 km at the equator (five arc-minutes) [38]. The SST is the water surface temperature measured in the top most meter of the ocean water column using monthly observations with a temporal range from 2002 to 2009, and was obtained by the level-3 pre-processed satellite data from the Sensor Aqua-MODIS [6]. The SST major sources of error in the radiometric determination are sun glint, water vapor absorption in the atmosphere, trace gas absorption, etc. [39]. However, since calibration is done using in situ measurements, the SST data can be considered accurate to ±0.4 °C [39].

The sea salinity variable with values in Practical *Salinity* Unit (PSU) indicates the dissolved salt content in the ocean. The data were collected by the World Ocean Database (WOD 2009) using DIVA interpolation of *in situ* measurements with a temporal range from 1961 to 2009 [5].

2.3. Self-Organizing Maps (Data-Driven Approach)

SOM is an artificial neural network based on competitive learning and non-supervised training [13,14]. It consists of organized units called neurons that are distributed in a regular low-dimensional grid where adjacent neurons are connected by a neighborhood relation, making what is often called as neural map [14,23]. The SOM and geovisualization tools were applied in this research to select groups of spatial dependent variables and to highlight environmental patterns that may influence the species distribution. The SOM parameters chosen for this work were: "Gaussian function neighborhood", "long training", batch algorithm, non-linear training, range transformation and the map neural size was defined according to the heuristics from Vesanto *et al.* [23] and the parameters will be further explained in the next paragraphs.

The SOM training is divided in three levels; competition, cooperation and learning [14]: first, random weights are distributed to each neuron of the neural map, then in each iteration (also called epoch) an Euclidian distance is calculated. Therefore, the shortest distance between the vector and its weight is called the winner neuron, also known as Best Matching Unit (BMU) (competition level) [14]. Next, the SOM algorithm identifies the closest neurons to the BMU and by Gaussian function local radius, the weights of excited neighborhood neurons are updated. A relatively large initial learning rate and neighborhood radius are used in the first phase to fine-tune the SOM approximately to the same space as the input data. In the second phase, both the learning rate and the neighborhood radius are small from the beginning, in order to achieve further fine-tuning of the SOM (cooperation level) [14,23]. Finally, the SOM converges based on learning rates which should decrease at each epoch (learning level) [14]. As clarified by Vesanto *et al.* [23], the SOM training algorithm moves the weight vectors so that they span across the data cloud and the map is organized in a way that neighboring neurons on the grid get similar weight vectors.

The batch training algorithm [14] displays all input vectors at once for the neural map before any adjustment is made. As a result the algorithm does not require a parameter of learning rate α (t) and does not need a random presentation of the input vectors [14,40]. In every epoch, the data set is partitioned according to the Voronoi regions, where each region corresponds to a unit on the neural map. Each input vector therefore belongs to a region in the neural map, in which it is closest. After the Voronoi regions have been defined, the average of the input vector is calculated from the centroid of each Voronoi region, thereby the weight vectors are updated [14,40].

To evaluate the SOM's results, two measurements of error were used: the mean quantization error and the topographic error [14]. The mean quantization error is the average distance between each data vector and its BMU, and thus measures map resolution. The topographic error represents the proportion of all data vectors for which 1st and 2nd BMU's are not adjacent, and is used for the measurement of topology preservation [14]. For this work, we used three geovisualization tools called: SOM component plan, D-matrix and SOM Labels and SOM Principal Component Analysis (SOM-PCA) [23].

The SOM component plan shows the attribute patterns formed by high and low values in a neural map where the relationship between variables can be identified by visual analysis [14] or automatically detected by the SOM-PCA that orders the SOM component planes by the similarity of patterns [23,41].

The Unified distance matrix (U-matrix) [42] is able to detect the topological relationship between neurons. It is based on the combination of variables used in that specific data set, measuring the degree of similarity by the Euclidean distance between adjacent neuron weight vectors where high and low distance values correspond to dissimilar and similar neighboring neurons, respectively [42]. For this work, we used the Distance Matrix (D-matrix) that is also called SOM cluster, because similar neurons can be seen as a cluster and dissimilar neurons as a boundary between the clusters [14]. Areas with similar colors are close to each other in the input space [43]. The D-matrix is an averaged version of the U-matrix that enhances the visibility of dissimilar areas in the neural map [43].

The SOM label map shows the geographical localization of the Brazilian states and the frequency of the samples in each neuron brought the spatial information to the D-matrix when we overlapped it. Samples in the same neuron indicate mangrove locations with similar environmental factors. Occasionally, more than one sample fits into a single neuron, mainly because the samples are extremely similar or due to the size of the neural map [44]. Analyzing the SOM label map together with component planes provides us an overview of the environmental factors that change according to the geographical space. The SOM methods were carried out using the SOM Toolbox in MATLAB software [23,45].

2.4. Descriptive Analysis

We used the SOM-PCA as a data-driven approach to assist a pre-selection of variables' group and two variables of each group were further analyzed. Scatterplots, cartographical and cartogram maps were computed and analyzed for the most important variables that are often used to determine structure, composition, abundance and distribution of mangroves [46,47].

Because the species richness declines from the north to the south (Figure 1 and Table 1), the latitude was used in the scatterplots as a dependent variable *versus* environmental factors as independent variables. This provides a better understanding of the environmental influence on species distribution. In addition, we spatialized cartogram maps, which are abstract maps distorted proportionally by the values of the selected variable [48] to overstate the contrast between regions with low and high values. To create the cartogram maps, we used the GeoDa software [49]; and all geoprocessing procedures and map building was done using ArcGIS 10 Desktop [50].

The missing values were excluded, but we also made sure that the deleted samples were surrounded by other point samples in their neighborhood. In this sense, we kept important locations, for instance at the distribution limits of mangroves or in isolated mangrove patches.

3. Results

3.1. Self-Organizing Maps

After the data cleaning process, the samples were reduced from 900 to 390, representing 43% of the total. Nevertheless, the remaining samples were well spread out, representing the entire distribution of Brazilian mangrove. The resulting neural map size had 98 neurons with dimensions of 14 × 7. The rough training phase had 12 epochs and fine tuning phase 44 epochs which generates a low quantization error

(0.28) and topological error (0.01). Here, we divide 25 variables in three groups showing the similarities and inverse correlations between variables based on the result of the SOM-PCA component planes. Group 1 consists of variables of air and sea surface temperature that approximately follow a latitudinal gradient. In this group, we only found one "precipitation" variable, which can, however, be linked to "temperature", as it is the precipitation of the "warmest" quarter of the year. Group 2 is represented by the variables of air temperature, precipitation and evapotranspiration. There is also a correlation between Groups 1 and 2, which is, however, less strong than their within-group correlations. Group 3 is represented by the variables of precipitation, aridity and salinity (Figure 3).

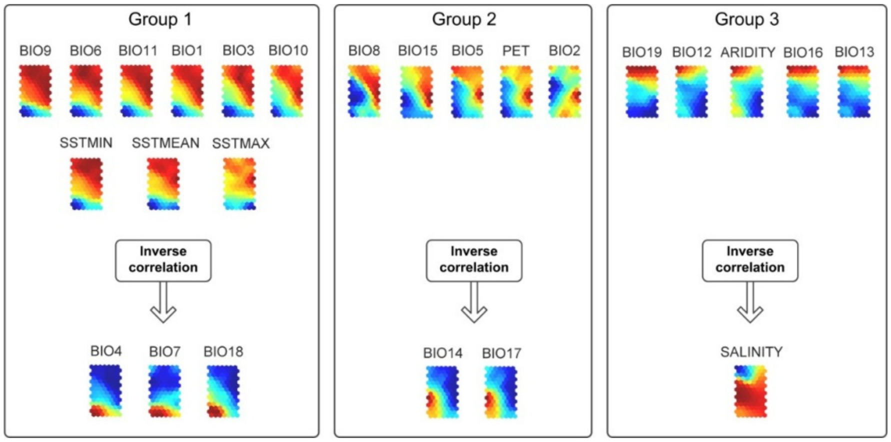

Figure 3. SOM Component planes. The component planes organized in three groups according to correlated components. High values are in red, intermediated values in yellow and green, and low values in dark blue.

Figure 4 provides useful information regarding the spatial location of states, the environmental dissimilarities within each and between states according to the D-Matrix and the lines roughly represent the distribution of species. To better understand these "climate barriers" in the D-Matrix neural map (Figure 4), it is necessary to further interpret the component planes of the variables (Figure 3). Keeping in mind the lines showed in the D-Matrix (Figure 4) and the component planes of the variables (Figure 3) some insights come up in order to understand which variables can provide explanations about species distribution. The patterns of low and high values in the component planes easily match some limits of the species distribution and we will expose some observations and insights based on these results.

The species *R. racemosa* and *R. harrisonii* are distributed where we can find high and intermediate values of precipitation and just after their limits are the low values (Figures 3 and 4) indicating that these species may be geographically limited by rainfall patterns, composed by the variables of Group 3, but also Group 2. By contrast, the species *A. germinans, C. erectus, R. mangle, A. schaueriana* and *L. racemosa* are likely more affected by temperature than by precipitation where their limits match with the low values of temperature, composed by the variables of Group 1. The high salinity value is mainly homogeneous over the mangrove areas, except by the low values in the north region. Therefore, it does not give us possible feedback or explanation about the species distribution.

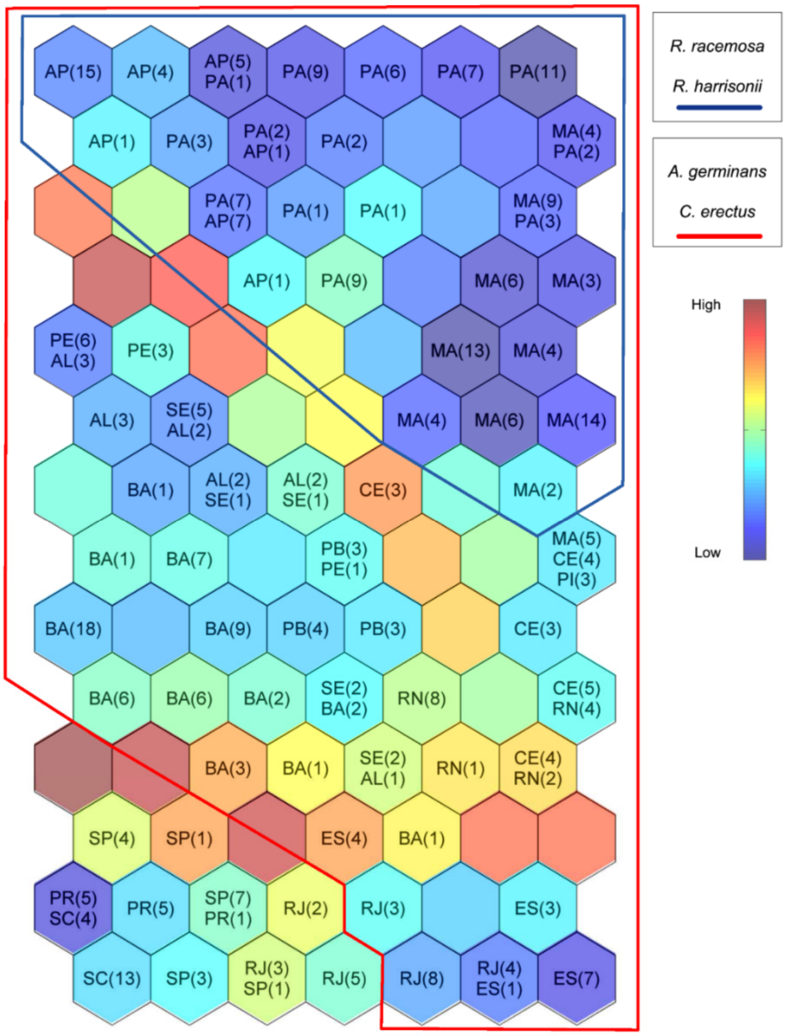

Figure 4. SOM labels and D-Matrix overlapped with species distribution. High values are boundaries between clusters and indicate high dissimilarities. Low values can be considered as a cluster, with more similarity and homogeneity. Brazilian States demarcate the localization on the neural map and the numbers indicate their frequency in each neuron. This figure represents the geographical location of samples that have a relation with component planes in Figure 3. At the top of the map are the northern states, in the middle the northeastern states, further down and to the right and center are the southeastern states and the lower left side shows the southern states where the mangrove reaches its limits. The red and blue polygons indicate the range of the mangrove species that are found along a section of the Brazilian coastline. Indicating the species that are found along the entire coastline would create a polygon around the entire neural map (not shown).

3.2. Environmental Description

In our database, we found 56 missing values for the PET and Aridity, in which were removed to compute the statistics because scatterplots cannot handle missing values, like the SOM methods can. A total of 334 sample points were used for the descriptive analyses focusing on at least two important variables from each group, showed on Figure 3, which are: BIO6, SSTMIN (Group 1); PET and BIO17

(Group 2); BIO12 and aridity index (Group 3). In the next section, we will give further explanation of these variables.

3.3. Air Temperature and Sea Surface Temperature

We found little difference in the minimum temperature of the coldest month (BIO6) and quarter (BIO11) for the species southernmost limits highlighting that *A. schaueriana* and *L. racemosa* reach the same distribution limit in Laguna (SC), but the limit of *R. mangle* is about 75 km more to the north.

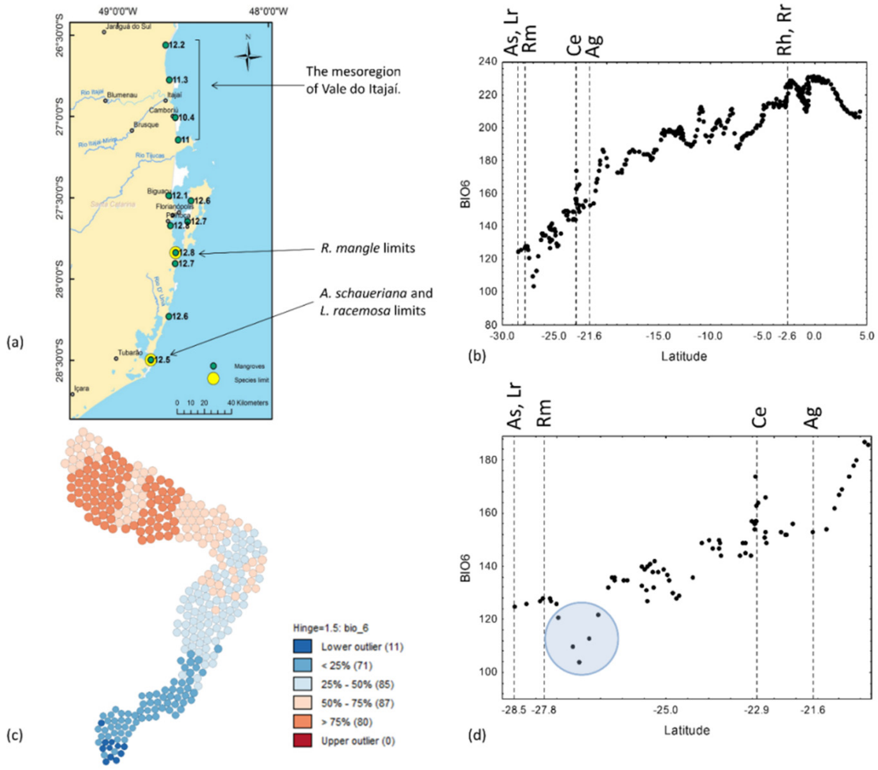

Figure 5. Detailed description of the Min temperature of coldest month (BIO6) (°C × 10) for mangroves in Brazil. (**a**) Detailed map of the south limits with their BIO6 values for each location of mangroves. (**b**) Scatterplot (n = 334) representing the BIO6 by latitude in decimal degree superimposed on species distribution limits of (vertical dashed lines from the right to the left) *R. racemosa* (Rr) and *R. harrisonii* (Rh) (at 2.6°S), *A. germinans* (Ag) (at 21.6°S), *C. erectus* (Ce) (at 22.9°S), *Rhizophora mangle* (Rm) (at 27.8°S), and finally *A. schaueriana* (As) and *L. racemosa* (Lr) (together at 28.5°S). The vertical dashed lines from the right to the left can therefore be seen as the increasing richness of mangrove trees species. (**c**) Cartogram map distorted by the high and low values of BIO6. Each circle represents a mangrove sample point location (however distorted), the circle size overstates the value of the variable (here BIO 6), and the circle color represents the lower outliers, the lower quartile, the inter-quartile range (split into an upper and lower part), the upper quartile and the upper outliers, in exactly the same way as a Box and Whisker plot. The legend also shows the number of samples per color between brackets. (d) Scatterplot of BIO6 with a detailed zoom on the surrounding of the southernmost species distribution limits (vertical dashed lines of the species limits) and the blue circle indicates the mesoregion of Vale do Itajaí with the lowest values of BIO6 in the Brazilian mangroves.

Despite the fact that BIO6 roughly follows the latitudinal gradient ($R^2 = 0.87$), our findings indicate that the minimum temperature of the coldest month found for all mangroves in Brazil is 10.4 °C located around 90 km to the north of the southernmost *R. mangle* limit in the estuary of the Camboriú river (Balneário Camboriú—SC) at Santa Catarina (Figure 5a). At the latitudinal limit of mangroves in Laguna, approximately 160 km more to the south, we found a minimum temperature of 12.5 °C, which is 2.1 °C higher than the minimum found in Camboriú. Therefore, we found the lowest values of the minimum air temperature of the coldest month for mangroves with lower values than what we found in the mangroves southernmost limit in the coastal mesoregion of Vale do Itajaí (Figure 5a).

The SSTMIN follows the latitude with a gradual decline in direction to higher latitudes ($R^2 = 0.86$) (Figure 6). Contrary to BIO6 (Figure 5), the lowest SSTMIN value is in Laguna (17 °C) and in the limits of *R. mangle* is 1 °C higher (18 °C) (Figure 6c and Table 3). From 2.6° S to 21.6° S of latitude, the SSTMIN decline gradually from 29 °C to 23 °C, however, it has a dramatic decline after the latitude 21.6° S to 28.5° S, with SSTMIN from 23 °C to 17 °C in a southerly direction (Figure 6b).

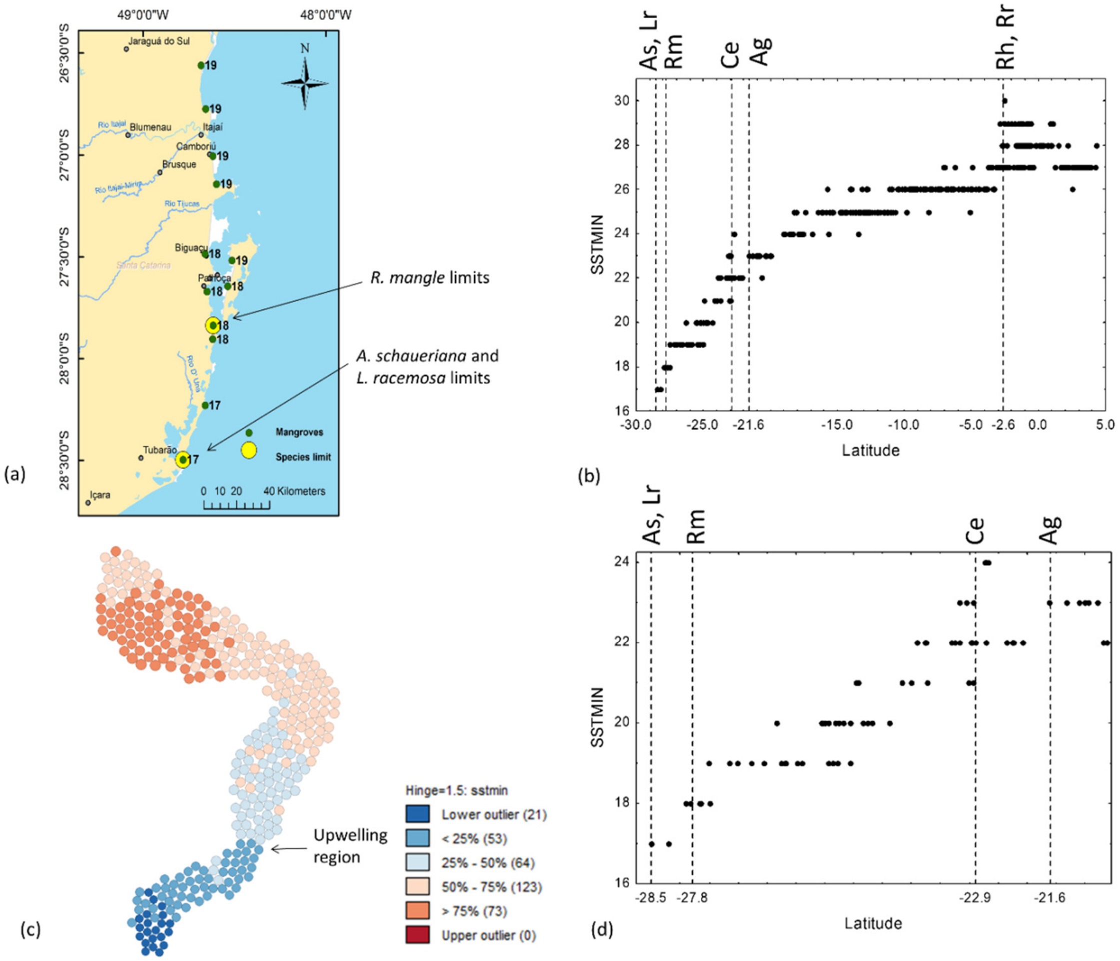

Figure 6. Detailed description of the Min sea surface temperature (SSTMIN) (°C) for mangroves in Brazil. (**a**) Detailed map of the south limits with their SSTMIN values for each location of mangroves. (**b**) Scatterplot (n = 334) representing the SSTMIN by latitude in decimal degree superimposed on species distribution limits (vertical dashed lines). (**c**) Cartogram map distorted by the high and low values of SSTMIN. (**d**) Scatterplot of SSTMIN with a detailed zoom of the surrounding area of the southernmost species distribution limits (vertical dashed lines of the species limits). Refer to Figure 5 for further explanations.

There is no difference between the values of SSTMEAN in the two southern limits (22 °C) and the minimum value of SSTMAX located at *R. mangle* limit, not in the extreme south. However, the SSTMIN is the only variable that demonstrates species' richness, even though these values are relatively close between the two successive species limits (Table 3).

Table 3. An overview of values of air temperature derivate and sea surface temperature derivate according to punctual values at latitudinal species limits and their species richness values for each limit.

Species	Latitude	Richness	BIO1	BIO6	BIO11	SSTMIN	SSTMEAN	SSTMAX
R. racemosa and R. harrisonii	2.6° S	7	27.3	22.1	26.7	27	29	29
A. germinans	21.6° S	5	23.0	15.3	20.7	23	26	28
C. erectus	22.9° S	4	23.0	17.4	20.9	22	25	27
R. mangle	27.8° S	3	20.0	12.8	16.4	18	22	26
A. schaueriana and *L. racemosa*	28.5° S	2	19.9	12.5	16.3	17	22	27

3.4. Annual Precipitation, PET and the Precipitation of the Driest Quarter

The "Annual precipitation" reaches a peak at 3.791 mm in Nazaré, Amapá followed by a dramatic fall until the lowest value of 600 mm in Macau, in Rio Grande do Norte state close to the border with Ceará (Figure 7b and Table 5). The next lowest value is in the surroundings of Arraial do Cabo in Rio de Janeiro with 870 mm. However, we also found lowest values of BIO12 in some sites in Ceará (937 mm), Bahia (990 mm) and Espírito Santo (1003 mm).

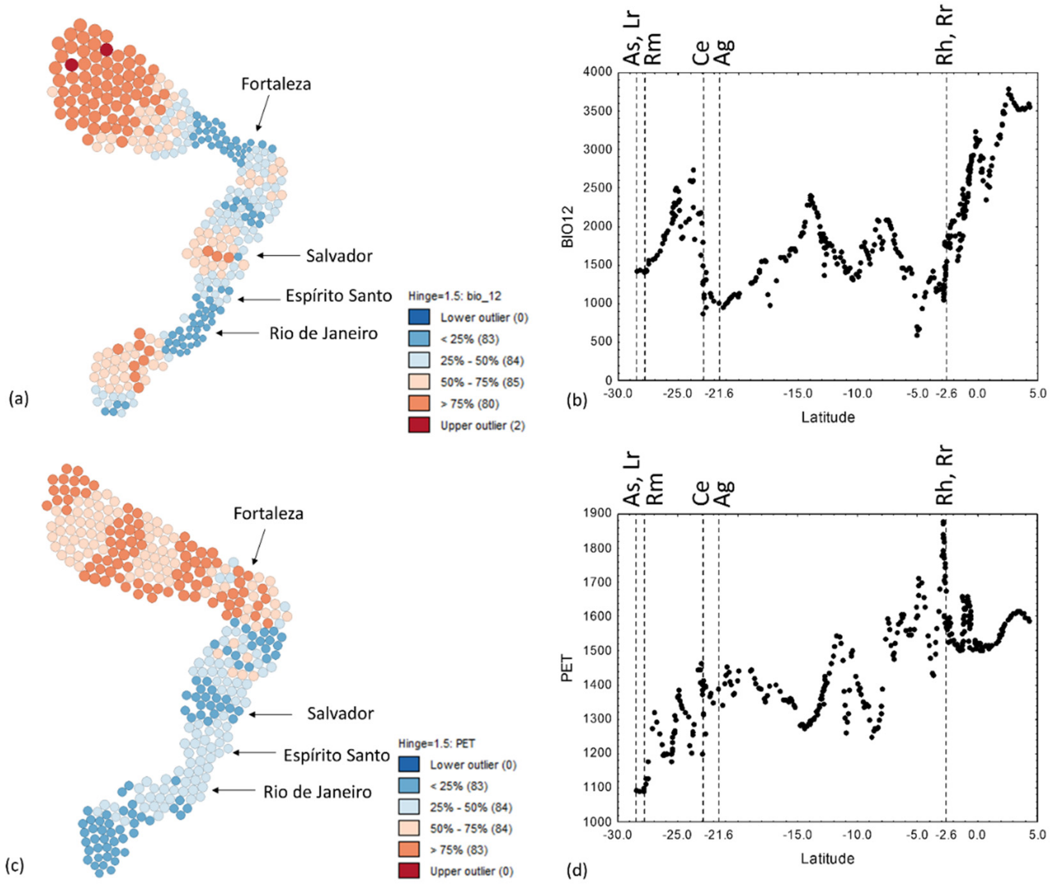

Figure 7. Detailed description of the Annual Precipitation (BIO12) and Potential Evapo-Transpiration (PET) for mangroves in Brazil. (**a**) The cartogram map distorted by the high and low values of BIO12. (**b**) Scatterplot (*n* = 334) representing the BIO12 by latitude in decimal degree superimposed on species distribution limits (vertical dashed lines). (**c**) Cartogram map distorted by the high and low values of PET. (**d**) Scatterplot (*n* = 334) representing the PET by latitude in decimal degree superimposed on species distribution limits. Refer to Figure 5 for further explanations.

The cartogram map (Figure 7a,c) enhances the spatial fluctuations of values of BIO12 and PET along the Brazilian coast while the highest values of PET are concentrated in the north and part of the northeast regions, the BIO12 present high and low values in all Brazilian regions (Figure 7).

The driest regions of Brazil's mangroves are located in the northeast states of Piauí, Ceará and Rio Grande do Norte (Figure 8a). After this region the precipitation of the driest quarter increases to the south, and reaches a peak of 466 mm in Camamu/Maraú in Bahia that has a remarkable and high amount of precipitation during the driest periods in comparison with other regions (Figure 8b,c). The cartogram of the precipitation of the driest quarter shows a strong restriction of precipitation during the driest season in the limits of the two species of *Rhizophora* (Figure 8c).

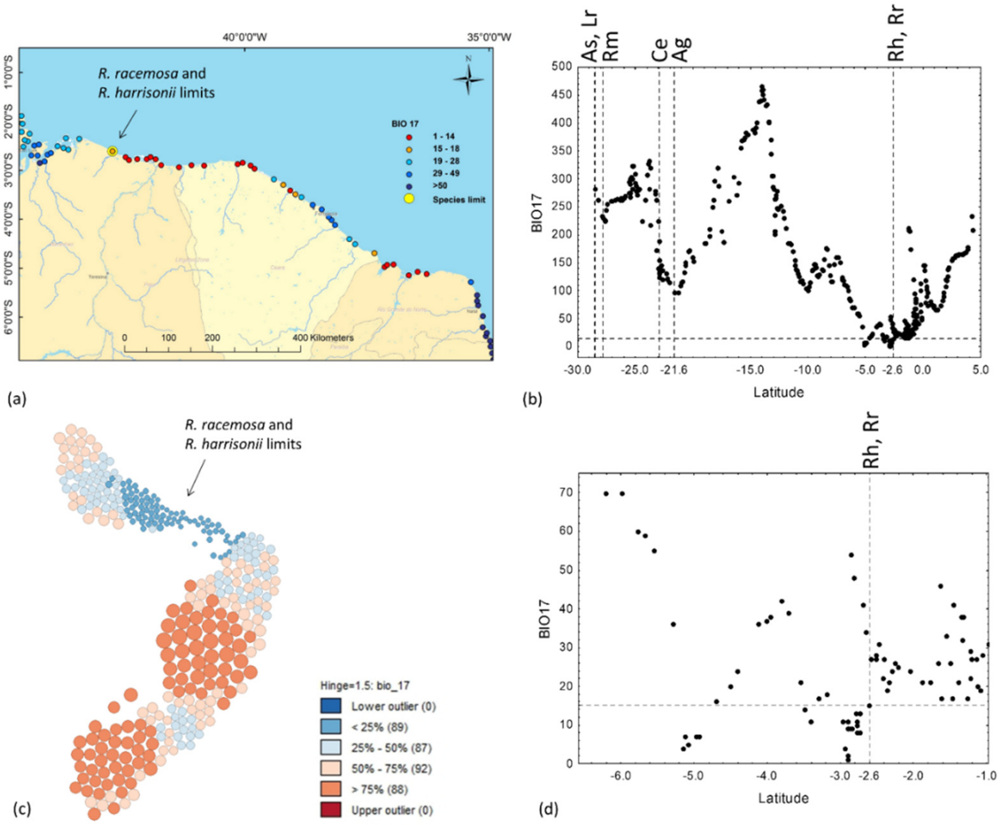

Figure 8. Detailed description of the Precipitation of the driest quarter (BIO17) for mangroves in Brazil. (**a**) Detailed map of the northeast limits with their BIO17 values for each location of mangroves. (**b**) Scatterplot (n = 334) representing the BIO17 by latitude in decimal degree superimposed on species distribution limits of (vertical dashed lines). (**c**) Cartogram map distorted by the high and low values of BIO17. (**d**) Scatterplot of BIO17 with a detailed zoom on the surrounding area of the northeast species distribution limits (vertical dashed lines of the species limits). The horizontal dashed lines in the BIO17 scatterplots indicate a barrier of <15 mm of precipitation for the *Rhizophora* species' northeast limits. Refer to Figure 5 for further explanations.

The scatterplot does not show the precise value of the BIO17 and Aridity at and after the limit (Figures 8b and 9b) due to the little latitudinal variation in the limits of *R. racemosa* and *R. harrisonii* (Figure 8b). For this reason, we spatialized the distribution of these variables in a map that can better reveal the influence of precipitation for the species limits. For instance, the two *Rhizophora* species are not distributed in areas with the "Precipitation of driest quarter" < 15 mm (Figure 8d), Aridity < 0.9 index (Figure 9d).

Brazilian mangroves are distributed mostly in humid areas (>0.65 Aridity index) with few exceptions of dry sub-humid areas in the border of Piauí and Ceará and semi-arid areas located in Rio Grande do Norte (Figure 9b) and just beyond the limits of *R. racemosa* and *R. harrisonii* (Figure 9a). We used a dashed line to indicate the humid areas with 0.9 of aridity index, because it seemed that a limit for these two species of *Rhizophora* genus (Figure 9b,d) and the detailed map (Figure 9a) help highlight the geographical space where their distribution is restricted to >0.9 of the aridity index.

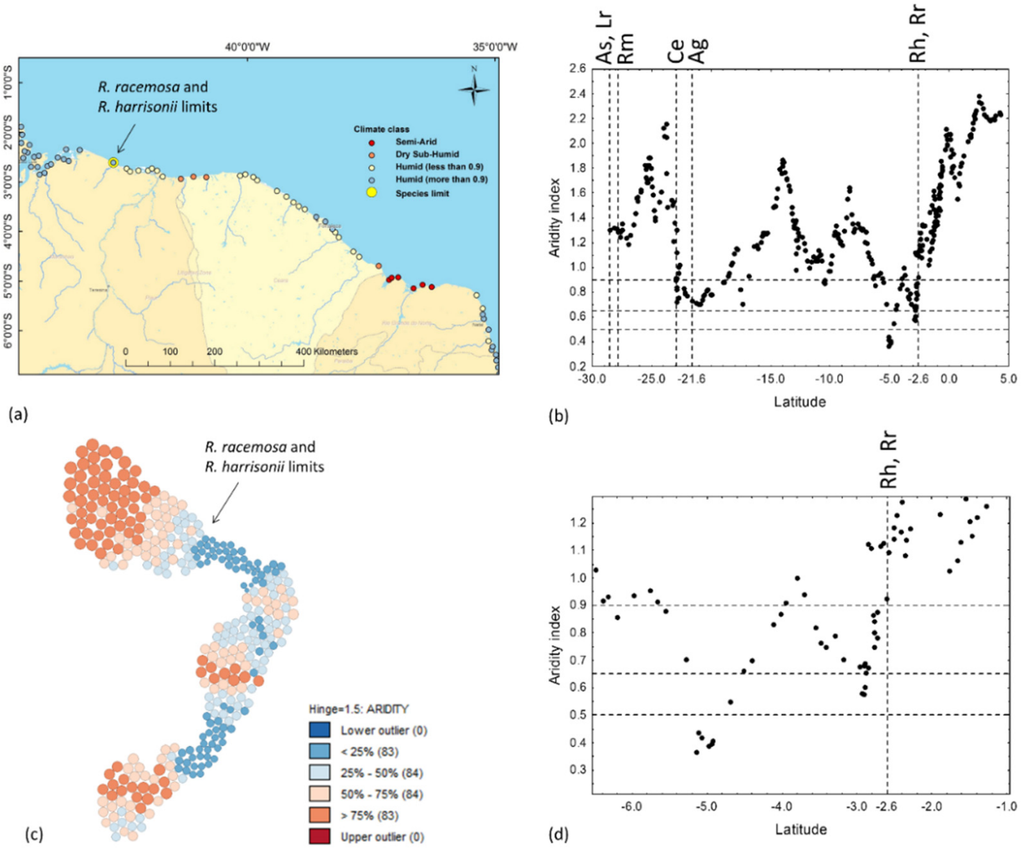

Figure 9. Detailed description of the Aridity index for mangroves in Brazil. (**a**) Detail spatial distribution map of the northeast limits with their Aridity values for each location of mangroves. (**b**) Scatterplot (n = 334) representing the aridity by latitude in decimal degree superimposed on species distribution limits of (vertical dashed lines). (**c**) Cartogram map distorted by the high and low values of aridity index. (**d**) Scatterplot of aridity with a detailed zoom on the surrounding of the northeast species distribution limits (vertical dashed lines of the species limits). The horizontal dashed lines in the aridity index indicate the climate class (0.2–0.5—Semi-Arid; 0.5–0.65—Dry Sub-humid; >0.65—Humid) [37], and we included an additional dashed line at aridity index 0.9, because as shown in (**a**) the two species of *Rhizophora* reach their southernmost limit around that value. Refer to Figure 5 for further explanations.

In the *R. racemosa* and *R. harrisonii* limits, Table 4 shows that the annual precipitation is favorable (1549 mm), however, the precipitation of the warmest quarter, and the driest quarter and month is low, at 16 mm, 15 mm and 5 mm, respectively.

Table 4. An overview precipitation derivate and aridity according to punctual information at latitudinal species limits and their species richness for each limit.

Species	Latitude	Richness	BIO12	BIO14	BIO17	BIO18	Aridity
R. racemosa and *R. harrisonii*	2.6° S	7	1549	5	15	16	0.92
A. germinans	21.6° S	5	1014	27	98	329	0.73
C. erectus	22.9° S	4	870	39	125	242	0.72
R. mangle	27.8° S	3	1420	72	230	535	1.29
A. schaueriana and *L. racemosa*	28.5° S	2	1431	89	282	434	1.30

4. Discussion

4.1. Explaining the Species Limits

As temperature is correlated with latitude, a similar sequence of species loss with increasing latitude should be discernible [46,51]. Where mangroves are not limited by aridity or precipitation, temperature is the major factor in reducing number of species correlated with latitude [51–53]. However, the opposite is also true: when the temperature is suitable for mangroves, the availability of precipitation may have a stronger influence on certain mangrove species' distributions [51]. Several reports have suggested that the distribution of mangroves on western coasts of southern continents is generally more limited by aridity than by temperature [51–53]. Having these facts in mind, and based on our results, we can delineate a deeper hypothesis for the species distribution along the Brazilian coast.

R. racemosa and *R. harrisonii* species are not distributed in areas with low precipitation <15 mm in a drier quarter or <5 mm in a drier month and <0.9 of aridity index. For these two species, temperature is not likely to be a limiting factor for the distribution of these congeners in Brazil because the "Mean temperature of the warmest quarter" is 28.7 °C in Camocim (CE), and the "Min temperature of the coldest month" is also >20 °C , which is still suitable for these species. A previous experimental study in Costa Rica confirmed that *R. racemosa* is inhibiting in its landward establishment because of drought and high soil salinities [54]. However, until now there are few studies about these two *Rhizophora* species, especially in Brazil.

According to the updated climate classification of Köppen-Geiger [55] in species limits of *R. racemosa* and *R. harrisonii* are described as equatorial savanna with dry winter (Aw), but *ca.* 350 km south of these species limits the classification changes to equatorial savanna with dry summer (As), and *ca.* 670 km after the limits is classified as arid zones of hot steppe or steppe climate (BSh). However, in this coastal stretch of 350 km, we found the humid (<0.9 aridity index) and dry sub-humid climate classes, and after *ca.* 670 km we found semi-arid classes are south of *Rhizophora* limits, based on UNEP [37] aridity index classification.

In Cabo Frio, the strongest of about seven coastal upwelling areas along the southeastern and southern coast of Brazil is found [56], and this coincides with the southernmost distribution limit of *A. germinans* and *C. erectus* (Table 1). This intense upwelling has been recognized as an important biogeographic barrier for the distribution of several algal taxa along the Brazilian coast [57–59]. Weather/climate patterns can be influenced by upwelling, which reduces precipitation and moderates temperatures [60].

At the species limits of *A. germinans* and *C. erectus*, we found the annual precipitation to vary between 870 and 1014 mm, which is one of the driest regions of the southeast and south of Brazil. Yet *A. germinans* and *C. erectus* are known to survive in more arid regions in the northeast (<600 mm of Annual precipitation). However, under upwelling conditions, sea surface temperature can reach as low as 13 °C [61] or 18 °C [62], which is below or close to the temperature limit known to inhibit propagule germination in the mangrove *A. germinans* [63]. Although also non-upwelling conditions with temperatures over 21 °C [61] exist, the upwelling conditions might also be a barrier for *A. germinans* and *C. erectus* and should be further investigated.

Our results suggest that at the southernmost limits of mangroves the air temperature is not as low as that found at lower latitudes such as in the Mesoregion Vale do Itajaí (Figure 5). This is exemplified by the min temperature of the coldest month (BIO6 = 10.4 °C) in Camboriú (Figure 5), *ca.* 90 km more north than the *R. mangle* limit (where BIO6 = 12.8 °C). However, *R. mangle* does not grow in Camboriú [64] and its distribution is therefore more discontinuous than that reported by other authors [7,8]. The same discontinuity was also reported for other mangrove species elsewhere in the world [65]. However, in

Brava Beach in Itajaí (BIO6 = 11.3 °C), just about 10 km north of Camboriú, there is a record of *R. mangle* [64], which leads us to question whether this is due to physiological or dispersal limitations.

Firstly, one could argue that a physiological limitation at temperatures below 11 °C exist, but experiments in Florida with *R. mangle* has demonstrated survival of this species at temperatures of 4 °C [66]. However, the natural population of *R. mangle* in Florida (USA) at Ponce Inlet grows under lower temperatures than in Brazilian mangroves (average minimum = 9.5 °C), and experiences severe freezes every eight years. [66], hence, these findings may not be extrapolated to mangroves in Brazil. To our knowledge, there are no data available to support any straightforward plant physiological limitation marking a limit between roughly 10 and 11 °C.

Secondly, dispersal limitations may be linked to the water current, the wind or physical barriers affecting large nautohydrochorous propagules but not small ones since *A. schaueriana* apparently has no restriction in establishing at Camboriú. Bias in the metadata sets available may be a possibility (see also below), but further research is needed to elucidate the absence of *R. mangle* in Camboriú. However, also here, there is no physiological or dispersal evidence at hand to explain this.

In contrast to Quisthoudt *et al.* [67] and to what we expected, in Brazil we did not find a clear difference for the minimum air temperature of the coldest month and quarter in the limits of *R. mangle*, *A. schaueriana* and *L. racemosa*.

Further research should concentrate on unveiling the importance of temperature variables that give differences between the distribution limit of the southernmost species, such as SSTMIN (Table 3).

4.2. Comparison Climate Databases

We identified differential maximum and minimum extreme values organized in a table (Table 5) comparing our results with those of Schaeffer-Novelli *et al.* [2], particularly in between the main coastal cities. For example, Camocim (CE), located between São Luís (MA) and Fortaleza (CE), is a peculiar location, with extreme values: the highest values for "Annual mean temperature", "Max temperature of warmest month", "Mean temperature of warmest and coldest quarter", "Mean diurnal range", "Precipitation seasonality", "Potential of Evapotranspiration" and the lowest for "Precipitation of driest quarter" (Table 5).

For the "Annual mean temperature", Schaeffer-Novelli *et al*. [2] found almost the same values as we did, however, we found them in different locations. In contrast, the minimum value of the "Min temperature of coldest month" that we found in Brazilian mangroves was 10.4 °C against 15.7 °C found by Schaeffer-Novelli *et al*. [2]. While just considering the southern mangrove limits, the min temperature of the coldest month that we found is 12.5 °C that differs 3.2 °C with that of previous works (15.7 °C) [2,68]. Soares *et al*. [68] also found 15.7 °C as a minimum air temperature in Laguna based on 55 years of monitoring at the Laguna meteorological station, operated by the Centro de Informações de Recursos Ambientais e de hidrometeorologia of Santa Catarina (CIRAM). This difference cautions us not to deliberate about climate change while we still are debating about the actual minimum temperature at the limits. Current research about the species distribution modelling and their extent range usually incorporate the same climate database [69,70] as we did. Also, Quisthoudt *et al*. [67] working on mangrove limits worldwide found the minimum air temperature of the coldest month for *Rhizophora* species to be 13.1 °C. However, just for the Brazilian mangroves, we found the minimum temperature of the coldest month at the limits of *Rhizophora mangle* in Praia do Sonho to be 12.8 °C, and from here towards the north, the temperature decreases to 11.3 °C in Praia Brava in Itajaí (*ca.* 110 km north of Praia do Sonho).

Table 5. Comparison of the minimum and maximum values of the environmental variables and their geographical location based on the results of Schaeffer-Novelli *et al.* (Schaeffer-Novelli *et al.* 1990) and the present study. *The maximum values of SSTMAX are found in four locations: Chaves, near to Bragança (PA) and two others locations in between São Luiz (MA) and Parnaiba (PI).

Variables		**Codes**	**This Study**		**S-N *et al.* (1990)**		**This Study**		**S-N *et al.* (1990)**	
			Min	**Location**	**Min**	**Location**	**Max**	**Location**	**Max**	**Location**
Annual Mean Temperature	Group 1	BIO1	19.8	Florianópolis/Biguaçu, SC	<20	Laguna, SC	27.9	Camocim, CE	*ca.* 26.8	Recife, PE
Isothermality		BIO3	43	Laguna, SC			89	near to Belém, PA		
Temperature Seasonality		BIO4	306	near to Belém, PA			3129	Paranaguá Bay, PR		
Temperature Annual Range		BIO7	8.5	Aracajú, SE	>1	Belém, PA	18.3	Camboriú, SC	>8	Laguna, SC
Mean Temperature of Driest Quarter		BIO9	16.2	Camboriú, SC			28.2	Acaraú, CE		
Mean Temperature of Warmest Quarter		BIO10	23.2	Florianópolis, SC			28.7	Camocim, CE		
Min Temperature of Coldest Month		BIO6	10.4	Camboriú, SC	15.7	Laguna, SC	23.2	Marajó Island, PA	*ca.* 25.5	Belém, PA
Mean Temperature of Coldest Quarter		BIO11	16.2	Camboriú/Biguaçu, SC			27.1	Camocim, CE		
Min Sea surface temperature		SSTMIN	17	Laguna, SC			30	Icatu, MA		
Mean Sea surface temperature		SSTMEAN	21.50	Imbituba, SC			31.21	Bequimão, MA		
Max Sea surface temperature		SSTMAX	25	Imbituba, SC			33	*Four locations		
Precipitation of Warmest Quarter		BIO18	7	Cajueiro da Praia, PI			1029	Cananéia, SP		
Mean Diurnal Range	Group 2	BIO2	57	Aracajú, SE			110	Camocim, CE		
Mean Temperature of Wettest Quarter		BIO8	22.5	Belmonte, BA			27.6	Areia Branca, RN		
Max Temperature of Warmest Month		BIO5	27.6	Laguna, SC			35.1	Camocim, CE		
Precipitation Seasonality		BIO15	9	Una, BA			118	Camocim, CE		
Precipitation of Driest Month		BIO14	0	Macau, RN			143	Camamu/Maraú, BA		
Precipitation of Driest Quarter		BIO17	1	Camocim, CE			466	Camamu/Maraú, BA		
Potential Evapotranspiration		PET	1092	Madre River, SC	*ca.* 950	Florianópolis, SC	1877	Camocim, CE	1600	Golfão-Belém, PA
Annual Precipitation	Group 3	BIO12	600	Macau, RN	1090	Rio de Janeiro, RJ	3791	Nazaré, AP	3250	Maracá, AP
Precipitation of Wettest Month		BIO13	114	Arraial do Cabo, RJ			613	Algodoal, PA		
Precipitation of Wettest Quarter		BIO16	300	Arraial do Cabo, RJ			1655	Nazaré, AP		
Precipitation of Coldest Quarter		BIO19	61	Areia Branca, RN			1634	Marajó Island, PA		
Aridity index		ARIDITY	0.36	Macau, RN			2.38	Nazaré, AP		
Salinity		SALINITY	27.96	Oiapoque River, AM			37.17	Belmonte, BA		

According to Schaeffer-Novelli *et al.* [2] in between Fortaleza (CE) and Rio de Janeiro the rainfall and the potential of evapotranspiration are similar throughout the year with a seasonal climate. Indeed, taking into account the annual precipitation in the cities of Fortaleza and Rio de Janeiro they are apparently similar around 1315 to 1450 mm, respectively. However, our results contrast their findings and show strong variability within and between these cities (Figure 7). For example, in Ceará the annual precipitation ranges between 937 mm and 1429 mm, in Rio Grande do Norte between 600 mm and 1624 mm, in Paraíba between 1665 and 2097 mm, in Pernambuco between 1686 and 2098 mm, in Alagoas between 1321 and 1794, and in Sergipe between 1327 and 1673 mm, indicating that the states of Paraíba and Pernambuco on one hand, and the states of Alagoas and Sergipe on the other hand, have a similar range. In Bahia, we found about 41% intra-state variation for the "Annual precipitation" with a minimum of 990 mm and a maximum of 2414 mm. Espírito Santo has a low annual precipitation variation between 1003 and 1340 mm, but in Rio de Janeiro we found a huge variation between 870 and 2182 mm. The high annual precipitation variability in Bahia and Rio de Janeiro can be explained by the large coastline and a significant latitudinal variation that provides a wide range of environmental conditions, but also due to the seasonal upwelling events that changes the climate conditions. In Bahia this is evident through the fluctuations of the Annual precipitation and for the precipitation of the driest quarter.

We also found extremely different results for the maximum and minimum values of "Annual precipitation" when compared with the previous study by Schaeffer-Novelli *et al.* [2]. For instance, we found the record with the minimum "Annual mean precipitation" to be 600 mm and to originate from Macau, whereas Schaeffer-Novelli *et al.* [2] found it to be 1090 mm and to originate from Rio de Janeiro, which is a difference of 490 mm from two sites >2000 km apart. However, Schaeffer-Novelli *et al.* [2] also found fairly low values in Aracajú (*ca.* 1150 mm) and in Fortaleza (*ca.* 1200 mm) about 650 km and 260 km distance from Macau, respectively. Likewise, we found the maximum "Annual precipitation" to be 3791 mm originating from Nazaré (AM) against 3250 mm found in Macapá in the same state (Table 5), amounting to a difference of 541 mm. In the mangroves next to Macapá we found values for the annual precipitation in between 3110 and 2710 mm, which are lower than the previous study [2].

4.3. Mangrove Mappings

In this study, we found differences between the three most recent global mangrove mapping exercises [7–9] with respect to the southernmost mangrove limits in Brazil. In contrast to Spalding *et al.* [7], the online datasets for both Spalding *et al.* [8] and Giri *et al.* [9] give a seemingly erroneous southernmost limit of mangroves in Brazil that is shown in Guarda do Embaú and next to Imbituba, respectively, instead of Laguna as indicated by Schaeffer-Novelli *et al.* [2], Spalding *et al.* [7] and Quisthoudt *et al.* [67]. In Giri *et al.* [9], the southernmost mangrove is close to Imbituba (SC), about 7 km from the coast located in the sea, however, we did not localize this mangrove position in any other mapping or reference. In addition, this location seems erroneous because we did not find an island that could make the establishment of mangroves possible. Therefore, we localize a nearest estuary using the high-resolution images on Google Earth in the surroundings of Imbituba (SC), that is, we moved this point from the sea to the nearest estuary.

4.4. Limitation of This Work

We analyzed the species assuming a continuous distribution, mainly owing to a lack of a reliable data of the species distribution and the fact that Brazilian mangrove species are usually mapped as though they had a continuous distribution from the northern to the southern limits [8]. However, a study conducted by Menezes *et al.* [71] in the Amazonia mangroves has shown that *R. racemosa* and *R. harrisonii* has a disjunct distribution. Wherever available, we used site-specific information (the absence of *R. mangle* in Camboriú), but given that this information is not systematically available for all species, we often focused on the limits of all species, keeping in mind the environmental range that species had to go through to reach their limit in the direction of higher latitudes.

Twilley *et al.* [72] developed a hierarchical classification system based on several studies related to the species distribution at different scales, and they showed that the main factor for the distribution of species at global scale is temperature. At others scales, the geomorphology types (*i.e.*, Lagoon, Delta, Estuary) and ecological type (*i.e.*, Basin, Fringe, Riverine and Scrub) [73] can also influence the distribution of species. However, considering the entire and latitudinally wide Brazilian mangrove coastline, and despite the species' distribution discontinuity, we were able to characterize mangroves at regional scale based on climate rather than local factors.

This study did not include the "tidal amplitude" as a variable. However, since "tidal amplitudes decrease southward along the Brazilian coast", as reported by Schaeffer-Novelli *et al.* [2], this variable undoubtedly correlates with other variables that follow a latitudinal gradient, but without any causal or relation whatsoever between these variables. On local scale, tide inundation, frequency and amplitude are important ecohydrological factors determining the mangrove zonation by limiting excessive build-up of salt within soil, controlling propagule dispersion [51], and other factors. However, on regional or global scales the distribution of species is more influenced by climate factors [72,74] than by local factors, such as tide.

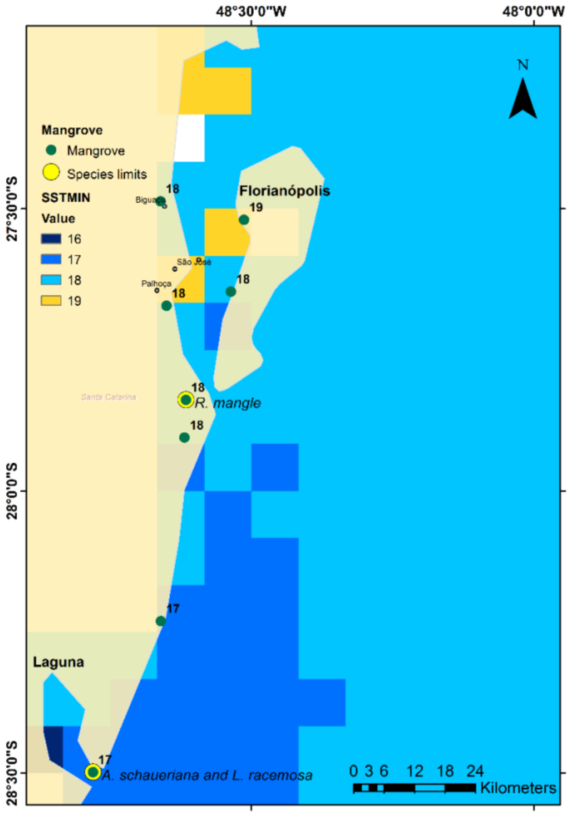

Figure 10. SSTMIN variation at the southernmost limit. Map showing the distribution and variation of SSTMIN at the mangrove limits in the state of Santa Catarina. Note that within Laguna, the SSTMIN variation ranges over 16 °C, 17 °C and 18 °C, averaging to 17 °C ± 1 °C. The yellow circle corresponds to the southernmost mangrove limits in Brazil.

The SST used in this study was obtained from global MODIS ocean water temperature surfaces. However, the local water temperature in mangroves will probably be higher than that of MODIS, because the soil absorbs the solar radiation and this process may also increase the local water temperature in contact with the warmer soil. In addition, the turbidity of the shallow coastal waters is known to affect the reflectance of the Sun, which in turn interferes with the radiometric determination of the SST. This local influence is a typical circumstance of Case II waters, that are affected by dissolved organic matter of terrestrial origin, inorganic mineral particles and various suspended sediments, in addition to phytoplankton and their associated debris. Although, *in situ* measurements are usually taken to calibrate the MODIS data [39], differences between surface data and field data may continue to exist. In any case, for this work on the characterization of mangroves along the Brazilian coastline, there were not enough local (in lagoons, mangrove creeks, *etc.*) temperature measurements at the scale of our study. In addition, variations may occur inside lagoons (Figure 10).

The same global *versus* local discussion can be valid for the air temperature stemming from the WorldClim database. WorldClim is a historical meteorological database with data from several stations worldwide that were interpolated using latitude, longitude and altitude as independent variables, creating what is called a climate surface. These climate surfaces allow us to estimate the climate in areas where there is a lack of climate data. For this reason, the proposed method enabled us to measure and cover climate gaps existing in previous studies [2,74].

The atmospheric climate variables are reliably observed by a limited number of meteorological stations [75], and according to Hijmans *et al.* [4] the geographic distribution of the stations is clearly not random and there are few stations in areas with low population density, such as in the Amazon. Possibly, a denser network of weather stations, more effectively covering the Brazilian coast would lead to finer results. The Worldclim database, however, already has a 400 times higher spatial resolution than previously available surfaces with more weather stations and more accurate global elevation data [4].

The ocean surface salinity was used in this research to understand the regional variation of salinity along the Brazilian coast, as ocean currents and the physicochemical properties of the water are of direct importance for the nautohydrochorous propagules [76]. The low ocean salinity found in the north of Brazil is probably due to the high precipitation and the huge freshwater discharge in the Atlantic Ocean from large rivers, such as the Amazon. The highest value of salinity from our database did not exceed 37 PSU, but local values of salinity have a strong variation on short distances and are known to have a high impact on mangrove ecosystems: depending on the topographical elevation and the season, the salinity in Bragança, for instance can range from 10 to 90 PSU [77]. Even in the north of Brazil where a high annual precipitation occurs, a prominent dry season, hypersaline conditions and rarely inundated areas can be found, resulting in monospecific dwarf mangrove forests [77–79]. In addition, higher values of salinity have been reported from other sites in the world [80–82]. For this reason, the salinity ocean surface used in this research did not bring enough relevant information to understand the species distribution.

5. Conclusions

The objectives of this study were achieved for the Brazilian mangroves. First, our study provides significant improvement to update the information regarding to climate using recent databases overcoming data gaps in previous studies [2,68]. These improvements have led us to the identification and location of extreme maximum and minimum values that differ from previous studies for certain variables. Second, relevant climate variables were exposed according to their spatial dependence, and three groups of variables were divided using the SOM-PCA geovisualization tools, which forms a new approach for mangrove studies. Third, this study could provide a better understanding of the fundamental niche for mangrove plant species giving insights about their distribution related to bioclimate factors.

In this sense, according to our findings the *R. racemosa* and *R. harrisonii* seem limited by extremely low precipitation during the dry season, *i.e.*, the high precipitation component planes coincide with the northeastern limits of the two species of *Rhizophora*. Because there is hardly any latitudinal variation in the coastline with suitable temperatures beyond their limits, temperature is not the main factor for these two species. In this sense, like others authors [51–53], we also conclude that when precipitation is the main limiting factor for a certain species' distribution, the declining of richness does not necessary follow a latitudinal gradient.

However, species that are more likely to be limited by temperature gradually follow the latitudinal gradient, which is the case for *A. germinans*, *C. erectus*, *R. mangle*, *A. schaueriana* and *L. racemosa.* In addition, we highlight the importance of the upwelling conditions that might be a barrier for *A. germinans* and *C. erectus*, but further investigation should be done in this respect.

However, our data indicate that the lowest min air temperatures of the coldest month are located at the mesoregion of Vale do Itajaí and not in the southernmost limit of mangroves, as we expected. Nevertheless, the SSTMIN follow gradually the latitudinal variation with the lowest values in the southernmost limit. For this reason, we believe that it is instead the minimum sea surface temperature that has a major influence on mangrove species distribution, rather than any other air temperature or mean or max sea surface temperature. Dana [83] made an observation on marine animals very close to what we found: "The cause which limits the distribution of species northward or southwards from the equator is the cold of winter rather than the heat of summer or even the mean temperature of the year".

This study also provides new information about the Brazilian mangroves characterizing it mostly in humid areas, with few exceptions in dry sub-humid and semi-arid areas in restricted regions in the northeastern states. The spatial localization of these sub-humid and semi-arid areas have never been identified by previous studies *cf.* [2,69]. In addition, we provide a pre-selection criterion for the bioclimatic variables that have been largely used as input data for species distribution modeling and/or environmental mapping. The pre-selection of the three groups of variables reduces the dimensionality of the data and it facilitates the analysis of modeling activities.

The reduction of dimensionality as the main characteristic of SOM methods did not give us detailed information of variables *versus* species limits. Therefore, descriptive statistical analyses, such as scatterplots and spatialization of the variables, are highly recommended to complement the SOM methods, and provide the extra detail needed to understand the possible influence of the variables on the species limits.

In this study, we also found some contradictions between the most recent mappings of mangroves that are important to emphasize. The most visible differences are based on the fact that the two most recent mappings [8,9] have ignored the southernmost limits of mangroves and only the old version of the World Mangrove Atlas [7] has properly mapped it. This gap could be explained by the fact that at their limits mangroves are scarce, so maybe they did not reach the minimum size area to be mapped by these new methods of classification. The mangrove limits at higher latitudes have important ecological aspects to be studied and they should not be ignored in global mappings. However, we also recognize the excellent effort of these two most recent worldwide mappings [8,9], because they continue to provide useful higher resolution global mappings for conservation projects and scientific studies.

The study of Schaeffer-Novelli *et al.* [2] was a very important review of the environmental and physiographic characterization of the Brazilian mangroves. In the 1990s, this work gave us an important overview the Brazilian mangroves and their relation to climate. However, nowadays a huge amount of information is available from satellite images and interpolated climate surfaces, providing new input data for such an analysis. For this reason, policy makers and other stakeholders may find the method proposed here useful for designing conservation strategies since it offers a more correct, complete and updated analysis of environmental factors driving mangrove tree distribution, or driving the distribution of any other coastal system (e.g., seagrass beds and coral reefs). If the design of policy, governance and management rules were to divide the Brazilian coast into sections, such as in Schaeffer-Novelli *et al.* [2], reliable data are paramount. For future research, we expect to expand this climate framework on a global scale.

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Supplementary information

Converting mangrove polygons into points can offer additional possibilities and flexibility when working with geoprocessing tools (Ximenes 2015; Ximenes *et al*. 2016). For this reason, Ximenes *et al.* (2016) adopted a methodological framework that consists in converting each mangrove polygon into a point. In order to eliminate redundant data and reduce spatial autocorrelation it is necessary to reduce the number of points. The main concern in this methodology is to maintain the points geographically well distributed in space, representing mangrove distribution.

Figure 1 shows the methodological framework adopted by Ximenes *et al.* (2016) for converting polygons into points, and how the number of points was reduced. To compare the results, this methodology was applied to the three mangrove maps in a clipping area of the Brazilian Amazon mangrove forest. However, Ximenes *et al.* (2016) used the first World Atlas of Mangroves (Spalding *et al.* 1997) because the data file is lighter when compared to other global mangrove maps, which facilitates geoprocessing analysis.

To reduce the number of points, a 3 km buffer was applied around the center of each point, recreating polygons. Buffers were then aggregated within a certain distance (in this case 100 m), creating a minimum distance between points of approximately 6 km. The aggregate buffers were subsequently converted back into points, thus reducing the number of redundant points (i.e., sample points located too close to each other) (Figure 1).

The conversion of polygons to points generated a greater number of points for the Giri *et al*. (2011) map, when compared to the two World Atlas of Mangroves (Spalding *et al.* 1997, 2010) (Figure 1). After converting aggregated buffers into points, it was possible to note differences between the number of points and their distribution. For instance, the Giri *et al.* (2011) map resulted in much fewer points than the other two maps of the World Atlas of Mangroves (Figure 1), since buffers close to each other were merged. It is important to highlight that this procedure was only done for a small area (window size in figure 6); therefore, the outcome may be different if we consider the global map, since the first World Atlas of Mangroves only contains 34,315 polygons compared to more than 1 million polygons in the other two maps.

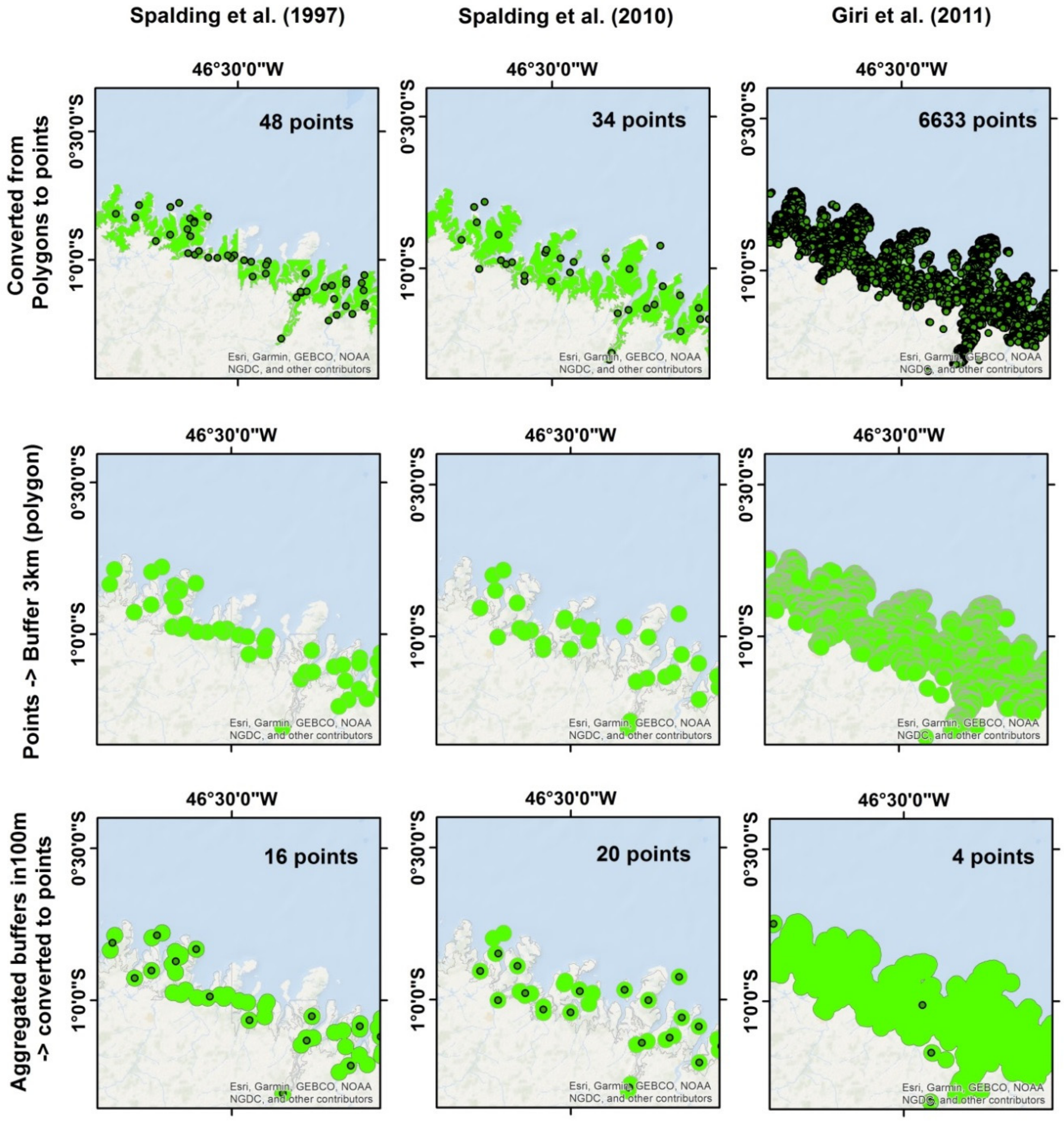

Figure 1. Methodological framework developed by Ximenes *et al.* (2016), which semi-automatically reduces the amount of point samples. Each column represents a different map and the number of points generated by the number of polygons in this window size. Three global maps were processed using the same methods for comparison. The first line represents the polygons converted into points (Polygons -> Points); each point is located inside the centroid of each polygon. The second line represents the 3 km buffers generated from the points (Points -> Buffer 3 km). The third line represents the aggregated buffers within a distance of 100 m, and these aggregated buffers were then converted back into points (Buffers -> Aggregated buffers within a distance of 100 m -> Points).

CHAPTER 5

Does Sea Surface Temperature Contribute to Determining Range Limits and Expansion of Mangroves in Eastern South America (Brazil)?

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and Farid Dahdouh-Guebas

> “To do science is to search for repeated patterns, not simply to accumulate facts.”
>
> **Robert MacArthur**

remote sensing

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Article

Does Sea Surface Temperature Contribute to Determining Range Limits and Expansion of Mangroves in Eastern South America (Brazil)?

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Abstract: Low Sea Surface Temperature (SST) is a climate barrier because it may inhibit and reduce seedling growth of mangrove propagules upon dispersal through seawater. Our objective is to analyze the spatio-temporal series of daily SST data from the Multi-scale Ultra-high Resolution (MUR)-SST in order to identify the occurrence of chilling events for mangrove plants at the Eastern South America mangrove limit and beyond. We focus our study on three key sites: (i) the *Rhizophora mangle* L. distribution limit (Praia do Sonho: 27°53′S), (ii) the Eastern South America mangrove limit (Laguna: 28°30′S) and (iii) one beyond mangrove areas, in Araranguá (28°55′S). Our results show that, in Araranguá, chilling events are more intense and occur more frequently than in the other two sites that have a mangrove cover. We conclude that, the chilling events of SST may play a role in restricting mangroves within their actual limits. In this sense, higher occurrences of chilling events of SST could be an explanation for the absence of *R. mangle* in Laguna. However, *Laguncularia racemosa* (L.) C.F. Gaertn. was reported to be tolerant to low temperatures, and yet it is absent from the southernmost study site. This may be an indication of the role of other factors than SST in determining a mangrove range expansion, such as dispersal constraints.

Keywords: wetland; climate; sea surface temperature; biogeography; remote sensing; species limits; Brazilian southernmost mangrove; Western South Atlantic mangroves

1. Introduction

The mangrove ecosystem is a wetland forest which is globally distributed at the sea–land interface in tropical and subtropical coastal environments, usually sheltered in deltas, lagoons, rivers and estuaries.

Ecologists have been questioning why mangroves have latitudinal limits, and which variables are affecting their distribution (Quisthoudt *et al.* 2012; Osland *et al.* 2017b; Cavanaugh *et al.* 2018).

Several authors observed the spatial agreement of specific values of Sea Surface Temperature (SST) isotherms and mangrove limits for many regions in the world (Barth 1982; Woodroffe & Grindrod 1991; Duke *et al.* 1998). These studies revealed the influence of SST in determining mangrove distribution limits. Thus, Duke et al. (Duke *et al.* 1998) suggested that mangroves are generally restricted to the SST winter isotherms around 20 °C, while Woodroffe and Grindrod (Woodroffe & Grindrod 1991) proposed a temperature of around 15 °C. However, all authors highlighted that the Eastern South America mangrove limit is an exception to the global pattern of SST isotherms.

One can argue how SST can affect mangrove distribution. First, it is required to know that mangrove tree species are dispersed exclusively by water (mostly marine) due to the properties of their propagules (Rabinowitz 1978), from short to long distances (Triest 2008; Ngeve *et al.* 2016). During the dispersal stage, water temperature is an influential variable that can regulate seedling growth of mangrove propagules (Steinke & Naidoo 1991; Oliveira 2005). The propagules' viability and seedling growth are conditioned by favorable temperatures, where low SST can initially already reduce or inhibit their germination or rooting and establishment (Steinke & Naidoo 1991; Oliveira 2005). In short, when mangrove propagules are transported by seawater, the main variable is the SST, which determines the success or failure of the establishment of mangrove propagules in new lands. This causes low values of SST to act as a barrier to mangrove expansion. Recently, a study revealed that the minimum SST decreases with higher latitudes in Eastern South America, for which it seems to be a prominent predictor of mangrove limits (Ximenes *et al.* 2016).

However, recently, the absolute daily minimum and below-zero air temperatures have received more attention in studies on mangrove distribution limits, for instance in the southeast of the United States (Stuart *et al.* 2007; Osland *et al.* 2013; Cavanaugh *et al.* 2014, 2015) and globally (Osland *et al.* 2017b), whereas daily SST data are being poorly evaluated at regional scales in mangroves. In this sense, there is a lack of detailed study analyzing seasonality patterns of SST at the limits of mangroves and quantifying daily occurrences of chilling events of SST at high resolution. For instance, the SST derivates used as a proxy of chilling events is the mean annual SST (Quisthoudt *et al.* 2012; Osland *et al.* 2017a) and the monthly mean of the minimum SST (Quisthoudt *et al.* 2012; Ximenes *et al.* 2016).

In Eastern South America, Soares et al. (Soares *et al.* 2012) suggested multiple limiting factors (or proxies of factors) inhibiting mangrove expansion to higher latitudes, namely, mean air temperature, annual mean SST, the occurrence of frost events, and the northward-directed longshore drift. Nevertheless, other authors consider also other non-climate variables, such as dispersal constraints and unavailable habitat, to better explain the absence of mangroves beyond their limit in Eastern South America (Osland *et al.* 2017b; Cavanaugh *et al.* 2018). Contrasting literature statements (Quisthoudt *et al.* 2012; Soares *et al.* 2012; Osland *et al.* 2017b; Cavanaugh *et al.* 2018) on the limiting factors reflects our lack of understanding on why mangroves do not cross their current limit in Eastern South America.

About 70 km south of the mangrove limits in Eastern South America, there is a narrow river parallel to the coastline forming a small lagoon with a marginal vegetation, which seems geomorphologically suitable for wetland ecosystems, but no mangroves have been observed in this site for more than three decades (Schaeffer-Novelli *et al.* 1990; Soares *et al.* 2012). Since apparently there is an availability of accessible habitat beyond actual Eastern South American mangrove limits, the absence of mangroves is intriguing. Although the Eastern South American mangrove limit is probably due to dispersal constraints

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(Osland *et al.* 2017a) or multiple factors, including low SST (Soares *et al.* 2012), a detailed analysis of SST data has never been done properly in this region, in order to better understand the limit of mangrove distribution. Currently, daily SST data with high spatio-temporal resolution have been improved, thanks to new products of remote sensing which merge satellite data from several missions and sensors, as well as in situ observations (Chin *et al.* 2017).

With new SST data being freely available, a detailed analysis of SST data in the light of previous laboratory experiments related with low SST stressing mangrove propagules is now possible. For this reason, a better understanding of SST data as a possible limiting factor in mangrove expansion in this region is necessary. Hence, the objective of the present paper is to assess SST data considering occurrences of daily chilling events and to characterize the seasonality patterns of SST fields in Eastern South America mangrove limit (Brazil).

2. Materials and Methods

2.1. Study Area

The Eastern South America mangrove limit, also known as the Brazilian southernmost mangrove limit, is located in Laguna (28°30'S) in the state of Santa Catarina, Brazil (Schaeffer-Novelli *et al.* 1990; Soares *et al.* 2012) (Figure 1). Our study covers three sites: two are within the current mangrove range, Praia do Sonho and Laguna, and one is beyond the mangrove limit, in Araranguá (28°55'S) (Figure 1). Therefore, in Araranguá, mangroves are absent; however, wetland vegetation is present (Soares *et al.* 2012). The distance between Praia do Sonho and Laguna is about 78 km, while Araranguá is about 70 km to the southeast of Laguna.

The geographical limit of *Avicennia schaueriana* Stapf & Leechm. ex Moldenke (Acanthaceae) and *Laguncularia racemosa* (L.) C.F. Gaertn. (Combretaceae) is in Laguna and the *Rhizophora mangle* L. (Rhizophoraceae) limit is in Praia do Sonho (27°53'S), in the city of Palhoça (Schaeffer-Novelli *et al.* 1990; Soares *et al.* 2012). All three mangrove trees species are present in Praia do Sonho. In Laguna, only the former two species are found (Figure 1), with *L. racemosa* being dominant and *A. schaueriana* represented by few isolated trees only (Soares *et al.* 2012). The floristic composition of the study sites was described by Schaeffer-Novelli et al. (Schaeffer-Novelli *et al.* 1990) and by Soares et al. (Soares *et al.* 2012). The structural development of the mangrove trees decreases according to higher latitudes (Soares *et al.* 2012). Hence, the Eastern South America mangrove limit in Laguna shows a lower degree of structural development compared to the mangroves north of the limit (Soares *et al.* 2012).

The three study sites are located in a region with warm temperate, fully humid and hot summer (Cfa), according to the Köppen-Geiger climate classification (Kottek *et al.* 2006). Our study areas are located in the same marine province, the Warm Temperate Southwestern Atlantic, but with respect to the marine ecoregions, the two mangrove study sites are in the Southeastern Brazil ecoregion, and Araranguá is localized in the Rio Grande ecoregion (Spalding *et al.* 2007) (Figure 1).

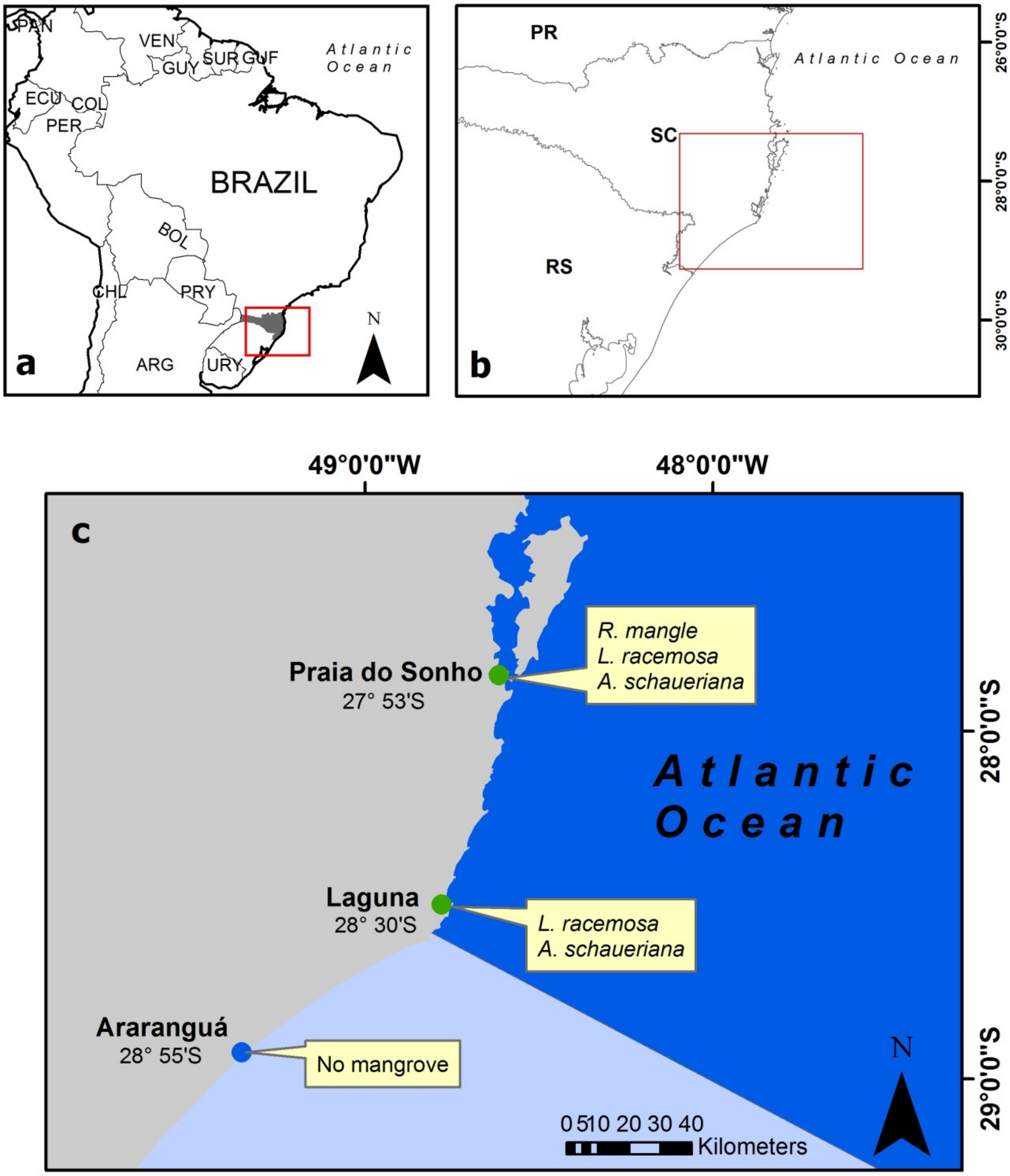

Figure 1. Study area at the eastern coast of South America. (**a**) Map of Brazil with Santa Catarina (SC) State marked in dark grey and the red rectangle is in detail above right; (**b**) SC State boundaries and the area within the red rectangle are shown in detail in the figure below; (**c**) detailed map of the Eastern South America mangrove limit located in Laguna, Brazil. The green circles represent the southernmost mangrove stands in Praia do Sonho and Laguna. The blue circle represents Araranguá estuary, beyond the Eastern South America mangrove limit. The pale yellow boxes list the mangrove tree species which occur, if any. Praia do Sonho and Laguna are located in the Southeastern Brazil marine ecoregion (dark blue on the Atlantic Ocean), whereas Araranguá, which is beyond the mangrove limits, is located in the Rio Grande marine ecoregion (light blue on the Atlantic Ocean). Laguna is very near to the boundary of the two marine ecoregions.

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2.2. Sea Surface Temperature

The temperature data was extracted from the Multi-scale Ultra-high Resolution (MUR)-SST Analysis-version 4 (L4) (Chin *et al.* 2017). This analysis was produced by the Jet Propulsion Laboratory (JPL) from the National Aeronautics and Space Administration (NASA). The data are freely available via the Open-source Project for a Network Data Access Protocol (OPeNDAP) platform.

MUR-SST is provided on a daily basis, since June 2002 to present, and at a longitude-latitude resolution of 0.01 degrees (~ 1 km). Such ultra-high resolution is achieved by combining data from several microwave (MW) and infra-red (IR) sensors, among them the NASA Advanced Microwave Scanning Radiometer-EOS (AMSRE), the US Navy microwave WindSat radiometer, the Moderate Resolution Imaging Spectroradiometer (MODIS) on the NASA Aqua and Terra platforms, Advanced Very High Resolution Radiometer (AVHRR) on a number of National Oceanic and Atmospheric Administration (NOAA) satellites, as well as in situ SST observations from the NOAA iQuam project.

The advantage of merging these complementary products relies in the fact that the IR presents high spatial resolution, but the measurements are affected by cloud coverage. Due to the reflectance promoted by clouds and water vapor, the retrieval of the real SST value may be biased and so the accuracy is reduced. Additionally, an undetected cloud is often found at the edges of the cloud cells which also may affect the SST accuracy. On the other hand, MW does not suffer this limitation and can improve the IR measurements, though it presents much coarser spatial resolution (Chin *et al.* 2017). Some other issues related to the SST data must be considered, since the reflectance captured by the sensors from the satellites is usually affected by suspended matter and various particles of the shallow coastal waters in which the reflectance of sunlight by these materials interferes in the radiometric determination of the SST. Thus, the SST coastlines near mangroves are the most difficult areas to accurately estimate, due to the high turbidity of river, lagoon and estuary waters. Then, to improve the estimative power of the SST, using several satellite images and sensors, in situ observations were taken to calibrate the MUR data, thus reducing error (Donlon *et al.* 2012; Chin *et al.* 2017). The data description from the provider is found through the following link: https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1.

For a complete description of MUR-SST methodology, the reader is referred to Chin et al. (Chin *et al.* 2017). In short, these authors make use of wavelet-based multi-scale signal expansion incorporated into a Multi-Resolution Variational Analysis (MRVA) scheme. The authors argue that this method is unique in addressing irregularity in measurement locations and scale-dependent interpolation issues, and as a consequence, the MUR-SST data present two main strengths as compared to the other available L4 SST datasets: (i) there is a better preservation of the spectral power in the SST measurements, and thus all SST features observed in the data are indeed due to the measurements; (ii) this is a "grid-less" analysis due to the use of a continuous basis function, which preserves the original coordinates of the measurements. These two advantages are illustrated in the JPL webpage (https://podaac.jpl.nasa.gov/Multi-scale_Ultra-high_Resolution_MUR-SST).

We have calculated monthly means from January 2003 to September 2018 by making the grid-point average of the respective daily fields within a certain month. Seasonal fields, namely summer, autumn, winter and spring, were calculated as the averages of January–February–March, April–May–June, July–August–September and October–November–December, respectively. All data processing and plotting were performed using Python 2.7.0 executed under in the Linux operating system (Ubuntu 16.04).

2..3. Chilling Events

We considered, as chilling events of SST, the values of ≤15 °C, ≤16 °C and ≤17 °C. These three values can be considered as three levels of intensity, and the number of occurrences of these daily temperatures is the frequency of such an event. Based on the scientific literature (see Section 4.1 for more details), these values were deemed to inhibit or reduce the seedling growth of the mangrove propagules, which we consider herein as chilling events. For example, propagules of *A. schaueriana* exposed to a water temperature of 15 °C did not germinate (Oliveira 2005). Moreover, the mean SST of the coldest month in Araranguá being *circa* 17 °C, a temperature of ≤17 °C was used as a reference for a chilling event (Table 1), since mangroves were reported absent from this site for decades (Schaeffer-Novelli *et al.* 1990; Soares *et al.* 2012).

Thus, the intensity of such events is represented by the temperature values, with lower values being more intense, and the frequency by the number of occurrences of chilling events observed along the years. These are the two metrics that are known to reflect factors in geographical distribution of species (Larcher 2003).

The frequency of low SST data was determined by the number of daily occurrences of chilling events that happened per year and by the cumulative daily occurrences over the studied years (June 2002 to September 2018). In order to evaluate and compare different sites, we used the same time span of the SST data for all three sites. This procedure allowed us to investigate differences between the studied sites.

3. Results

The values of the SST isotherm were expectedly different according to the season of the year and location (Figure 2 and Figure 3). The lowest values during the winter mean of SST (and absolute minimum daily SST) were 17.90 °C (14 °C) in Praia do Sonho, 17.54 °C (13.13 °C) in Laguna and 16.86 °C (11.81 °C) in Araranguá (Table 1). The SST isotherm in autumn and in spring are intermediate, reaching between 21 °C and 22 °C in Laguna and Praia do Sonho and between 20 °C and 21 °C in Araranguá (Figure 2). During summer, all studied sites present SST higher than 24 °C (Figure 2). The temporal monthly variability of SST data for the three sites is similar, though Araranguá is marked by colder temperatures during almost the entire time span, being more pronounced in winter (Figure 3).

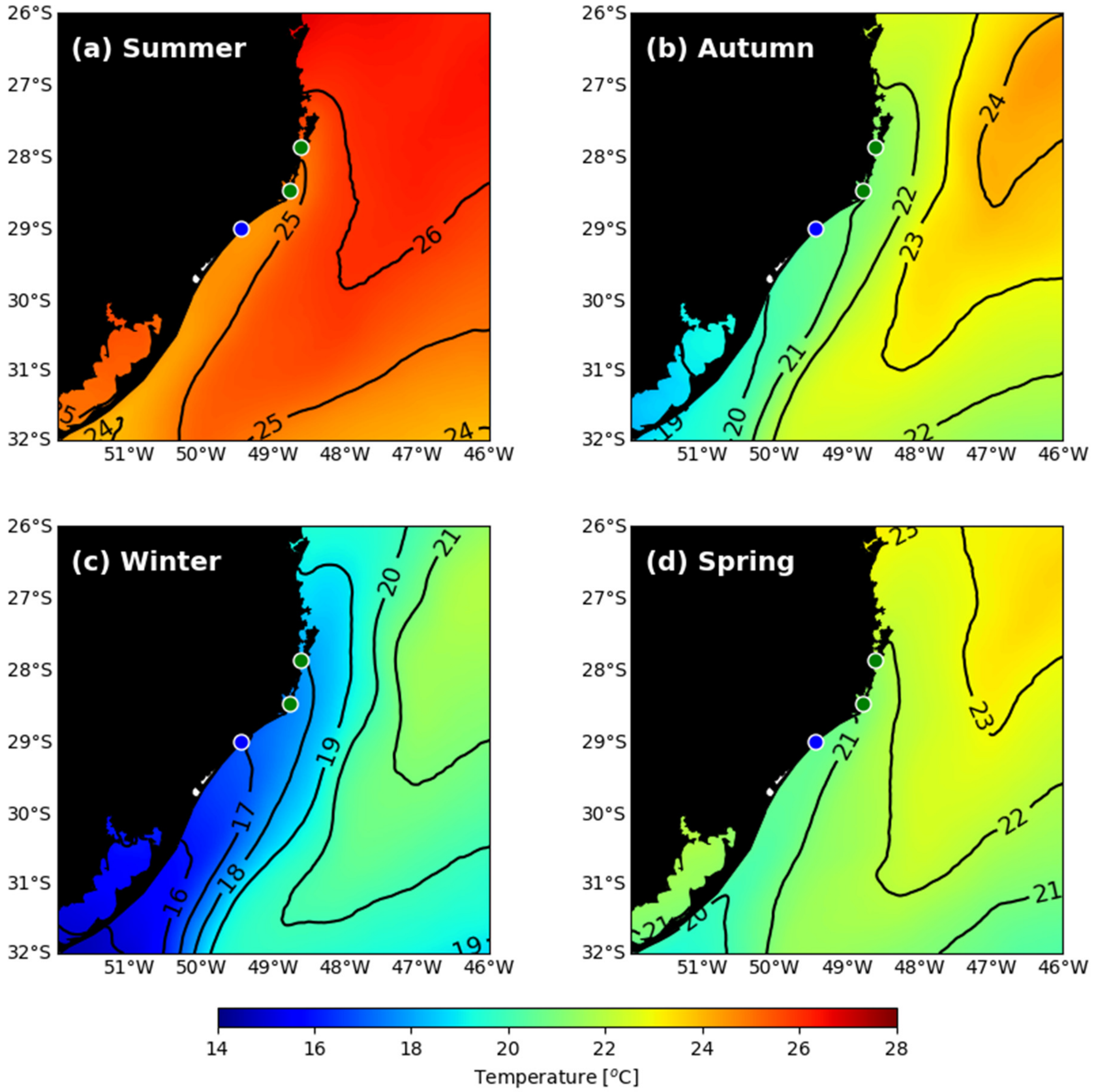

Figure 2. Seasonal fields of Sea Surface Temperature (SST): (**a**) summer (January, February, and March), (**b**) autumn (April, May, and June), (**c**) winter (July, August, and September) and (**d**) spring (October, November, and December). The isotherms and their associated temperatures are represented by the black lines and the respective values are shown. Seasonal averages were calculated from January 2003 to December 2017, since this is the period for which MUR-SST provides data for all months of the year. From north to south, the green circles indicate the locations of Praia do Sonho and Laguna, respectively, and the blue circle indicates the location of Araranguá.

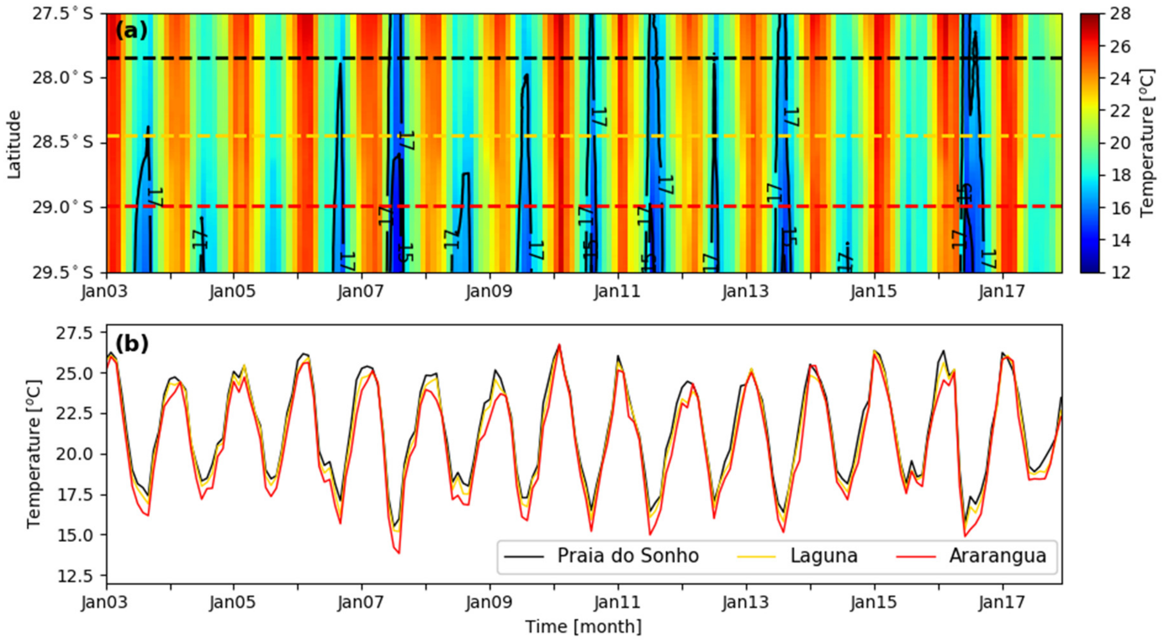

Figure 3. (**a**) Monthly averages of SST along the Brazilian South Coast, from 27.5°S to 29.5°S (January 2003 to December 2017). The isotherm of 17 °C is highlighted by the black isolines. The latitudes of Praia do Sonho (southernmost distribution limit for *R. mangle*), Laguna (southernmost distribution limit for *L. racemosa* and *A. schaueriana*) and Araranguá (beyond southern mangrove limit) are indicated by the black, yellow and red lines, respectively. (**b**) Monthly averages of individual SST time series from the three geographic locations mentioned above.

We evaluated the occurrences of chilling events from data shown in Figures 4 and 5. Araranguá showed a higher occurrence of chilling events for SST than the other two mangrove sites (Figures 4 and 5; Table 1). In Praia do Sonho, the SST had 36 days with temperatures of ≤15 °C, while Laguna had 59 days of such temperatures, but in Araranguá, we observed temperatures of ≤15 °C for 216 days over a 16-year period (Figures 4 and 5; Table 1). For the SST of ≤16 °C, the cumulative occurrences of chilling events were 495 days in Araranguá, i.e., around 31 days per year, with 222 more days than in Laguna (Table 1). The two mangrove sites within the mangrove range limit, Praia do Sonho and Laguna, showed less frequent events with an SST of ≤17 °C than Araranguá. For SST equal to or below 17 °C, in Araranguá, 928 days of occurrences of chilling events were found over a 16-year period while Laguna had 589 days and Praia do Sonho had 442 days (Table 1). Although the chilling events were found mostly during the winter period, low values were also found in other seasons, for example, during autumn. Comparing the two mangrove sites, Praia do Sonho and Laguna, the SST differences are about ≥0.3 °C for the annual mean, winter mean, and mean SSTs in July, August and September. Moreover, Laguna has more chilling events than Praia do Sonho (Figures 4 and 5; Table 1).

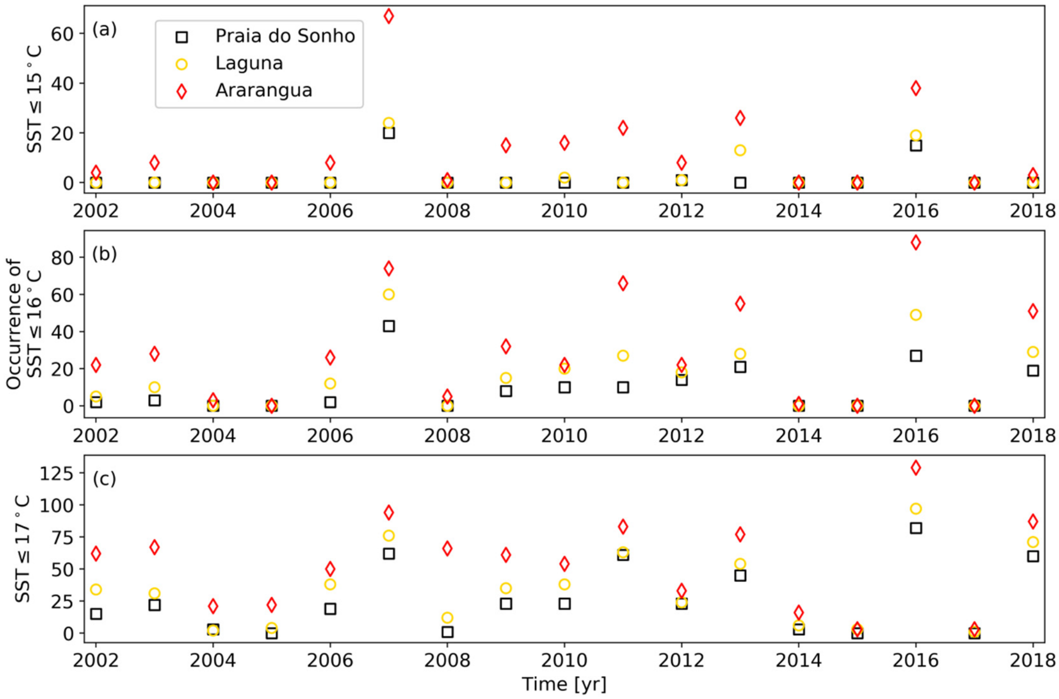

Figure 4. The number of occurrences of daily SST per year equal to or below the defined threshold. (**a**) Daily SST of ≤15 °C; (**b**) daily SST of ≤16 °C; and (**c**) daily SST of ≤17 °C. The SST data were analyzed for a period of 16 years (June 2002–September 2018).

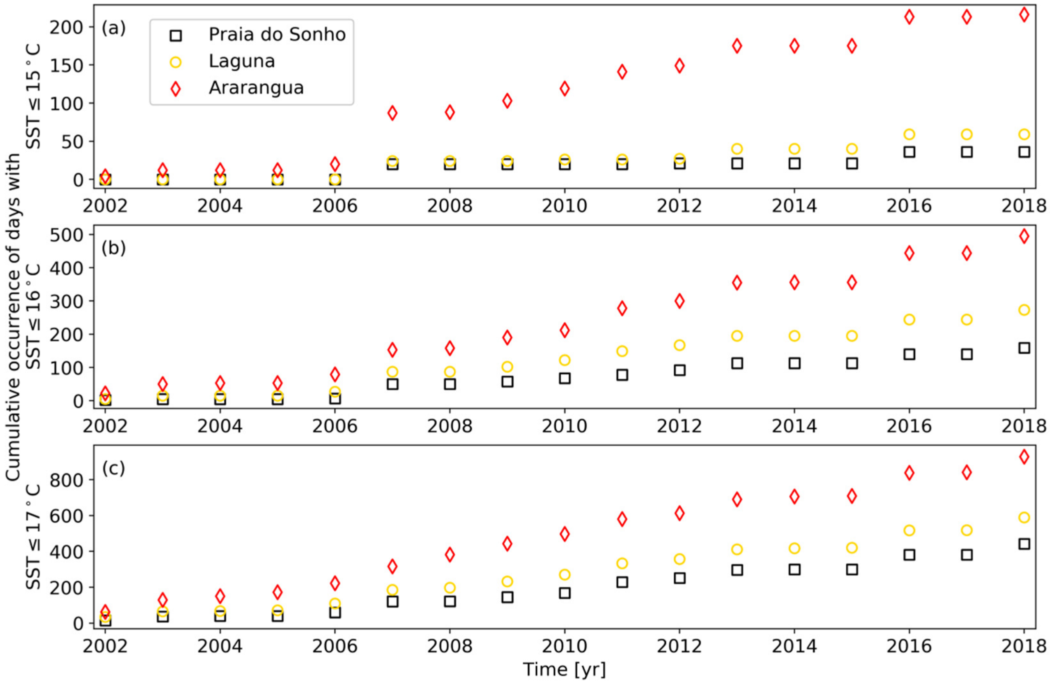

Figure 5. The cumulative occurrence of days of SST data equal to or below the defined threshold. (**a**) Daily SST of ≤15 °C; (**b**) daily SST of ≤16 °C; and (**c**) daily SST of ≤17 °C. The SST data were analyzed for a period of 16 years (June 2002–September 2018).

On average, SST is lower in Araranguá compared to that in Laguna, and a maximum difference of about 0.76 °C was observed in July, considered as the coldest month. For the entire winter (July, August and September), the mean SST difference is about 0.68 °C (Table 1). Moreover, within and beyond the mangrove limit, we found higher differences up to 1.32 °C for the absolute minimum daily SST data and 1.29 °C for the mean SST of the 10 coldest days (Table 1).

Table 1. The SST (°C) derivate was obtained from the Multi-scale Ultra-high Resolution (MUR). Cumulative occurrence of chilling events is the accumulated days of chilling events using a total of 16 years for SST (SST daily). * P–L: differences between Praia do Sonho and Laguna. ** L–A: differences between Laguna and Araranguá. When the differences are negative, it means that Laguna* or Araranguá** presented more occurrences of chilling events.

	Variables	Praia do Sonho	Laguna	Araranguá	P—L*	L—A**
Sea Surface Temperature	Annual mean SST	21.43 (±3.09)	21.09 (±3.12)	20.61 (±3.28)	0.34	0.48
	Winter mean SST	17.90 (±1.30)	17.54 (±1.34)	16.86 (±1.47)	0.36	0.68
	Mean SST in July	17.70 (±1.38)	17.41 (±1.39)	16.65 (±1.46)	0.29	0.76
	Mean SST in August	17.63 (±1.27)	17.20 (±1.32)	16.53 (±1.49)	0.43	0.67
	Mean SST in September	18.41 (±1.11)	18.02 (±1.15)	17.41 (±1.30)	0.39	0.61
	Absolute minimum daily SST	14.00	13.13	11.81	0.87	1.32
	Mean SST of the 10 coldest days	14.32 (±0.20)	13.76 (±0.27)	12.47 (±0.39)	0.56	1.29
	Number of days with daily SST of ≤15 °C	36	59	216	−23	−157
	Number of days with daily SST of ≤16 °C	156	273	495	−117	−222
	Number of days with daily SST of ≤17 °C	442	589	928	−147	−339

4. Discussion

Relatively low SST values were reported to negatively impact seedlings of certain mangrove species (Steinke & Naidoo 1991; Kao *et al.* 2004; Oliveira 2005). They can be considered an important limiting factor for mangrove expansion. For the SST, values lower than or equal to 15 °C seem to reflect an important threshold for species distribution (Woodroffe & Grindrod 1991). Empirical experiments with *A. schaueriana* propagules showed that no seedling germination occurred when propagules were exposed to a water temperature of 15 °C (Oliveira 2005).

A higher occurrence of chilling events for the SST of ≤15 °C in Araranguá (216 days) was observed; at the same time, these events were less frequent in Laguna (59 days) and in Praia do Sonho (36 days) (Table 1).

Experimental laboratory research on establishment and early growth of propagules of *Avicennia marina* (Forssk.) Vierh. showed that seedlings at an SST of 25 °C developed well, but growth was strongly reduced at a water temperature of 17 °C (Steinke & Naidoo 1991). *A. marina* does not occur in Brazil, but it has a wider latitudinal range than the Brazilian mangrove congeneric species, and hence a threshold for the SST of 17 °C is probably an indication of an acceptable and conservative barrier to the establishment of the mangrove seedlings. In Araranguá, over the studied years, there were about 1.6 times more occurrences of SST of ≤17 °C than in Laguna, and about 2.1 times more than in Praia do Sonho (Table 1).

The fewer occurrences of SST of ≤15 °C and ≤17 °C in Praia do Sonho may favor the presence of *R. mangle*, reaching its southernmost occurrence along the Brazilian coastline. Since *A. schaueriana* and *L. racemosa* are found in Laguna estuary, no dispersal constraint for *R. mangle* to reach this estuary is expected either. However, despite its longer capability to float as opposed to *L. racemosa* propagules, *R. mangle* is absent in Laguna estuary. More occurrences of chilling events could be an explanation for this absence.

Genetic diversity of *R. mangle* (on a basis of microsatellites) was found to be lower in the southern as opposed to the northern Brazilian mangroves (Pil *et al.* 2011). The authors attributed this pattern to the populations' recent historical age (Pil *et al.* 2011), a pattern for peripheral populations that was found with other mangrove species elsewhere (De Ryck *et al.* 2016). The lower genetic diversity in Brazilian southern populations of *R. mangle* can reduce the phenotypic plasticity of this species, the individuals of which become less resilient to constraining factors such as low temperature.

Despite the chilling events being a physiological stress to mangrove plants (Chen *et al.* 2017b), experimental research with *L. racemosa* propagules showed significant seedling growth even at SST below 15 °C (Oliveira 2005). Although this advantage can tolerate lower SST than *A. schaueriana* (McMillan 1971), the *L. racemosa* propagules have a shorter viability period while floating (and dispersing) than other mangrove species (Rabinowitz 1978), which contributes to restrict dispersal, and hence range expansion (Duke *et al.* 1998).

Nevertheless, we observed that the *L. racemosa* population is dominant and only a few isolated trees of *A. schaueriana* were found in Laguna estuary (Soares *et al.* 2012). This means that *L. racemosa* contributed more to expanding mangrove limits in Eastern South America than *A. schaueriana*. This dominance of *L. racemosa* at the Eastern South America mangrove limit (Soares *et al.* 2012) can be interpreted by higher resistance of *L. racemosa* to low SST, enabling seedlings to growth, as observed in experimental studies (Oliveira 2005).

5. Conclusions

The use of new products of SST data in our study allowed us to analyze spatio-temporal series of chilling events which affect the mangroves propagules at high resolution. The latest works for mangrove on a large scale used the SST temporal scale for a 5-year period (from 2009 to 2013) (Osland *et al.* 2017b) and an 8-year period (from 2002 to 2009) (Ximenes *et al.* 2016). For this reason, we used a historical SST data with 16 years (June 2002 to September 2018) that can be considered within an appropriate time period. Moreover, our study makes use of state-of-the-art SST data, with finer spatio-temporal resolution compared to previous studies. To our knowledge, this is the first research considering daily SST data affecting mangrove ecosystems.

For sure, there are multiple factors constraining mangrove expansion, and they were summarized in previous studies (Soares *et al.* 2012; Osland *et al.* 2017b); however, here we focused our analysis on SST data constraining mangrove expansion and abundance at the distribution limits. In this study, we demonstrate the usage of SST data with respect to mangrove dispersal. Each mangrove species has a threshold of SST that can inhibit primordial physiological functions of the plants and a response to seasonal SST patterns. Based on the literature, we know that the *R. mangle* and *A. schaueriana* propagules can be affected by low SST of around ≤17 °C, and no seedling germination occurred in *A. schaueriana* when exposed to SST of 15 °C (Oliveira 2005). For SST, comparative evaluation showed that in Araranguá (beyond the mangrove limit), there was a higher occurrence of chilling events (SST of ≤17 °C) than in the two sites having mangrove cover, at lower latitudes. The higher frequency of such chilling events (SST of ≤17 °C) may constrain mangrove expansion, at least for *R. mangle* and *A. schaueriana*. For narrowing down this explanation, the daily temperature patterns should be matched with propagules production phenology, for which no historical or retrospective data are available.

On the other hand, the *L. racemosa* propagules are more physiologically tolerant to SST of ≤15 °C (Oliveira 2005). For this reason, another explanation, instead of low SST, is needed; for instance, unfavorable directions of sea currents (Siegle & Asp 2007) consequently dispersal constraint (Soares *et al.* 2012; Osland *et al.* 2017b) seems a possible explanation. However, the dominance in abundance of the *L. racemosa* population at the mangrove limit (Laguna) can be explained by the species' resilience to low SST while *A. schaueriana* is less tolerant and occurred with few isolated individuals. Moreover, *L. racemosa* propagules have a shorter viability period while floating when compared with the other two species (Rabinowitz 1978), which renders long-time dispersal difficult and epic colonization events rare.

For the future, we urge more research on the influence of low SST on the viability of mangrove propagules for different species and populations in different geographical sites, since the relative importance of ecological factors may be different (and hence also response to environmental change). We call for sampling propagules at the Eastern South America mangrove limits in Laguna and Praia do Sonho, to initiate physio-ecological studies, since respective propagules are likely to be more resilient to low SST than the mangrove populations from northern sites. We need to better know the physiological thresholds for low values of SST in regard to the viability and functionality of mangrove propagules. For this reason, laboratory and/or field experiments should be conducted in that direction, for instance, exposing mangrove trees propagules to seawater with different threshold temperatures (controlled in the lab or in different locations at sea), during a typical period in which the propagules stay immersed in seawater. After this exposition, propagules should be planted in appropriate soil in order to test their viability. New physiological studies in regard to SST thresholds influencing propagule viability, aligned with satellite images merged with interpolated in situ data of SST, are a crucial approach to modeling mangrove species distribution.

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CHAPTER 6

Discussion and Conclusions

"A journey of a thousand miles begins with a single step". **Confucius**

Discussion & Conclusions

The main focus of this PhD project was to fill some of the gaps in our knowledge with respect to the macroecology of mangroves at regional to global scales. This PhD thesis relies on knowledge derived from research developed by various authors in the fields of botany, ecology, biogeography, plant physiology, climate science, oceanography, remote sensing, geoprocessing, and GIS. Yet, the methodology used in all chapters was only possible because of recent and freely available databases, such as those connected to the global mangrove maps (Spalding *et al.* 1997, 2010; Giri *et al.* 2011), the mangrove species distributions (Polidoro *et al.* 2010; IUCN 2016), the surface climate databases (Hijmans *et al.* 2005; Zomer *et al.* 2006, 2008; Tyberghein *et al.* 2012), the remote sensing products of SST data (Tyberghein *et al.* 2012; Chin *et al.* 2017), the maps outlining upwelling zones of intensity (Hoekstra *et al.* 2010) and the body of scientific literature on oceanographic processes (i.e. upwelling zones and sea currents).

Terrestrial conditions and oceanographic processes influence mangrove distribution (Chapman 1975, 1976; Duke 1992; Duke *et al.* 1998; Tomlinson 2016). Since the first life stage of mangroves, the dispersal process of buoyant propagules, happens in seawater (Rabinowitz 1978; De Ryck *et al.* 2012; Lo *et al.* 2014; Ngeve *et al.* 2016; Ximenes *et al.* 2018), oceanographic processes determine, though not solely, the success of mangrove propagule establishment (Triest 2008; Soares *et al.* 2012). Seawater is essential for the distribution of mangrove species and contributes to their establishment. For instance, floating time (upon viability) determines the distance that can be covered by propagules (Rabinowitz 1978; Duke *et al.* 1998; Drexler 2001), and sea currents provide direction and speed of dispersal (Duke 1992; Triest 2008; Lo *et al.* 2014; Ngeve *et al.* 2016, Van der Stocken *et al.* 2019). Conversely, low sea surface temperatures could constrain propagule viability (McMillan 1971; Steinke & Naidoo 1991; Oliveira 2005). Sea surface temperature and currents are intrinsically associated, and both warm and cold currents exist in oceans. These two factors contribute to mangrove distribution, and are responsible for the success or failure of mangrove seedling establishment. The important influence of oceans currents and seawater as a vector in the distribution and viability of mangrove propagules was established. Little is however known about the tolerance of most mangrove species to different temperature conditions. A few physiological studies have been done specifically on key mangrove species in certain regions. Other factors are certainly involved in the success of mangrove seedling establishment. For example, seedlings must reach an appropriate substrate in a geomorphological context such as lagoons, estuaries, deltas and bays (Thom 1967; Chapman 1975; Hutchings & Saenger 1987). Then wave energy may impede succesful establishment (Hurst *et al.* 2015). Following their primary establishment in an appropriate substrate, both oceanographic and terrestrial conditions will be more directly associated with the success of mangrove seedling recruitment.

Historically, scientists tried to find a general causal explanation for worldwide mangrove geographical containment within their range limits. For many years, at a global scale, the SST isotherms were considered to reflect the main restriction of mangroves at their range limits (Barth 1982; Woodroffe & Grindrod 1991; Duke 1992). However, Duke (1992) pointed out exceptions to this pattern of a common SST isotherm amongst the mangrove limits in Brazil, East Australia and New Zealand. Other authors claimed that minimum air temperature of the coldest month and annual mean air temperature isotherms are factors delimiting global mangrove distribution (Macnae 1963; Chapman 1977). Quisthoudt *et al.* (2012) compared many mangrove range latitudinal limits throughout the world, for their environmental conditions. They found that SST and air temperature isotherms at the range limits are highly variable, not obeying a common isotherm. Indeed, expecting a single and common isotherm worldwide for one species specifically or for mangroves in general, assumes that the same responses play everywhere, while combinations of determinants and even intra-species variability would probably not support such an assumption.

Strikingly, Osland *et al.* (2017b) recognized that sea temperatures play an important role by modulating air temperature, soil temperature, and rainfall regime (factors strongly associated with mangrove distribution); however, they maintain that minimum air temperature and rainfall regimes are more directly relevant than sea surface temperature. On the other hand, many authors believe that ocean currents and SST may interfere directly with delimiting mangrove range limits and distribution (Chapman 1975; Woodroffe & Grindrod 1991; Duke 1992; Soares *et al.* 2012; Ximenes *et al.* 2018).

To obtain a comprehensive understanding of mangrove species' range limits and spatial assessment of environmental constraint factors, we investigated mangrove plant species distribution at three large scales: **global** (worldwide mangroves), **continental** (> 6000 km of Brazilian mangrove extension), and **regional** (southernmost mangrove range limits at Eastern South America). I consider that a study covering three mangrove estuaries constitutes a regional study (CHAPTER 5), whereas the entire Brazilian coastline constitutes a continental scale, because of the extensive dimensions and wide latitudinal and longitudinal variations (CHAPTER 4). Finally, global scale means that the two major mangrove regions in the worlds, the Atlantic East Pacific (AEP) and Indo-West Pacific (IWP), were incorporated into the model (CHAPTER 3).

Global mangrove range limits

Chapman (1975) observed coincidences of upwelling cold waters and southern mangrove limits at the western side of South America, Africa and Australia. However, precipitation is likely to be more important than temperature in defining mangrove range limits at the western side of continents (Saenger 2002), or it may be working in combination with temperature (Osland *et al.* 2017b). The two main factors (i.e. temperature and precipitation) associated with mangrove species' range limits are also connected to the upwelling phenomenon. In this PhD project, we investigated the relationship between mangrove species range limits and the upwelling phenomenon. I identified several mangrove range limits that coincide with upwelling zones, and therefore suggest that these spatial agreements are due to the upwelling characteristics related to the deep sea cold water (i.e. low temperature) that triggers arid conditions, as colder waters reduce evaporation and, consequently, promote strong temperature inversion and minimize precipitation (Shi *et al.* 2000a; Adams 2007). Hence, there may be multiple physiological effects of the conditions caused by an upwelling phenomenon (low temperature, drought or relative humidity).

At this point, I argue that upwelling intensities can affect patterns of mangrove species distribution, which will intrinsically affect global mangrove range limits (Figure 1). Mangrove plant distribution display a pattern of highest abundance under the influence of the lowest upwelling intensities (i.e. more suitable biotopes), whereas absent or lower abundance was seen adjacent to the highest upwelling intensities (i.e. zones with conditions which are less or not tolerated).

On a global scale, we note a relationship between the upwelling intensity level and mangrove distribution and abundance (in terms of cover), and hence consideration of upwelling systems will enrich our scientific debate on mangrove range limits. More importantly, our results disrupt a long-term scientific consensus among the mangrove scientific community that assumes the AEP and IWP regions are intrinsically environmentally similar (Chapman 1976; Duke 1992; Ricklefs *et al.* 2006). If we compare the upwelling intensity for each biogeographical region, it is possible to note that the strongest upwelling intensities are found in the AEP region, which is very different from the IWP region in that respect (CHAPTER 3).

Upwelling events are intrinsically associated with sea currents. Globally, sea currents are distinct at the two sides of an ocean and behave quite differently: the Eastern Boundary Current (EBC) has a slower velocity compared to its counterpart, the Western Boundary Current (WBC).

At the west sides of continents, where mangroves do not reach high latitudes, a general pattern with strong upwelling intensity is associated with the Eastern Boundary Current (EBC); these are the Canary, Benguela, California, and Humboldt currents. However, this global pattern is not observed in Western Australia because of the warm water of the Leeuwin Current (Hanson *et al.* 2005). Generally, upwelling zones are found to coincide with mangrove latitudinal range limits, with the exception of western Australia, south Australia, New Zealand and south Japan. These mangrove range limits are mainly restricted by minimum temperature and rainfall (Saenger 2002; Duke 2006; Semeniuk 2013; Osland *et al.* 2017b). Moreover, we found upwelling zones coinciding with absence of mangroves in South Australia (e.g. Bonney upwelling).

For western Australia, Semeniuk et al. (2000) proposed that the anomalous coastal warm currents from the Leeuwin Current may favour mangrove extent beyond 30°S. We agree with this statement. Nevertheless, we believe that mangrove extension in western Australia is mainly caused by the Leeuwin Current inhibiting the development of strong upwelling cells. However, at least two minor upwelling zones are found (Cape Currents and Ningaloo) (Hanson *et al.* 2005) (CHAPTER 3).

At other mangrove limits, for instance, the frequency of freezing events has been indicated as the major factor responsible for mangrove restriction (Osland *et al.* 2013; Cavanaugh *et al.* 2014 for Florida, USA). However, we found some upwelling zones in east Florida that might have an additional effect on the restriction of mangrove range limits and in the low species number in that region (CHAPTER 3).

To the best of our knowledge, Hoekstra *et al.* (2010) offer the only global database for upwelling presence and intensity map. The upwelling presence and intensity is indicated for each marine province *sensu* Spalding *et al.* (2007). This was sufficiently accurate to show the main global upwelling patterns. Unfortunately, the upwelling index that could provide a more detailed intensity of the upwelling zones was not globally available.

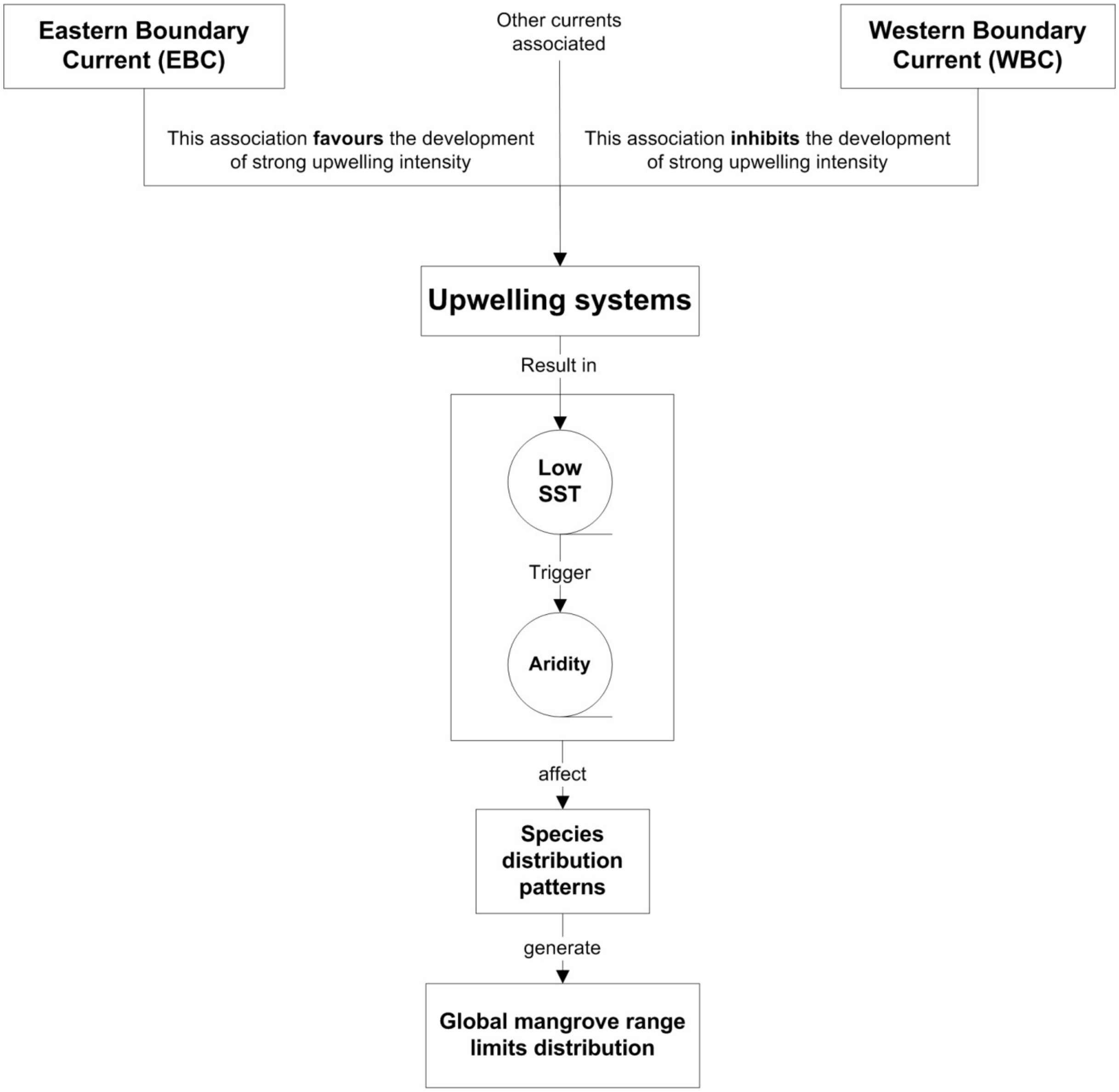

Figure 1: A general scheme of the upwelling systems associated with sea currents that result in low SST and triggers aridity in surroundings areas. These two variables, lower SST and aridity, have been described as potential variables affecting mangrove species distribution patterns, and by consequence also influence mangrove range limits on a global scale. Despite it is not mentioned in this scheme, it is important to highlight that the warm Leewin Current in west coast of Australia reduces the strength of the upwelling systems in that region, which is an exception to the EBC pattern of strong upwelling systems.

Brazilian mangroves – Continental scale

The Brazilian coastline is extensive, it runs for more than seven thousand kilometres and ~36 degrees latitude (from 4°N to 33°S), and mangrove forest covers most of it, for more than six thousand kilometres (from 4°N to 28°S). Mangroves are encountered in sheltered estuaries, deltas, lagoons, and bays (Saenger *et al.* 1983). There are five sites of mangrove species limits along the Brazilian coastline (Schaeffer-Novelli *et al.* 1990), but some of them are close to each other, and, at low scale, I roughly represent them as three key sites of species range limits (Figure 2).

Osland *et al.* (2017b) indicated that temperature rather than precipitation explains the mangrove species distribution along the Brazilian coastline. However, two mangrove species *R. racemosa* Meyer and *R. harrisonii* Leechman have their range limits located in the northeast of Brazil, where we find the lowest values of precipitation in the driest month, the driest quarter and aridity of the entire Brazilian mangrove distribution. At the same time, temperature was consistently suitable through the years in the northeastern region (CHAPTER 4; Figure 2). Yet, in areas where temperature is suitable, other variables (e.g. as represented by precipitation of the driest season) play a role to determine mangrove species range limits (Saenger 2002; Ximenes *et al.* 2016). For these reasons, I conclude that low 'precipitation of the driest season' and aridity are probably reflecting the conditions that play the main role in defining *Rhizophora* species limits in the northeast of the Brazilian coastline, rather than temperature (CHAPTER 4; Figure 2). In addition, near to the two species limits found in northeastern Brazil mentioned above, we identify sub-humid and semi-arid areas (CHAPTER 4) that were to our knowledge never identified in previous studies (cf. Blasco 1983; Schaeffer-Novelli *et al.* 1990; Osland *et al.* 2017b). For this reason, we believe that precipitation is more important for species distribution than temperature in the northeast of Brazil (Figure: 2).

Yet, in southeastern America, the range limits of *Avicennia germinans* (L.) Stearn and *Conocarpus erectus* L. coincide with areas where cold waters of two upwelling systems are found (São Tomé Cape and Cabo Frio). These were suggested as a causative agent for these mangrove species limits (Ximenes *et al.* 2016). In fact, not only upwelling of cold water may play a role, but also aridity in the southeast of Brazil (Figure 2), which probably reflects the two upwelling systems in that region.

We suggested that in the Brazilian southernmost limits the minimum sea surface temperature has a major influence on mangrove species distribution, rather than any other air temperature derivatives or mean or maximum sea surface temperature (Ximenes *et al.* (2016) and CHAPTER 4). In this sense, species that are more likely to be limited by temperature gradually follow the latitudinal gradient, which is the case for *A. germinans*, *C. erectus*, *R. mangle*, *A. schaueriana* and *L. racemosa.*

Nowadays, the availability of databases is much better than a few years or decades ago. For example, the WorldClim is a historical meteorological database with data from several stations worldwide that were interpolated using latitude, longitude and altitude as independent variables, creating what is called a climate surface (Hijmans *et al.* 2005). The WorldClim database already has more weather stations and more accurate global elevation data, providing a 400 times higher spatial resolution than previously available climate surfaces (Hijmans *et al.* 2005). However, this database still presents shortcomings, such as the (still too) limited number of meteorological stations, fewer stations in areas with low population density and the non-randomness of station distribution, which are all potential causes of possibly inaccurate data in certain sites (Droogers & Allen 2002; Hijmans *et al.* 2005). Also, local conditions in mangroves may differ from even nearby meteorological stations. Nevertheless, for the entire Brazilian mangrove distribution, the WorldClim database allowed us to detect important patterns associated with mangrove species distribution and climate factors (Figure 2).

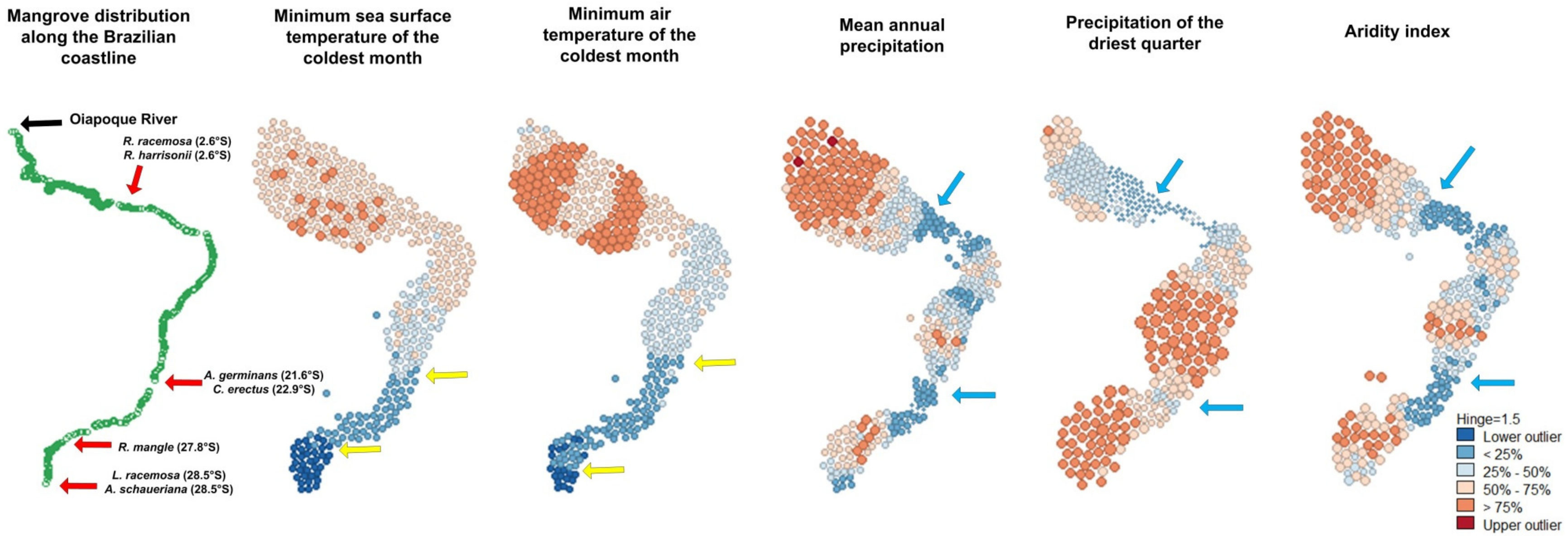

Figure 2: Mangrove distribution along the Brazilian coastline in green points (left side). The red arrows roughly indicate the mangrove species range limits with their respective names and decimal degree coordinates of their range limits. The other five climate maps are 'cartogram maps' (Anselin *et al.* 2006) distorted by the high and low values of each variable. Each circle represents a mangrove sample point location (however distorted), where circle size overstates the value of the variable, and circle colour represents the lower outliers, lower quartile, inter-quartile range (split into an upper and lower part), upper quartile and upper outliers, in exactly the same way as a Box and Whisker plot. The yellow arrows point at the location of temperature transition as the main factor for species range limits. Blue arrows – precipitation as the main factor. Adapted from Ximenes *et al.* (2016).

Mangrove range limits in eastern South America – Regional scale

What is limiting mangrove expansion in eastern South America? This was the fundamental question that inspired this research. Air temperature derivatives were indicated as main factors to explain the mangrove absence beyond their limits in eastern South America (Schaeffer-Novelli *et al.* 1990). Soares *et al.* (2012) suggested a combination of climate and oceanographic factors of mean annual air temperature, minimum air temperature of the coldest month, occurrence of frost, sea surface temperature, upwelling events and the direction of coastal currents. We suggested that, in the Brazilian southernmost limits, minimum sea surface temperature has a major influence on mangrove species distribution, rather than any other air temperature derivatives, mean or maximum sea surface temperature (CHAPTER 5). Other authors bring forward dispersal constraints and/or lack of potential habitat (Osland *et al.* 2017b). However, there is a geomorphologically suitable and accessible biotope for mangroves ~75 km beyond the mangrove limits in eastern South America, yet no mangroves are present. Therefore, if habitat availability is apparently not limiting, what could be confining mangroves to a lower latitude?

Because of this unexpected pattern, we proposed a detailed study to understand and explain the mangrove range limit in eastern South America (i.e. Brazilian southernmost limits) (CHAPTER 5). Here, we described in more detail the daily SST data influence the viability of propagules dispersal from satellite images and *in situ* measurements

Osland *et al.* (2017b) used the mean annual sea surface temperature data from UNEP-WCMC (2015), for the period between 2009 and 2013, with a spatial resolution of 5 arc minute (~10 km). Quisthoudt *et al.* (2012) used the SST database V2 from NOAA (National Oceanographic and Atmospheric Administration) with 1° degree of spatial resolution (~110 km) for a period between 1971 and 2000 (Reynolds *et al.* 2005). Both studies explaining mangrove range limits consider annual and mean temperature of the coldest month as a surrogate for extreme conditions of SST. However, observations revealed that some days exposure to low SST are sufficient to reduce seedling growth and success rate of propagule establishment (Steinke & Naidoo 1991).

In this sense, to the best of our knowledge, temporal data for *daily* sea surface temperature (SST) have never been applied to elucidate the mangrove latitudinal limits. For this reason, we analysed the Multi-scale Ultra-high Resolution (MUR) SST data which provides daily estimates with a spatial resolution of ~1 km for the period of June/2002 to Sept/2018 (Chin *et al.* 2017), which we believe gave us strongly refined **daily** temporal and spatial resolutions data applied to mangrove studies, gathering SST data of both our sites with mangroves and the site beyond the current range distribution, hence without mangroves. The advantage in analyzing daily SST data is the possibility to obtain the number of occurrences of certain chilling events throughout the years. Moreover, the temporal analysis allowed us to identify the absolute minimum daily SST, SST seasonality, annual and monthly means.

The higher frequency of such chilling events may constrain mangrove expansion, at least for *R. mangle* and *A. schaueriana*. Although, *L. racemosa* propagules are more physiologically tolerant to SST ≤15°C (Oliveira 2005), they have shorter viability while floating when compared to the two other species (Rabinowitz 1978), which makes long time dispersal difficult. This inference seems valid for Eastern South America, however, other mangrove range limits around the world can have distinct explanations for their restricted distribution. For this reason, another explanation besides low SST is needed; for instance, unfavourable direction of sea currents (Siegle & Asp 2007) and consequent dispersal constraints (Soares *et al.* 2012; Osland *et al.* 2017b; Ximenes *et al.* 2018).

According to Chuine & Beaubien (2001) the phenology of trees is a major determinant for their species range distribution. Biological processes of survival and reproductive success must be incorporated into the model. However, no historical or retrospective data are available for the mangrove limits in Brazil of propagules production phenology

The predation of propagule by crabs is a biotic factor that could restrict mangrove distribution (see in Langston *et al.* 2017). One could assume that within a cohort the chance of escaping predation is greater than coping with unfavourable environmental conditions, which would mean that the determining power of predation and e.g. cold or drought is not similar. This PhD project was however not designed to address predation, however we recognize that experimental approaches are required to assess unfavourable biotic conditions beyond the actual range limits.

Future perspectives - Applicability of this PhD thesis

According to MacArthur (1972) a prediction is possible when some sort of repetition exists. In this sense, the repetition of spatial agreement between upwelling zones and mangrove species range limits implies a possible prediction.

This thesis states that upwelling systems are characterised by factors that are causally associated with mangrove distribution, such as cold water and aridity. Thus, the intensification or spatial dynamics of upwelling zones can likely change the mangrove species distribution. Some predictions of the intensification of upwelling zones have been made (Bakun 1990; Sydeman *et al.* 2014). For future projects, we believe that predictive scenarios of the intensification or spatial dynamics of upwelling zones must be applied to forecast changes in mangrove range limits.

This work can contribute even indirectly to the systematic conservation planning as knowledge of what causes a species range limits can allow to predict changes in the species' range limits through time, shifting by expansion and retreat. This PhD thesis was not designed to develop scenarios for the future, but rather to first prioritize identification of direct or indirect causal factors of mangrove distribution.

According to Sexton et al. (2009) the ecological niche in space is essentially expressed by the range limits of species. Taking into consideration that we described climate factors in the Brazilian mangroves, focusing on species range limits, we provided a better understanding of the ecological niche of mangrove species. For the future perspective, we need to better know the physiological thresholds for low values of SST in regard to the viability and functionality of mangrove propagules. New physiological studies in regard to SST thresholds influencing propagule viability, aligned with satellite images merged with interpolated *in situ* data of SST is crucial approaches for better understand mangrove species distribution.

More research is needed with respect to the physiology of propagules and established mangrove seedlings. Understanding their tolerance to seawater and air temperature may improve our knowledge of species distribution, and hence better models can be developed to predict future scenarios.

Climate change in a changing world

During Earth's history, climate has been changed by many factors. However, the Intergovernmental Panel on Climate Change (IPCC 2014) reported an excessive emission of CO_2 since industrialization. These CO_2 emissions increase the greenhouse effect that causes global warming (IPCC 2014). Nowadays, it is known that global warming directly affects biodiversity due to changes in species distribution, shifting their limits and range (Thomas 2010). For this reason, mangrove specialists are debating about the mechanisms that influence mangrove distribution.

Moreover, specific models for mangrove ecosystems have predicted changes in their distribution in case of sea-level rise (Lovelock *et al.* 2015). According to the Fifth Assessment Report from the IPCC (2014), global mean sea level rose by *circa* 19 cm (17 to 21 cm) during the last century.

This PhD thesis was designed mainly to understand which variables are influencing mangrove distribution based on current climate conditions and, for this reason, scenarios of climate change were not incorporated. However, this PhD project is useful for future studies, since it gives emphasis to important variables that should be addressed when predicting changes on mangrove distribution. It is important to identify upwelling as a constraint factor to mangrove expansion since increasing trends of such events have been observed, mainly in the Eastern Boundary Currents (Varela *et al.* 2015). These trends of intensification of upwelling can likely inhibit the expansion of mangrove limits. In this sense, I urge that new approaches for future scenarios of mangrove distribution also include the changes in strength of upwelling systems into the models, including its combination with sea-level rise predictions.

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Ximenes, A.C. (2015) Global mangrove mapping: a critical tool for conservation. *GLP news*, **12**, 65–69.

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Ximenes, A.C., Amaral, S. & Valeriano, D.M. (2012) *Os impactos dos cenários gerais de mudanças climáticas sobre as ecorregiões da Amazônia Legal*, INPE, São José dos Campos.

Ximenes, A.C., Maeda, E.E., Arcoverde, G.F.B. & Dahdouh-Guebas, F. (2016) Spatial Assessment of the Bioclimatic and Environmental Factors Driving Mangrove Tree Species' Distribution along the Brazilian Coastline. *Remote Sensing*, **8**, 451.

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Education

PhD **Université Libre de Bruxelles (ULB),** Science, 2018
Joint **PhD Vrije universiteit Brussel** (VUB)
Thesis title: Mangrove species range limits and species diversity: A Macroecological approach from regional to global scales.
Advisors: Dr. Farid Dahdouh-Guebas and Dr. Nico Koedam

MSc **National Institute for Space Research, INPE**, Remote Sensing,*05/06/2008*
Dissertation: Self-Organizing Map for boundary ecoregions Madeira-Purus interfluvium in Amazon forest: an approach of ecological biogeography.
Advisors: Dr. Silvana Amaral and Dr. Antonio Miguel Vieira Monteiro

Pontifical Catholic University of Rio de Janeiro, PUC
Environment and Analysis Assessment, *30/11/2005*
Dissertation: Structure of mangrove plant formation at the Itaipu Lagoon.
Advisor: Dr. Rogério Oliveira

BS **University Santa Úrsula, USU**, Biological Science, *09/01/02004*
Bachelor's degree
Dissertation: Modelling mangrove restoration using GIS and geoprocessing.
Advisor: Dr. Philip Conrad Scott

Honors and Awards

2016 – I was awarded in 500 euros as a financial support from the University Foundation of Belgium (Universitaire Stichting van België/Fondation Universitaire de la Belgique US-FU) to publish an open access article in the Remote sensing journal.

2011 – I received the ArcGIS 10 ArcInfo with main extensions, such as: Spatial Analyst, 3D Analyst, Geostatistical Analyst, Tracking Analyst, Data Interoperability as a grant for a Conservation Project from ESRI.

2009 - Awarded ArcView licenses for presenting a work in the SCGIS Brazil meeting.

Teaching Experience

Masters Students Advised (tutor)

1. **Caroline Laroye**. Distribution of threatened mangrove tree species analysed using the Mangrove Reference Database and Herbarium and geographical information systems. 2013. Dissertation (Biologie) - Université Libre de Bruxelles

2. **Della Kemalasari**. Spatial analysis of fragmentation on mangroves across multiple scales: study case in the Unites States, Kenya, Sri Lanka and South Africa. 2013. Dissertation (Biology) - Vrije Universiteit Brussel.

Undergraduate student (Advised)

Gabriel M. Matos. Descriptive statistics for mangroves worldwide. 2014. - Vrije Universiteit Brussel

Maria Flávia Xavier – Building a database for mangrove plants, 2014. Vrije Universiteit Brussel

Teaching

Visiting Professor at Universidade Santa Úrsula, 2010
Credit Hours: 32 / undergraduate
Subject: Principles of Natural Resources

Visiting Professor at Universidade Santa Úrsula, 2010
Credit Hours: 32 / undergraduate
Subject: Nature Conservation

Monitor

2007 – 2008 - Monitor of the course Spatial Dynamic Modelling at INPE, supervised by Prof. Dr. Claudia Almeida.

Work Experience

1. **Université Libre de Bruxelles - ULB**

Laboratory of Systems Ecology and Resource Management

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08/2011 - 2018 PhD student

2014 – 2016 - PhD student with scholarship from the National Council for Scientific and Technological Development (CNPq).

08/2011 - 2014 - PhD student with scholarship from the Le Fonds de la Recherche Scientifique (FNRS).

2011 – 2013 – Project - **Coastal Research Network on Environmental Changes** - To understand the complex linkages between selected wetland functions, ecosystem services, and indirect effects of climate change at organismal, population and community levels. To develop and test scientifically sound methodologies for assessing long term changes of coastal ecosystems in order to provide effective tools for their rehabilitation and management. To identify existing and potential conflicts affecting the human society, and emerging from the environmental changes.
Dr. Farid Dahdouh-Guebas – Coordinator

2. **Vrije Universiteit Brussel - VUB**

Laboratory of Plant Biology and Nature Management

2011 - 2018 Joint PhD student

3. National Institute for Space Research - INPE

Image Processing Division – DPI

2010 - 2011	Research Fellow from the Foundation for Applied Sciences and Space Technology, FUNCATE.
2008 - 2010	Research Fellow from the National Council for Scientific and Technological Development - CNPq – Level 7D.
2006 - 2008	Master Student

2006 - 2011 - GEOMA Project - Aims to analyse and model the spatial patterns of biodiversity in the Amazon, to support the choice of priority areas for conservation and also for the implementation of public policies of sustainable use of biological resources in various tiers. Site: www.geoma.lncc.br
Dr. David Oren - Coordinator

2010 - 2011 - Biomes Project (Impacts of climate change in the Brazilian Biomes). Description: Nationwide study of the consequences of climate change and biodiversity in the Brazilian biomes, based on future climate scenarios from global climate models of medium spatial resolution and regional models of high spatial resolution for South America. Dr. Carlos A. Nobre - Coordinator

2009 - 2010 - PIME Project - The Integrated Project MCT - Embrapa (PIME) was designed to evaluate the sustainability of social, economic and environmental aspects of the Forest District of the road BR-163 (DFS BR-163), established by Presidential Decree of 13 February 2006. One of his goals is to promote the integration of the skills developed within the major research projects focused on the MCT is the Amazon (LBA GEOMA, PPBio) and Embrapa, focused on the development of regional technologies. Dr. Ana Luisa Kerti Mangabeira Albernaz – Coordinator

4. University Santa Úrsula – USU

Laboratory of Geographic Information Systems

2010	**Visiting Professor**, Credit Hours: 32 / undergraduate Subject: Principles of Natural Resources
2010	**Visiting Professor**, Credit Hours: 32 / undergraduate Subject: Nature Conservation
2000 - 2001	Trainee, workload 30 hours

2000 - 2001 Restoration ecology of mangrove and GIS - The internship consisted of data collection during field trips and abiotic modelling of mangrove restoration at the lagoon of Itaipu - RJ, using geoprocessing techniques. In 2001 the project was granted by the NGO Institute Itaipu, where maps were drawn to delimit the areas of permanent preservation of the study area, according to the environmental laws of the Forest Code. Site: http://www.laquasig.bio.br/

5. **Associação Mico-Leão-Dourado - Golden Lion Tamarin Association**

Conservation Project for Private Areas

2005 - 2006 Researcher assistant, workload: 40 hours, excusive dedication for 4 months.

Forest corridors - Aiming to restore the connectivity of the landscape, AMLD has been working with landowners seeking forest corridors' implementation, which are forest strips that connect two or more remaining's of Atlantic Forest. Site: www.micoleao.org.br

6. **National Institute of Amazonian Research – INPA**

Ecology Department

2001 Trainee, workload: 30 hours, exclusive dedication for 2 months.

Ecology of Palms - The understanding of how palms respond to variation in the forest structural components may help to explain their abundance and richness in a given area of Ducke Reserve. In this study, we describe a palm community and analyse how the palms are affected by forest micro-environmental heterogeneity.

7. **State University of Rio de Janeiro – UERJ**

Laboratory of Radioecology and Climate Change - LARAMG

2002 - 2003 Trainee, workload 30 hours.

MATLAN Project – Data collection and research were made to estimate forest biomass and carbon sequestration in the region of Nova Friburgo - RJ. The work also consisted of classifications of satellite images of Niterói - RJ, evaluating the different types of land use. Site: http://www.meioambiente.uerj.br/destaque/proj_matlan.htm

Publications

Journal Publications

1. **Ximenes**, A. C., Ponsoni, L., Lira, C., Koedam, N., Dahdouh-Guebas, F. (2018). Does Sea Surface Temperature contribute to determining range limits and expansion of mangroves in Eastern South America (Brazil)? **Remote Sensing**, 10, 1787; (Impact factor 3.40) DOI: 10.3390/rs10111787

2. Bispo, P.C., Balzter H., Malhi, Y., Santos, J.R., Valeriano, V.M., Renno, C.D., Slik, F., Aragão, L., Espirito Santo, F.D., **Ximenes**, A.C., Bispo, P.C. (2017). Drivers of metacommunity structure diverge for common and rare Amazonian tree species. **PlosOne**. 12(11): e0188300. (Impact factor 3.54). DOI: https://doi.org/10.1371/journal. pone.0188300

3. **Ximenes**, A.C., Maeda, E.E., Arcoverde, G.F.B. & Dahdouh-Guebas, F. (2016). Spatial Assessment of the Bioclimatic and Environmental Factors Driving Mangrove Tree Species' Distribution along the Brazilian Coastline. **Remote Sensing**, 8, (6) 451. (Impact factor 3.18) DOI:10.3390/rs8060451

4. **Ximenes**, A.C., Gondim, F.R., Scott, P.C. & Dahdouh-guebas, F. (2016). Spatial analysis framework for mangrove forest restoration: A theoretical case for Itaipu Lagoon, Brazil. **Caminhos de Geografia**, 17, 32–50. DOI: http://dx.doi.org/10.14393/RCG175903

5. **Ximenes**, A.C. (2015). Global mangrove mapping: a critical tool for conservation. **GLP news**, 12, 65–69.

6. Maeda, E. E.; Almeida, C. M.; **Ximenes**, A. C.; Formaggio, A. R.; Shimabukuro, Y. E.; Pellikka, P. Dynamic modelling of forest conversion: simulation of past and future scenarios of rural activities expansion in the fringes of the Xingu National Park, Brazilian Amazon. **International Journal of Applied Earth Observation and Geoinformation**, v. 13, p. 435–446, 2011. (Impact factor 3.93)
Accessed: (doi:10.1016/j.jag.2010.09.008)

7. Arcoverde, G. F. B.; Almeida, C.; **Ximenes**, A. C.; Maeda, E. E.; Araújo, L. S. Identifying priority areas for forest restoration using neural network Self-Organizing Maps. **Boletim de Ciências Geodésicas**, v. 17, p. 379-400, 2011. (in portuguese).

8. **Ximenes**, A. C.; Amaral, S. Prediction of structural tropical forest parameters with Fourier Transform techniques and manual delineation crown application in high-resolution imagery. **Caminhos da Geografia**. v. 11, p. 202-207, 2010. Accessed: <http://www.caminhosdegeografia.ig.ufu.br/viewarticle.php?id=1010>
(in portuguese).

9. **Ximenes**, A. C.; Amaral, S. Valeriano, D. M. Ecoregions - concepts and mapping methods. **Geografia**. v. 35, p. 219-227, 2010. (in portuguese).

10. Fook, K. D.; Amaral, S.; Monteiro, A. M. V.; Câmara, G.; **Ximenes**, A. C.; Arasato, L. S. Making species distribution models available on the web for reuse in biodiversity experiments: Euterpe edulis case study. **Revista Sociedade & Natureza**, v. 21, n. 1, p. 39-49, 2009.
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11. **Ximenes**, A. C.; Almeida, C.; Amaral, S.; Aguiar, A. P. D.; Escada, M.I.S. Dynamic deforestation modelling in the Amazon. 2008. **Boletim de Ciências Geodésicas**, v. 14, n. 3, p.370-391, 2008. (in portuguese).
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12. Cintra, R.; **Ximenes**, A. C.; Gondim, F.; Kropft, M. S. Spatial heterogeneity of forest and palm richness, abundance and community composition in Terra Firme forest, Central Amazon. **Brazilian Journal of Botany**, v. 28, p.75-84, 2005. Accessed: <http://www.scielo.br/pdf/rbb/v28n1/26256.pdf>

Paper submission in 2018

Ximenes, A. C., Maeda. E. E., Ponsoni, L., Koedam, N., Dahdouh-Guebas. F. Large influence of upwelling intensity on mangrove distribution and patterns of species richness. In preparation for submission.

Chapter of Book

Ximenes, A. C.; Almeida, C.; Amaral, S.; Escada, M.I.S., Aguiar, A. P. D. Spatial Dynamic modelling of deforestation in the Amazon. In: **Cellular Automata**: Simplicity behind complexity. Ed. Alejandro Salcido. ISBN: 978-953-307-230-2, INTECH, 2011. p. 47-66. http://www.intechopen.com/articles/show/title/spatial-dynamic-modelling-of-deforestation-in-the-amazon

Technical research

Ximenes, A. C.; Amaral, S.; Valeriano, D. M. Os impactos dos cenários gerais de mudanças climáticas sobre as Ecorregiões da Amazônia Legal Brasileira. São José dos Campos, SP: INPE, 2012. (Scientific research report). http://mtc-m19.sid.inpe.br/col/sid.inpe.br/mtc-m19/2012/09.14.14.48/doc/publicacao.pdf

Valeriano, D. M.; Amaral, S.; **Ximenes**, A. C.; Sousa, A.F. Application of ALOS/PALSAR in support to Brazilian Forest Monitoring Program. Tokyo: JAXA EORC NDX-1000003 (2010). http://www.eorc.jaxa.jp/ALOS/en/kyoto/phase_1/KC-Phase1-report_INPE_Valeriano.pdf

Conference Papers

1. Arcoverde, G., Maeda, E., Ximenes, A.C., Souza, B. Avaliação da influência do fenômeno El Niño realizada por índice de aridez em áreas suscetíveis à desertificação. XVII Brazilian Remote Sensing Symposium, Apr 25-28, 2015. Accessed: http://www.dsr.inpe.br/sbsr2015/files/p1655.pdf

2. Amaral, S.; Costa, C. B.; Arasato, L. S.; Ximenes, A.C.; Renno, C. D. AMBDATA: Variáveis ambientais para Modelos de Distribuição de Espécies (MDEs) In: XVI Simpósio Brasileiro de Sensoriamento Remoto, 2013, Foz do Iguaçu. **XVI Brazilian Remote Sensing Symposium**: INPE, 2013. p.6930 – 6937.
Accessed: http://www.dsr.inpe.br/sbsr2013/files/p0944.pdf

3. **Ximenes**, A. C. & Amaral, S. Mapping of ecoregions of Sustainable Forest District of the BR-163 in the Brazilian Amazon using Neural Networks. In: **XV Brazilian Remote Sensing Symposium**. Curitiba, Brasil, INPE, 2011, p.3094-3102. (in portuguese). Accessed: <http://www.dsr.inpe.br/sbsr2011/files/p0430.pdf>

4. **Ximenes**, A. C.; Amaral, S.; Arcoverde, G. F. B.; Monteiro, A. M. V. Neural networks for selection of environmental variables in the species distribution modelling in northern Brazil. In: **XIV Brazilian Remote Sensing Symposium**. Natal, INPE, 2009, p. 5531-5538. (in portuguese).
Accessed: <http://urlib.net/dpi.inpe.br/sbsr@80/2008/11.17.20.33>.

5. Amaral, S.; Valeriano, D. M.; Sánchez, G. A.; **Ximenes**, A. C.; Souza, A. F. ALOS/PALSAR Images & carbon at the Brazilian Amazonia Forest monitoring program using satellite. In: **XIV Brazilian Remote Sensing Symposium**. Natal, INPE, 2009, p. 5065-5072. (in portuguese).

Accessed: <http://urlib.net/dpi.inpe.br/sbsr@80/2008/11.16.22.26>.

6. Arasato, L. S.; Amaral, S.; **Ximenes**, A. C. Drainage density and HAND (Height Above the Nearest Drainage) by SRTM for species distribution modelling of palm trees in Brazil. In: **XIV Brazilian Remote Sensing Symposium**. Natal, INPE, 2009, p. 5089-5097. (in portuguese).
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7. Miceli, M. F. L.; Scott, P. C.; **Ximenes**, A. C. Selection of Marine Protected Areas for potential fisheries management: a case study from south-eastern and southern Brazil. In: **XIV Brazilian Remote Sensing Symposium**. Natal, INPE, 2009, p. 4085-4092. (in portuguese).
Accessed: <http://urlib.net/dpi.inpe.br/sbsr@80/2008/11.17.19.01.42>.

8. **Ximenes**, A. C.; Ribeiro, J. R.; Amaral, S. Self-Organizing Maps and geophysical parameters to characterize the landscape. In: **XIII Brazilian Remote Sensing Symposium**. Florianópolis, INPE, 2007, p. 3219-3226. (in portuguese). Accessed: <http://urlib.net/dpi.inpe.br/sbsr@80/2006/11.16.02.04.59>.

9. **Ximenes**, A. C.; Almeida, C.; Amaral, S.; Aguiar, A. P. D. Dynamic deforestation modelling in the Amazon: study of case in city of São Felix do Xingu - Pará. In: **XIII Brazilian Physical Geography and Applied Symposium**. Natal, UFRN, 2007. (in portuguese).

11. **Ximenes**, A. C.; Scott, P. C. Selecting suitable sites for red mangrove restoration. In: **XIII Brazilian Remote Sensing Symposium**. Florianópolis, INPE, 2007, p. 4331-4338. Accessed: <http://urlib.net/dpi.inpe.br/sbsr@80/2006/11.16.01.51.48>.

12. Mantelli, L. R.; **Ximenes**, A. C.; Amaral, S.; Fonseca, L. Analysis of algorithms for digital image classification of TM / Landsat data using aerial videography to identify land cover in a region of the Madeira-Purus rives. In: **XIII Brazilian Remote Sensing Symposium**. Florianópolis, INPE, 2007, p. 5927-5934. (in portuguese). Accessed: <http://urlib.net/dpi.inpe.br/sbsr@80/2006/11.18.00.58>.

Summary published in proceedings of conferences

1. **Ximenes, A.C.**, Maeda, E.E., Arcoverde, G.F.B. & Dahdouh-Guebas, F. (2016). Spatial Assessment of the Bioclimatic and Environmental Factors Driving Mangrove Tree Species' Distribution along the Brazilian. **MMM4 Meeting on Mangrove ecology, functioning and Management** (Florida, USA).

2. **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Spatial analysis of threats on mangrove worldwide. **7th Annual Meeting of the Specialist Group on Macroecology of the Gesellschaft fur Okologie**, Göttingen: 13-15/03/2013.

3. Kemalasari, D.; **Ximenes**, A. C.; Dahdouh-Guebas, F.; Koedam, N. Global Vulnerability Assessment of Mangrove Forest Fragmentation. **7th Annual Meeting of the Specialist Group on Macroecology of the Gesellschaft fur Okologie**, Göttingen: 13-15/03/2013.

4. **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Spatial analysis of the socio-economic factors affecting mangrove forests worldwide. **13th VLIZ Young Marine Scientists Day**. Bruges.15 Feb 2013.

5. Laroye, C.; **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Distribution of threatened mangrove tree species analyzed using the Mangrove Reference Database and Herbarium and geographical information systems. **13th VLIZ Young Marine Scientists Day**, Bruges.15 Feb 2013.

6. **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Self-Organizing Maps to determine global distribution patterns of mangrove plant species and analysis of threats using socio-economic indicators. **Meeting on Mangrove ecology, functioning and Management** (MMM3), Sri Lanka. 2012.

7. **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Fundamental niche of the trees in mangrove forests. In: 12th VLIZ Young Marine Scientists Day, 2012, Bruges. **Young Marine Scientists Day**. Bruges: VLIZ. 2012.

8. **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Species distribution modelling of the trees on mangrove forest. In: Young Botanist Day, 2012, Leuven. **Young Botanist Day**. Leuven. 2012.

9. **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Global analysis of threatened mangrove tree species. **1st Annual Meeting on Plant Ecology and Evolution** (AMPEE). Brussels. 2012.

10. Koedam, N.; Mukherjee, N.; **Ximenes**, A. C.; Satyanarayana, B.; Kairo, J. G.; Bosire, J. O.; Mohamed, M. O. S.; Quisthoudt, K.; Van der Stocken, T.; De Ryck, D.; Dahdouh-Guebas, F. Mangroves as an ecosystem-similarities and differences in a wide comparison. **50th ECSA Conference: Today's science for tomorrow's Management**. Venice, Austria, 2012. Presented orally by Koedam, N.11. Laroye, C.; **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. GIS analysis of climate impacts on threatened mangrove trees. **1st Annual Meeting on Plant Ecology and Evolution** (AMPEE). Brussels. 2012.

12. Kemalasari, D.; **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Does shape matters? A global vulnerability assessment of fragmented mangrove forests against climate changes. **1st Annual Meeting on Plant Ecology and Evolution** (AMPEE). Brussels. 2012.

13. **Ximenes**, A. C.; Maurenza, D.; Amaral, S. Heterogeneidade da composição florística arbórea numa região do interflúvio Madeira-Purus In: **International Scientific Conference Amazon in Perspective, 2008, Manaus. Integrated Science for a Sustainable Future**.2008.

14. **Ximenes**, A. C.; Amaral, S.; Monteiro, A. M. V. Redes neurais para a identificação de ecorregiões no interflúvio Madeira-Purus: uma abordagem da biogeografia ecológica In: **International Scientific Conference Amazon in Perspective, 2008, Manaus. Integrated Science for a Sustainable Future**. 2008.

15. Amaral, S.; Costa, C. B.; Iwashita, F.; **Ximenes**, A. C.; Valeriano, D. M. Estudos de Modelagem de Distribuição de Espécies no Componente Biodiversidade na Rede GEOMA In: **I Simpósio da Rede GEOMA**, 2007, Petrópolis. I Simpósio da Rede GEOMA. 2007.

16. **Ximenes**, A. C. Avaliação rápida do uso do solo na região noroeste fluminense utilizando Sensoriamento Remoto e Geoprocessamento In: IV Semana de Biologia e Meio Ambiente, 2004, Rio de Janeiro. **IV Semana de Biologia e Meio Ambiente**. 2004.

17. Cintra, R.; **Ximenes**, A. C.; Gondim, F.; Kropft, M. S. Forest spatial heterogeneity and palm richness, abundance and community composition in Terra Firme forest, Central Amazon In: **Simpósio Internacional Projetos Ecológicos de Longa Duração**, 2004, Manaus. Simpósio Internacional Projetos Ecológicos de Longa Duração. 2004.

18. Cintra, R.; Ximenes, A. C.; Gondim, F.; Kropft, M. S. Some Forest strutural components affecting the richness, abundance and comunity composition of palms in the Amazon Forest. In: **55 congresso Nacional de Botânica**, 2003, Belém - PA.

Presentations and Invited Lectured

1. **Ximenes**, A.C., Maeda, E.E., Arcoverde, G.F.B. & Dahdouh-Guebas, F. Spatial Assessment of the Bioclimatic and Environmental Factors Driving Mangrove Tree Species' Distribution along the Brazilian Coastline. In: Universidade Federal do Rio de Janeiro – UFRJ. (2017). Presented orally by Ximenes, A. C.

2. **Ximenes**, A. C.; Dahdouh-Guebas, F. Global spatial dependence of the bioclimatic and environmental variables on the mangrove ecosystem. **8th Annual Meeting of the Specialist Group for Macroecology of the Ecological Society of Germany, Austria, and Switzerland** (Integrating Mechanisms into Macroecology), Halle. 4th - 6th March 2014. Presented orally by Ximenes, A. C.

3. **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Global mangrove biogeographic regions based on species composition and historical events. **7th Annual Meeting of the Specialist Group on Macroecology of the Gesellschaft für Ökologie**, Göttingen: 13-15/03/2013. Presented orally by Ximenes, A. C.

4. **Ximenes**, A. C.; Koedam, N.; Dahdouh-Guebas, F. Delimitation of global mangrove biogeographic regions based on species composition using Self-Organizing Maps. **Meeting on Mangrove ecology, functioning and Management** (MMM3), Sri Lanka, 2012. Presented orally by Ximenes, A. C.

5. Amaral, S.; Valeriano, D. M.; Gildardo, A. S.; **Ximenes**, A. C.; Souza, A. F. ALOS/PALSAR Images & carbon at the Brazilian Amazonia Forest monitoring program using satellite. 2009. **XIV Brazilian Remote Sensing Symposium**. Presented orally by Ximenes, A. C.

6. **Ximenes**, A. C.; Amaral, S. Proposal for Ecoregions based on self-organizing maps in the area of influence of the PIME. 2009. **Seminars on Project Results PIME**. Presented orally by Ximenes, A. C.

7. **Ximenes**, A. C.; Amaral, S. Neural networks for the selection of climatic variables in species distribution modeling in Northern Brazil. 2008. **OpenModeller Workshop**. Presented orally by Ximenes, A. C.

Professional Training

2017 OCELET Simulation of Spatial Dynamics. (Credit Hours: 32h).
Emprapa Solos – Rio de Janeiro and CIRAD – France.

2013 Multivariate analysis for Biologists, ecologists and environmental scientists, using PRIMER. (Credit Hours: 35h).
Marine Biological Association of the United Kingdom, Plymouth - Devon, United Kingdom.

2012 How applied statistics can work against you. (Credit Hours 8h).
Vrije Universiteit Brussel, VUB, Belgium.

2012 Introduction to R: an open-source statistical toolbox (Credit Hours: 8h).
Vrije Universiteit Brussel – VUB, Belgium.

2011 Geographic Information Systems with ArcGIS Desktop 10 - Module II (Credit Hours: 24h).
State University of Rio de Janeiro – UERJ - LABGIS

2011 Spatial Analyst 2D and 3D with ArcGIS 10. (Credit Hours: 24h).
State University of Rio de Janeiro – UERJ – LABGIS

2011 Meta-heuristics and combinatorial optimization: applications in environmental problems. (Credit Hours: 6h).
National Institute for Space Research - INPE

2011 Topics in applied computational intelligence in space technologies. (Credit Hours: 6h).
National Institute for Space Research - INPE

2011 Visualization and computational analysis of time series in environmental science and space. (Credit Hours: 6h).
National Institute for Space Research - INPE

2010 Self-Organizing Maps. Neural Network (Credit Hours: 24h).
Commonwealth Scientific and Industrial Research Organisation – CSIRO and UNICAMP

2009 Geographical Database. (Credit Hours: 40h).
National Institute for Space Research - INPE

2009 Global Positioning System - GPS. (Credit Hours: 36h).
National Institute for Space Research - INPE

2008 Principles of statistical modelling. (Credit Hours: 8h).
National Institute for Space Research - INPE

2008 Species Distribution Modelling. (Credit Hours: 36h).
Wildlife Conservation Society - WCS and University of Kansas

2008 ALOS Data Analysis Training Seminar. (Credit Hours: 72h).
Remote Sensing Technology Center of Japan.

2007 MATLAB. (Credit Hours: 10h).
National Institute for Space Research - INPE

2006 Spatial and Space-Time Scan for Cluster Detection. (Credit Hours: 8h).
National Institute for Space Research - INPE

Professional Service

Peer-Reviewed Articles for:

- 2013 - International Journal of Applied Earth Observation and Geoinformation
- 2006 - 2014: Revista Ambiente e Água - An Interdisciplinary Journal of Applied Science.

Languages

English: Comprehends Very Well, Speaks Very Well, Reads Very Well, Writes well.

French: Comprehends Very Well, Speaks Well, Reads Very Well, Writes Reasonably.

Portuguese: Native Language

English courses
2013 - Academic English Speaking (Credit Hours: 60 h). C.V.O. Brussels, Belgium.
2013 – English nível 2. (Credit Hours: 60 h). C.V.O. Brussels, Belgium.
2013 Academic English – ULB – (Credit Hours: 24 h), Brussels, Belgium.
20.08.2012 – 20.01.2013 – English for Academic and research purposes – CVO, Brussels, Belgium.
2012 - English for Academic and research purposes, Doctoral Schools VUB. Brussels, Belgium.

French courses
20.01.2014 – 20.06.2014 –French course, nível 2A. Brussels, Belgium.
2013 – French course level UF2. Institut Supérieur de Formation Continue d'Etterbeek (I.S.F.C.E). Brussels, Belgium.
2012 – French course level UF1. Institut Supérieur de Formation Continue d'Etterbeek (I.S.F.C.E). Brussels, Belgium.

Computer Skills

Programming: good knowledge in R software and R studio, notions of: Matlab R2010b.
Applications: Word, Excel, PowerPoint, Visio, Access, EndNote and Mendeley.
Platforms: Windows and notions of Linux Ubuntu.
Software - Statistica 7, PRIMER, PCORD 4.
GIS software - ArcGIS 10.5 and extensions, Envi 4.5, notions of QGIS, Spring, Global Mapper v.11, GeoDA, Garmin MapSource, and TrackMaker.

Other

Fieldwork Experience

2012 - **Pampala, Chilaw and Galle mangrove, Sri Lanka**. (Duration: 4 days)
2012 - **Gazi Bay mangrove, Kenya**. (Duration: 30 days)
2007 - **Amazon Forest, Brazil** (Duration: 28 days)
Participation on expeditions for the GEOMA Project during 28 days, 40 km from Porto Velho in the Amazon Rain Forest. Granteed by: Geoma Project
2007 - Ximenes, A. C. **Scientific Documentary of GEOMA Project Expedition in Amazon Forest.**
2006 - **Air survey in Amazon forest. Porto Velho, Rio Branco and Manaus**. Participation on flights for GEOMA Project at the Madeira-Purus interfluvium in the Amazon Rain Forest. Granteed of: Geoma project and INPE. (Duration: 5 days)
http://www.dpi.inpe.br/geoma/videografia/relatorio.pdf
2003 - **Atlantic Forest, Nova Friburgo, Macaé de cima** (Duration: 10 days)
2001 - **Amazon Forest – Reserve Adolph Ducke, Manaus** (Duration: 2 months)
2001 - **Itaipu Lagoon - Mangrove in formation, Rio de Janeiro** (Duration: 10 days)