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The Effect of Climate Change and Anthropogenic Activities on Mangrove Ecosystems

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The Effect of Climate Change and Anthropogenic Activities on Mangrove Ecosystems

A dissertation submitted in partial satisfaction of the
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in Geography

by

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ABSTRACT OF THE DISSERTATION

The Effect of Climate Change and Anthropogenic Activities on Mangrove Ecosystems

by

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Doctor of Philosophy in Geography
University of California, Los Angeles, 2021
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Mangroves are critical tropical coastal ecosystems and provide essential ecological and societal services. Mangroves have been rapidly changing over the last fifty years, and geospatial technologies provide a tool to measure such changes around the world. As a response to climate change and rising temperatures, mangroves have been encroaching into salt marshes at many mangrove-salt marsh ecotones in sub-tropical areas, rapidly shifting their distributions poleward. Although mangroves have faced substantial degradation and deforestation due to human activity, we have seen a rise in anthropological efforts towards their preservation and reforestation in recent years. This dissertation examines both climatic and anthropogenic drivers of change for mangrove ecosystems, using a combination of remote sensing, climate modeling, and manipulative experiments. First, we investigate mangrove range limit dynamics on the Atlantic and Pacific coasts of North America, where the same three species of mangroves are found. Using gridded climate data, remote sensing and manipulative experiments, we compared the realized and fundamental niches of the Atlantic and Pacific mangroves, and found notably different responses to environmental conditions, resulting in contrasting range dynamics. We then focused specifically on the Pacific range limit, where further manipulative experiments on cold water temperatures and aridity highlighted the fact that mangroves' response to changes in climate is highly species- and location-specific. Therefore, aspects particular to each range population must be taken into consideration to best understand and predict mangrove response to climate change. Lastly, we focused on anthropogenic impacts on mangrove ecosystems. Using the island of Madagascar - a major biodiversity hotspot - as a case study, we conducted a remote sensing analysis of mangrove dynamics over fifty years. Results show that mangroves have faced considerable loss. However, recent awareness arising over the last twenty years has led to better conservation and preservation efforts, resulting in an increase in overall mangrove cover during this period.

The dissertation of Rémi Bardou is approved.

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2021

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Introduction

Understanding the processes that limit the geographic ranges of species is one of the central goals of ecology and biogeography. This issue has become particularly important given that climate change, habitat loss and degradation, and biological invasions are altering the range and abundance of species worldwide (Rosenzweig *et al.*, 2008). For example, temperate and tropical plants are moving poleward in response to global warming, displacing native species, altering biodiversity patterns, and impacting ecosystem structure and function (Parmesan & Yohe, 2003; Cavanaugh *et al.*, 2014). The highest 'velocity' of climate-driven change is occurring in the coastal zone (Loarie *et al.*, 2009), a region that includes more than 70% of the world's population and some of our most biologically productive ecosystems (Agardy *et al.*, 2005). Amongst the most important of these ecosystems are mangroves, which are generally limited to tropical and sub-tropical climates (Duke *et al.* 1998).

Mangrove ecosystems consist of a diverse, yet small group of tropical species, which have developed special physiological and morphological adaptations in order to grow in dynamic and highly saline inter-tidal conditions (Lugo & Snedaker, 1974; Chapman, 1976; Tomlinson, 1995). Mangroves are also considered foundation species, since they provide food and habitat for a diverse array of marine and terrestrial communities, as well as valuable services to human communities. They protect and stabilize shorelines (Ewel *et al.*, 1998), serve as nurseries for commercially important fisheries (Aburto-Oropeza *et al.*, 2008), filter sediments and nutrients from upland runoff (Robertson & Phillips, 1995), and sequester large amounts of carbon (Hogarth, 1999; Alongi, 2012). The value of the services provided by mangroves has been estimated at over US$1.6 trillion annually (Costanza *et al.*, 1998). Mangroves represent an ideal system for examining general questions about range limitation and anthropogenic impacts in plants. Mangroves are widely distributed along tropical coastlines around the world, and are typically restricted to coastal wetlands below latitudes of ~30ºN and ~40ºS, but the latitude of the poleward range limit varies a great deal from region to region (Spalding *et al.*, 2010). This widespread distribution is leading them to experience a wide range of environmental conditions (e.g., air temperature, sea surface temperature, precipitation, aridity, and salinity) (Osland *et al.*, 2017), as well as different levels of anthropogenic threat or conservation varying across countries and local policies (Fent *et al.*, 2019).

Mangroves are rapidly responding to climate change. There have already been observations of mangroves expanding poleward near their range limits (Cavanaugh *et al.*, 2014; Saintilan *et al.*, 2014), yet much uncertainty remains regarding the factors that control the poleward range limits of mangroves in different parts of the world. Conventional wisdom asserts that these distributions are constrained by the colder air and water temperatures found at higher latitudes (Duke et al. 1998). However, our real understanding of this phenomenon is surprisingly limited.

Despite the increases observed at poleward range limits, globally mangroves have been been extremely degraded as a result of human activities such as clearing for urban development, aquaculture, farming and resource extraction, as well as pollution and sedimentation (Alongi, 2002; Duke *et al.*, 2007). It is estimated that between the 1980s and early 2000s, 20% to 30% of mangroves have been lost globally (FAO, 2007; Giri *et al.*, 2011), and while mangrove deforestation is rampant throughout the tropics, overall studies have identified higher rates of deforestation among developing countries (Spalding *et al.*, 2010; Giri *et al.*, 2011). However, this widespread degradation has been happening in the context of a global scientific awakening to climate change-induced threats, and more specifically to the necessity of maintaining mangroves' ecosystem and societal services (Nicholls & Lowe, 2004; Alongi, 2008; Gilman *et al.*, 2008).

This dissertation uses a combination of methods to investigate the impacts of climatic and anthropogenic changes on mangrove ecosystems at different levels, from landscape-scale to the individual level. By integrating remotely sensed observations, climate modeling, as well as controlled physiological tolerance experiments, the goal of this dissertation is to improve our understanding and projections of how climate change and human activity will impact species' distributions. The first chapter focuses on analyzing the North American mangroves on both the Atlantic and Pacific coasts, by characterizing and comparing the fundamental versus realized thermal niches of two mangrove species found near their northern range limits on both coasts of North America. This chapter uses a combination of remote sensing, climate modeling and manipulative experiments to model range-specific distributions based on threshold survival responses to cold treatments, and to compare these predictions to current distributions and climate envelopes. The second chapter focuses specifically on the northernmost mangrove range limit of the Pacific coast of North America in arid Central Baja California, where mangroves grow under sub-optimal conditions. To test whether the interaction of cold water and aridity has significant, species-specific effects on mangroves, we designed a controlled experiment in which we tested the interactions of cold water and aridity stressors. The last chapter focuses on Madagascar, a biodiversity hotspot where mangroves have been highly endangered, and where previous studies have highlighted alarming rates of mangrove deforestation (Giri & Muhlhausen, 2008). This work consisted of a long-term remote sensing survey examining regional mangrove dynamics over a multi-decadal timeframe, and allowed for a better identification and comparison of mangrove dynamics.

Gaining a better understanding of the processes that control mangrove dynamics, whether climate-driven or due to anthropogenic activity, is a critical step towards accurately predicting how these foundation species will change in the future and respond to different stressors or facilitators.

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Chapter 1: Variability in the Fundamental Versus Realized Niches of North American Mangroves

1.1. Abstract

Climate change is leading to large-scale shifts in species' range limits. Mangroves, for example, are encroaching into saltmarshes at numerous tropical-temperate transition zones. However, mangrove expansion varies geographically, in large part because mangroves might not be fully occupying their fundamental niches across their range limits. Here, we characterize and compare the fundamental versus realized thermal niches of two mangrove species found near their northern range limits on both coasts of North America. Red and black mangrove propagules were collected near range limits on the Atlantic and Pacific coasts and experimentally exposed to simulated overnight freezes ranging from -0.5°C to -15°C, and grown in water temperatures ranging from 13°C to 25°C. We then modeled range-specific distributions based on threshold survival responses to cold treatments and compared these predictions to current distributions and climate envelopes. On the Atlantic coast, laboratory physiological thresholds closely matched realized distributions for both black and red mangroves. The Pacific black mangroves were less tolerant to freezes than the Atlantic populations, but laboratory determined thresholds essentially matched their realized distributions. In contrast, Pacific red mangroves were surprisingly freeze tolerant, and our laboratory threshold-based model predicted suitable habitat far north of their current range limit. Our cold-water tolerance experiments indicate that mangroves can tolerate chronically colder water temperatures than are currently experienced at either range limit. On its own,

cold water temperature does not seem to be a limiting factor on either coast of North America. On the Atlantic coast, range limits for both mangrove species are set by extreme cold air temperatures and are rapidly shifting in response to climate change. On the warmer but more arid Pacific coast, range limits for black mangroves only appear to be limited by cold air temperatures, but neither species seems to be undergoing climate-change related migration. This underlines the magnitude of other range-restricting factors, such as aridity and dispersal limitation. Thus, distribution models need to incorporate species and range-specific physiological data to predict the effects of climate change on population-specific range limits.

1.2. Introduction

Facets of climate change, in particular increases in temperature, are impacting numerous ecosystems worldwide (Rosenzweig et al., 2008). For example, rising temperatures have shifted the abundance and distributions of hundreds of plant species towards higher latitudes and elevations (Chen et al., 2011). Climate-related impacts to foundation species, species that provide food and habitat for entire ecological communities, are likely to be especially consequential due to the critical influence these species have on ecosystem structure and function (Ellison et al., 2005). In order to predict how species' distributions will respond to climate change, we need to understand the processes that currently control those distributions.

If a species' range is limited by climate, then climate change is likely to lead to distributional changes. In this case, a species' fundamental niche, i.e. the set of conditions under which species can survive and reproduce (Chase & Leibold, 2003; Peterson, 2006), will be similar to its realized niche, the environmental and climatic conditions of the areas that the species actually inhabits (Austin et al., 1990; Vetaas, 2002). However, species often do not fully occupy their fundamental niche due to processes such as biotic interactions (e.g., competition, predation) and dispersal limitation (Elith & Leathwick, 2009; Gaston, 2009; Schurr et al., 2012). In practice, characterizing both realized and fundamental niches is challenging. Realized niches are often described using correlative distribution models, which identify relationships between species' distributions and climatic and environmental variables (Guisan & Zimmermann, 2000; Dormann et al., 2007; Kearney et al., 2010b). However, these models typically assume that species' distributions are in equilibrium, and they can produce misleading results when species' range do not match their physiological boundaries (Austin & Smith, 1990; Sagarin et al., 2006; Jiménez-Valverde et al., 2008; Jarnevich et al., 2015). For example, the fundamental niches of species can vary among populations due to local adaptation to climatic and environmental factors at specific range edges (Soberón & Peterson, 2005; Atkins & Travis, 2010). Nevertheless, most species distribution models neglect biological mechanisms and species tolerance to environmental factors, despite the fact that these interactions can often explain unexpected responses to climate change (Austin et al., 2009; Urban et al., 2012; Martínez et al., 2015; Kotta et al., 2019). To assess these shortcomings, we need more manipulative experiments characterizing species' fundamental niches (Guisan & Thuiller, 2005; Kearney & Porter, 2009; Peterson & Soberón, 2012). Recent studies have found that integrating mechanistic and correlative models is a key step in predicting species distributions and range dynamics, especially in the complex context of a rapidly-changing climate (Kearney et al., 2010a; Kotta et al., 2019; Rodríguez et al., 2019).

Mangroves can be considered an informative system for examining questions about range limitation and local adaptation (Gabler et al., 2017; Sippo et al., 2018). Mangroves are widely distributed along tropical and sub-tropical coastlines and experience a range of environmental and climatic conditions (Saenger, 2002; Spalding et al., 2010). Restriction to coastal intertidal zones simplifies the task of identifying range limits, as latitudinal ranges for a given region generally vary relatively little across longitude. Species richness and abundance also generally decline with increasing latitude, coincident with changes in large scale climatic conditions, notably air temperature, sea temperature, and precipitation (Feher et al., 2017; Osland et al., 2017b, 2019). Mangrove ranges are increasingly impacted by climate change, specifically changes in temperature and rainfall patterns (Alongi, 2015; Lovelock et al., 2016; Osland et al., 2019). We are already observing dramatic responses in many coastal wetlands near tropical-temperate transition zones, where mangroves have rapidly been encroaching into salt marshes (Cavanaugh et al., 2013; Saintilan et al., 2014; Osland et al., 2017a). However, mangrove distributions can be restrained by a wide range of abiotic and biotic factors (e.g., competition, predation, dispersal) (Hutchings & Saenger, 1987; Duke et al., 1998; Devaney et al., 2017). There is also evidence of local adaptation in mangroves, as mangroves have developed freeze-tolerant phenotypes at some range limit populations (McMillan & Sherrod, 1986; Stuart et al., 2007; Cook-Patton et al., 2015; Lovelock et al., 2016). As a result, there is a clear need for a better mechanistic understanding of regional variability in the factors that set mangrove range limits (Cavanaugh et al., 2015; Rogers & Krauss, 2018; Osland et al., 2020).

In this study, we focus on two common species of mangroves found along the Atlantic and Pacific coasts of North America - Avicennia germinans (black mangrove), and

Rhizophora mangle (red mangrove). Interestingly, black mangroves are the northernmost mangroves on the Atlantic coast, whereas red mangroves are the northernmost mangroves on the Pacific coast. Populations of each species have been evolving separately on opposite sides of the North American continent for more than three million years since the rise of the isthmus of Panama, potentially developing different physiological traits based on local environmental conditions (Duke, 1995; Saenger, 1998).

Our goals were to examine the biogeographic factors controlling large-scale mangrove distributions in North America and to characterize inter- and intraspecific variability in tolerance to cold air and water temperatures. Are the mangrove ranges on the east and west coast controlled by the same set of environmental conditions? We hypothesize that the biogeographical range of these two mangrove populations is controlled by different factors, which may potentially explain their contrasting responses to climatic changes. We argue that physiological experiments can be combined with observational data to better understand whether climate or other factors limit range edge populations. Integrating range-specific physiological data also allows us to incorporate local adaptation into distribution models. We focused on the thermal niche in terms of air and water temperatures based on the assumption that temperature is an important driver of mangrove range limitation in many parts of the world (Duke et al., 1998; Osland et al., 2017b). We conducted controlled laboratory experiments to characterize the fundamental thermal niches of mangroves from populations near range limits on both the Atlantic and Pacific coasts of North America. We then compared each species' fundamental niche to their realized niche using data on the current distribution of mangroves.

1.3. Materials and Methods

1.3.1. Study Area

Our study area includes coastal wetlands along the Atlantic and Pacific coasts of North America from 21°N to 34°N (Fig. 1.1). Three species are found near range limits on both the east and west coasts of North America: *Avicennia germinans* (black mangrove), *Rhizophora mangle* (red mangrove), and *Laguncularia racemosa* (white mangrove). On the Atlantic coast, the current northern limit of mangroves (black mangrove) is located on the south end of Amelia Island, Florida (at 30.52°N), based on recent ground observations by I.C Feller. On the Pacific coast of Baja California (BC), Mexico, the current mangrove range limit (red mangrove) is in central BC, at Punta Abreojos (26.8°N). We focused this study on red and black mangroves as these are the two mangrove species that set the northern range limits on each coast.

Mangrove range limits on the Pacific versus Atlantic coasts experience significantly different climatic and environmental conditions (Quisthoudt *et al.*, 2012) (Figs. 1.1, S1, Table 1.1). Mangroves on the north Atlantic coast experience frequent mild freezes as well as sporadic hard freezes (occurring a couple of times per decade) where some cold snaps can reach overnight temperatures below -10°C (Rogers & Rohli, 1991; Miller & Downton, 1993; Osland *et al.*, 2013). Precipitation averages 1300 mm annually (Table 1.1). The Pacific coast is characterized by occasional mild frost (0°C to -1°C), while more pronounced freezes (up to -4°C) are more common on the Sonoran desert coast of the Gulf of California (Turnage & Hinckley, 1938; Bowers, 1981; Felger *et al.*, 2001). Due to upwelling and a prevailing cold countercurrent, the Pacific water temperatures are on average 1°C cooler than water at the Atlantic range limit (Fig. 1.1, Table 1.1). The Pacific mangrove range limit is also characterized by arid conditions, averaging only 200 mm of annual precipitation (Table 1.1). Aridity, along with the lack of freshwater input and hypersalinity, can lead to highly inhospitable conditions to vascular plants and be a major stressor to mangrove growth and development (Flores-Verdugo *et al.*, 1993; Glenn *et al.*, 2006; López-Medellín & Ezcurra, 2012; Adame *et al.*, 2020).

Coast	Latitude of range limit	Species found at the range	Minimum air temperature of coldest day	Mean sea surface temperature of coldest month	Mean annual precipitation
Pacific	26.79°N	*Rhizophora mangle*	-0.9°C	15.4°C	206 mm
Atlantic	29.95°N	*Avicennia germinans*	-11.7°C	16.4°C	1308 mm

Table 1.1. *Latitude and climatic conditions for Rhizophora mangle and Avicennia germinans established range limits on the Atlantic and Pacific coasts of North America. Distributional data: Giri et al., 2011. Temperature data (1983-2013), Livneh et al., 2015. Sea surface temperature data (2002-2010), Sbrocco and Barber, 2013.*

1.3.2. Seedling Source Populations

In the fall of 2016, mangrove propagules were collected from parent trees along the Baja California and Florida coastlines (Fig. 1.1) and immediately transported back to the laboratory at the Smithsonian Environmental Research Center, in Maryland, USA. Propagules were kept moist in plastic bags until planting approximately three weeks after collection. Propagules were placed in plastic trays with a thin layer of wet potting soil/sand until they had emerging radicles, initiated leaf-out, and thus were considered mangrove seedlings. Healthy seedlings were measured for length, matched for relative size, and planted into individual RayLeach Cone-tainers (2.5 cm diameter, 12.1 cm length; 49 ml volume) filled with a 2:1 mixture of potting soil and sand. Cone-tainers were placed into large plastic tubs (38 cm wide, 43 cm long, 23 cm high), each holding 100 tubes and filled with a solution of de-ionized water and Instant Ocean at 35 Practical Salinity Units (PSU). In total, we planted 1,200 black and red mangroves from both the Atlantic and Pacific coasts (N=300 per species per coast). Each tub was placed in a walk-in Environmental Growth Chamber with controlled temperature (12am-6am: 16°C, 6am-12pm: 21.5°C, 12pm-6pm: 27°C, 6pm-12am: 21.5°C). Humidity was kept constant at 65%. Temperature and humidity were monitored and logged using "HOBO" Loggers (model # UX100-011A, Onset Computer Co. Bourne, MA, USA). Water salinity was checked weekly with an Accumet AP85 probe, with deionized water or Instant Ocean used to bring salinities back to 35PSU.

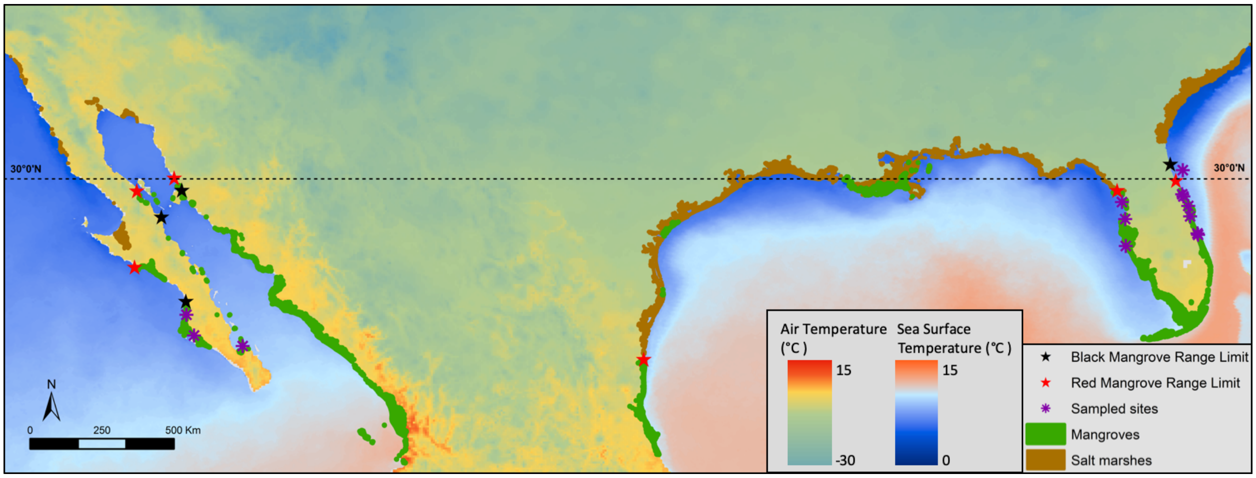


Figure 1.1. *Geographic distribution of mangroves (Giri et al., 2011) and salt marshes (Mcowen et al., 2017) across North America under CURRENT climatic conditions, including absolute minimum temperature from 1983-2013 (Livneh et al., 2015), and average sea surface temperature of the coldest month from 2002 to 2010 (Sbrocco and Barber, 2013).*

1.3.3. Air Temperature Experiments

We conducted an overnight experiment to test mangrove tolerance to freezing air temperatures. We imposed freeze treatments to one year-old seedlings over a range of air temperatures: -0.5°C, -2°C, -4°C, -5°C, -6°C, -7°C, -8°C, -9°C, -10°C, -12°C, and -15°C. We randomly distributed ~30 black and red mangrove individuals from both Florida and BC into 11 trays, each with 100 Cone-tainer capacity. Freeze treatments were then imposed to all ~60 seedlings in a single tray over a 24-hour period in a freeze-thaw chamber (Caron 7901-33) with three separate temperature phases: 1) a 12-hour ramp starting from 21°C and declining to the target temperature, 2) a 4-hour period at the target temperature, and 3) an 8-hour ramp back to 21°C. HOBO temperature loggers recorded temperature at 5-minute intervals in the water, a Cone-tainer holding only soil, and air temperature at leaf level in the middle of the tray.

Freeze damage was apparent as brown or black scorching on the leaves and/or the tip of the seedling and generally evident within 48-72 hours following the freeze. Heavily damaged seedlings typically died within two to three weeks following the freeze. Surveys were conducted one and three months after the freeze, with any seedlings that recovered in this interval counted as alive for the entirety of the survey.

1.3.4. Water Temperature Experiments

A second experiment assessed mangrove tolerance to cold water temperatures. Ten three-months old seedlings from each species were randomly assigned to one of ten coolers, held at room temperature for one week, after which water temperatures in each cooler were progressively decreased or increased by 1°C increments per day to their final set points. Set points in each cooler were: 13°C, 15°C, 17°C, 21°C, and 25°C, with two replicate coolers per temperature. Replicate coolers for each temperature were placed on different sides of the growth chamber, with temperature treatments randomly dispersed.

Water temperatures in the 13°C, 15°C, and 17°C coolers were controlled by individual chillers (Chill Solutions CSXC-1). Two coolers were left at room temperature (21°C), and two were equipped with submersible aquarium heaters to elevate temperatures to 25°C. All coolers were outfitted with aquarium pumps to circulate water. Water temperatures in each cooler throughout the experiment were recorded with free-floating HOBO temperature loggers (model # UA-002-64). Air temperature and humidity in the room were monitored with a HOBO logger (model # UX100-011A). This system enabled us to achieve very consistent water temperatures. Water temperatures and salinities within coolers were checked five days/week with an Accumet AP85 probe, with set points on chillers and heaters adjusted accordingly. We used deionized water or Instant Ocean to bring salinities back to 35PSU. We then let the plants grow in the coolers for six months. At the end of every week, we recorded seedling survival, with mortality evident as withered brown stems and leaves.

1.3.5. Analysis of Air and Water Temperature Experiments

For each experiment, we used linear logistic regression to determine the 50% survival threshold in response to varying water and air temperature, with separate curves modelled for black and red mangroves from both BC and Florida. We chose a 50% threshold as it is widely used in the ecophysiology and toxicology fields to estimate population mortality rates after exposure to various abiotic stressors (Lagarto Parra *et al.*, 2001; Randhawa, 2009; Weir *et al.*, 2016). However, we also calculated thresholds determined from the 25% and 75% mortality rates (Supplemental Table S1).

All seedlings were considered individual replicates for the water temperature experiment; preliminary analyses showed no qualitative differences when responses were averaged by cooler. Seedlings were also the unit of replication for the air temperature experiment as each species/population experienced only a single freeze treatment.

1.3.6. Environmental Modeling

1.3.6.1. Determining the Realized Niche

We characterized the realized niches for mangroves on both the Atlantic and Pacific coasts by examining remotely sensed mangrove presence/absence data with gridded climate data. Presence/absence data were obtained from a global mangrove distribution dataset (Giri *et al.*, 2011). This mangrove presence/absence dataset relies on 30-m Landsat pixels, and thus can detect large stands of mangrove but not scattered individuals. This dataset does not differentiate species, therefore range limits from this dataset represent the northernmost species found on each coast (black mangroves on the Atlantic and red mangroves on the Pacific). The Giri dataset had one notable inconsistency on the Pacific coast, allocating mangroves north of their actual range in Central BC, within the Laguna Ojo de Liebre. On the Atlantic coast, this dataset incorrectly had mangrove pixels in north Galveston Bay, as well as one errant pixel in southern Texas, 30km inland from Padre Island. We manually removed these pixels from our mangrove presence data. We then identified the secondary range limits for red mangroves on the Atlantic side and for black mangroves on the Pacific side (Fig. 1.1). To maintain consistency with our mangrove presence/absence dataset, we based these range limits only on established mangrove stands (i.e. not individual trees) which were referenced in the early 2010s as current range populations (Whitmore *et al.*, 2005; Stevens *et al.*, 2006; Quisthoudt *et al.*, 2012).

Daily temperature data from 1983 to 2013 were obtained through a gridded (1/16° resolution, or about 6 km cells) hydrometeorological dataset (Livneh *et al.*, 2015).We calculated the absolute minimum temperature over the 1983-2013 time period. We obtained sea surface temperature (SST) data for 2002-2010 from the Marspec dataset (Sbrocco & Barber, 2013). We selected the sea surface temperature of the coldest month (Biogeo14 variable), which has a 30-arcseconds resolution, equivalent to about 1km. We then calculated the mean SST of the coldest month from 2002 to 2010. All data were processed into ArcMap 10.5 (Environmental Systems Research Institute, Redlands, CA). Since the geographic resolution of the temperature data was 1/16°, we statistically degraded the mangrove presence/absence and sea surface temperature data to a similar resolution. We then isolated the coastal areas by selecting cells which were within 10km from the coastline. Each 1/16° coastal cell was then assigned a binary code denoting presence or absence of mangroves based on the mangrove occurrence dataset. Our analysis extended from central Mexico to central California (Point Conception) on the Pacific, and to North Carolina on the Atlantic coast (Figs. 1.1, S3a, b).

Similar to the physiological experiments, we then conducted linear logistic regression analyses to determine threshold responses to climate variables. We used mangrove presence/absence as a dependent variable, and each of the two selected climate variables (absolute minimum air and mean minimum water temperatures) as independent variables. We used the 50% inflection point from the logistic regressions as the climate-based threshold for modeled presence/absence. This threshold represents a climatic value for which rapid changes can occur from a mangrove ecosystem (above threshold) to non-mangrove (salt marshes) below. Although this 50% can be considered as a conservative threshold, it has been used in studies of a similar scope (Osland *et al.*, 2013, 2017b, 2020; Cavanaugh *et al.*, 2015). We also calculated thresholds using the 25% and 75% probabilities (Table S1).

1.3.6.2. Fundamental Niche Model

We created a simple model to map the fundamental niche of mangroves over the landscape using the results from the laboratory survival data. Based on the assumption that physiological thresholds can be correlated with climate, laboratory data were projected to the same gridded climate datasets used for correlative modeling. We characterized coastal cells as suitable for mangroves if their absolute minimum temperature and mean SST of the coldest month were above the 50% temperature thresholds identified by the laboratory experiments. For this model we isolated potential estuarine habitats by combining our mangrove distribution dataset with a global saltmarsh dataset (Mcowen *et al.*, 2017). This worldwide saltmarsh dataset is a reference in coastal habitats distribution and modeling, similarly to what the Giri dataset is to mangroves. Doing so excluded areas that were considered unsuitable from lack of habitat due to coastal morphology. We assumed that low-lying coastal areas with sufficient freshwater input to support saltmarshes could also support mangroves, recognizing that this could lead to a potential overestimation of suitable mangrove habitat. Focusing our analysis on these habitats helped account for the fact that we did not include precipitation or aridity in our fundamental niche model. This analysis was performed within the ArcMap software.

1.4. Results

1.4.1. Current Mangrove Distributions

Mangrove distributions along both coasts are associated with steep gradients in air and water temperature, as well as aridity (Figs. 1.1, S1). The range limit on the Pacific coast has warmer minimum air temperatures, but colder minimum water temperatures compared to the Atlantic coast. Minimum air and sea surface temperatures were positively related on both coasts (Figs. S2a, b).

1.4.2. Air Temperature Thresholds

On the Pacific coast, the presence/absence of red and black mangroves exhibited inflection points at ~0°C, indicative of their restriction to regions on this coast that do not typically experience freezes (Fig. 1.2a). This result was mirrored in the overnight freezing experiments for black mangroves, where the 50% mortality temperature threshold was -0.92°C (Fig. 1.2b, see Table S1 for 25% and 75% threshold temperatures). In contrast, red mangroves from the Pacific exhibited a significantly colder 50% mortality temperature threshold of -6.71°C (Fig. 1.2b). On the Atlantic coast, black mangroves are found at locations with consistently colder minimum air temperatures than red mangroves (-8.81°C versus -7.3°C, respectively, Fig. 1.2c). These presence/absence data were remarkably consistent with laboratory experiments, where black mangroves were more tolerant to overnight freezing air temperatures when compared to red mangroves (-8.65°C versus -7.27°C, respectively, Fig. 1.2d).

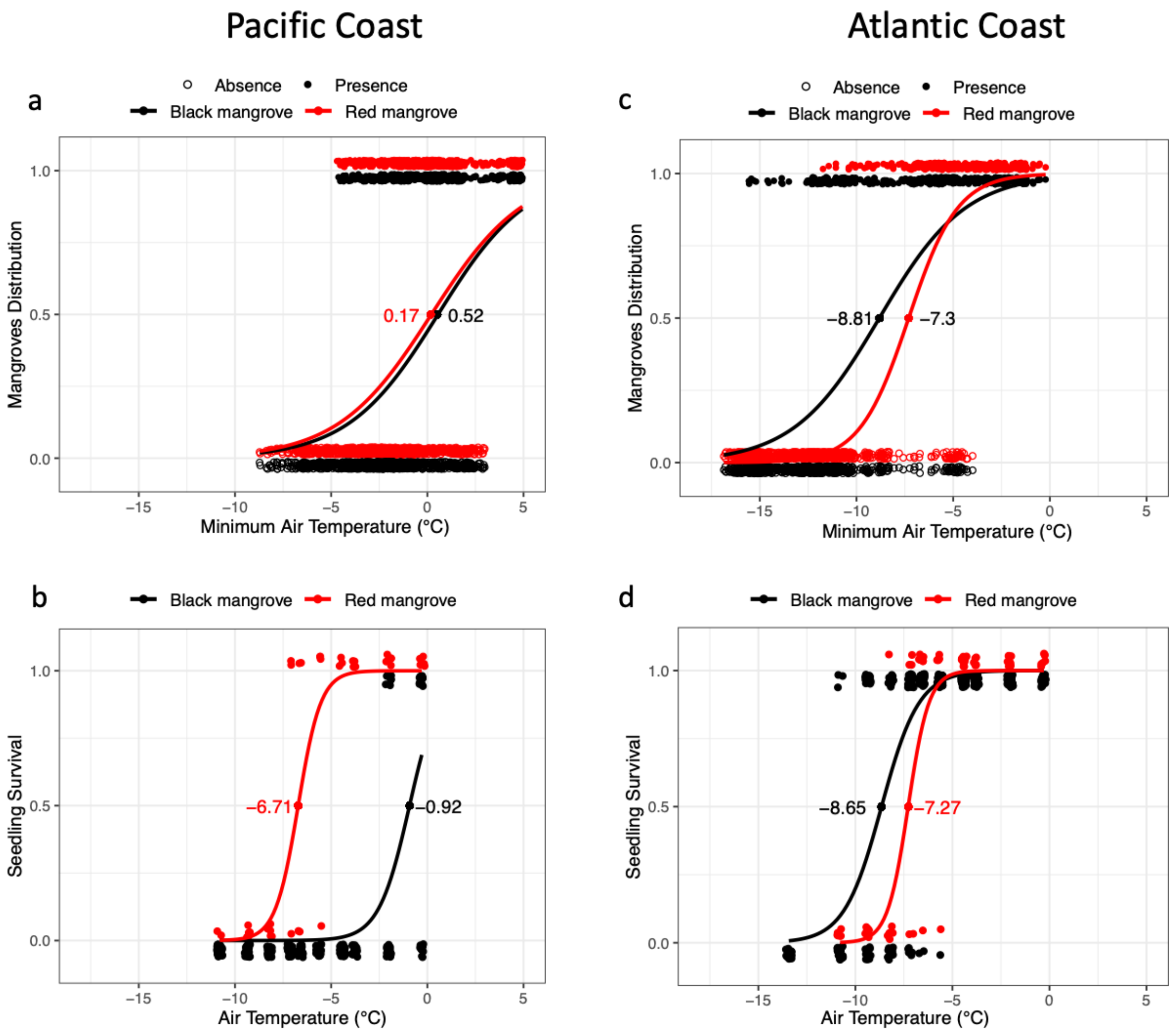


Figure 1.2.

(a) *Relationship between absolute minimum air temperature (1983 to 2013, Livneh et al., 2015) and presence/absence of mangroves in 6 km cells along the Pacific coast. Curves and midpoints are from logistic regressions (black mangroves: p<0.001*

(b) *Pacific coast seedling survival 3 months after exposure to overnight air temperatures in the laboratory. Curves and midpoints are from logistic regressions (black mangroves: p<0.001, r2=0.561; red mangroves: P<0.0001, r2=0.688).*

***(c)** Relationship between absolute minimum air temperature (1983 to 2013, Livneh et al., 2015) and presence/absence of mangroves in 6 km cells along the Atlantic coast. Curves and midpoints are from logistic regressions (black mangroves: $p<0.001$, $r2=0.395$; red mangroves: $P<0.0001$, $r2=0.688$).*

***(d)** Atlantic coast seedling survival 3 months after exposure to overnight air temperatures in the laboratory. Curves and midpoints are from logistic regressions (black mangroves: $p<0.001$, $r2=0.536$; red mangroves: $P<0.0001$, $r2=0.721$).*

1.4.3. Water Temperature Thresholds

The 50% sea surface temperature thresholds for mangrove presence/absence occurred at ~18°C on both coasts (Figs. 1.3a, 1.3c). In our experiments, however, 50% mortality temperature thresholds for red and black mangroves from the Pacific were substantially lower at 14.4°C and 14.8°C respectively (Fig. 1.3b). In contrast, Atlantic coast mangroves exhibited 50% mortality temperature thresholds that were close to their presence/absence thresholds, 17.6°C for red mangroves and 17.8°C for black mangroves (Fig. 1.3d).

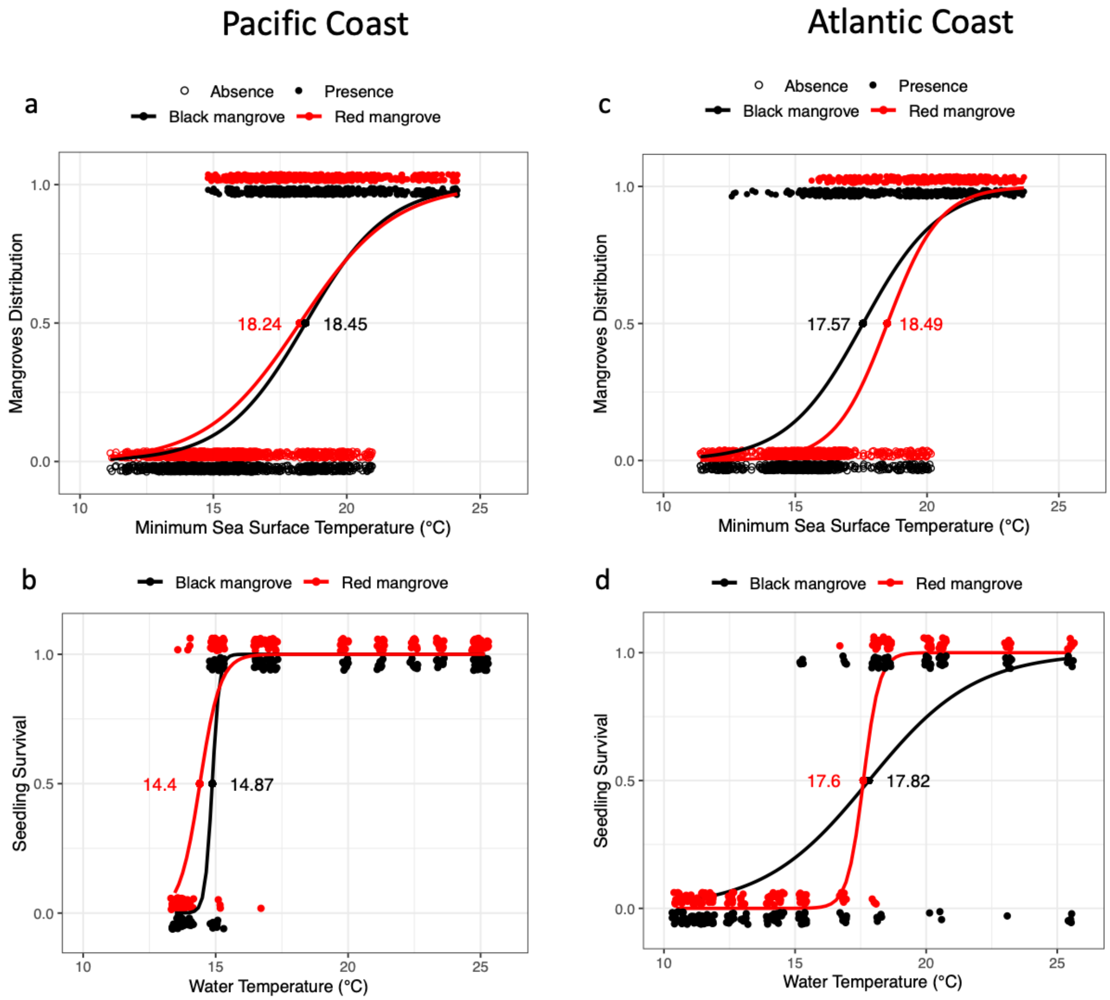


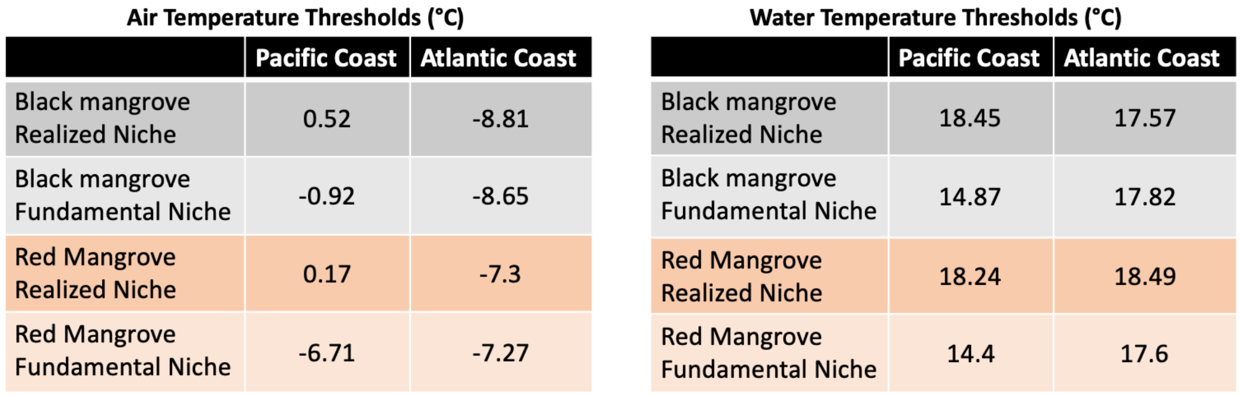
Figure 1.3.

(a) *Relationship between mean sea surface temperature of the coldest month (2002 to 2010, Sbrocco and Barber, 2013) and presence/absence of mangroves in 6 km cells along the Pacific coast. Curves and midpoints are from logistic regressions (black mangroves: p<0.001, r2=0.311; red mangroves: P<0.0001, r2=0.260).*

(b) *Pacific coast seedling survival 6 months after exposure to cold water temperatures in the laboratory. Curves and midpoints are from logistic regressions (black mangroves: p<0.001, r2=0.845; red mangroves: P<0.0001, r2=0.686).*

(c) *Relationship between mean sea surface temperature of the coldest month (2002 to 2010, Sbrocco and Barber, 2013) and presence/absence of mangroves in 6 km cells along the Atlantic coast. Curves and midpoints are from logistic regressions (black mangroves: p<0.001, r2=0.366; red mangroves: P<0.0001, r2=0.562).*

(d) *Atlantic coast seedling survival 6 months after exposure to cold water temperatures in the laboratory. Curves and midpoints are from logistic regressions (black mangroves: p<0.001, r2=0.415; red mangroves*



Air Temperature Thresholds (°C)

	Pacific Coast	Atlantic Coast
Black mangrove Realized Niche	0.52	-8.81
Black mangrove Fundamental Niche	-0.92	-8.65
Red Mangrove Realized Niche	0.17	-7.3
Red Mangrove Fundamental Niche	-6.71	-7.27

Water Temperature Thresholds (°C)

	Pacific Coast	Atlantic Coast
Black mangrove Realized Niche	18.45	17.57
Black mangrove Fundamental Niche	14.87	17.82
Red Mangrove Realized Niche	18.24	18.49
Red Mangrove Fundamental Niche	14.4	17.6

Table 1.2*. Summary of Realized and Fundamental niche thresholds for mangroves on the Pacific and Atlantic Coasts.*

1.4.4. Fundamental Niche Models

Fundamental niche models incorporating cold air and water thresholds from laboratory experiments modeled black mangroves in three primary areas where they are currently absent: 1) the salt marshes of southern California, 2) Punta Abreojos in central BC (where red and white mangroves are present), and 3) along the northern Gulf of Mexico coastline in Mexico, just south of the US border (Fig. 1.4a). In addition, the fundamental niche models failed to predict black mangroves in several areas where they are currently found, including the Sonoran coast of Mexico in the Sea of Cortez, the upper Gulf of Mexico in Louisiana, and the northernmost populations in west and eastern Florida (Fig. 1.4a).

Results for red mangroves were similar but slightly shifted northward, with models showing suitable but currently unoccupied habitats in southern California, the mouth of the Colorado River at the uppermost portion of the Sea of Cortez, the Laguna Ojo de Liebre (a salt marsh complex sheltered from the Pacific Ocean), and along the northern Mexico coastline in the Gulf of Mexico (Fig. 1.4b). The fundamental niche model for red mangrove also failed to predict mangroves at the northernmost populations in western and eastern Florida (Fig. 1.4b).

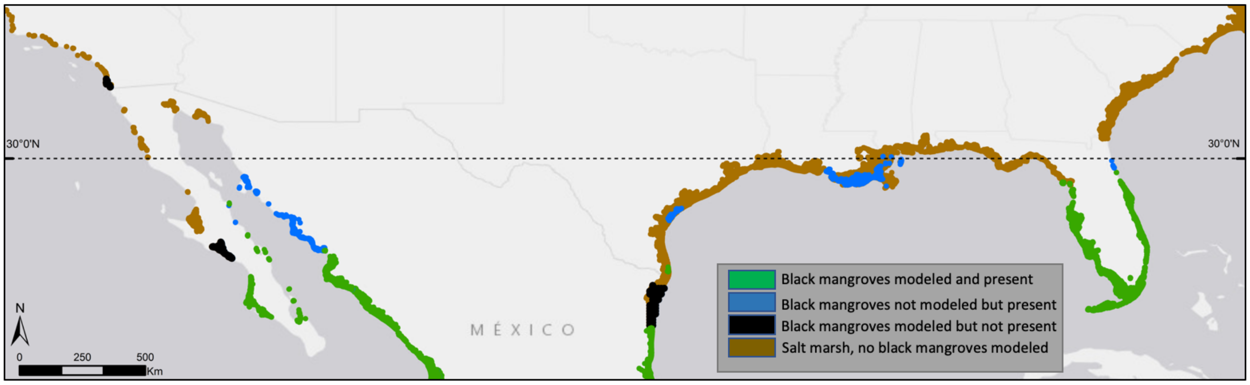


Figure 1.4. *Model of black mangrove suitability across North America based on laboratory-derived tolerance to minimum air and water temperatures.*

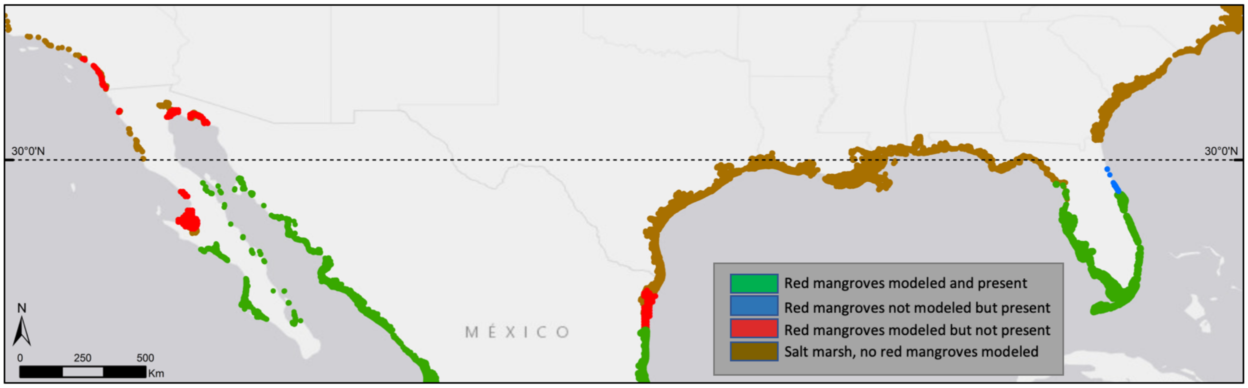


Figure 1.5. *Model of red mangrove suitability across North America based on laboratory-derived tolerance to minimum air and water temperatures.*

1.5. Discussion

Laboratory experiments demonstrated differences in the fundamental thermal niche of red and black mangrove populations at their range limits on the east and west coasts of North America. This suggests local adaptation to different climatic conditions. Consequently, physiologically-informed niche models showed discrepancies between the fundamental and realized niches for red and black mangrove populations on both coasts, signifying different sensitivities to climate change and different processes responsible for range limitation across North America.

1.5.1. Differences in the Fundamental Niches of Mangroves Between the Atlantic and Pacific Coasts of North America

We found substantial differences in freeze tolerance among populations of black mangroves on the Atlantic and Pacific coasts, and Atlantic black mangroves were more freeze tolerant by ~7°C (Figs. 1.2b, 1.2d, Table 1.2). In contrast, freeze tolerances of Pacific red mangroves were within ~1°C of the Atlantic threshold. On the other hand, both species of mangroves in Baja California showed a significantly higher tolerance (~3°C) to cold water than their Floridian counterparts (Figs. 1.3b, 1.3d, Table 1.2). This lower tolerance to cold air and water temperature may be explained by different adaptive responses of Pacific mangroves to long-term differences in climate, although more genetic work is required to test these hypotheses. There are significant genetic disparities between mangroves on the Atlantic versus Pacific coastlines, which split apart from core populations around the Central American Isthmus approximately 3 million years ago (Cerón-Souza *et al.*, 2015). Recent comparative phylogeography studies revealed an asymmetric historical migration characterized by higher gene flow from the Atlantic to the Pacific (Sandoval-Castro *et al.*, 2012). This suggests the possibility that Pacific mangroves might have retained some of the cold air tolerance traits exhibited in mangroves from the Atlantic coast.

Furthermore, although both red and black mangrove populations in BC exhibit low levels of genetic diversity (Sandoval-Castro *et al.*, 2012, 2014), shared alleles also point to closer affinity of red mangrove populations compared to black mangroves. For example, Pacific red mangroves share 50% of alleles with Atlantic coast red mangroves, while black mangroves on the Pacific coast only share 29% of alleles with Atlantic black mangroves, a difference which may have been caused by a more extensive distribution of red vs. black mangroves before the closure of the Central American Isthmus (Sandoval-Castro *et al.*, 2014; Hodel *et al.*, 2016). These differences in dispersal potential persist and are embodied in present distributional patterns, as studies have found that the northernmost populations of black mangroves on Mexico's west coast have only established recently from range expansion from southern populations (Nettel & Dodd, 2007; Triest, 2008; Sandoval-Castro *et al.*, 2014). Genetic analyses indicate that this recent black mangrove colonization occurred following the Holocene warming period 10,000 to 8,000 years Before Present (Metcalfe *et al.*, 2000; Lozano-García *et al.*, 2013), indicating that these northernmost black mangrove populations may retain more of their ancestral, tropical state relative to the longer established red mangroves (Ochoa-Zavala *et al.*, 2019). Indeed, genetic predisposition to cold air may allow Pacific coast red mangroves to occupy more northern, colder habitats compared to Pacific black mangroves.

1.5.2. Cold Water Temperature Does Not Seem to be a Limiting Factor on Either Coast of North America

The fundamental water temperature niche of both black and red mangroves (as characterized by laboratory experiments) was colder than their realized niche (based on current distribution data), and this observation is valid on either side of North America (Fig. 1.3). As a result, cold water by itself does not seem to be a key limiting factor for either species of mangroves on the Atlantic and Pacific coasts. The difference between fundamental and realized niches was relatively narrow for the Atlantic mangroves (within 1°C, Figs. 1.3c, 1.3d, Table 1.2). This gap was significantly wider for the Pacific mangroves, their fundamental niche being 4°C colder than conditions currently encountered at their northernmost range edge (Figs. 1.3a, 1.3b, Table 1.2).

1.5.3. Agreement Between Fundamental and Realized Niche on the Atlantic Coast

There was remarkable congruence between the realized and fundamental niche for both mangrove species on the Atlantic coast (Table 1.2), suggesting nearly complete range infilling of their thermal niche space. Therefore, the distribution of black and red mangroves on this coast seems to be largely climate-limited. This conclusion is supported by observations that populations near the range limit on the Atlantic coast are particularly sensitive to climate variability (Cavanaugh *et al.*, 2018, 2019; Osland *et al.*, 2020). As minimum winter temperatures rapidly rise, the number of hard and prolonged freezes are decreasing, extending the mangrove niche further north. In response to such changes, we are already seeing strong evidence of a rapid poleward migration on the Atlantic and Gulf of Mexico coasts (Cavanaugh *et al.*, 2013, 2019; Armitage *et al.*, 2015; Osland *et al.*, 2017b). On the Atlantic coast of Florida, recent field observations from Dr. Feller found black mangroves establishments up to Amelia Island, just south of the Georgia border.

This recent expansion is also reflected in our physiologically-based suitability model. The northernmost areas of the current mangrove distribution on both sides of Florida were predicted as non-suitable for red and black mangroves by our model (Fig. 1.4). Fig. 1.4a also shows areas of Texas and Louisiana where black mangroves are present, but which were not modeled as suitable. These underestimates of suitability may be artifacts of methodology. First, we used a conservative 50% mortality threshold from the laboratory experiments to define suitability. Only a few successful seedlings can establish new range populations, and a 50% population threshold is conservative relative to what is likely to happen demographically. Second, the climate data used to predict mangrove presence was averaged from 1983 to 2013. In the last two decades there have been marked declines in the frequency of extreme cold events (Cavanaugh *et al.*, 2013, 2019), which may have led to very recent (i.e., sub-decadal) changes in the climatic suitability of some northern areas. Furthermore, differences between macro- and micro-climates in northernmost mangrove populations in Florida can be ~2-3°C (Devaney *et al.*, 2017), differences that are large enough to substantially alter patterns of survival and leaf damage from freezing (Cook-Patton *et al.*, 2015; Osland *et al.*, 2015). Thus, even though a climate cell might have a minimum air temperature below our 50% physiological threshold, local conditions within an estuary or a sheltered bay could be more favorable for mangrove survival. It is also important to note that we conducted our experiments on young seedlings. This makes our models even more conservative, as we can argue that established trees would have an even higher survival rate after exposure to freezing air temperatures. Lastly, our physiologically-based suitability model was built on data averaged over multiple mangrove populations collected across the range. Pioneer mangrove individuals occupying the current northernmost range have been shown to benefit from specific physiological adaptations to chilling or salinity tolerance (Madrid *et al.*, 2014; Cook-Patton *et al.*, 2015; Lovelock *et al.*, 2016). Our experimental physiological thresholds would likely have been higher if testing only range limit populations.

Another limitation of our modeling approach lies within the fact that while we did use a broad-scale and somewhat coarse mangrove dataset, we are aware of recent mangrove populations growing outside of our mapped distributions. This is the case for the northernmost mangroves in eastern Florida (where black mangroves are found only a few miles from the Georgia border), or in the Apalachicola region in northwestern Florida, where there have been accounts of both black and red mangroves being present (based on recent field observations from Ilka Feller and Karen Cummins). It is also the case for southern Texas, where black and red mangroves are increasingly present along the Rio Grande River and up to Corpus Christi (based on field observations from Ilka Feller and Ed Proffitt). While we recognize these limitations, our approach goes along the lines of previous mangrove modeling studies which used similar data (Osland *et al.*, 2017b; Cavanaugh *et al.*, 2018), therefore benefiting from continuity. This approach makes our model somewhat conservative, however we were not seeking to predict and forecast the very last northernmost tree, but were rather focused on modeling large mangrove stands (i.e. detectable from 30m resolution satellite imagery).

On the other hand, our fundamental niche model predicted black and red mangroves to be present on the northern part of Mexico, just south of the Texas border (Figs. 1.4a, 1.4b), where no mangroves were assumed to be found (Spalding *et al.*, 2010; Giri *et al.*, 2011; Rodríguez-Zúñiga *et al.*, 2013). This portion of the Gulf of Mexico meets the thermal niche thresholds in terms of water and air temperature conditions, although it is significantly drier than the upper and lower parts of the Gulf, receiving on average only 650 mm of rain per year (Buskey *et al.*, 1998; Méndez & Magaña, 2010). Changes in mangrove abundance, diversity, and morphology are closely following a latitudinal gradient throughout the Gulf of Mexico, resulting from changes in temperature and precipitation (Lot Helgueras *et al.*, 1975; Méndez-Alonzo *et al.*, 2008; Osland *et al.*, 2014; Feher *et al.*, 2017). This is one of the drier areas of the Gulf of Mexico, and it is characterized by the presence of the Laguna Madre and delta del Rio Bravo, a large lagoonal complex extending from the mouth of the Río Soto la Marina in Mexico, to the US border at the Rio Grande (Tunnell & Judd, 2002). Hypersaline conditions in this shallow and semiarid lagoon dominated by salt flats and sand dunes are a challenge to vegetation growth, including mangroves (Hedgpeth, 1947; Lot Helgueras *et al.*, 1975; Tunnell & Judd, 2002; Yando *et al.*, 2017). This is preventing mangroves from establishing large stands potentially visible from remote sensing imagery, which is why global mangrove datasets do not account for the presence of mangroves in this lagoon (Spalding *et al.*, 2010; Giri *et al.*, 2011; Rodríguez-Zúñiga *et al.*, 2013). However, recent ground observations reported both black and red mangrove individuals scattered throughout the lagoon up to the more established mangrove stands at the mouth of the Rio Grande at the US border. This suggests that although conditions in this vast lagoon are challenging, it is still viable for mangrove development.

While some uncertainty remains, it is believed that climate change might lead to an increase of moisture and precipitation around the Gulf of Mexico (Mulholland *et al.*, 1997; Keim *et al.*, 2011; Biasutti *et al.*, 2012). In combination with a decrease in minimum winter temperatures (Keim *et al.*, 2011; Osland *et al.*, 2013), such conditions would certainly favor mangrove establishment and expansion throughout the Gulf of Mexico (Osland *et al.*, 2013, 2020; Armitage *et al.*, 2015).

1.5.4. The Pacific Coast Mangrove Distribution Does Not Meet Their Fundamental Thermal Niche

Our models indicate greater potential for range infilling along the Pacific coast compared to the Atlantic coast. The water and air temperatures at the Pacific coast range limits are higher than the experimental physiological thresholds (Table 1.2). Such divergence indicates that neither air nor water temperatures seems to be the sole factor setting the Pacific mangrove range. These disparities are reflected by our fundamental niche models, as there are substantial habitats categorized as suitable where mangroves are currently absent (Figs. 1.4a, 1.4b). This difference between fundamental and realized niches is more pronounced for red than for black mangroves.

Our fundamental niche model indicates suitable habitats for black mangroves near the range limit of red mangroves, as well as some areas in southern California (Fig. 1.4a). There was a larger difference between the experimental and observational cold air thresholds for red mangroves (-6.7°C and 0.17°C, respectively) (Figs. 1.2a, 1.2b). As a result, the fundamental niche model for red mangroves identified large areas of suitable but unoccupied habitats (Fig. 1.4b). This includes a vast lagoonal complex, the Laguna Ojo de Liebre where salt marshes are extensive, as well as other estuarine habitats in northern BC and southern California. The model also identifies suitable habitats around the Colorado River delta in the Gulf of California. It is possible that these regions are too arid to support mangroves. However, some of these areas of northern BC and southern California characterized by an absence of mangroves receive from 200 mm to 350 mm of precipitation, well within the range of precipitation encountered in areas currently occupied by mangroves (206 mm at the current range, Table 1.1). These conditions are favorable to vascular plants growth, and are enabling the presence of extensive salt marshes (Phleger & Ewing, 1962; Orme, 1973; Glenn *et al.*, 2006). As a result, we believe that a significant portion of these areas could indeed be suitable for mangroves.

On the other hand, in some areas of mainland Mexico on the Sea of Cortez, black mangroves are currently found along a stretch of coastal habitat which was not modeled as suitable (Fig. 1.4a). This is due to the fact that climate data indicates freezing minimum temperatures ranging between -1°C and -4°C, higher than our physiological survival levels, which remain fairly conservative. We also did not run physiological experiments on seedlings from these mainland Mexico mangroves, and it is possible that these populations have been established for longer periods of time than the BC populations, thereby enabling them to adapt to colder temperatures (Sandoval-Castro *et al.*, 2012; Ochoa-Zavala *et al.*, 2019).

Surprisingly, although black mangroves (*Avicennia germinans*) in particular and the genus *Avicennia* in general are widely considered to be among the most freeze- and salt-resistant mangroves (Markley *et al.*, 1982; Duke, 1990; Pickens & Hester, 2011; Hayes *et al.*, 2020;

Osland *et al.*, 2020), the Pacific coast black mangroves were freeze intolerant, in stark contrast to both black mangroves from the Atlantic coast and sympatric Pacific red mangroves (Table 1.2). The generally higher freeze- and salt-resistance of *Avicennia* have been used to explain the observation that along most other mangrove range limits around the world, *Avicennia* have a greater latitudinal extent than *Rhizophora* (Quisthoudt *et al.*, 2012; Madrid *et al.*, 2014; Cook-Patton *et al.*, 2015; Lovelock *et al.*, 2016; Otero *et al.*, 2016; Chen *et al.*, 2017; Osland *et al.*, 2017a). For example, Quishoudt *et al.* (2012) found that *Avicennia* have a higher latitudinal limit than *Rhizophora* at 18 out of the 21 range limits they examined. In fact, Baja and the islands of southern Japan are the only regions where *Rhizophora* has a more poleward distribution than *Avicennia*.

Mangrove distributions in BC and northwestern Mexico have been stable over the last 50 years, and although there are some signs of inland migration, they have not been expanding beyond their existing latitudinal range (López-Medellín *et al.*, 2011; Rodríguez-Zúñiga *et al.*, 2013; Riosmena Rodriguez *et al.*, 2014). In addition, dynamics of populations near the range limit do not appear to be sensitive to annual climate variability (Cavanaugh *et al.*, 2018). These observations support the hypothesis that this range is not strongly limited by climate. The significant mismatch between mangrove thermal tolerance and environmental conditions on the Pacific coast suggests that other factors may control Pacific mangrove range limits. A potential limiting factor could be dispersal. Factors contributing to dispersal limitation could include geographical features such as headlands, equatorward currents, and large gaps in suitable habitats along the coastline, which could limit stepping stone dispersal (Bernardi *et al.*, 2003; Van der Stocken *et al.*, 2019). We observe a similar pattern on the Gulf of California side, where general current patterns seem to be preventing mangroves from dispersing further north (Sandoval-

Castro *et al.*, 2012). In addition to these obstacles, the coastal landscape north of the range is rugged and dominated by rocky and sandy shoreline, with only a few saltmarshes found in seasonal river mouths and estuaries or sheltered bays (Hammond, 1954). These coastal patterns are different than the continuous availability of salt marshes habitats found on the Atlantic coast. The dispersal limitation hypothesis is supported by the occurrence of grey mangroves (*Avicennia marina*) in Southern California in the Mission Bay salt marsh, next to San Diego. These mangroves have been thriving since being introduced as an experiment between 1966-1969, despite efforts to eradicate them (Mission Bay Park Natural Resource Management Plan, 1990). These invasive mangroves are growing in an area that was determined suitable for both black and red mangrove by our fundamental niche model (Figs. 1.4a, 1.4b), thus suggesting that if mangrove propagules managed to reach such suitable habitats, they would likely establish new range limits.

An alternative hypothesis is that the Pacific mangroves could be limited by a combination of environmental stressors, including aridity. The Pacific coast range limit is an arid habitat (Table 1.1), and previous research indeed described this mangrove range as being controlled by both temperature and precipitation (Felger *et al.*, 2001; Turner *et al.*, 2005; Osland *et al.*, 2017b). Range limits with a more arid climate have mean air and water temperatures warmer than more humid range limits, suggesting that the combination of low temperatures and aridity may result in exacerbated water stress on mangrove trees (Clough, 1993; Lovelock *et al.*, 2016; Osland *et al.*, 2017b). While we did not include aridity treatments in our experimental manipulations, aridity likely has a role in limiting mangrove growth on the arid BC coast. Several studies focusing on arid mangrove range limits have shown that latitudinal increases in rainfall are correlated with significant increases in mangrove area accompanied with a decrease in salt marshes (Bucher & Saenger, 1994; Osland *et al.*, 2014; Feher *et al.*, 2017; Duke *et al.*, 2019). Aridity or hypersalinity can even negatively impact mangroves over a short period of time, and have resulted in massive dieback events such as the recently studied ones in Australia (Duke *et al.*, 2017; Lovelock *et al.*, 2017). Consequently, aridity and prolonged periods of drought could potentially be a key factor preventing the Pacific mangrove range to expand further north.

In addition, there could be interactions among aridity and cold air and water temperatures that inhibit mangrove reproduction, recruitment, and growth. Finally, the fundamental niche of mangroves likely varies by life stage, and conditions suitable for the survival of adult mangroves may not be the same as the conditions necessary for recruitment of mangrove seedlings (Krauss *et al.*, 2008; Osland *et al.*, 2015). Forecasting mangrove dynamics at arid or semi-arid range limits have been proven challenging, as there can be substantial regional variation based on changes in rainfall and freshwater availability, temperature, evaporation or transpiration (Ward *et al.*, 2016). There still is uncertainty towards determining whether and how will these mangrove range populations be impacted in terms of abundance, dynamics, and composition (Field, 1995; Gilman *et al.*, 2008; Semeniuk, 2013; Osland *et al.*, 2014; Lovelock *et al.*, 2016). Uncertainty remains very high as to how climate change will impact northwestern Mexico and southern California, but models tend to agree towards a generalized significant decrease in precipitation as well as an increase in temperature, which would affect mangrove populations negatively (Peterson *et al.*, 2002; Cavazos & Arriaga-Ramírez, 2012; Ashraf Vaghefi *et al.*, 2017).

1.5.5. Inferring Biogeographical Range Dynamics from Ecological Niches

By coupling thermal tolerance experiments with observational data across multiple range limits for two mangrove species, we revealed species and range-specific differences in thermal niches. While no populations are in perfect equilibrium when comparing their realized and fundamental niches, there is an asymmetry between coasts, with a much greater disequilibrium for the Pacific mangroves. Running these experiments under laboratory conditions enabled us to compare these two populations under similar conditions, which could not have been possible through only field measurements. We recognize that experimental freeze treatments in the laboratory may differ from freezes that plants experience in the field. For example, conditions in the field will be more variable with respect to the intensity and duration of cold events. Also, variability in long-wave radiation emissions, wind, and microclimates, can lead to small-scale variability in exposure among individuals (Devaney *et al.*, 2017). However, our experimental results are remarkably consistent with previous studies of freeze impacts on mangroves, whether these were conducted under laboratory or field conditions (Osland *et al.*, 2013, 2020; Cavanaugh *et al.*, 2015; Cook-Patton *et al.*, 2015). For example, Osland *et al*. 2020 conducted field surveys of freeze damage to *Avicennia germinans* on the Gulf of Mexico and Atlantic coasts and found temperature thresholds for plant mortality of ~-7°C, close to our laboratory thresholds of -8.65°C.

These patterns have implications for the response of mangrove distributions to climate change, as our results support recent observations that on the Atlantic coast both species of mangroves are rapidly shifting their distribution in response to climate change (Perry & Mendelssohn, 2009; Cavanaugh *et al.*, 2013, 2019; Armitage *et al.*, 2015). We hypothesize that the relatively stable populations on the Pacific coast indicate other barriers to range expansion, including dispersal limitation, biotic factors, and/or a combination of climate stressors, mostly linked to the lack of freshwater availability. As a result, we can assume that a potential increase in aridity due to climate change might actually result in a decline in abundance and composition of the Pacific coast mangroves, following similar patterns observed at other arid range limits (Semeniuk, 2013; Lovelock *et al.*, 2016; Duke *et al.*, 2019).

We also contend that controlled laboratory experiments can be useful proxies for reciprocal transplant experiments to determine whether climate outside of the range is suitable (Lee-Yaw *et al.*, 2016), particularly given that reciprocal transplant experiments outside the range are often unfeasible. Overall, our approach combining experimental data with observational patterns provides a benchmark for integrating physiological tolerance experiments, remotely sensed observations of species' range limit dynamics, and distributional modeling to improve our projections of climate change impacts on species distributions. This approach can help improve our ability to model species responses to a rapidly changing climate and under the appearance of non-analogue climates (Williams *et al.*, 2007; Urban *et al.*, 2012; Kotta *et al.*, 2019). This is particularly pertinent to widely distributed species with multiple range limits, where environmental conditions and individual responses can be highly population-specific.

1.6. References

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Chapter 2: Species-Specific Acclimation and Adaption of Mangroves to Cold Water and Aridity at the Range Edge in Baja California, Mexico

2.1. Abstract

Climate change has the potential to alter the abundance and distribution of mangroves, which will have dramatic impacts on the structure and function of present-day temperate coastal ecosystems. However, we still know relatively little about how climate change will alter mangrove distributions, which limits our ability to predict and adapt to changes in these ecosystems. This paper focuses on the northernmost mangrove range limit of the Pacific coast of North America in arid Central Baja California (Baja), where mangroves grow under sub-optimal conditions. The constraints at this range edge are potentially different than most investigated ranges, as it has two distinctive characteristics. First, although air temperatures are relatively mild with only infrequent subfreezing temperatures, often known to limit mangroves elsewhere, Baja is both extremely arid and is characterized by relatively cold water due to the California Countercurrent. We hypothesize that the combination of aridity and cold water is physiologically stressful and thus potentially limiting to mangroves given their mostly tropical and humid distributions. Second, it is one of the few range edges where red and white mangroves (Rhizophora spp. and Laguncularia spp., respectively), not black mangrove (Avicennia spp.), are the most poleward distributed. This is unusual, as Avicennia spp. are widely thought to be the hardiest mangrove, tolerant of a range of physiologically stressful environments. We hypothesize that ecophysiological differences among Baja mangrove species explain their relatively unique distributions in Baja, which we investigate through manipulative experiments.

Specifically, we tested whether the interaction of cold water and aridity has significant, species-specific effects on mangrove survival, and ecophysiological traits in a controlled experiment in two climate-controlled growth chambers using propagules from all three species collected from the range limits in Baja. We exposed seedlings to a wide range of water temperatures (13-30°C) at two different humidity levels (40% and 65% relative humidity). We then measured key ecophysiological traits to provide insight into how mangroves respond to these environmental stressors.

We found that cold water and aridity interactively but differentially affected the survival and ecophysiological traits of all three species, with potential implications for their latitudinal range limits. In these extreme conditions, all species have adopted dramatically different strategies, and these different physiological responses appear to fit their unique distributions at this range. The two northernmost species, red and white mangroves, both had consistently lower stomatal conductance across a range of water temperature and humidity levels. Although lower stomatal conductance would likely restrict photosynthesis and thus result in slower growth, it would also effectively conserve water loss from evapotranspiration under the arid Baja conditions. In contrast, black mangroves had higher turgor loss points (the ability of leaves to retain water), suggesting a different strategy for alleviating drought stress. Despite these physiological differences, black mangroves consistently experienced higher mortality rates from cold water temperatures compared to red and white mangroves that persisted across humidity levels. The relative inability of Baja black mangroves to tolerate cold water mirrors their inability to tolerate mild freezing air temperatures highlighted in Chapter 1. Thus, we suggest that the rather unique distributions of mangroves in Baja, where black mangroves are not found at the most northern range limits, reflects their range-specific inability to tolerate cold temperatures, both air and water. This intolerance to cold air and water seems unique for the Avicennia genus which generally occupies the most poleward distributions across a range of global mangrove range limits. Thus, the Baja mangrove ecosystem provides an interesting and novel opportunity to understand natural selection for cold tolerance in tropical plants. Ultimately, we suggest that although conditions for mangrove growth and survival exist further north of their current range limits, a combination of dispersal limitation (red and white mangroves) and mild cold temperatures (black mangroves) limits their ultimate and species-specific range limits.

2.2. Introduction

Climate change is altering the distribution, dynamics, and functions of ecosystems around the world (Thomas *et al.*, 2004; MacDonald *et al.*, 2008; Rosenzweig *et al.*, 2008; Chen *et al.*, 2011). Temperate and tropical plants are moving poleward in response to global warming, displacing native species, altering biodiversity patterns, and impacting ecosystem structure and function (Parmesan & Yohe, 2003; Cavanaugh *et al.*, 2013). The highest velocity of climate-driven environmental changes is occurring in the coastal zone (Loarie *et al.*, 2009), a region that includes more than 70% of the world's population and some of our most biologically productive ecosystems (Agardy *et al.*, 2005). Amongst the most important of these ecosystems are mangroves, which are generally limited to tropical and sub-tropical climates (Duke *et al.* 1998), and salt marshes, which dominate more temperate coastlines (Frey & Basan, 1978). Conventional wisdom asserts that these distributions are constrained by freezing air temperatures and winter sea surface temperatures (SST) below 20°C, which are conditions found at higher latitudes (Duke *et al.*, 1998). It has been recognized that freeze tolerance is the principal range limiting factor in setting the global distribution of mangroves at many range limits (Stuart *et al.*, 2007; Lovelock *et al.*, 2016; Osland *et al.*, 2017b). As a result, changes in climate, particularly an increase in minimum temperatures, could lead to further expansion of mangroves, encroaching into mid-latitude salt marshes and significantly altering them (Cavanaugh *et al.*, 2013; Chen *et al.*, 2017; Osland *et al.*, 2020). Therefore, mangroves are particularly relevant for examining general questions about range limitation in plants. However, our actual understanding of this phenomenon is still surprisingly limited, and the increasing availability of higher resolution and more accurate datasets obtained from remote sensing, climate data, and field observations, is revealing a more diverse and wider range of temperature thresholds than previously thought across mangrove range limits (Osland *et al.*, 2017b; Cavanaugh *et al.*, 2018). For instance, Quisthoudt et al. (2012) showed high variability in terms of mean water temperature at upper latitudinal limits across the world, ranging from 12.5°C to 32°C.

Although studies have examined the response of a single abiotic stressor in terms of mangrove growth and physiology (Cavanaugh *et al.*, 2015; Chen *et al.*, 2017; Osland *et al.*, 2020; Gu *et al.*, 2021), research remains to be conducted as to how mangroves may be physiologically impacted by the combination and additive effects of multiple environmental stressors. Recent studies on range dynamics have focused on integrating multiple climate variables (i.e. air and water temperature, salinity, relative humidity, precipitation) (Lenoir & Svenning, 2015; Bradie & Leung, 2017; McHenry *et al.*, 2019). Studies that have focused on the impact of high vapor pressure deficit (VPD) – a factor of both air temperature and relative humidity and a measure of the drying capacity of air, have demonstrated that this combination can have a more significant impact on plant mortality than temperature alone (Eamus *et al.*, 2013; Devaney *et al.*, 2020).

In terms of mangrove dynamics, new studies have underlined the potential effect of cold temperatures and aridity combined, illustrated by mangrove latitudinal boundaries occurring within significantly warmer temperatures at ranges under arid conditions (Quisthoudt *et al.*, 2012; Osland *et al.*, 2017b; Cavanaugh *et al.*, 2018; Duke *et al.*, 2019). Analyzing the interactive effects of minimum air and water temperature and aridity on mangrove growth and development is essential to better understand and predict potential mangrove range shifts under changing climatic conditions. However, much of the evidence underlying these assumptions derives from remote sensing, climate data, and field observations, and seldom from experimental studies specifically testing the thresholds of mangrove's physiological tolerances to various environmental stressors (Ross *et al.*, 2009; Cavanaugh *et al.*, 2015).

The poleward range limit of mangroves does not always encompass areas that experience sporadic freeze events. This is the case for the range limit on the Pacific coast of North America, occurring in Baja California, Mexico. This range shares similar species to those found on the Atlantic range limit, where freezing temperatures are restricting poleward expansion (Cavanaugh *et al.*, 2013). However, the mangroves of Baja California (Baja) are unlikely to experience significant freeze events, and the factors which are currently setting their range are unclear. Previous studies have argued that cold water temperatures might set the mangrove range limit in Baja (Duke *et al.* 1998), while others seem to indicate that mangroves in arid regions could have an overall lower resistance to cold air and water temperatures (Quisthoudt *et al.*, 2012). However, there is surprisingly little experimental data on the cold-water tolerance of mangroves, and there have been few studies investigating mangrove ecophysiological response to combined water temperature and aridity stressors. A recent paper (Devaney *et al.*, 2020) focused on the role of low humidity and hypersalinity in reducing the cold tolerance of the Florida mangroves, thus highlighting the importance of accounting for interactions between multiple abiotic factors. Identifying the environmental tolerance thresholds of mangroves in terms of cold water and aridity is critical for improving our understanding of how future changes in sea surface temperature and air moisture content and precipitation will impact the abundance and distribution of these important coastal foundation species.

The Baja California mangrove range limit is unique for two reasons. First, it is one of the few ranges where red and white mangroves, not black, are the most poleward distributed. This is globally interesting, as the black mangrove genus is widely thought to be the hardiest mangrove and largely resistant to cold temperatures (Duke, 1990; Pickens & Hester, 2011; Hayes *et al.*, 2020b; Osland *et al.*, 2020). We hypothesize that this singularity may be due to ecophysiological differences among these species in Baja California, as well as species and range-specific dispersal limitation. Second, although air temperatures in Baja are relatively mild, this Pacific coast mangrove range is characterized by an arid environment and cold coastal waters, which we hypothesize are difficult conditions for mangroves given their mostly tropical, humid distributions, as cold roots can limit water uptake of tropical plants (Atkin *et al.*, 2005; An *et al.*, 2012). Mangroves, as trees living in salt water, are almost constantly under water stress (Lugo & Snedaker, 1974; Parida & Jha, 2010), however the combination of cold water and aridity as potential added stress has been an under-investigated hypothesis in mangrove ecology. Based solely on air temperature tolerance, the Baja mangroves' range should be much further north than its current edge.

There is a large amount of variability in air and water temperatures as well as humidity along the Pacific coast, and we argue that rather than being limited by a single factor such as cold air or cold water temperature, the Baja California mangroves range could be restricted by a combination of environmental factors, including cold temperatures, aridity, and dispersal potential. This paper tests whether the combination and interaction of cold water and aridity has significant, species-specific effects on mangrove growth and survival. We set up a controlled experiment in growth chambers using propagules from all three species collected from mangroves in Baja, and measured key ecophysiological traits to provide insight into how mangroves respond to these environmental stressors. We then compared these to current environmental conditions, and hypothesized on the main range-setting components, as well as the reasons why the Pacific range limit has not been expanding poleward unlike other ranges such as the Atlantic coast mangrove range (Cavanaugh *et al.*, 2013). Analyzing the additive effects of cold-water temperature and aridity on mangroves is thus required in order to better understand and inform predictions of the Pacific mangrove range dynamics as well as other arid mangrove ranges, as the integration of range-specific physiological data can enable us to incorporate local adaptation into distribution models.

2.3. Materials and Methods

2.3.1. The Coastal Environment of Baja California

Baja California is a 1350 km-long peninsula, located in the northwestern part of Mexico, just south of the border with the United States. It covers 71,777 km^2, extends about 1,300 km from north to south, and is also associated with 65 islands. Its geomorphology and climate create favorable conditions for stunning biogeographical diversity, ranging from coastal wetlands and sandy beaches to forested mountain ranges and rugged deserts (Minch *et al.*, 1998; Riemann & Ezcurra, 2005). Deserts represent 65% of the peninsula and its largest, the Vizcaíno Desert, is located in its central portion. Although mostly desertic, Baja contains such high levels of endemism that it has been designated a protected Biosphere Reserve by the United Nations (Kumar, 2013; Minch et al., 1998). The Baja peninsula is separated from mainland Mexico by the Gulf of California, also called Sea of Cortez, from a distance of 250 km at its widest, and features about 3,000 kilometers of coastline, supporting an array of critically important fauna and flora (Whitmore *et al.*, 2005).

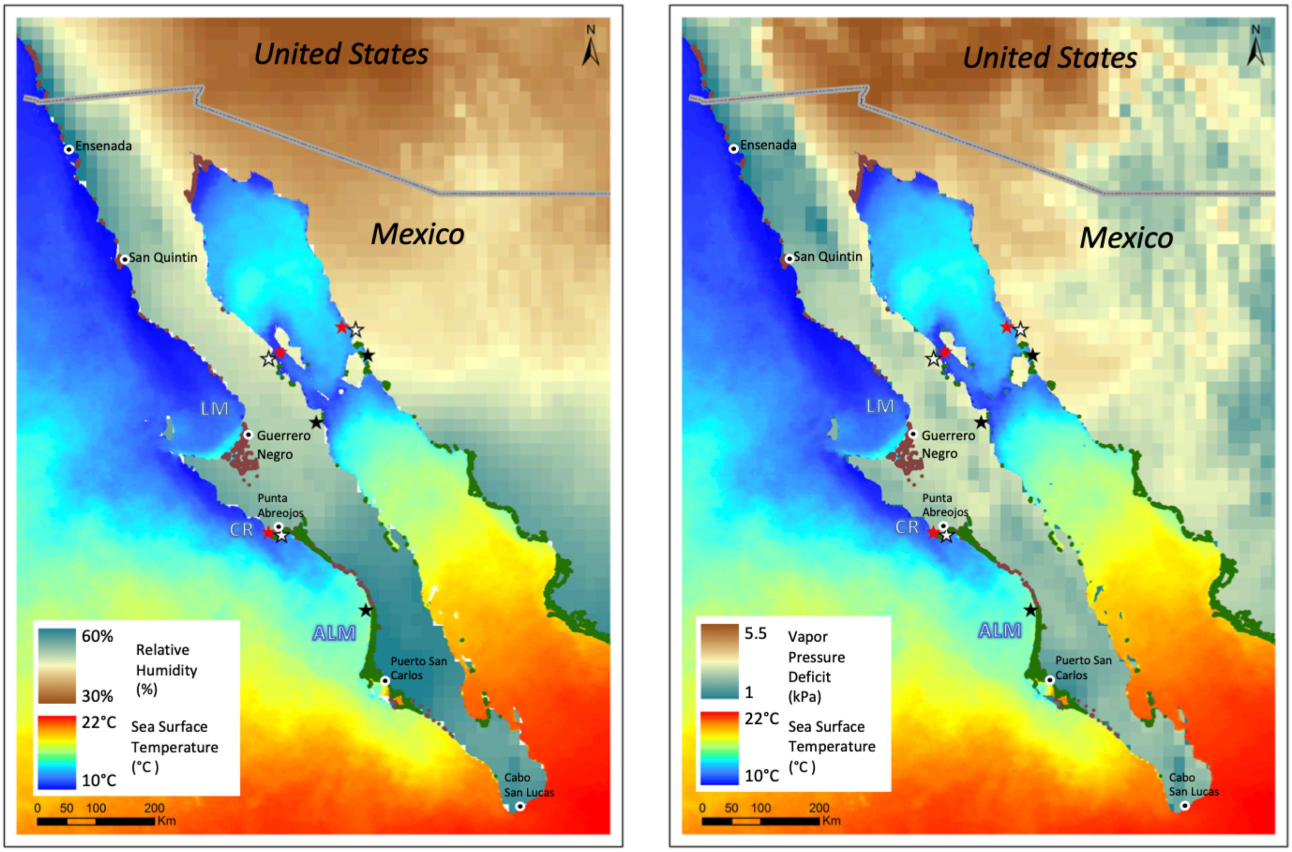

Figure 2. 1. *Distribution and range limits of the Baja California mangroves under current environmental conditions. Species-specific ranges are symbolized by stars corresponding to the three species (red, white and black mangrove). Sea-surface temperature is the average of the coldest month from 2002 to 2010 (Sbrocco and Barber, 2013). Relative Humidity and Vapor*

Pressure Deficit are the average of daily values for the month of August over the years 1961-1990 (Kriticos et al., 2012). The location of Hobo sensors (Fig. 2.4) is marked by their initials.

The geomorphic characteristics of coastal Baja California are not generally conducive to extensive mangrove and salt marsh development. The coast is dominated by a series of uplifted and warped marine terraces of Quaternary age resulting in cliffs, rocky shoreline, and low-lying areas, which are subject to tidal inundation and are limited in occurrence and extent (Orme, 1973). Sheltered estuaries and lagoons characterized by Holocene tidal-flat sedimentation are sparse, and permanent fresh water supply from riverine flows are not reliably found (Alvarez-Leon, 1993; Portillo & Ezcurra, 2002; Tovilla & Orihuela, 2002; Sánchez-Núñez & Mancera-Pineda, 2011).The major lagoons currently present in Baja California, such as the Laguna Ojo de Liebre and the Laguna Santo Domingo (Fig. 2.1), have originated from fringing beaches on the coastal plain at a time where sea level was about 12 meters lower than presently (Phleger & Ewing, 1962). With sand and sediments supplied by rivers, such barriers grew upwards as sea level rose. In the last 1,800 years, these sand barriers have been displaced seaward about just over a kilometer (Phleger & Ewing, 1962).

The climate of Baja California spans from Mediterranean on the northern part of the peninsula to mostly tropical as the southern end, which lies within the Tropic of Cancer (Fig. 2.1). The majority of the peninsula however is under arid conditions, with 69% of the region considered as desertic. Coastal areas are unlikely to experience major hard freeze events, and average winter temperatures rarely fall below freezing, although freezing temperatures (-1°C to -5°C) do occur occasionally (Fig. 2.2). Overall, climatic conditions are progressively changing over a north to south gradient, dividing the peninsula into two major climatic zones. The northern part of Baja is under the influence of a Mediterranean climate similar to Southern California, consisting of mild, wet winters, and hot, dry summers. Northern Baja is also influenced by atmospheric subtropical high pressure and maritime polar air from the Pacific, bringing fog, drizzle and moderate precipitation during the winter and spring months (Hastings & Turner, 1965; Comrie & Glenn, 1998). Summer and winter temperatures increase moving south (Fig. 2.2) along a distinct north to south climatic transition, which is the consequence of the influence of the North American summer monsoon (also referred to as the Southwest monsoon). As the monsoon gets stronger further south, precipitation regimes shift in timing and intensity. Summer and autumn thunderstorms bring significant amounts of rainfall, associated with the presence of low-pressure systems centered to the south and west of Baja California (Hales Jr, 1974; Douglas *et al.*, 1993; Higgins *et al.*, 1997; Anderson *et al.*, 2000). The proximity of the Tropic of Cancer creates the potential for hurricanes during the late summer and autumn seasons (García-Oliva *et al.*, 1991). Although major hurricanes are seldom encountered in this area of the Pacific, they have the potential to carry surges of moist maritime tropical air leading to significant amounts of rain and fierce winds (Hastings & Turner, 1965; Hales, 1972; Wilkinson, 2014). Southern Baja is subject to a dry season that extends from November to June, although sporadic winter rains periodically occur, while northern Baja receives much of its precipitation during winter storms (Díaz *et al.*, 2001).

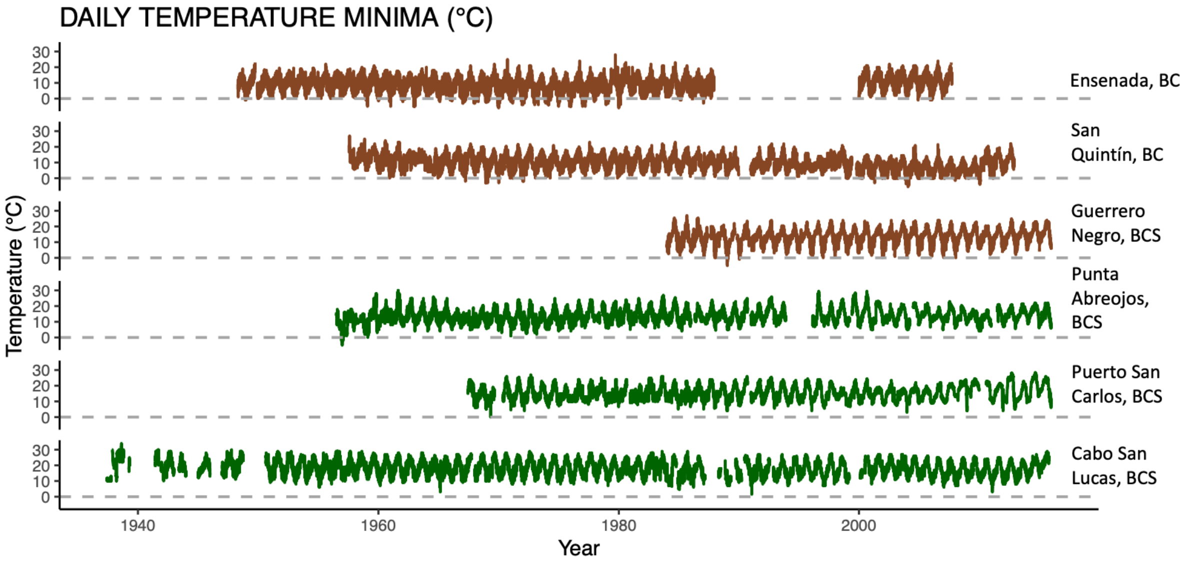

Figure 2. 2. *Daily temperature minima (°C) across costal Baja California from north to south, based on weather stations data. Green lines are stations next to mangroves, brown lines are stations next to salt marshes north of the range. Station locations are geographically referenced in Figure 2.1.*

Oceanic conditions are significantly different on each side of the peninsula (Fig. 2.1). Water is cooler on the Pacific side due to the California current, a stream of cold water along the west coast of North America, flowing from British Columbia down to Baja California (Hickey, 1979; Lynn & Simpson, 1987). Water temperature is significantly warmer on the eastern side of the Peninsula, on the Sea of Cortez. The Baja California Peninsula is also subject to the influence of the El Niño–Southern Oscillation (ENSO). In this area of the Eastern Pacific, ENSO is considered to be the most important source of interannual climatic variation (Neelin & Latif, 1998; Díaz, et al., 2001; Folland, Karl, & Vinnikov, 1990; Stahle & Cleaveland, 1993). Strong ENSO events have the potential to bring significant amounts of rainfall caused by abnormally warm water and an increase in subtropical moisture and activity. On the other hand, La Niña years consistently coincide with years of below average precipitation, sometimes leading to prolonged periods of extreme droughts (Hastings & Turner, 1965; Díaz *et al.*, 2001; Durazo, 2009).

2.3.2. Characterizing the Mangroves of Baja California

Mangrove ecosystems consist of a diverse, yet small group of tropical species, which have developed special physiological and morphological adaptations in order to grow in dynamic and highly saline inter-tidal conditions (Lugo & Snedaker, 1974; Chapman, 1976; Tomlinson, 1995). In the context of Baja California, mangroves have to adapt to the harsh environmental conditions of the peninsula, characterized by aridity and low water temperatures (Hutchings & Saenger, 1987; Jiménez, 1988; Fernandes, 1999; Riosmena Rodriguez *et al.*, 2014). Although population density in Baja is relatively low, mangroves have still been under increasing anthropogenic pressure, mostly from tourism and shrimp farming (Páez-Osuna *et al.*, 1999, 2003; Glenn *et al.*, 2006; Aburto-Oropeza *et al.*, 2008). However, the Baja mangroves have gained more attention in terms of the environmental and societal services they provide, and as of today all mangroves are subject to special protection status by the Official Mexican Standard (NOM-059-ECOL-2001). A study from Ezcurra *et al* (2016) showed that mangroves along the Baja coast have compensated for sea-level rise during the last two millennia by accreting on their own root remains, accumulating large amounts of carbon in their sediments (900–3,000 Mg C/ha) at rates considered higher than tall and lush tropical mangrove forests. Mangroves thus represent the largest carbon sink per unit area in Mexico's northern drylands (Ezcurra *et al.*, 2016). Unlike other mangrove range limits, the Mexican mangroves have shown no sign of poleward migration over the last 200 years, and their dynamics have been relatively stable (Riosmena Rodriguez *et al.*, 2014). Such characteristics emphasize on the importance of mangroves conservation in this region, and the need to comprehensively understand their behavior and dynamics.

2.3.2.1. Mapping Mangrove and Salt Marshes of Pacific Coast Ecotone

In order to obtain a clear depiction of the distribution of coastal wetlands along the Baja California coast, we created a mangrove and salt marsh dataset using Landsat 8 Operational Land Imagery satellite data at a 30-meter spatial resolution. We selected 14 atmospherically and geometrically corrected Landsat tiles from 2019, covering the Pacific Coast from the southern tip of Baja California north to Southern California. For each satellite tile, we operated an unsupervised classification using the ISODATA clustering algorithm. Each pixel was divided into a range of 30 to 50 spectral cluster classes, based on a change threshold of 10%. The minimum number of pixels in each class was set to 500, and the classification was instructed to run for ten iterations. We manually grouped the resulting spectral clusters into mangrove or salt marsh classes, based on visual interpretation. The selected mangrove/salt marsh classes were then combined and imported into the ArcMap software for visual representation. We replicated this analysis tile by tile then merged all mangrove and salt marsh outputs within a common shapefile covering the entire Pacific coast ecotone. The accuracy of our final mangrove and salt marsh cover was then assessed and compared to existing global mangrove (Spalding *et al.*, 2010; Giri *et al.*, 2011) and salt marsh (Mcowen *et al.*, 2017) datasets. We based this accuracy assessment on 2019-2020 Google Earth imagery (provided by Maxar Technologies) at a spatial resolution of 0.5 meters. We randomly generated 200 points within our mangrove and salt marsh classifications, and overlaid this point-cloud into Google Earth Pro. Based on this very high-resolution imagery, we attributed values of 0 or 1 depending on whether or not these were within actual mangroves and salt marshes. Each of the 200 reference points was compared to our final dataset in order to determine a total accuracy percentage. We repeated this similar accuracy assessment for the existing mangrove and salt marsh datasets (**Error! Reference source not found.**). Since our mangrove classifications did not allow for species-specific characteristics, we identified range limits particular to each species from field data collected between 2016 and 2020 at every range limit across the peninsula (Fig. 2.1).

Dataset	Mangroves Accuracy	Salt Marshes Accuracy
Giri *et al.*, 2011	52%	n/a
Spalding *et al.*, 2010	69%	n/a
Mcowen *et al.*, 2017	n/a	87%
Bardou *et al.*, 2021	96%	92%

Table 2. 1. *Accuracy assessment of our Baja California mangrove / salt marsh dataset, and comparison to existing datasets.*

2.3.2.2. Geographic Extent of Mangrove and Salt Marsh Distributions

Mangrove forests are distributed from the southern tip of the Baja California peninsula to the arid shores of the Sonoran Desert, at Punta Abreojos and the Estero La Bocana (~26.8°N) on the Pacific side, and at Bahia de Los Angeles (~29.0°N) on the Gulf of Mexico side (Fig. 2.1). Due to the aridity of the region and the lack of rainfall and permanent rivers, mangroves usually grow under sub-optimal conditions and are characterized by smaller heights and less developed structure and extension (Flores-Verdugo *et al.*, 1992; Whitmore *et al.*, 2005), as seen on Figure 2.3. Mangrove forests in this region are typically found in coastal lagoons and small bays

(Contreras-Espinosa & Warner, 2004), and the San Ignacio Lagoon and Bahia Magdalena hold the largest mangrove coverage in Baja (López-Medellín & Ezcurra, 2012). The three species of mangroves found in Baja California are *Rhizophora mangle* (red mangrove), *Laguncularia racemosa* (white mangrove), and *Avicennia germinans* (black mangrove). Red and white mangroves have the northernmost distributions in Baja, while the northernmost black mangroves are only found further south, in the northern part of Bahia Magdalena (Pacific; ~25.8°N) and in Bahia de Concepcion (Gulf of California; ~27. 0°N) (Fig. 2.1). At their respective range limits, all three species are characterized by small but healthy-looking pockets of small, shrubby mangrove trees (Fig. 2.3). This pattern of latitudinal distribution contrasts with mangrove range limits in most other parts of the world where Avicennia distributions typically extend further poleward than those of Rhizophora and Laguncularia due to their typically higher tolerance to cold temperatures (Stuart *et al.*, 2007; Cavanaugh *et al.*, 2013; Cook-Patton *et al.*, 2015). When comparing mangrove datasets accuracy, we noticed that data from Giri et al. (2011) shows a vast area of mangroves north of Punta Eugenia, in the Vizcaíno Bay and the Laguna Ojo de Liebre (Fig. 2.1), a vast estuary where mangroves have not been found to this day. Such differences in mangrove mapping are mainly due to remote sensing interpretation and mis-classification. This difference is nonetheless noteworthy, as the incorrectly classified mangrove around Vizcaíno Bay is most likely a result of the vegetation density and large size of the wetland, and it tends to support the hypothesis that this lagoon could potentially be a suitable habitat for mangroves under different climatic conditions.

Figure 2. 3. *Red mangroves (Rhizophora mangle) in Bahía de Los Ángeles. Author (Rémi Bardou) is seen for scale.*

2.3.2.3. Describing the Baja California Mangroves' Realized Niche

Conditions vary widely across coastal ecosystems in Baja California, from the mostly tropical mangroves of the southern peninsula to the arid range, and up to the most temperate salt marshes of the north. The current environmental and climatic conditions under which mangroves thrive, also described as the mangroves' realized niche (Austin *et al.*, 1990; Vetaas, 2002) reflect this diversity. We used gridded temperature and relative humidity climate data to spatially characterize differences in environmental conditions across the mangrove – salt marsh ecotone (Fig. 2.1). Data on mean sea-surface temperature of the coldest month (Sbrocco & Barber, 2013) was used to represent the most challenging conditions to mangrove growth. We also used CliMond data (Kriticos *et al.*, 2012) to characterize relative humidity across the Peninsula, using the mean 3pm daily relative humidity for the month of August. We then calculated maximum Vapor Pressure Deficit (VPD) values. VPD, as a dependent of air temperature and humidity, is considered a good indicator of plant transpiration and water loss (Abtew & Melesse, 2013; Eamus *et al.*, 2013). To obtain maximum VPD, we first calculated Saturation Vapor Pressure (SVP) from CliMond maximum daily August temperature. We then extracted VPD values using SVP and 3pm relative humidity, following established calculation methods (Abtew & Melesse, 2013). Mean sea-surface temperature of the coldest month, mean August afternoon relative humidity and mean maximum VPD in August were all represented Figure 1.

To complement gridded climate data, we gathered data obtained from weather stations across Baja California. Daily minimum temperature data from the 1950s to 2012 was downloaded from the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), using the Clicom platform (http://clicom-mex.cicese.mx).

However, neither stationary nor remotely sensed data fully reflect actual condition encountered within mangroves, and we additionally obtained in-situ data on air temperature and humidity, as well as water temperature. During a 2017 field campaign, we installed Hobo temperature and humidity sensors along the Baja California mangrove and salt marsh ecotone in order to better characterize current environmental conditions. We used free-floating Hobo temperature loggers (model # UA-002-64) to log water temperature, and temperature/relative humidity external probes (model # U23-001A). These sensors logged at a 30-minutes interval for 18 months. This in-situ data enabled us to obtain daily data on air temperature and relative humidity, as well as actual water temperature encountered right within mangrove roots. Vapor pressure deficit was computed from this data

2.3.3. Seedling Experiments on Water Temperature and Aridity

2.3.3.1. Experimental Design

To test whether the combination of cold water and aridity has significant species-specific effects on mangrove growth and survival, we set up a controlled experiment in growth chambers using propagules from all three species collected from mangrove populations in Baja California. We collected mangrove propagules in November 2016 from trees along the Pacific and Sea of Cortez sides of Baja. We sampled propagules on the Pacific coast in Bahía Magdalena, around San Carlos, and further north in the mangroves surrounding Adolfo López Mateos. Propagules were also collected on the Sea of Cortez side around La Paz. Propagules from individual parent trees were kept separate and tracked for potential maternal effects. After collection, propagules were immediately transported to the laboratory at the Smithsonian Environmental Research Center, in Maryland (USA). We kept propagules moist in plastic bags until planting. We then placed propagules in plastic trays over a layer of mixed wet potting soil and sand. Once propagules had emerging radicles and initiated leafout (about three weeks later), they were considered mangrove seedlings ready for experimentation. We selected only healthy seedlings, measured their initial fresh mass to the nearest mg, and planted them into individual RayLeach Cone-tainers (2.5 cm diameter, 12.1 cm length; 49 ml volume) filled with a 2:1 mixture of potting soil and sand. Cone-tainers were then placed into large plastic tubs (38 cm wide, 43 cm long, 23 cm high), each holding 100 tubes and filled with a solution of de-ionized water and

Instant Ocean at 35 Practical Salinity Units (PSU). We planted a total of 750 red, white, and black mangroves, 250 seedlings per species. After planting, we let seedlings acclimate under similar conditions for 60 days before submitting them to our water temperature and air humidity treatments.

Our experiment was designed around six water temperatures and two levels of relative humidity. We set up two walk-in Environmental Growth Chambers with similar controlled temperatures over a 24-hour cycle (12 a.m.–6 a.m.: 16°C, 6 a.m.–12 p.m.: 21.5°C, 12 p.m.–6 p.m.: 27°C, 6 p.m.–12 a.m.: 21.5°C). Each room was equipped with controlled de-humidifiers to maintain constant humidity levels, with one room set to 65% and the other to 40%. In both rooms, temperature and humidity were monitored and logged at 30-minute intervals using Hobo Loggers (model # UX100-011A, Onset Computer Co.). We then established 12 coolers (9-liters capacity) in each room filled with a solution of de-ionized water and Instant Ocean at 35PSU. Next, using aquarium pumps, individual chillers (Chill Solutions CSXC-1), and submersible heaters, we established a gradient of six different water temperatures (13°C, 15°C, 17°C, 21°C, 25°C and 30°C), with two replicate coolers per temperature. Chillers were used in the 13-17°C treatments, 21°C coolers lacked chillers/heaters but tracked ambient room temperature, and 25°C and 30°C coolers contained heaters. Replicate coolers for each temperature were placed in different sides of the growth chamber with temperature treatments randomly dispersed throughout each room.

We then planted into each cooler healthy three-month old seedlings from each species with seedlings paired by parent tree and by relative size. Each pair was randomly assigned to a given water temperature and to either the 40% or the 65% room. In total, each cooler was outfitted with 30 seedlings (n=10 seedlings per species). Water in all coolers was first held at constant room temperature for one week to let plants acclimate, after which water temperature in each cooler was progressively lowered or increased by 1°C increments per day to their final set points. We lowered humidity in the 40% room by 10% increments per day. Throughout the experiment, water temperatures in each cooler were recorded with free-floating Hobo temperature loggers (model # UA-002-64). Water temperatures and salinities within coolers were also checked five days/week with an Accumet AP85 probe, with set points on chillers and heaters adjusted accordingly. When needed, we used deionized water or Instant Ocean to bring salinities back to 35PSU. Treatments were maintained at equivalent volume by adding deionized water to coolers when required, in order to minimize the effects of differential evaporation. This design enabled us to achieve consistent water temperatures across rooms and within each treatment.

2.3.3.2. Measurements

We measured key ecophysiological traits to provide insight into how mangroves respond to cold water temperature in conjunction with aridity. After being placed in coolers, each seedling was measured for height from the root collar to the highest living apical bud, and number of leaves. Each of these measurements were also recorded at the end of the experiment, eight months later. We also recorded final wet and dry mass, which was separated into root mass, leaf mass, stem mass, and propagule mass for red mangroves. Survival was recorded weekly throughout the experiment. Seedling survival was based on functional mortality and defined as displaying no photosynthetic tissues, resulting in withered, brown stems and leaves.

Stomatal conductance, a measure of leaf gas exchange that is critical to photosynthesis, was measured twice during this experiment. Initial measurements were taken one month after the beginning of the experiments, and final measurements were taken seven months later. We measured stomatal conductance (mol m^{-2} s^{-1}) of the upper, most fully expanded leaf from all seedlings of each species per cooler and per treatment using a diffusion porometer (Leaf Porometer, model SC-1; Decagon Devices Inc., Pullman, WA, USA). All measurements were taken under the same room temperature conditions, between 9am and 12pm when room temperature was at a constant 21.5°C. We also estimated trichome density, which can potentially impact the rate of leaf gas exchange (Franks *et al.*, 2009; Galdon-Armero *et al.*, 2018) on the underside of black mangrove leaves, as red and white mangroves lack trichomes.

After seven months, we also measured turgor loss point, a measure of a plants' capacity to maintain cell turgor during dehydration and which is strongly predictive of plant response to drought. We adapted these measurements from previous experimental designs designed to obtain precise measurements of sap osmotic potential (Ball & Oosterhuis, 2005; Bartlett *et al.*, 2012, 2014). We conducted osmometer measurements on 180 seedlings. Two leaves were selected per seedling, measured for leaf area, mass, and thickness. We then collected from each leaf an 8mm disk with a cork borer, placed each disk in coin envelopes, and froze them overnight at -18°C. The next day, osmotic potential measurements were taken using a Vapor Pressure Osmometer (Vapro 5600, Wescor, Logan, UT, USA). Each frozen disk was wrapped in foil to limit condensation, plunged them into liquid nitrogen for 5 minutes, and then punctured at least 5 times using sharp-tipped forceps to facilitate evaporation through the cuticle. Punctured disks were immediately placed into the osmometer chamber before thawing, and pressure readings were taken every two minutes until the osmometer indicated equilibrium. Lastly, leaves and their corresponding discs were placed into coin envelopes and into a drying oven for 14 days, after which their mass was added back to the total dry mass per leaf for that seedling. From these leaf area and dry mass, we calculated specific leaf area (cm^2 g-1), the amount of leaf area relative to leaf mass, an indicator of plant growth strategy that also varies with exposure to cold air temperatures in mangroves (Cook-Patton et al. 2014).

2.3.3.3. Analyses

Survival was characterized as an overall response by species and treatment, as well as over time. All seedlings were considered individual replicates, and preliminary analyses showed no qualitative differences when responses were averaged by cooler. Because of inherent differences in physiological traits and growth rates between red, white, and black mangroves, and because propagules were collected from different locations, separate statistical analyses were conducted for each species. For established seedlings, we tested the responses of stomatal conductance and stem elongation at initial vs. final stages of growth in temperature and humidity treatments, with averaged values per cooler as replicates (n = 24 coolers per humidity treatment for each species). Stomatal conductance measurements for black mangroves only included seedlings with full coverage of leaf trichomes. Osmotic potential measurements enabled us to obtain turgor loss point values for each of the measured leaves, based on established equations (Ball & Oosterhuis, 2005; Bartlett *et al.*, 2012).

2.4. Results

2.4.1. Current Environmental Conditions at the Mangrove/Salt Marsh Ecotone

The geographical distribution of mangrove and salt marshes along the Pacific coast of North America (Fig. 2.1) is remarkably different than most mangrove range limits around the world. Red and white mangroves are further poleward compared to black mangroves, which are widely considered the most environmentally tolerant of extreme conditions such as cold air, cold water, and high salinity (Duke, 1990; Sobrado & Ewe, 2006; Pickens & Hester, 2011). However, Fig. 2.1 also illustrates that constraints at this range edge are potentially different than most investigated range limits, as cold water and extremely dry conditions create simultaneous stresses on above and belowground biomass. Conditions around the red and white mangrove range edge are particularly inhospitable, as central Baja is under the driest conditions (Fig. 2.1). For instance, Punta Abreojos receives only an annual average of 62 mm of precipitation. From the range northward, around Punta Eugenia, water becomes colder, and the rugged shoreline does not contain significant suitable habitats for coastal vegetation until the vast Laguna Ojo de Liebre. The northern section of Baja is not as arid; however, water remains cold. Going northward from this vast estuarine lagoon, there are only a few small salt marsh habitats until the larger San Quintin and Ensenada coastal wetlands. Figure 2 shows that freezing temperatures are extremely rare within the mangrove range. Freezes can occur north of the range, but are very mild, reaching temperatures only a few degrees below 0°C.

Our field Hobo temperature and humidity data (see Fig. 2.1 for location) reflect dramatic differences in abiotic conditions across Baja (Fig. 2.4). The southernmost Hobo (Adolfo Lopez Mateos – ALM) was placed within Bahia Magdalena and indicates warm air, warm water, and high relative humidity. VPD was also below 1 for most of the observation period. Environmental conditions at the range edge (Campo Rene – CR) are much more challenging. This range edge is characterized by hot and dry conditions, thus very high VPD. VPD consistently stays above 1, and spikes above 2 and even 3 kPa are not uncommon. This is an extremely moisture-starved environment, and trees at this location were stunted. Water temperatures were also much colder than that of Bahia Magdalena, and in the winter of 2017, roots regularly experienced water temperatures below 15°C, with some days dipping below 10°C (Fig. 2.4). Conditions above the mangrove range limit, represented by the Laguna Manuela (LM) Hobo, located within Laguna Ojo de Liebre, were not as dry as those at the range limit, and VPD values were not as severe as those of Campo Rene. The Laguna Manuela Hobo did record significant spikes in VPD, temporarily reaching values over 2 to 3 kPa. Water temperatures within this sheltered estuary were also higher than water temperatures encountered at Campo Rene, where the range for red and white mangroves ends.

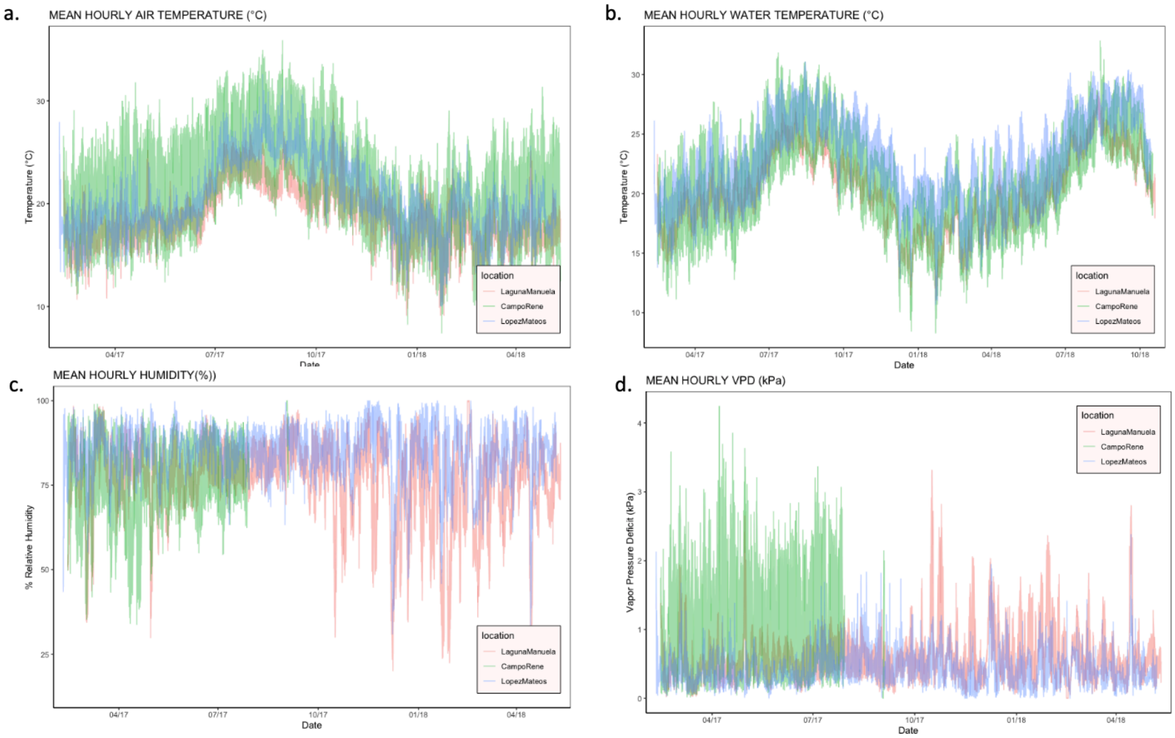

Figure 2. 4. *Field data on air temperature (a), water temperature (b), relative humidity (c), and vapor pressure deficit (d) across the mangrove - salt marsh ecotone in Baja California, placed in the Laguna Manuela (LM), Campo Rene (CR), and Adolfo Lopez Mateos (ALM). Hobo sensors*

locations are geographically referenced Figure 1. The Campo Rene relative humidity sensor (c) stopped logging in 07/17.

2.4.2. Growing Conditions Within a Controlled Experimental Environment

Working with two walk-in growth chambers enabled us to achieve consistent and comparable environmental conditions (Fig. 2.4). Daily temperature conditions followed a similar pattern and temperature differences were minimal (Fig. 2.4a). Transitions between temperature thresholds were sharper in the dry room (40% relative humidity). This can be explained by the specific heat capacity of water within the air, making it more difficult to shift temperatures in the humid room (65% relative humidity). Humidity data stayed consistent and around our established set points, and Figure 4b illustrates the massive difference in relative humidity between rooms. VPD values (Fig. 2.4c) showed that the 65% humidity room stayed at or below 1, while the 45% room reached VPD values above 2 during the warmer hours of the day.

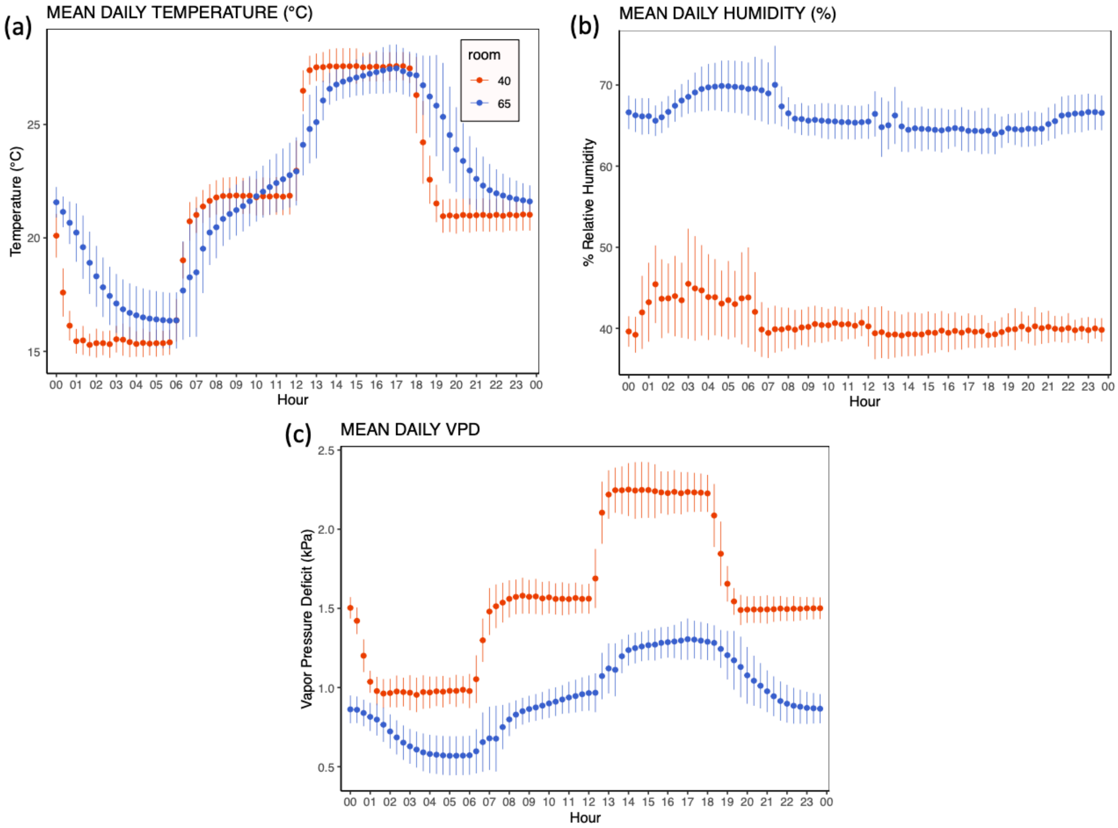

Figure 2. 5. *Daily experimental room conditions. (a) Mean daily air temperature, (b) Mean daily relative humidity, (c) Mean daily vapor pressure deficit (VPD).*

2.4.3. Response to Cold Water Temperature Stress Under Variable Humidity

Figure 5 clearly illustrates that all three species are intolerant of cold-water temperatures (13°C). However, the Baja black mangroves showed a significantly lower tolerance to cold water, as their survival time in 13°C water was much shorter than the survival of red and white mangroves. Humidity played a significant role, and all species in the 65% relative humidity room survived longer than seedlings in the 40% room. Higher humidity enabled stronger red and white mangrove survival in 13°C cold water, whereas all black mangroves in 13°C water died.

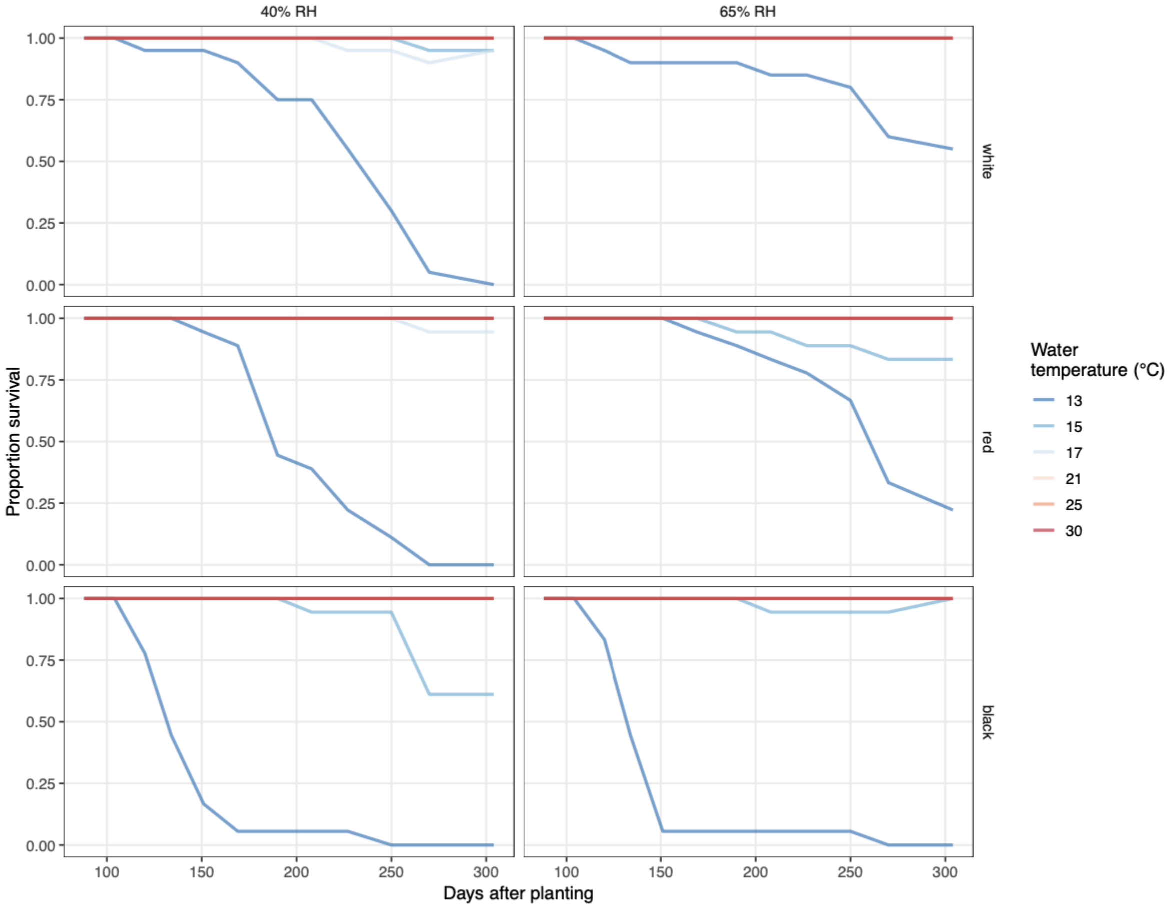

Figure 2. 6. *Proportion survival of white, red and black mangrove plants over nine months in different water temperature (13, 15, 17, 21, 25, 30°C) and relative humidity (40%, 65%) treatments. Errors bars are not shown for clarity. Water temperature is based on actual temperature readings (See Supplemental Figure 1 for details on water temperature accuracies).*

Turgor loss point (Fig. 2.5a) was strongly species-specific and affected by humidity, but the effect of water temperature was minimal. Black mangroves had the lowest turgor loss points, followed by red and white mangroves. More negative turgor loss points indicate stronger capacity to maintain cell turgor during dehydration, suggesting that black mangroves have the highest drought tolerance levels of these three species. Extra humidity made plants less drought resistant overall, but maintained the same rank differences across species.

Stomatal conductance measurements show different and species-specific leaf gas exchange strategies for acclimating to cold water and low humidity (Fig. 2.6b). White mangrove stomatal conductances were static across temperatures and humidities, indicating non-acclimation to cold water and humidity. Black and to a lesser extent red mangrove exhibited the opposite response, as they were highly dynamic across water temperatures and humidities. As water temperature increased, stomatal conductance increased for both black and red mangroves. Black and red mangroves also increased their stomatal conductance in the higher humidity room, indicating that both black and red mangroves have the plasticity to acclimate to their conditions and start taking in more air, even under sub-optimal conditions. Although stomatal conductance of white mangroves does not vary significantly between treatments, their high survival rate (Fig. 2.6) indicates a relatively strong tolerance to changes in water temperature and humidity despite the slower growth suggested by reduced leaf gas exchange.

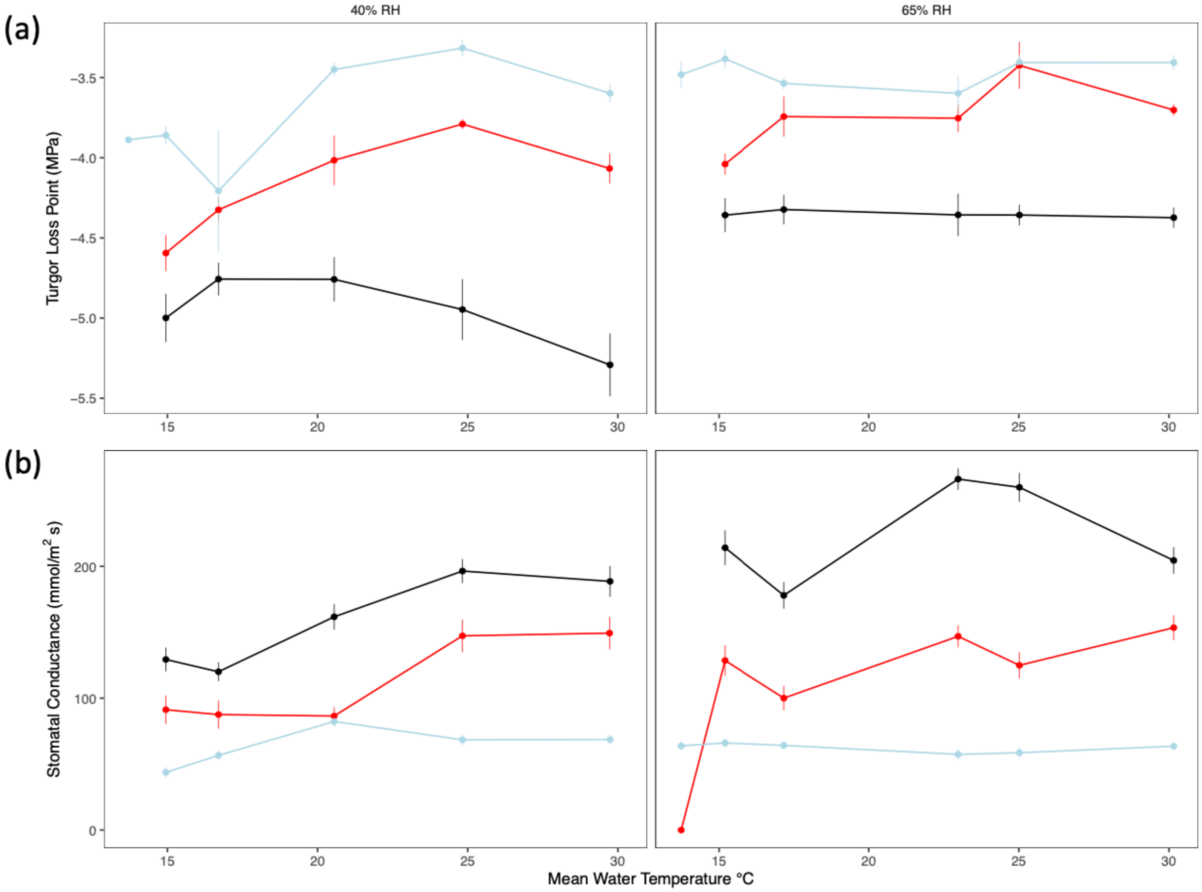

Figure 2. 7. *Physiological traits at the eighth month of white, red and black mangrove plants in water temperatures (13, 15, 17, 21, 25, 30°C) and relative humidity (40%, 65%) treatments. (a) Turgor Loss Point (MPa) and (b) Stomatal Conductance (±1 S.E.; mmol* m^{-2} s^{-1}*)*

2.5. Discussion

Cold water and aridity interactively but distinctly affected the survival and ecophysiological traits of all three species of the Baja California mangroves, revealing potential implications for their latitudinal range limits. Conditions at this range edge are unique, and the combination of high VPD with cold sea surface temperature is widely considered challenging to mangroves. Under these extreme conditions, all three species have adopted dramatically different physiological strategies in terms of their capacity to take CO_2 out of the air and transpire water. These different physiological responses appear to fit their unique distributions at this range. Although these experiments suggest that the Baja black mangroves have some traits displaying adaptation to drought conditions (Fig. 2.7a), they cannot tolerate cold water (Fig. 2.6). This key difference in cold-water adaptation could be a main factor as to why the Baja black mangroves are not as far north as red and white mangroves, as field data suggests that the Baja coastline is uniquely characterized by very demanding environmental conditions: hot air, dry relative humidity, and seasonally cold water.

The water temperature and air and water temperature sensors placed in the field revealed much colder water temperatures and higher VPD than what was initially expected from gridded climate data analysis (Fig. 2.4). Water temperature at Punta Abreojos, the range limit, dipped below 15°C in many occasions during the winter and spring, which is significantly colder than minimum water averages often used in mangrove modeling studies (Quisthoudt *et al.*, 2012; Osland *et al.*, 2017b). These cold water temperature values can be explained by strong upwelling events, and can bring extremely cold water rushing into coastal lagoons and estuaries, lowering overall water temperature at the mangrove root level (Huyer, 1983; Zaytsev *et al.*, 2003). The Punta Abreojos range was also characterized by extremely high VPD due to the combination of hot air temperature and low relative humidity (Fig. 2.4). VPD values above 1 are often considered physiologically challenging to plant establishment and growth (Eamus *et al.*, 2013; Yuan *et al.*, 2019; Grossiord *et al.*, 2020). These differences between field measurements versus gridded climate data suggest caution when relying on gridded climate data to conduct species range modelling. Gridded climate data is often averaged over longer time scales, and does not take into account daily extremes (Donat *et al.*, 2014; Behnke *et al.*, 2016; Timmermans *et al.*, 2019). In this case, both station and Hobo data show extreme intra-day and inter-annual variability in terms of air temperature and humidity but also water temperature (Figs. 2, 3). Intra-day temperature variability is particularly important, as it has been shown that a single extreme event such as a hard overnight freeze can be a critical threshold (Cavanaugh *et al.*, 2013). Intra-day relative humidity is also significant in the context of mangrove growth under arid conditions. A recent study demonstrated that mangroves could survive the daily extreme temperature swings occurring in Baja by taking in water through the air where relative humidity is at its highest, during short windows before dawn or when coastal fog rolls out (Hayes *et al.*, 2020a). These extremes are critically important facets of mangrove life at highly dynamic range limits such as Baja California, where temperature or relative humidity values can change dramatically within a few hours. This suggests that incorporating finer-grained data would improve modelling and predictive efforts under future climate change scenarios.

2.5.1. Ecophysiological Explanations to Species-Specific Mangrove Distribution in Baja California

Mangroves have developed special physiological and morphological adaptations in order to grow in dynamic and highly saline intertidal conditions (Lugo & Snedaker, 1974; Chapman, 1976; Tomlinson, 1995). Baja California mangroves in particular must adapt to the harsh environmental conditions of the peninsula characterized by aridity (high VPD) and cold-water temperatures, and both variables were tested in these experiments. At low humidity (40%), all species experienced major mortality, while higher humidity seemed to favor red and white mangroves (Fig. 2.6). This white – red – black mangrove hierarchy in terms of adaptation to a combination of cold water and high VPD, mirrors their current distributions (Fig. 1). This suggests that dynamics at this range limit could have a physiological basis, explaining why red and white mangroves are at the range edge, but not black mangroves.

Stomatal conductance (Fig. 2.7b) results indicate that the northernmost species (red and white mangroves) have overall lower conductance rates, thus enabling them to grow slowly while conserving water and protecting themselves from high VPD. Meanwhile, black mangroves have different responses, as their conductance remains high, especially at warmer water temperatures, potentially leading to water stress under high VPD conditions. Black mangroves are the only species for which conductance declined with decreasing water temperature in the 45% room, showing signs of adaptive traits to drier conditions. Gas exchange is crucial to taking up CO_2 and thus photosynthesizing and growing, but detrimental in terms of water loss to the atmosphere (Pereira, 1995; Sánchez-Blanco *et al.*, 2009). The significantly higher stomatal conductance of black mangroves in high VPD and low water temperature conditions (Fig. 2.7b) exposes them to the risk of drying out, potentially compromising their survival. This different behavior may explain why black mangroves experience higher environmental stress than red and white mangroves at this arid Pacific range limit, and why they are found further south, where conditions are more favorable. Low conductance seems to be a paying strategy at this arid range limit, although it possibly results in little photosynthesis and slow growth (Carlson *et al.*, 2016; Liu *et al.*, 2018). This also explains the physical appearance of mangroves at the range limit, in which while being short and stunted, mangroves are remarkably dense and healthy (Fig. 2.8).

The physiological tolerance to aridity tested by turgor loss point analysis reveals opposite characteristics, as black mangroves have the lowest values, much below red and white mangroves. A low turgor loss point and leaf osmotic potential (the point at which leaves start wilting and die), has been successfully associated to plant tolerance to dry conditions (Rada *et* *al.*, 1989; Bartlett *et al.*, 2014; Kunert *et al.*, 2021). In this case, the low turgor loss point of the Baja black mangroves indicates their higher resistance to arid conditions. Figure 6a also demonstrates that the combination of cold water and aridity is increasing drought resistance, as TLP in cold water temperatures was significantly lower than the TLP of the same water temperatures in the humid room. TLP thus differs within species as a function of aridity and cold water. This tends to support the idea that TLP is species-specific but also plastic, and can respond to environmental stresses.

Although black mangroves appear more drought resistant (Fig. 2.7a), their ability to widely open their stomates in order to take in more CO_2 puts them at risk of drying out (Fig. 2.7b). Meanwhile, red and white mangroves might not be as adapted to drought, but their conservative stomatal conductance gives them an edge, enabling them to survive for longer. The Baja California range limit is an extreme environment in terms of air and water temperature and relative humidity, and conditions vary widely on a diurnal, daily and seasonal basis (Fig. 2.4). This would favor species with hyper conservative survival and growth strategies, and red and white mangroves seem to have adapted better than black mangroves. Our chronic experimental conditions, however, did not fully reflect field conditions encountered in Baja California, where air temperature and relative humidity can drastically change over a few hours. The daily swings in humidity and temperature (morning dew or afternoon fog) could be enough to rescue plants during highly stressful VPD conditions.

Figure 2. 8. *Red and white mangroves (Rhizophora mangle and Laguncularia racemosa) at the Punta Abreojos range limit. Co-authors Kyle Cavanaugh and John Parker are seen for scale.*

2.5.2. The Singularity of the Baja California Black Mangroves

Black mangroves and the genus Avicennia in general are considered a tough species, able to expand at poleward range limits, or to occupy hypersaline areas with sparse inundation (Duke, 1990; Suarez & Sobrado, 2000; Pickens & Hester, 2011; Madrid *et al.*, 2014). However, the Baja California mangroves appear to be much different than their global archetype. Our recent study comparing survival thresholds of black mangroves from the Atlantic (Florida) and Pacific coasts (Baja California) showed that the Baja black mangroves were not able to withstand even the slightest level of freezing air temperatures, while the Baja red and white mangroves were able to tolerate cold air much better and on par with their counterparts in the cold Florida ecotone (Cavanaugh *et al.*, 2015; Bardou *et al.*, 2021). This paper demonstrates that although the Baja black mangroves have some traits that suggest adaptation to drought conditions, they cannot tolerate cold air nor cold water. Such lower physiological tolerance for black compared to red mangroves in particular is entirely different than every other range edge ever investigated (Stokes *et al.*, 2010; Cavanaugh *et al.*, 2015; Cook-Patton *et al.*, 2015; Osland *et al.*, 2020; Kennedy *et al.*, 2021), and could explain why black mangroves are not found at this range limit. Conditions at the Punta Abreojos range edge are characterized by cold water, and our data shows several months where water temperature dipped below 15°C (Fig. 2.4), a temperature at which black mangroves have displayed major mortality (Fig. 2.6).

Higher humidity increases the stomatal conductance of black mangroves, especially for higher water temperatures, suggesting that elevated humidity could potentially favor black mangroves over red and white mangroves. Conversely, our results indicate that lower aridity can remove this advantage, supporting a physiological limitation to the Baja black mangroves at this extremely arid range limit. Under more humid conditions, the high gas exchange ability of black compared to red and white mangroves could be a competitive advantage, leading them to deal with challenging environmental conditions such as freezing temperatures or high salinity better than other species by promoting establishment, survival and faster growth. However, under cold water temperatures combined with high VPD, we speculate that higher stomatal conductance could lead to excess loss of internal water vapor, resulting in a quicker death, while the lower stomatal conductance of white and red mangroves, although slowing growth, might actually be more stable by preventing death.

The first chapter of this dissertation highlighted the fact that the Baja California black mangroves are fully freeze intolerant, and experienced significant mortality during simulated overnight freezes of as low as -0.5°C (Bardou *et al.*, 2021). Weather stations and our field air temperature data accounts for infrequent but nonetheless occurring freezing temperatures, from the current range at Punta Abreojos northward (Figs. 2, 3). Previous studies stated these single events, which have such potential for mass mortality, can be considered threshold events and are important drivers of mangrove range limits (Cavanaugh *et al.*, 2013). These determining events could have even more severe impacts in Baja California, where growth is so slow that mass mortality resulting from an overnight freeze could have significant and lasting consequences on range dynamics.

2.5.3. Phylogenic and Genetic Explanations to Intra-Specific Differences in Adaptation Strategies

Such a contrast between species could be a result of different phylogenic and genetic pathways. From a global standpoint, there are no indications that mangroves have all evolved from a single center of origin, and it is believed that mangroves may have evolved independently as many as 15 times (Ricklefs & Latham, 1993; Spalding *et al.*, 2010). Paleobotanical records suggest that mangroves have been present in the Americas since the Eocene, as mangrove species colonized the American Pacific coast from the Atlantic coast through the open Central American Isthmus (Rico-Gray, 1993; Graham, 1995, 2006; Rull, 1998). Rhizophora and Avicennia originated during the Eocene in the Indo-Malayan region, and they migrated to America through the ancient Tethys Sea; however, as this route closed during the Oligocene, new mangrove genera were unable to reach the Pacific coast of America. There are some reports that *Rhizophora mangle* actually colonized the Pacific before *Avicennia germinans*, resulting in the opportunity to accumulate more genetic variation (Takayama *et al.*, 2009). This could be an explanation for the observations of higher genetic diversity of *Rhizophora mangle*, in terms of allelic richness and heterozygosity (Riosmena Rodriguez *et al.*, 2014).

Low levels of genetic diversity for range populations away from their ancestral populations is a well documented phenomenon (Triest, 2008). Such characteristics have been thought to be the result of harsher environmental conditions, small population sizes, the scarcity of pollinators, and dispersal limitation (Maguire *et al.*, 2000; Giang *et al.*, 2003; Arnaud-Haond *et al.*, 2006; Krauss *et al.*, 2008). The mangroves of Baja California are geographically isolated due to the lack of appropriate habitats, and we would expect to find high levels of both inbreeding and genetic structure. However, the Riosmena Rodriguez et al. (2014) study on genetic structure did not find significant inbreeding. This low genetic diversity could be partially explained by sporadic founder events from a small number of individuals, which do not fully represent the ancestral gene pool (Sandoval-Castro *et al.*, 2012).

Sandoval-Castro *et al*. (2014) used genetic diversity data in order to demonstrate compelling evidence that unlike *Avicennia germinans, Rhizophora mangle* presence has been widespread throughout Baja California, and that the northernmost populations illustrated signs of recent colonizations. Alternatively, they determined that *Avicennia germinans* have an overall stronger potential for northward dispersal than *Rhizophora* (Sandoval-Castro et al., 2012, 2014). However, due to the longer presence of *Rhizophora* at the northern edge of mangrove populations, it can be expected that *Rhizophora* may serve as a better adapted gene pool than *Avicennia germinans* for latitudinal advances under climate change. Populations with a longer history at a site are likely to be better adapted to local conditions than founders from populations under more benign conditions. Under this scenario, even though *Avicennia germinans* is often thought of as the most successful species in terms of poleward migration (Osland *et al.*, 2017a, 2020; Langston & Kaplan, 2020), *Rhizophora mangle* would be better adapted for colonization at higher latitudes, as the climate becomes more favorable for mangrove establishment (Riosmena Rodriguez et al., 2014; Sandoval-Castro et al., 2012, 2014). On this Pacific coast range limit, red and white mangroves could also have an edge over black mangroves due to their genepool. It has been shown that red and white mangroves share more alleles with the East coast of North America, whereas black mangroves seem to resemble mostly tropical populations found further south in Central America (Sandoval-Castro *et al.*, 2012, 2014; Ochoa-Zavala *et al.*, 2019). By retaining more of tropical traits than red and white mangroves, black mangroves could thus be at a disadvantage, leading to poor resistance to cold temperatures.

Dispersal can also influence mangrove distributions along the Baja California coast (Sandoval-Castro *et al.*, 2012; Van der Stocken *et al.*, 2019a). *Avicennia* propagules have been shown to sink rapidly and to require stranding in order to establish, unlike *Rhizophora* and *Laguncularia* propagules (Rabinowitz, 1978; Van der Stocken *et al.*, 2019b). In the context of Baja California, where there are significant rocky and sandy streches between mangrove and salt marsh habitats, the potential for dispersal can be an important limiting factor (Jacobs *et al.*, 2004). As previously discussed, the current mangrove range in Punta Abreojos is characterized by challenging conditions for mangrove growth: high VPD, low precipitation, and cold water temperatures. Although water remains cold from the range edge moving north, conditions in terms of VPD and precipitation significantly improve. However, in order to reach the more suitable habitats such as the Laguna Ojo de Liebre, mangrove propagules would have to travel northwest around Punta Eugenia and fight prevailing southernly oceanic currents (Sandoval-

Castro *et al.*, 2012), before shifting their course eastward, towards the shore. The distinctive shape of the Baja peninsula coastline, divided in two in its central part by the prominent Punta Eugenia (Fig. 1), has been shown as being a significant geographical barrier to dispersal of coastal species such as kelp (Jacobs *et al.*, 2004). The dispersal limitation hypothesis is supported by the occurrence of *Avicennia marina* in Southern California, found in the Mission Bay salt marsh next to San Diego. These mangroves have been thriving since being introduced as an experiment between 1966-1969, despite efforts to eradicate them (Mission Bay Park Natural Resource Management Plan, 1990). Although non-native to North America, these invasive mangroves persisting in a Southern California salt marsh are suggesting that if mangrove propagules physically managed to reach such suitable habitats, they would likely be able to establish new range limits populations.

Another barrier to northbound migration of all three species lies within the shift in precipitation regimes, from summer-dominated to winter-dominated. There is evidence that on the Baja Peninsula, limited fresh water availability may well play a role in mangrove reproduction (Lot Helgueras *et al.*, 1975; Rico-Gray & Palacios-Rios, 1996). Mangroves, which are tropical trees, are known to reproduce during the rainy season (Hutchings & Saenger, 1987; Jiménez, 1988; Tomlinson, 1995; Fernandes, 1999). There are noteworthy variations between species, *Rhizophora mangle* has been shown to flower and reproduce after heavy-rainfall events, which makes it responsive all year long (Tovilla, 1998; Hernández & Belmonte, 2002). Meanwhile, for other species such as *Avicennia germinans*, reproduction is only restricted to a prolonged humid period, which makes flower production varying on a latitudinal gradient, depending on the length of the wet season (Duke, 1990; Clarke & Myerscough, 1993; Schmitz *et al.*, 2007). Riosmena-Rodriguez et al. (2015) analyzed the three Baja species, and found that under these arid conditions, flowering episodes of all species commonly occur between the months of June and July. The following month (August) marks the beginning of the rainy season, which is highly favorable to propagule development (Helgueras *et al.*, 1975; Tovilla, 1998; Riosmena Rodriguez *et al.*, 2014). Riosmena Rodriguez *et al.* (2015) also found that flowering of all three mangrove species had a positive correlation with relative humidity, and benefited from the tropical influence of monsoonal summer conditions. One major difference between what has been observed in wet tropical regions and Baja California is the high rate of propagule abortion in the fall, due to salt stress caused by an excessive aridity, and Riosmena-Rodriguez *et al.* (2015) observed that the propagules' survival rates dropped considerably during years of low pacific tropical activity, resulting in prolonged periods of drought.

2.5.4. Implications for the Pacific Coast Mangroves' Response to Climate Change

Environmental conditions affect the Baja California mangroves in many ways, as this arid range limit is characterized by the unique combination of high VPD (high temperature and low humidity), low precipitation, and cold-water temperatures. In the context of a changing climate, each of these variables will be impacted differently, resulting in potential shifts in mangrove range dynamics. The hypothetical effects of climate change in Baja California are not fully understood yet, however the consensus tends to be towards overall higher air temperatures (Cavazos & Arriaga-Ramírez, 2012). Sea-surface temperature is forecast to increase overall (Fumo *et al.*, 2020), however studies have also shown a recent increase in wind-driven upwelling along the Pacific coast (Snyder *et al.*, 2003; Arellano & Rivas, 2019). There is higher uncertainty in terms of predicting precipitation and relative humidity changes along the Pacific coast, as models trend toward large interannual variation (Cavazos & Arriaga-Ramírez, 2012). Recent studies have identified a significant overall increase in VPD around the world, which could be accelerating under a changing climate (Ficklin & Novick, 2017; Cárcer *et al.*, 2018; Yuan *et al.*, 2019). The role of humidity changes on species' response to climate change is not fully understood yet, but is critical in predicting mangrove range shifts along the arid Pacific coast. Range dynamics could shift significantly based on whether Baja California and Southern California become wetter or dryer, as well as whether the bulk of the moisture comes as winter storm or summer monsoon. The increase in hurricane activity, which is often seen as an important stepping stone facilitator of mangrove dispersal (Gillespie *et al.*, 2012; Kennedy *et al.*, 2020), could also have an important role to play.

Significant shifts in the Baja California mangrove ranges are plausible, and palaeoecological evidence supports this hypothesis. There have been reports of mangroves extending all the way to Southern California, potentially reaching San Diego during warmer periods of the mid-Holocene. A 2011 study revealed paleoecological evidence of the first documentation of mangrove migration as far north as San Diego in the mid-Holocene (Scott *et al.*, 2011). In this study, mangrove pollen was found in one Southern California salt marsh, Los Peñasquitos lagoon, north of San Diego. They retrieved *Laguncularia racemosa* and *Rhizophora mangle* pollen from around 3,000 to 6,000 BP. Evidence of mangrove presence in Southern California between 3,000 to 6,000 years BP could be the consequence of a warmer and wetter climate, which potentially allowed for both white and red mangroves to thrive much further north than they currently are. This supports the idea that mangroves might be able to expand northward again under more favorable (warmer and more humid) conditions along the Baja California and Southern California coasts.

2.6. Conclusion

Understanding and modeling future range shifts as a response to climate change is one of the central goals of ecology and biogeography. In the context of climate change, coastal ecosystems and the mangrove-salt marsh ecotone are of major biogeographical interest, as climatic factors such as increasing air and water temperatures could lead to even further mangrove expansion, significantly altering temperate coastal ecosystems. There is evidence of non-linear relationships between climate variables and mangrove habitat suitability (Devaney *et al.*, 2017; Cavanaugh *et al.*, 2018). As a result, these mangrove-salt marsh ecotones might be near climate-related thresholds. If this is the case, then relatively small changes in environmental conditions could lead to dramatic, landscape-scale ecological transitions, which will clearly have a large impact on the structure and function of these coastal wetlands. Understanding and modeling species response to climate change will require examining multiple macroclimatic biotic and abiotic variables, and the interactions between them. It cannot solely rely on wide-scale modeling data, and needs to take into account local environmental conditions, as well as species-specific adaptation traits and physiological responses.

2.7. References

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Chapter 3: Assessing Mangrove Cover Change and Dynamics in Madagascar (1972 to 2019)

3.1. Abstract

Much like mangrove dynamics around the tropics, studies on the mangroves of Madagascar have identified a steadily decline from the years 1970s to 2000s. However, current studies estimating Madagascar's mangrove extent and dynamics reveal important inconsistencies, and estimates widely vary, ranging from extents as low as 2,000 km^2 to over 4,000 km^2. The now fifty-years temporal coverage offered by Landsat satellites is making possible a repeatable and comparable method of classifying the island's mangroves to produce a comprehensive and up-to-date dataset.

This study applied unsupervised classifications to atmospherically and geometrically corrected images, in order to obtain a refined and comparable dataset of mangrove area in 1972, 1989, 1999, 2009 and 2019. Results showed an overall decrease of 8%, from 2935 km^2 in 1972 to 2699 km^2 in 2019. Mangroves decreased steadily between 1972 and 2009, annually losing in average 0.4% from 1972 to 1989, 0.39% from 1989 to 1999, and 0.21% from 1999 to 2009. This steady decline was mainly the consequence of anthropogenic action such as timber extraction and habitat loss due to human development, and was most evident in the northern part of the island. The southern tier of Madagascar saw a correlation between mangrove degradation and prolonged periods of drought, as detrimental environmental conditions lead to a loss of habitat.

In contrast, the last decade reflected a significant increase in mangrove area from 2009 to 2019 of 4.9%. Such reversal is the result of a combination of mangrove degradation slowing down, favorable environmental conditions, and significant efforts in the conservation,

preservation and reforestation of mangrove ecosystems since the early 2000s. This resulted in an overall increase in mangrove area, especially within the central and southern tiers of the island, and most regrowth has been observed in newly protected or regulated areas. The northern tier of the island did not seem to benefit from similar positive dynamics yet, and has been facing a continuing decline in mangrove area.

3.2. Introduction

Mangroves are an essential coastal ecosystem widely distributed along tropical and sub-tropical coasts across the globe (Hogarth, 1999; Spalding *et al.*, 2010). They are highly valuable, productive, and are considered amongst the most carbon-rich ecosystems (Chmura *et al.*, 2003; Kristensen *et al.*, 2008; Donato *et al.*, 2011; Alongi, 2012). In addition to this significant carbon sequestration ability, mangroves are providing a wide range of ecological, human and societal services. They protect and stabilize shorelines (Ewel *et al.*, 1998), serve as nurseries for commercially important fisheries and coral reefs (Aburto-Oropeza *et al.*, 2008; Walters *et al.*, 2008), and filter sediments and nutrients from upland runoff (Robertson & Phillips, 1995). Overall, the value of ecological and societal services provided by mangroves has been estimated at over US$1.6 trillion annually (Costanza *et al.*, 1998).

Despite their tremendous ecological and societal importance, mangroves have been extremely degraded as a result of anthropogenic activities such as clearing for urban development, aquaculture, farming and resource extraction, as well as deterioration resulting from pollution and sedimentation (Alongi, 2002; Duke *et al.*, 2007). In 2007, a consortium of scientists published a letter in *Science* raising concerns about “the prospect of a world deprived of mangroves, perhaps within the next 100 years” (Duke *et al.*, 2007). This alarmist communication was based on early 2000s global mangroves surveys, stating that every year 1% to 2% of mangroves disappear worldwide (Wilkie & Fortuna, 2003), a rate which was considered greater than or equal to declines observed in adjacent coral reefs and tropical rainforests (Valiela *et al.*, 2001; Duke *et al.*, 2007; Stone, 2007). It is estimated that between the 1980s and early 2000s, 20% to 30% of mangroves have been lost globally (FAO, 2007; Giri *et al.*, 2011). Although mangrove deforestation is widespread throughout the tropics, overall studies have identified higher rates of deforestation among developing countries (Spalding *et al.*, 2010; Giri *et al.*, 2011). Such widespread degradation has been happening in the context of a global scientific awakening to climate change-induced threats, and more specifically to the necessity of maintaining mangroves' ecosystem and societal services (Nicholls & Lowe, 2004; Alongi, 2008; Gilman *et al.*, 2008). The importance of mangroves for billions of coastal populations is perceived as increasingly critical, especially in terms of climate change mitigation (sea-level rise and storm impacts), and the sustainability of coastal resources and fisheries (Field *et al.*, 1998; Barbier, 2006; Alongi, 2008; Ostling *et al.*, 2009). As a result, a major focus has now been placed on protecting, restoring and reforesting these ecosystems (Walton *et al.*, 2006; Alongi, 2008; Bosire *et al.*, 2008). The most recent studies conducted in various parts of the tropics seem to indicate a decline in the rate of deforestation, and an increase in regeneration or reforestation due to conservation and replanting efforts (Walton *et al.*, 2006; Hamilton & Casey, 2016; Romañach *et al.*, 2018; Friess *et al.*, 2019).

Mangroves have been generally inaccessible, and the exhaustive study of their distribution and dynamics was marginal until the advance of geospatial technologies and the launch of the first civilian satellites for Earth observation in the 1970s (Gillespie *et al.*, 2008; Wang & Sousa, 2009). Based directly on satellite imagery, of which the quality and spatiotemporal resolution is steadily advancing, new studies of mangrove's extent and dynamics are being increasingly prevalent (Kuenzer *et al.*, 2011; Giri, 2016; Bunting *et al.*, 2018; Wang *et al.*, 2019). The majority of the research which has relied on large-scale remote sensing studies, has prominently focused on mangrove cover loss, and often reported alarming rates of deforestation (Duke *et al.*, 2007; Giri *et al.*, 2011). While it is clear that anthropogenic action plays a significant role in mangrove loss and degradation, it has also been shown that long-term patterns of mangrove decline and degradation are reflecting natural fluctuations (Duke *et al.*, 2017; Bulleri *et al.*, 2018; Mafi-Gholami *et al.*, 2020). Furthermore, it has now been shown that human interference, such as protection, restoration and replantation programs, can also promote positive dynamics (Bosire *et al.*, 2008; López-Portillo *et al.*, 2017; Romañach *et al.*, 2018; Fent *et al.*, 2019).

Twenty years have passed since the turn of the century, and we investigate whether mangroves are still critically under threat, or whether a higher awareness of the ecological and societal services they provide increased their protection, or at least decreased the rate of mangrove degradation. We have chosen to focus our analysis on Madagascar, which can be considered as a representative benchmark. This island is a low-income developing country displaying astonishingly high biological diversity (Myers *et al.*, 2000). However, environmental degradation is critically threatening its biodiversity. Madagascar is often considered an "ecological jewel", as it is one of seven countries in the world that houses an exceptional ecological richness (Ramiarantsoa *et al.*, 2012). The island's remarkable biodiversity, endemism, but also high level habitat loss, lead it to be ranked as one of the world's biodiversity hotspots (Myers *et al.*, 2000). Madagascar has been subject to a mainly negative narrative regarding its environmental degradation since the early twentieth century. This narrative continues to have a profound effect on how we perceive the Malagasy environment (Kull, 2000; Pollini, 2010; Quemere *et al.*, 2012). However, as a result of its exceptionally renown biodiversity, Madagascar has benefited from global awareness, and we are starting to see positive impacts pertaining to the protection and conservation of its environment (Ferraro, 2002; Duffy, 2006b,a; Ratsimbazafy *et al.*, 2019).

The Malagasy mangroves have also benefited from this increasing environmental awareness, as scientists, non-governmental and for-profit organizations began focusing their attention on these ecosystems, and initiating efforts towards their preservation, restauration and replantation (Clausen *et al.*, 2010; Jones *et al.*, 2014; Benson *et al.*, 2017; Herr *et al.*, 2017). Despite increasing interest, island-wide mangrove dynamics are mostly uncertain. Although estimations of mangrove area vary widely, from as low as 2,000 km^2 to up to 4,500 km^2, all studies agree that the Madagascar mangroves have been widely deforested (Giri & Muhlhausen, 2008; Jones *et al.*, 2016a). However, there is a high disparity amongst studies, as dynamics varied significantly depending on geographical area and time period studied (Giri & Muhlhausen, 2008; Rakotomavo & Fromard, 2010; Renoux, 2011). This lack of certainty on the present status and of temporal dynamics of mangroves ecosystems limits conservation and management programs and strategies (Rasolofoharinoro *et al.*, 1998; Friess & Webb, 2011).

The goal of this study is to apply a rigorous and repeatable remote sensing method to examine regional mangrove dynamics over a multi-decadal timeframe, enabling us to better identify and compare mangrove dynamics. Our work capitalizes on the benefits of having continuous remote sensing coverage for over fifty years, and seeks to provide a clear picture of multi-decadal mangrove dynamics in Madagascar as we ask the following questions. Are we seeing evidence of widespread mangrove loss since the 1970s, and if so, are these following certain patterns? Are dynamics similar within different regions, and can we infer whether they are mainly due to human action or natural causes? Have the recent attempts at preserving, protecting and replanting mangroves had an impact at slowing down or even reversing negative trends?

This work was conducted using a combination of remote sensing and geospatial analyses. First, we will use remote sensing of Landsat satellite imagery to assess the extent and change of mangrove forest coverage in Madagascar between 1985 and 2019. We will be taking advantage of recent improvements in the geographic and atmospheric correction of Landsat imagery, which enables consistent classification of time series data (Vuolo *et al.*, 2015; Vermote *et al.*, 2016). Second, we will identify sub-regions of mangrove change that stand out against overall trends and whether these are positive or negative. Lastly, we will discuss the bio-physical and socio-economic processes that may contribute to Madagascar's mangrove forest mosaic and heterogenous dynamics.

3.3. Materials and Methods

3.3.1. Madagascar: A Biodiversity Hotspot Under Stress

Madagascar is the world's fifth largest island, and is constantly ranked as one of the ten poorest countries in the world (Fritz-Vietta *et al.*, 2011). It is mostly known for its biodiversity, caused by biogeographical isolation resulting in exceptional endemism and a variety of climates (Dandouau, 1922; Flacourt & Allibert, 2007). The island's extremely rich biodiversity was broadly promoted when it was designated as one of the world's 25 biodiversity hotspots, as a place with exceptional species richness and a large concentration of endemic species that is undergoing an exceptional loss of habitat (Myers *et al.*, 2000). The island owes this fame to its exceptional biodiversity as it is estimated that about 90% of plants (approximately 10,000) and animals are endemic (Ganzhorn *et al.*, 2001; Goodman & Benstead, 2005). However, this diversity is critically threatened, mostly by the overexploitation of timber and mining resources, and the expansion of agricultural and grazing areas, often using slash-and-burn agriculture (Green & Sussman, 1990; Kull, 2000; Harper *et al.*, 2007a). Madagascar's environment is perceived as being under such intense pressure that it is commonly referred to as one of the "hottest" biodiversity hotspots (Ganzhorn *et al.*, 2001). While there is no doubt that the Malagasy environmental richness is under threat, it is important to note that such considerations are deeply rooted in a strong narrative about Madagascar's environmental degradation. This discourse is based on the idea that the island was fully-forested prior to human settlements, and that the patchwork of primitive rain forests and exacerbated erosion we experience today is the result of anthropogenic degradation (Humbert, 1927; Kull, 2002; Pollini, 2010). However, recent studies combining paleobotany, archaeology, palynology and paleontology have unveiled new documentation that challenges this belief of a fully-forested primitive island which has been tirelessly deforested (Kull, 2000; Klein, 2002; Pollini, 2010; Quemere *et al.*, 2012). These may have helped combat the notion of alarmist environmental degradation of the island that remains under significant threat.

3.3.2. The Mangroves of Madagascar, a Critical Ecosystem Often Overlooked

While most of the ecological focus has been placed on Madagascar's eastern side and its extensive tropical primitive forests (Harper *et al.*, 2007a), the Malagasy mangroves are consequent and are amongst the most mangrove-rich countries in Africa, accounting for about 15% of the African mangroves (FAO, 2007; Spalding *et al.*, 2010). Mangroves, by creating an interface between terrestrial and marine environments, have a fundamental ecological role in maintaining healthy coastal ecosystems (Duke, 1992; Tomlinson, 1995; Kathiresan & Bingham, 2001). Mangroves are critical to the Malagasy coastal populations which largely rely on them. These communities have maintained ancestral and traditional lifestyles characterized by a very close relationship with mangroves, using them daily as part of a subsistence economy (Rasolofo, 1997; Iltis & Ranaivoson, 1998). Mangroves have an essential role in supporting coastal food webs. The nature of its substrates, and the multitude of wave protected channels provide refuge, nursery and food for many species of fish, mollusks and crustaceans (Rasolofo, 1997; Goedefroit *et al.*, 2002; Chaboud, 2006; Renoux, 2011). Mangroves are also a main provider of wood and timber supply, especially in coastal areas further south were a prolonged dry season makes steadily harvesting vegetation challenging. Due to their linear shape, as well as their rot and termite resistant properties, mangroves provide highly valuable timber resources used in traditional houses, fencing, canoe building, and fish traps (Iltis & Ranaivoson, 1998; Renoux, 2011). Additionally, coastal communities often derive charcoal from mangrove wood as cooking fuel. This dense and slow-burning wood delivers good quality charcoal, and is often favored (Iltis & Ranaivoson, 1998; Renoux, 2011). Lastly, mangroves offer critical protection against storms, coastal erosion, and sea-level rise (Alongi, 2008; Clausen *et al.*, 2010).

Madagascar’s mangroves are composed of nine different species (see Appendix 1 for further description), and cover about one quarter of the island’s coastline (Fig. 3.1). They are primarily found along the west coast, away from dominant easterly trade winds, and along Madagascar’s main bay and estuaries. Their distribution follows a latitudinal gradient, as the largest and most diverse species' stands are found on the northern and central areas, under a more humid climate. Although their habitat is characterized by fairly even water and air temperatures, mangroves do encounter a strong rainfall gradient. Rainfall is abundant over the northern segment of the island (around 2,000 mm). Meanwhile, the dry season becomes longer and more pronounced moving south, as precipitation decreases significantly to averages as low as 350 mm, resulting in mangrove ecosystems losing size and diversity (Kiener, 1972; Lebigre, 1990; Kramkimel *et al.*, 1992).

The Malagasy mangroves have long been overlooked and even marginalized, often perceived negatively as unhealthy swamp-like breeding grounds for mosquitoes and diseases (Lebigre, 1990). Most Malagasy mangroves are located in particularly remote areas, making them extremely difficult to access. As a result, they have been understudied for the majority of the 20th century. This strenuous work has only recently been facilitated with the help of advances in mapping and geospatial technologies that allowed for remote sensing data to make studying them possible (Heumann, 2011; Kuenzer *et al.*, 2011). Earliest field and aerial surveys of the twentieth Century estimated mangrove cover at around 3,500 to 4,000 km^2 (Perrier de La Bâthie, 1921; Humbert & Cours Darne, 1964) and mangrove dynamics were seen as fairly stable, and possibly slightly improving throughout their seaward side, due to encroachments into newly-formed sediment banks (Kiener, 1972; Kramkimel *et al.*, 1992; Rakotomavo & Fromard, 2010). Mangroves started to gain more attention in the 1970s, following the first extensive studies (Lebigre, 1990; Iltis & Ranaivoson, 1998). These studies began to raise awareness about the environmental and societal importance of mangroves for the island. In 2002, the World

Wildlife Fund (WWF) in partnership with the Missouri Botanical Garden published the report *The Global 200: Priority ecoregions for global conservation.* In this report, the Malagasy mangroves were considered as one of the flagship marine ecoregions representing the mangroves' exceptional biodiversity, and were ranked as "critical or endangered", the highest level of threat (Olson & Dinerstein, 2002). In 2007, a global report from the Food and Agriculture Organization of the United Nations (FAO), classified Madagascar as one of the five countries suffering the most from mangrove deforestation within the 1980-2005 period (FAO, 2007).

Figure 3. 1. *Mangroves and protected areas distribution throughout Madagascar, as of 2019.*

To this day, there are still contradicting reports calculating mangrove area in Madagascar. Multiple attempts at estimating mangroves' extent have been conducted, and their results have varied widely over the years, ranging from 4,500 km^2 to as low as 2,200 km^2 (see Fig. 3.2 for a list of all compiled studies). Such variation may be the result of each study's differing characterization of mangroves, since some studies may categorize salt flats (known as *tannes* in Madagascar) as part of the mangroves (Renoux, 2011). Different research methods (i.e. extrapolations from fieldwork, aerial surveys, remote sensing) have also played a role in the varying results. Furthermore, the mangroves of Madagascar are an extremely dynamic ecosystem that can change from one year to the next due to shifts in sediment loads, and even on a daily basis since the tides' amplitude can be very pronounced (Fig. 3.3). Such dynamics pose a challenge to taking accurate and consistent measurements.

There have been localized attempts at studying mangrove dynamics within specific areas of interests, such as major bays and estuaries. These studies have accounted for a variety of outcomes, from critical deforestation to underscoring areas of tangible progression (Guillet *et al.*, 2008; Rakotomavo & Fromard, 2010; Renoux, 2011; Jones *et al.*, 2015, 2016b). An island-wide study on mangrove dynamics was conducted in 2008 by Giri *et al*, using Landsat data to map mangrove distributions from 1975 to 2005. They identified an overall decline by 7% to 2,797 km^2 in 2005, but also contrasted regional dynamics within years and geographic areas (Giri & Muhlhausen, 2008). Across all studies, the overall consensus tends to point to widespread degradation due to anthropogenic activities such as resource extraction for firewood, timber and mining, land conversion for agricultural and urban development, and over-sedimentation often due to sediment runoff from upstream deforestation (Iltis, 1998; Giri & Muhlhausen, 2008; Rakotomavo & Fromard, 2010; Renoux, 2011; Scales & Friess, 2019).

Island-wide estimations and dynamics remain vague to this day (Fig. 3.2). By analyzing the early 2000s, which were the focus of several global remote sensing studies, we see some disagreement regarding mangrove extent. The two broadly-used worldwide mangrove datasets (Spalding *et al.*, 2010; Giri *et al.*, 2011) estimated Madagascar's mangrove extent as respectively 3,006 km^2 in 2003, and 2,377 km^2 in 2000, a difference of about 600 km^2. Such difference can be explained by the three years difference in data analysis, but would reflect a net increase of 600 km^2 if it were to be the case. Additional estimations from NGOs or International Agencies such as the FAO showed an even wider range of numbers (Fig. 3.2).

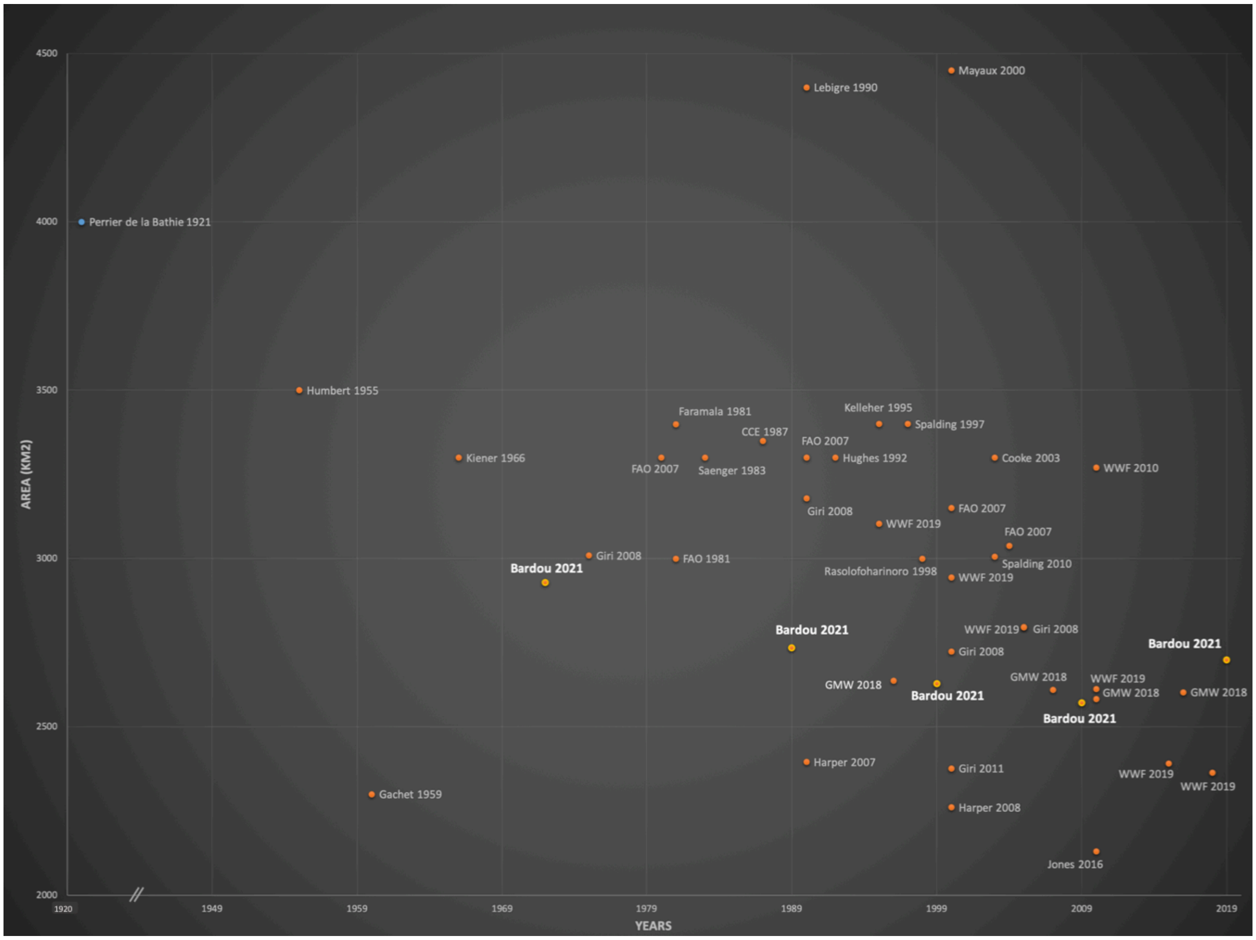


Figure 3. 2. *Comparison of studies estimating mangrove cover change in Madagascar throughout the century. The date following the author's name is the publication date. The blue dot represents the first estimation, conducted in 1921 from Perrier de La Bâthie. Our study is represented by orange dots.*

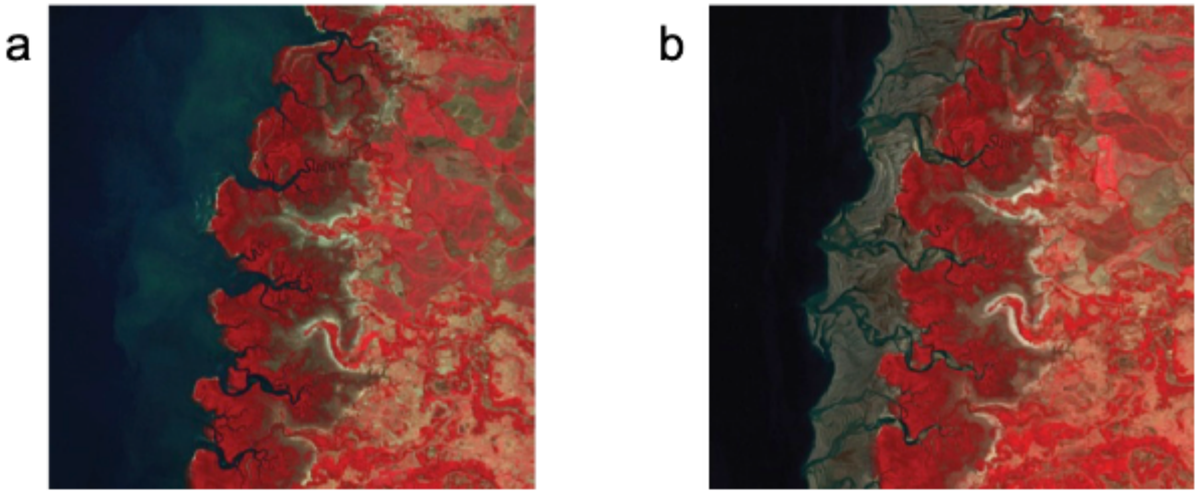


Figure 3. 3. *Comparing two Landsat 5 images at high and low tides. a- Picture taken on July 22d 2011, during high tide (water height 3.31m). b- Picture taken on August 30th 2008, during low tide (water height 0.71m). Color composite of near-infrared, red and green bands.*

3.3.3. Remote Sensing Analysis

We analyze a time-series of Landsat imagery every decade from 1972 to 2019, with the exception of the years between 1972 and 1989, as we were not able to obtain sufficient data due to the lack of imagery. Our overarching goal was to begin by examining processes rather than known patterns, and developing an understanding of mangrove dynamics from this starting point (Laney, 2004). In our case, this allowed for a better identification of processes, and the assessment of whether the intensity of mangrove degradation corresponds with periods of intensified environmental or anthropogenic stress. This approach was informed by remote sensing work underlining the importance of examining spatiotemporal variability (Walsh *et al.*, 2003; Crews-Meyer, 2006; Mishra *et al.*, 2016).

Downloading sufficient cloud-free satellite images that covered the entire island was a challenge in this area of the tropics, since the availability of cloud-free satellite scenes can be sparse. In order to minimize seasonal impacts, all images were collected during the dry season (from May to September), when cloud cover is minimal and the contrast between green mangrove and the surrounding drier tropical landscape is at its strongest. We monitored changes in mangrove extent using a combination of Landsat 1 Multispectral Scanner System, Landsat 5 Thematic Mapper, Landsat 7 Enhanced Thematic Mapper, and Landsat 8 Operational Land Imagery. Images downloaded for Landsat 5, 7 and 8 have a spatial resolution of 30 meters. The first island-wide survey based on Landsat 1 was at a coarser spatial resolution of 60-meters pixels. We only downloaded atmospherically corrected Landsat Surface Reflectance data which met strict quality and cloud cover standards, from the USGS Earth Resources Observation and Science Center Global Land Survey, as well as Landsat Collection 2 Archives. This data choice enabled us to take advantage of recent improvements in atmospheric correction of Landsat imagery (Gutman *et al.*, 2013; Vuolo *et al.*, 2015; Vermote *et al.*, 2016), facilitating consistent classification of time series data. Each Landsat tile covers an area of approximately 185 km × 185 km, and in order to cover the entire west and north coasts, we downloaded 15 tiles. We obtained imagery during the following years: 1972, 1989, 1999, 2009, and 2019. These dates reflect the availability of cloud-free imagery, which was very sparse until the launch of Landsat 8 in 2013. We conducted our remote sensing analysis using ENVI 5.5 (L3Harris Geospatial, Boulder, Colorado), while subsequent geospatial analysis and mapped results were produced using ArcMap 10.7 (Environmental Systems Research Institute, Redlands, CA).

This work covers a substantial geographical extent encompassing highly diverse habitats, from dense tropical rain forest to shrubs and open grasslands. We first extracted a subset of each

Landsat tile to include only low-lying coastal areas where mangroves are present. We used 30-meter spatial resolution elevation data from the Shuttle Radar Topography Mission (SRTM), in order to isolate pixels which were below 20 meters, thus excluding upland dense tropical forests which can often be misclassified as mangroves. We also applied a coastline mask to our Landsat scenes to address any confusion from sediments-rich water pouring out of mangroves, which could otherwise overwhelm our classifications. We used a Madagascar coastline shapefile, which enabled us to isolate anything that was not land. We allocated a 1-km buffer to this coastline mask, in order to include any area of mangrove which may have formed off the coast, at the mouth of bays and estuaries. Combining these two resulted into a final mask covering only a thin strip of coastline encompassing our study area, including only low-lying coastal areas.

The mapping of mangrove extent was performed by operating an unsupervised classification on each image subset, using the ISODATA clustering algorithm. Each pixel was divided into a range of 50 to 75 spectral cluster classes, based on a change threshold of 10%. The minimum number of pixels in each class was set to 1000, and the classification was instructed to run for ten iterations. We manually grouped the resulting spectral clusters into mangrove and non-mangrove classes, based on visual interpretation. The selected mangrove classes were then combined and imported into the ArcMap software for visual representation and statistical analysis. We replicated this analysis tile by tile, then merged all mangrove outputs within a common shapefile covering their entire island for a given year. We performed a dissolving operation in order to avoid overestimations due to overlapping data around each tile's edges. We conducted a final data cleanup at the island-wide level, by overlapping all mangrove shapefiles and looking for outlier pixels which may have occurred in forested areas close to the coast. We then calculated the total area covered by mangrove forests for every decade available as well as individually for several areas of interest. Lastly, we calculated the percent change in mangrove area between each of these time periods for each of our study regions.

Once complete and accurate datasets were available, we calculated mangrove cover by decade. We first intersected two consecutive dates (i.e. 2009 and 2019) to obtain a layer of stable mangroves. We then subtracted areas where mangroves were present only for one of the given years (i.e. 2009 or 2019), providing us with data on the mangroves lost (i.e. 2009 only), and gained (i.e. 2019 only). We conducted these comparisons for each timeframe available: 1972-2019, 1972-1989, 1989-1999, 1999-2009, 2009-2019.

In order to supplement our data analysis, we divided our coverage datasets into two sub-sections: by region and by protected areas. We used administrative boundaries to subset mangroves by regional extent, thus obtaining mangrove dynamics by region. We also used a dataset listing all of Madagascar's protected areas to collect mangrove dynamics within and without protected areas. Administrative data on regions and protected areas was obtained from the Madagascar Protected Area System (SAPM) as well as Protected Planet.

3.4. Results

3.4.1. Overall Trends in a Mangrove Extent

Mangrove area in Madagascar followed a diminishing trend from 2935 km^2 in 1972 to 2699 km^2 in 2019 (Fig. 3.4). We observed a steady and linear decline from 1972 to 2010, however, mangrove loss has slowed over time, with annual rates of 0.4% from 1972 to 1989, 0.39% from 1989 to 1999, and 0.21% from 1999 to 2009 (Fig. 3.5). he decade 2009-2019 featured a significant rebound, and mangroves gained 4.96% overall (Fig. 3.5). This positive change is the result of a slowing down of lost mangrove, as well as an increase in mangrove area.

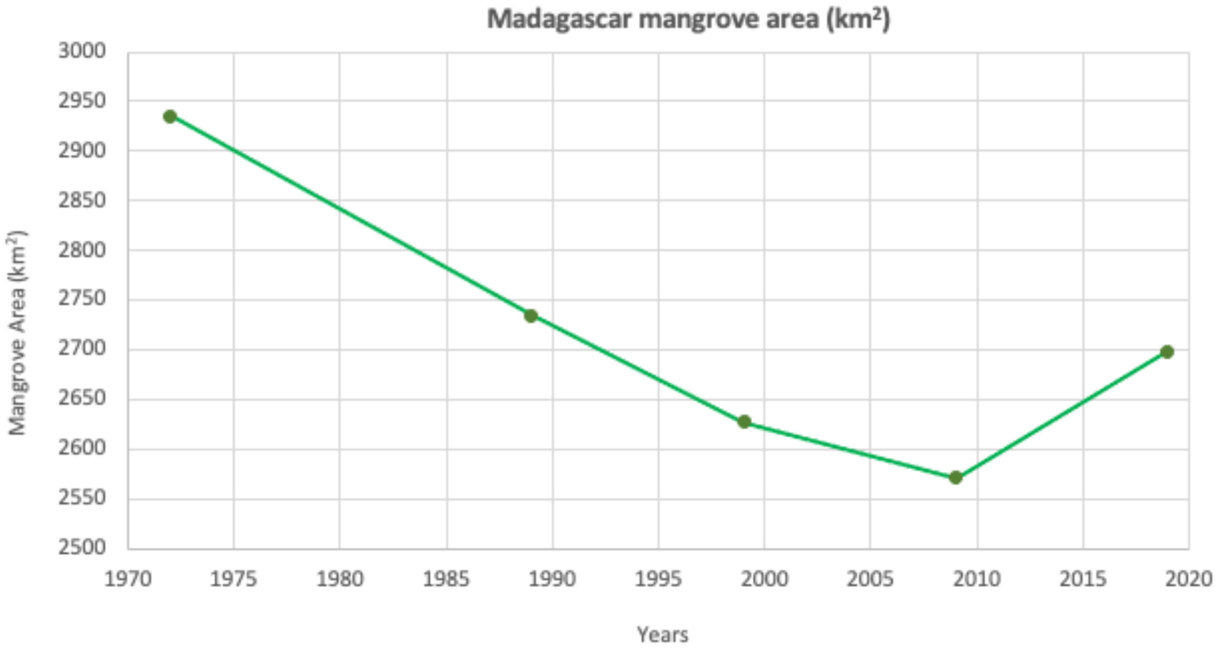
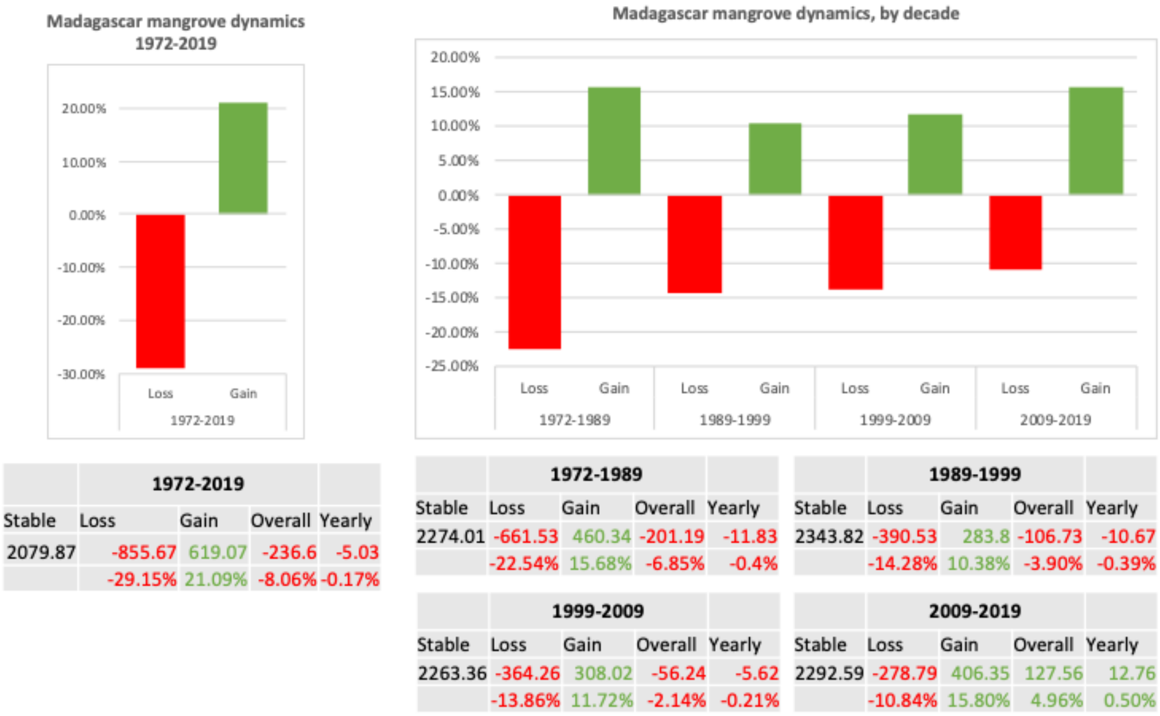


Figure 3. 4. *Madagascar mangrove area in 1972, 1989, 1999, 2009 and 2019.*



	1972-2019			
Stable	Loss	Gain	Overall	Yearly
2079.87	-855.67	619.07	-236.6	-5.03
	-29.15%	21.09%	-8.06%	-0.17%

	1972-1989			
Stable	Loss	Gain	Overall	Yearly
2274.01	-661.53	460.34	-201.19	-11.83
	-22.54%	15.68%	-6.85%	-0.4%

	1989-1999			
Stable	Loss	Gain	Overall	Yearly
2343.82	-390.53	283.8	-106.73	-10.67
	-14.28%	10.38%	-3.90%	-0.39%

	1999-2009			
Stable	Loss	Gain	Overall	Yearly
2263.36	-364.26	308.02	-56.24	-5.62
	-13.86%	11.72%	-2.14%	-0.21%

	2009-2019			
Stable	Loss	Gain	Overall	Yearly
2292.59	-278.79	406.35	127.56	12.76
	-10.84%	15.80%	4.96%	0.50%

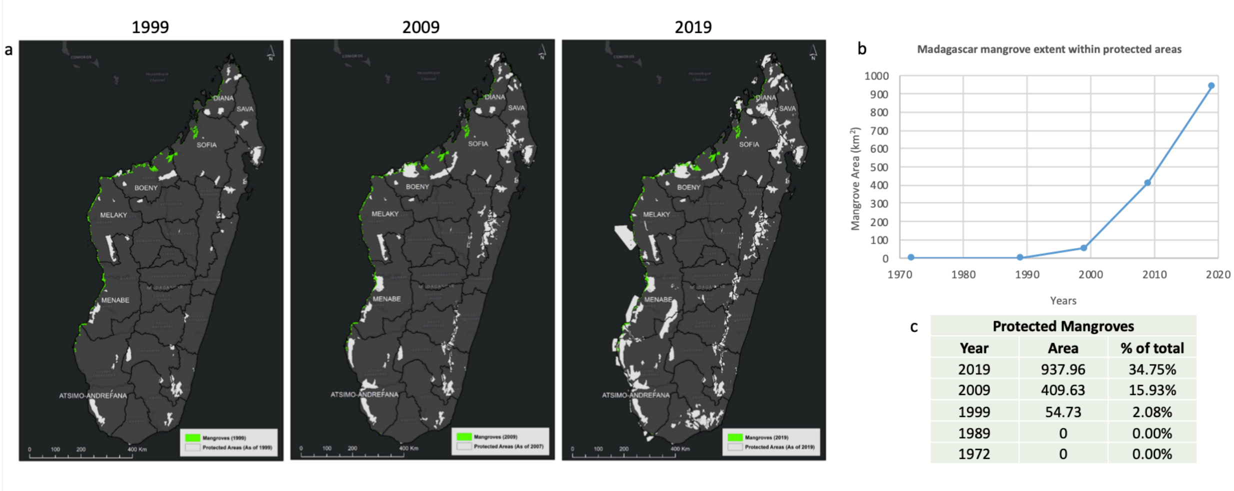
Figure 3. 5. *Fifty years of Madagascar mangrove dynamics from 1972 to 2019 and divided by decadal changes. Values for stable, lost and gained mangrove are in square kilometers.*

3.4.2. The Impacts of Protected Areas on Mangrove Dynamics

Protected areas in Madagascar were very sparse until the early 2000s, where they benefited from significant development (Fig. 3.6a). This development encompassed mangrove areas, and while there were only about 55 km^2 of mangroves within protected areas in 1999, there was a dramatic rise in the following two decades, and as of 2019 there were 938 km^2 of mangroves within protected areas across the island (Figs 3.6b, 3.6c).

The strong rebound in mangrove area in the years 2010s seemed to have been facilitated by mangrove conservation and protection, as mangroves within protected areas gained 8.7%

(Fig. 3.7a). Outside of protected areas, mangroves did increase as well, but to a much lesser extent, gaining 3% from 2009 to 2019 (Fig. 3.7b).



Protected Mangroves		
Year	**Area**	**% of total**
2019	937.96	34.75%
2009	409.63	15.93%
1999	54.73	2.08%
1989	0	0.00%
1972	0	0.00%

Figure 3. 6.

(a) *Madagascar's Protected Areas system as of 1999, 2009, and 2019.*

(b) *Evolution in mangrove area (km2) within protected areas.*

(c) *Area and change percentage of total mangroves within protected areas.*

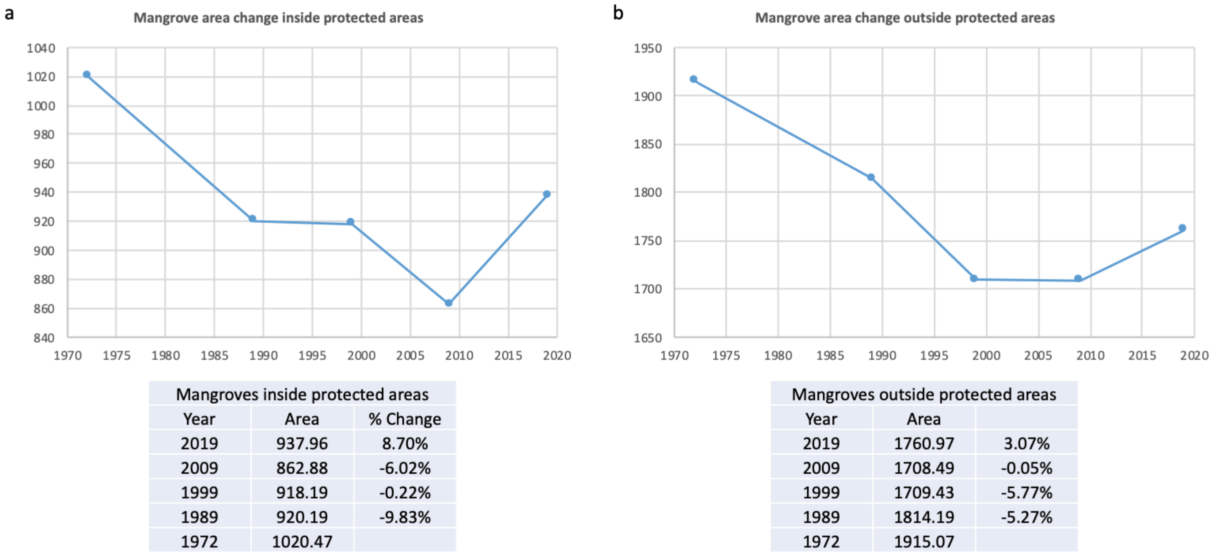
3.4.3. Contrasted Regional Mangrove Dynamics from North to South

Dividing mangrove change by administrative region allows us to see a change of pattern moving from north to south (Fig. 3.8). With the exception of Sava, which has very little mangroves (25 km^2), the northernmost regions of Diana, and Sofia have faced a long declining trend. Although they experienced a small rebound in the 1999-2009 decade, they lost ground once again during the last decade. Diana and Sofia, where the sharpest declines have been observed, were the regions with the least protected mangroves (respectively 14% and 11% in 2019). These are also densely populated regions (46.2 and 29.9 habitants per km^2). Meanwhile, the regions in which we observed the strongest rebounds were the central and southern regions, which significantly benefited from more protection (Fig. 3.8). Regions with the smallest population density, Melaky (8 habitants per km^2) and Menabe (15 habitants per km^2), demonstrated the strongest rebounds in the last decade, with mangrove area expanding 12.5% and 17.7 %.

Satellite images and cartographic representations reflect these regional dynamics in a more qualitative way. In the northern regions such as Diana, mangrove loss appears widespread, and continued well into the last decade (Fig. 3.9). Within central Madagascar, we focused our analysis on the Boeny region, which hosts most of the island's mangroves (Fig. 3.8), including the vast Bombetoka and Mahajamba Bays (Fig. 3.10). Contrasted dynamics are observed in this area, as major areas of the inland fringe have been lost, while the outside fringe along the coast and estuaries has seen a large increase in mangroves (Fig. 3.10). In the Boeny region, which holds multiple protected areas, we compared decadal dynamics both in terms of mangrove area and development of protected areas (Figure 11) that illustrates a very dynamic situation, where mangroves were considerably impacted between 1972 and 1989 (Fig. 3.11a). This negative trend then slowed down in the years 1989-1999, especially in the southern part of the region, where the first protected areas were implemented (Fig. 3.11b). Over the next two decades, as protected areas became more and more implemented, we see a persistent trend characterized by the interior mangrove losing area, but to a lesser extent (Figs. 3.11c and d).

From 1972 to 1989, the Maroambitsi Bay lost significant areas (Figs. 3.11a and12) However, by 1999 most of it had recovered (Figs. 3.11b, Fig 3.12). The 2019 image even showed prominent areas of progression along its edges and in the outer parts of the bay, to extents larger than those of 1972 (Fig. 3.12).

Mangrove dynamics in the southern parts of the island are characterized by significant loss until the 2009-2019 decade (Fig. 3.8). There still is evidence of mangrove degradation along the interior fringe (Figs. 3.13, 3.14), both figures show subsequent gains in mangrove area on its outside fringe, along the coast and at the mouths of major rivers (Figs. 3.13 and 3.14). These new mangrove settlements are a central explanation towards positive increases in mangrove area in southern Madagascar.

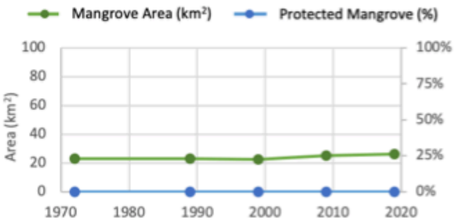


Mangroves inside protected areas		
Year	Area	% Change
2019	937.96	8.70%
2009	862.88	-6.02%
1999	918.19	-0.22%
1989	920.19	-9.83%
1972	1020.47	

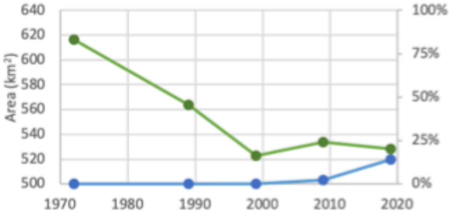
Mangroves outside protected areas		
Year	Area	
2019	1760.97	3.07%
2009	1708.49	-0.05%
1999	1709.43	-5.77%
1989	1814.19	-5.27%
1972	1915.07	

Figure 3. 7. *Mangrove cover change inside* ***(a)*** *and outside* ***(b)*** *protected areas from 1972 to 2019.*

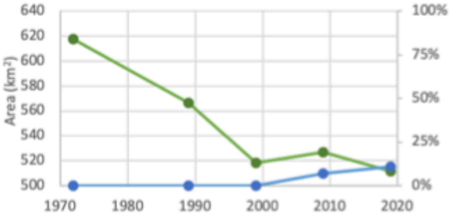
Region			Population	Pop. Density
Sava			1,123,013	44.0
Year	Area	Dynamics (%)	Protect. Mang.	% protected
2019	25.92	2.94%	0	0.00%
2009	25.18	12.66%	0	0.00%
1999	22.35	-3.08%	0	0.00%
1989	23.06	0.70%	0	0.00%
1972	22.9		0	0.00%



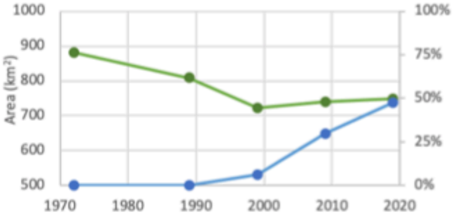
Region			Population	Pop. Density
Diana			889,736	46.2
Year	Area	Dynamics (%)	Protect. Mang.	% protected
2019	528.33	-1.01%	74.15	14.03%
2009	533.72	2.08%	11.91	2.23%
1999	522.83	-7.23%	0.42	0.08%
1989	563.56	-8.53%	0	0.00%
1972	616.13		0	0.00%



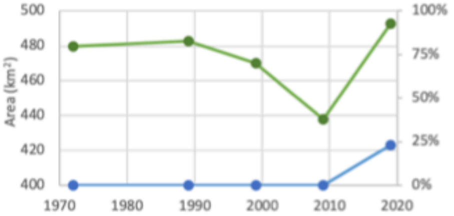
Region			Population	Pop. Density
Sofia			1,500,227	29.9
Year	Area	Dynamics (%)	Protect. Mang.	% protected
2019	511.76	-2.87%	55.98	10.94%
2009	526.89	1.68%	36.58	6.94%
1999	518.18	-8.55%	0	0.00%
1989	566.6	-8.24%	0	0.00%
1972	617.45		0	0.00%



Region			Population	Pop. Density
Boeny			931,171	30.0
Year	Area	Dynamics (%)	Protect. Mang.	% protected
2019	747.82	1.11%	355.13	47.49%
2009	739.63	2.22%	219.09	29.62%
1999	723.6	-10.52%	45.69	6.31%
1989	808.69	-8.32%	0	0.00%
1972	882.11		0	0.00%



Region			Population	Pop. Density
Melaky			309,805	8.0
Year	Area	Dynamics (%)	Protect. Mang.	% protected
2019	492.63	12.46%	114.09	23.16%
2009	438.05	-6.80%	0	0.00%
1999	470.01	-2.63%	0	0.00%
1989	482.72	0.63%	0	0.00%
1972	479.72		0	0.00%



Region			Population	Pop. Density
Menabe			700,577	15.2
Year	Area	Dynamics (%)	Protect. Mang.	% protected
2019	387.72	17.70%	246.41	63.55%
2009	329.4	-15.43%	140.16	42.55%
1999	389.49	5.18%	8.62	2.21%
1989	370.32	-17.67%	0	0.00%
1972	449.8		0	0.00%

Region			Population	Pop. Density
Atsimo-Andrefana			1,799,088	27.2
Year	Area	Dynamics (%)	Protect. Mang.	% protected
2019	135.13	7.65%	100.06	74.05%
2009	125.53	-6.01%	0.13	0.10%
1999	133.55	-4.22%	0	0.00%
1989	139.43	-23.51%	0	0.00%
1972	182.28		0	0.00%

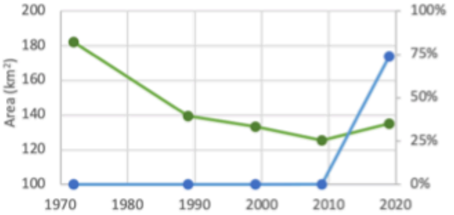


Figure 3. 8. *Regional mangrove dynamics. Demographic data (population and population density per region as of 2018 census survey), total mangrove area and change by region, and amount of mangroves within protected areas. Regions are organized from north to south.*

3.5. Discussion

Throughout Madagascar, remote sensing imagery over the past fifty years shows that mangroves have been significantly deforested. These findings confirm previous work highlighting the fact that Madagascar's mangroves were being deforested at concerning rates (Giri & Muhlhausen, 2008; Jones *et al.*, 2016a). However, we have seen that negative trends have significantly slowed throughout the island over the last two decades, as we are now witnessing an increase in overall mangrove area for the first time. This reversal appears to be due to a decrease in mangrove degradation and deforestation, as well as an overall increase in mangrove area resulting from both anthropogenic and environmental consequences.

3.5.1. Widespread Mangrove Deforestation is Slowing Down

Madagascar's mangroves experienced a loss from the 1970s to 2000s (Fig. 3.4). These negative dynamics were mostly caused by anthropogenic action, as mangroves were degraded and deforested, and reflect what has been observed in other developing countries across the tropics (Duke *et al.*, 2007; Polidoro *et al.*, 2010; Friess *et al.*, 2019). Throughout the island, mangroves have been targeted for their wood, since their strength and rot-resistant properties make them valuable timber and fishing material (Ewel *et al.*, 1998; Brander *et al.*, 2012). Mangrove wood is also a main provider of charcoal, a necessary cooking staple, for coastal populations(Smith & Berkes, 1993; Kridiborworn *et al.*, 2012). Another reason for mangrove decline is loss of habitat, due to clearing for rice farming, aquaculture and shrimp farming, salt and lime production, and even mineral (especially sapphire) extraction (Giri & Muhlhausen, 2008; Jones *et al.*, 2016b; Scales *et al.*, 2018).

In terms of regional dynamics, we noticed that in the northern regions (Diana and Sofia) where population density is higher, mangroves seem to suffer the most from human activity. There was no positive rebound within the last decade, and although there was a slight rebound in the 1999-2009 decade, mangroves have been steadily declining over the years. The mangroves of Ambanja and Ambaro Bay have been one of the most degraded by human activity (Jones *et al.*, 2016b), especially around the Ambato Peninsula. These areas of intense deforestation seem to indicate that close proximity to dense populations and major roads has become a significant threat to mangrove ecosystems. We observe similar negative trends in the Boeny region, where major mangroves (Mahajamba and Bombetoka Bays) which are situated next to densely populated areas, are facing high levels of degradation. Although they are more remote and benefit from significantly less population density, the central and southern parts of Madagascar have also suffered from evident deforestation and was confirmed by Scales *et al*., 2018 and Scales & Friess, 2019.

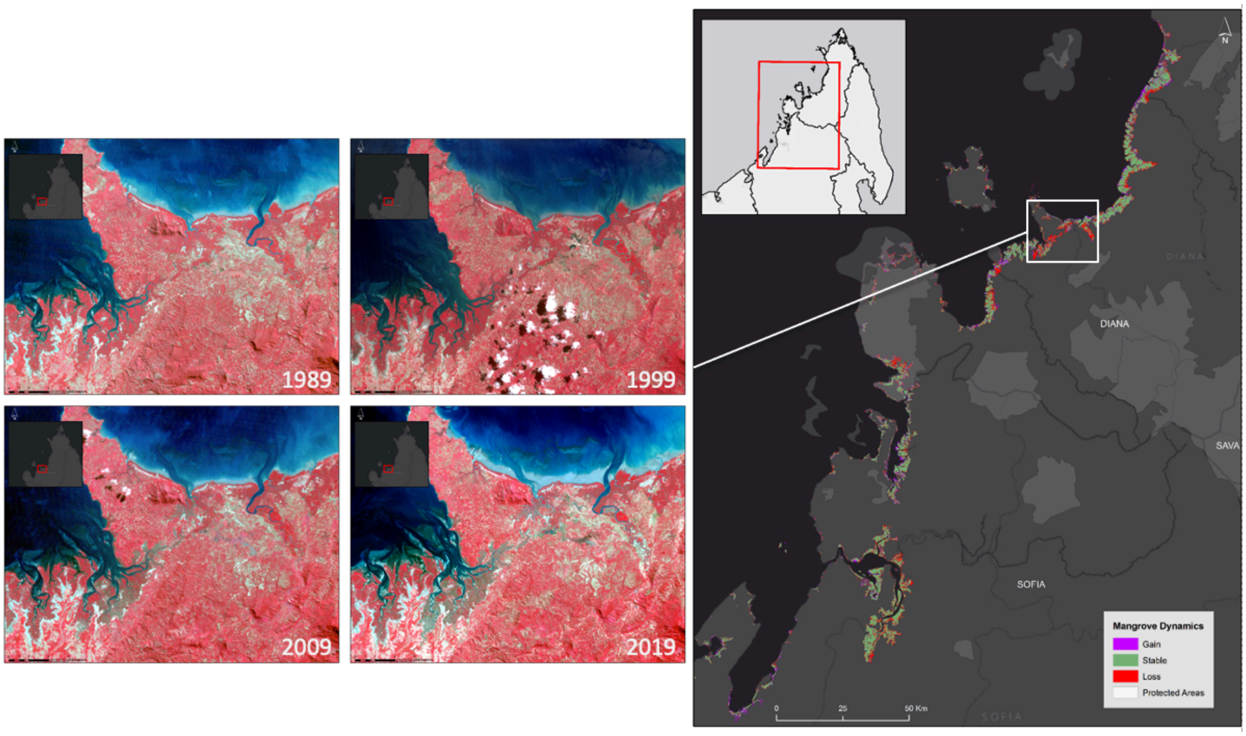


Figure 3. 9. *Mangrove area change around the Ambato Peninsula (Diana) from 1972 to 2019. Satellite imagery: Landsat 5, 7 and 8, with a color composite of Near-Infrared, Red, and Green.*

3.5.2. Mangrove Loss Due to Environmental Causes

Other possible reasons for mangrove loss could be environmentally driven. In areas of the southern tier of the island, the 1982-1999 decade has been depicted as significantly dry, and more prolonged and intense dry seasons resulting in a suffering vegetation and increase in wildfires (Ingram & Dawson, 2005). Such patterns are not specific to Madagascar, and seem to be correlated with the El Niño Southern Oscillation (ENSO), which can bring prolonged droughts to southeastern Africa, including Madagascar (Janowiak, 1988; Cook, 2001; Ingram & Dawson, 2005). Studies on ENSO's influence on southern Africa drought indicated an increase of 120% in drought probability for the year following an El Niño event (Ropelewski & Halpert, 1987; Thomson *et al.*, 2003). Although extensive historical precipitation data is difficult to obtain for Madagascar, we know that major ENSO events in 1982-1983 and 1997-1998 resulted in severe droughts in southern Madagascar the following years (Ingram & Dawson, 2005; Desbureaux & Damania, 2018). During this period, dry conditions prevailed, impacting vegetation and facilitating the spread of wildfires which consumed thousands of square kilometers (Kull, 2002; Ingram & Dawson, 2005). There is not enough continuous temporal coverage of Landsat data available within the 1980s decade to assess such correlation with accuracy, but mangroves certainly suffered from this prolonged drought similarly to the rest of the vegetation. The lack of rainfall as well as freshwater and sediments input from low rivers may have particularly affected the mangrove's inland fringe, where prolonged dryness and excessive salinity can create destructive conditions (Rakotomavo & Fromard, 2010; Duke *et al.*, 2017; Adame *et al.*, 2020). Although we do not have sufficient climatological data, we can identify that the highest loss percentages of the island were encountered within the southernmost and most arid regions, Menabe and Atsimo-Andrefana (Fig. 3.8).

Another potential environmental cause for loss of mangrove area lies within the destruction resulting from major cyclones. Madagascar is prone to being targeted by strong cyclones during the summer monsoon, and the stronger storms have had an impact on its vegetation (Ganzhorn, 1995; Dunham *et al.*, 2011; Lewis & Bannar-Martin, 2012). Mangroves have been shown to be impacted by cyclones and hurricanes which result in defoliation, flooding, mudflows and asphyxiation (Smith *et al.*, 1994, 2009; Imbert, 2018; Krauss & Osland, 2020). However, cyclone impacts on mangroves have mostly resulted in short-term damage, and if left undisturbed, mangrove ecosystems can quickly recover (Sherman *et al.*, 2001; Paling *et* *al.*, 2008; Aung *et al.*, 2013; Krauss & Osland, 2020). This might have been the case for Maroambitsi Bay, in the Boeny region, which lost the majority of its mangroves between 1972 and 1989, but regained most of its coverage the following decade and has been slowly progressing (Figs. 3.11, 3.12). The years 1983 and 1984 resulted in higher than average cyclonic activity (Mavume *et al.*, 2009). Two major cyclones hit the island: Category 3 Andry in 1983, a direct hit to Maroambitsi Bay, and Category 1 Kamisy which caused landfall about 100km to the north in 1984. These may have contributed to widespread mangrove degradation around Maroambitsi Bay.

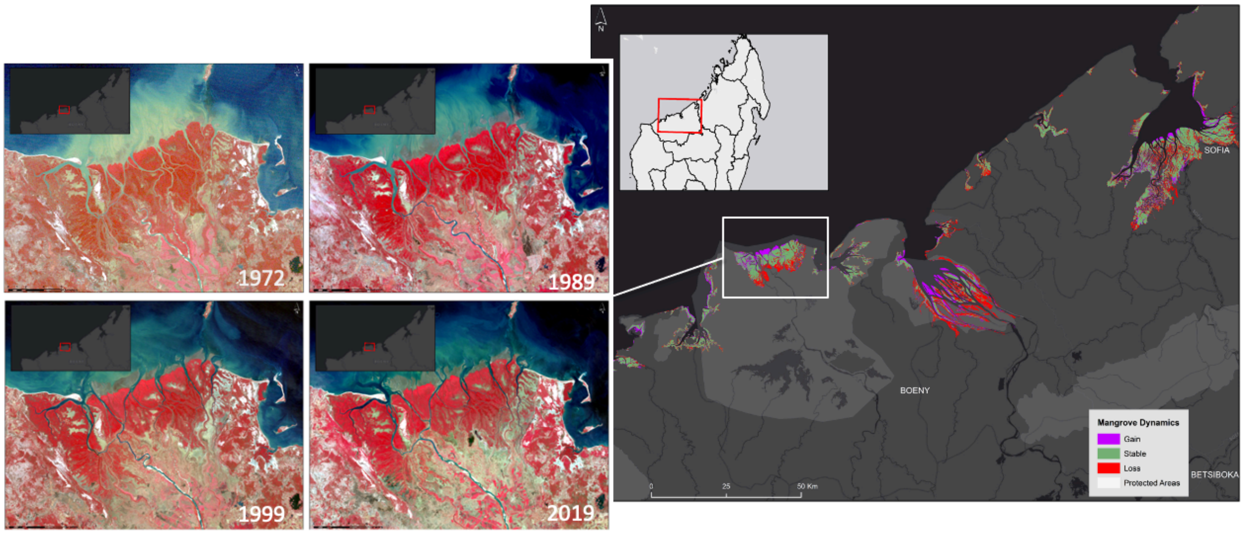


Figure 3. 10. *Mangrove area change in central Madagascar (Boeny), from 1972 to 2019. Satellite imagery: Landsat 1, 5, 7 and 8, with a color composite of Near-Infrared, Red, and Green.*

3.5.3. The Increasing Impact of Mangrove Expansion

The recent dynamics shift leading to mangrove expansion has only occurred within the last two decades. Mangrove increase started on a more localized scale in the 2000s, as some regions experienced positive dynamics for the first time (Fig. 3.8). This positive trend then became prevalent through island-wide dynamics for the 2009-2019 decade, with mangroves gaining 127.5 km^2 (Figs. 3.4, 3.5). Such results confirmed a trend that had been detected within previous studies. Giri and Muhlhausen (2008) identified positive changes in Bombetoka and Mahajamba Bays from 2000 to 2005. Other smaller-scale studies focusing on specific parts of the Malagasy mangroves also identified positive dynamics over the past two decades (Rakotomavo & Fromard, 2010; Jones *et al.*, 2014; Andriatsiaronandroy Onjanamboara *et al.*, 2017). This increase in mangrove area is the result of multiple climate and human induced trends, involving natural regeneration, preservation and conservation, or even reforestation.

Although Madagascar's protected areas were first declared in the 1930s, their coverage remained minimal for decades until the 1980s, as Madagascar's biodiversity started to become a popular topic of discussion (Randrianandianina *et al.*, 2003; Kull, 2014; Gardner *et al.*, 2018). The protected area network counted only 36 sites in the mid-1980s, and has been expanding rapidly since, from 122 in 2016, to 171 as of 2019 (Gardner *et al.*, 2018). Conservation and protection can be challenging to implement nevertheless, as monitoring vast and remote areas is often costly and resource-intensive (Nolte *et al.*, 2013; Gardner *et al.*, 2018). Such issues are all the more relevant to mangrove ecosystems, since accessing and monitoring them is particularly difficult and requires boats and personnel. Several studies have shown a lack of enforcement and the continuation of illegal practices in newly-implemented protected mangroves (McNally *et al.*, 2011; Fent *et al.*, 2019). However, Madagascar's conservation practices have been proven to be relatively efficient (Eklund *et al.*, 2016; Gardner *et al.*, 2018), and mangroves have benefited from such a positive setting. As the network of protected areas expanded throughout the island, an increasing number of mangrove ecosystems benefited from protection status. Mangroves within protected areas increased by more than 8% over the last decade, versus a slight rebound of 3% for mangroves outside of protected areas. This smaller but nonetheless significant increase in mangrove area outside of protected areas may have been driven by a 2014 Decree from the Ministry of the Environment (number 32100/2014), which ratified the nationwide ban on mangrove wood extracting, collecting, and selling. Although such drastic measures will be difficult to implement throughout the island, this Decree demonstrates a certain acknowledgement of the high ecological and societal value of mangroves on behalf of the Malagasy government, and its will to protect it.

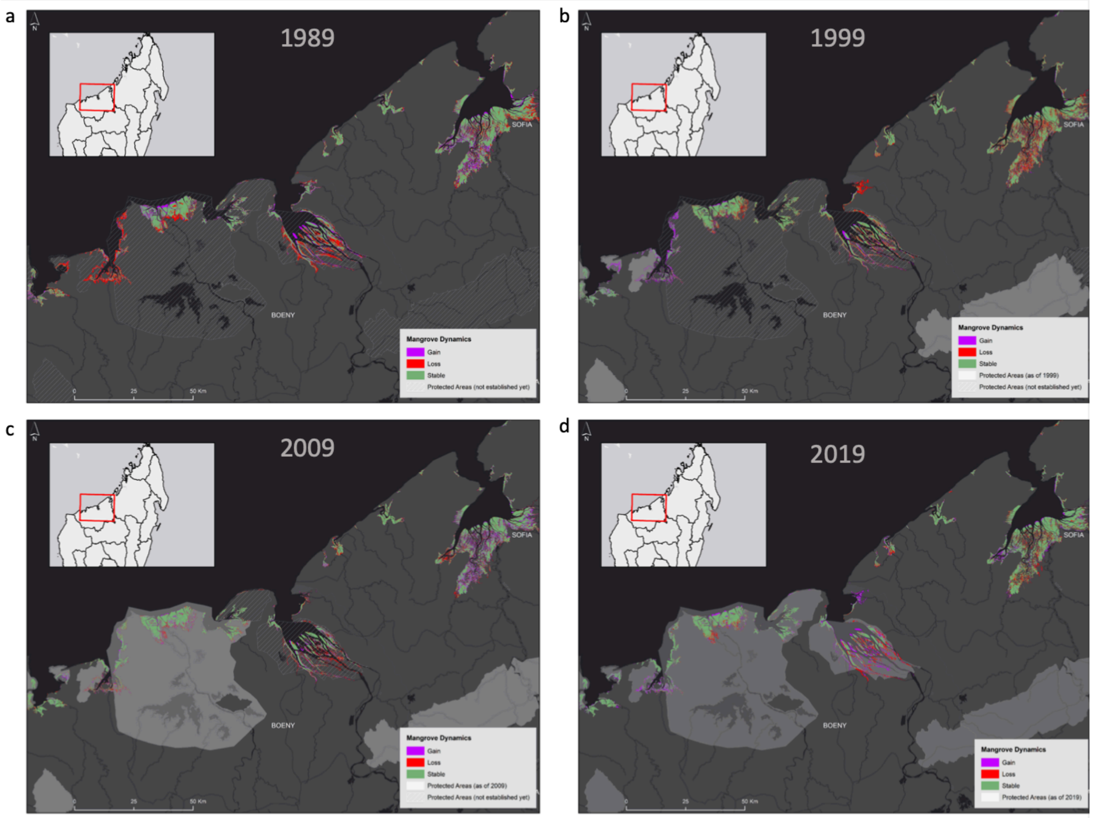


Figure 3. 11. *The evolution of mangroves and protected areas in the Boeny region, from 1972-1989* ***(a)****, 1989-1999* ***(b)****, 1999-2009* ***(c)****, and 2009-2019* ***(d)****.*

Mangroves within protected areas are at driving positive dynamics, and are a major factor in overall positive mangrove change from 2009 to 2019. This is especially true in the central and southern tiers of the island, where we find the largest extent of protected mangroves. Although overall dynamics within protected areas are positive, protected mangroves do not always exhibit widespread successful regeneration. Regions such as Diana, Sofia and Boeny struggled to inverse a negative trend, despite progressively expanding their protected areas. These are also the most populated areas, which indicate a sharp contrast between densely populated regions and the most remote and sparsely populated regions of southern Madagascar, where mangrove conservation appears to be highly successful. The evolution of mangroves and protected areas altogether in Boeny, demonstrates how mangrove dynamics evolved in protected areas as the years progress. Most protected areas targeted mangroves facing extreme threat and degradation, and attempting to slow down or reverse such trends can take years. Some areas, especially those of the inner fringe, may never recover after widespread losses, while others are able to regain full mangrove coverage within a decade.

Besides protection and conservation, the Malagasy mangroves have recently attracted the attention of reforestation and carbon credit initiatives, due to their unrivaled potential as carbon sink (Jones *et al.*, 2015; Benson *et al.*, 2017). This has led to newly implemented mangrove planting projects along its west coast, however, these projects are relatively new and small-scale. The lack of data in combination with the medium spatial resolution of our analysis did not enable us to rule out these dynamics, as it might take years for seedlings to develop canopies large enough to be detected from space. The studies of major mangrove reforestation throughout the tropics have shown disparities regarding strategies and success rates, as they strongly depend on the species planted and local environmental conditions (Elster, 2000; Walton *et al.*, 2006; Bosire *et al.*, 2008).

Another reason for positive mangrove dynamics lies within their natural ability to rapidly regenerate if left healthy and undisturbed (Roth, 1992; Elster, 2000; Baldwin *et al.*, 2001). In Madagascar, we found that degraded areas, whether as a result of environmental or anthropogenic disturbances, are able to recover considerably within one decade. Figure 12 demonstrates that although the Maroambitsi Bay lost significant area before 1989, decades of regeneration, coupled with the benefits from a newly-protected status, led to its mangroves being restored to levels even higher than those of 1972. Such regeneration potential can be an important factor in mangrove response to short-term disturbances such as cyclones, droughts, and deforestation.

The majority of positive dynamics detected across the island are located at the mangrove's outer edges along the coast and at the mouth of bays and estuaries. This seems to be enabled by an increase in sediment outflow and alluvial deposits from upstream erosion and deforestation, creating new habitats and facilitate mangrove encroachment (Rakotomavo & Fromard, 2010). As upland deforestation still is a major issue in Madagascar (Green & Sussman, 1990; Gade, 1996; Harper *et al.*, 2007a), this could in turn result in more downstream sedimentation, thus creating more favorable conditions for new mangrove encroachment.

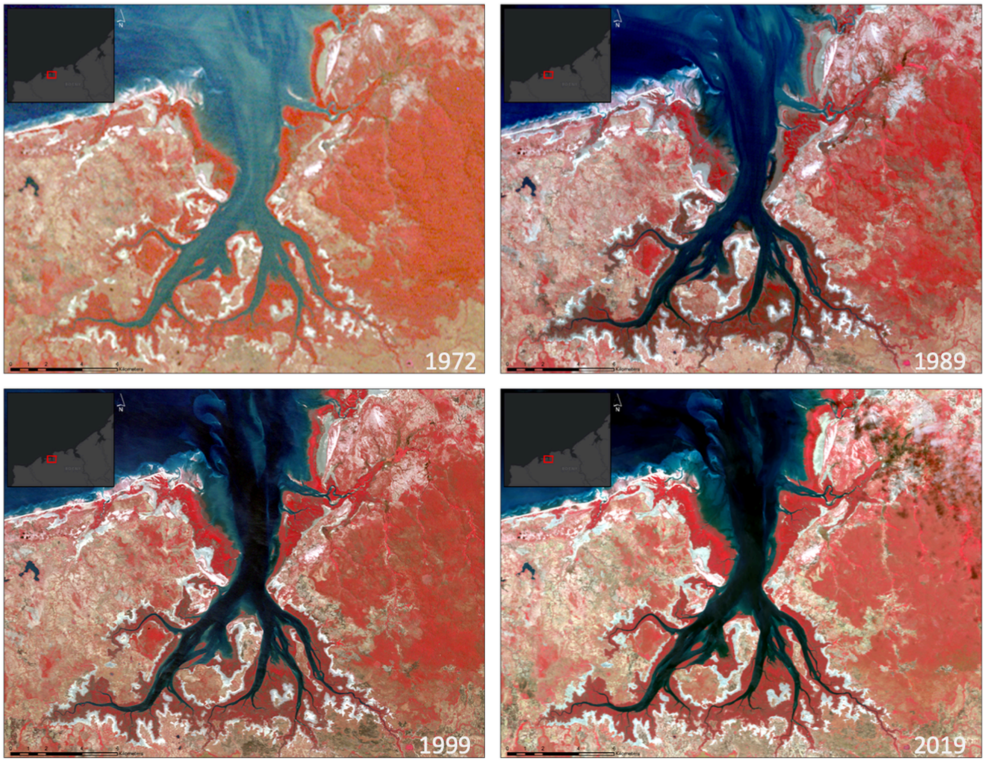


Figure 3. 12. *Maroambitsi Bay in the years 1972, 1989, 1999, and 2019. Satellite imagery: Landsat 1, 5, 7 and 8, with a color composite of Near-Infrared, Red, and Green.*

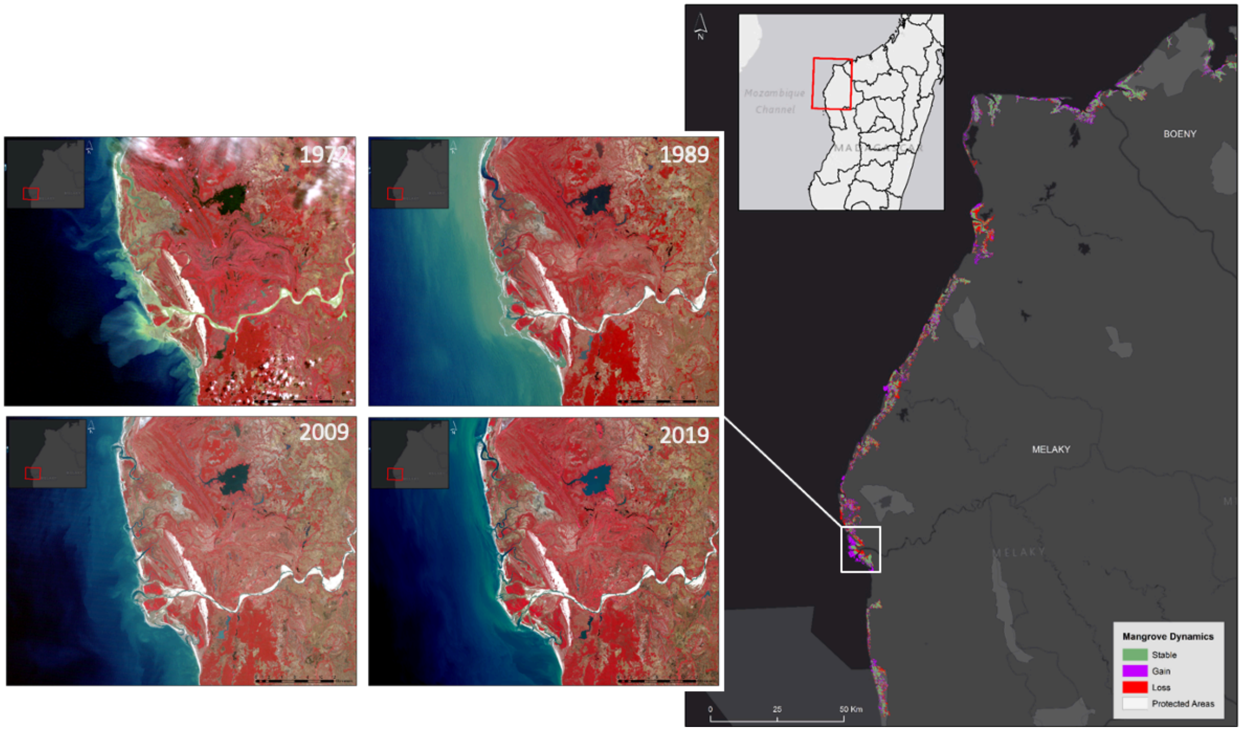


Figure 3. 13. *Mangrove area change in southern Madagascar (Melaky) from 1972 to 2019 Satellite imagery: Landsat 1, 5, 7 and 8, with a color composite of Near-Infrared, Red, and Green.*

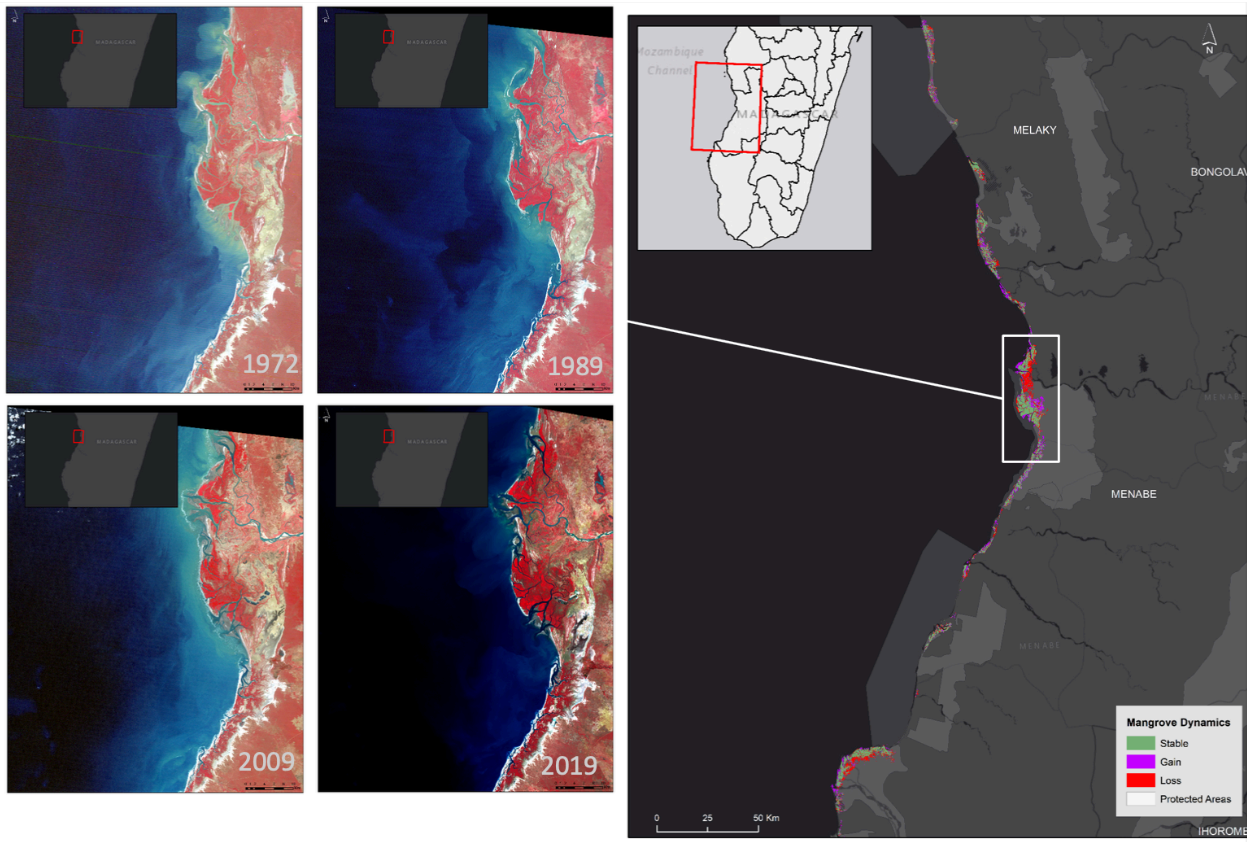


Figure 3. 14. *Mangrove area change in southern Madagascar (Menabe) from 1972 to 2019 Satellite imagery: Landsat 1, 5, 7 and 8, with a color composite of Near-Infrared, Red, and Green.*

3.5.4. Strengths and Limitations

The contrasting dynamics compared to recent studies published in the years 2010s, as well as the evidence of a trend change later this decade, underscores the importance and need for a continuous survey of mangrove dynamics through a repeatable and comparable approach. The constantly expanding Landsat archive is extremely valuable in conducting such long-term analysis, and will continue to do so throughout the 21st Century. However, there are caveats to such approach, as a 30-meter resolution is moderate and can prove a challenge in identifying small-scale processes, such as wood extraction and even reforestation efforts on a small parcel (Tang *et al.*, 2010; Giri, 2016). For instance, some degradation processes might not be captured by our approach if wood gathering is happening only within the undergrowth, thus leaving the canopy relatively intact. Similarly, the most recent reforestation projects will take multiple years before new seedlings have a canopy wide enough for a Landsat pixel to detect mangrove coverage. This is why a decadal timeframe seemed appropriate in our approach, as it allows enough time to detect positive changes in terms of mangrove cover.

When conducting this island-wide mangrove cover analysis at a moderate spatial resolution, distinguishing mangroves from adjacent tropical forests can be a challenge, since both reflect similar spectra. This is especially true for the northern regions of Madagascar, where important rainfall maintains the productive terrestrial vegetation and bright green, even throughout the dry season. The same is true along the coast's major bays and estuaries, where mangroves progressively meld into low-lying shrublands or tropical forests. Through a well-defined coastal mask excluding most of the upland vegetation and final post-classification editing, our method was able to produce mangrove classes of a high accuracy. Although it can be a challenge to distinguish mangroves from tropical terrestrial forests, narrowing the analysis down to mangrove habitats, in combination with a rigorous classification process, followed by final editing can lead to high accuracies.

This large-scale remote sensing analysis was targeted at mangrove dynamics, and was not meant to differentiate between species. For instance, our classifications did not distinguish *Rhizophora* from *Avicennia*, which have significantly different roles within coastal ecosystems and population livelihoods. *Rhizophora* is adapted to frequently or permanently submersed areas, and is mostly present on the outer fringe, where mangroves seem to be expanding. *Rhizophora* is also prone to being harvested, as it is a prime resource for building and fishing material, while *Avicennia* thrives in upland areas receiving less frequent inundation and is more vulnerable to prolonged dry conditions, it is also more accessible by foot in order to be harvested (Walters, 2005; Nordhaus *et al.*, 2019). Studies have been able to successfully detect mangrove species at a smaller scale (Wang *et al.*, 2004; He *et al.*, 2020; Peng *et al.*, 2020), however, due to the reliance on higher-resolution data and more complex methods (i.e. object-based classification, Radar and Lidar imagery), such studies would be challenging to implement island-wide and are historically comparable.

Another limitation to this study lies within the lack of ground data available. The island of Madagascar is vast, and extensive field work is a challenge, especially within mangroves along remote stretches of coastline. Meteorological and stream gaging data, which could provide relevant details on precipitation, temperature, water level and discharge rates, is still very limited. As a result, it can be difficult to identify the causes of remotely sensed dynamics, and to assert with certainty how much variation is natural and how much is anthropogenic. The strength of this study, however, lies within the fact that this medium-scale approach is enabling us to maintain a repeatable process over the years, and it is adapted to assess mangrove cover change consistently at a decadal scale (Gutman *et al.*, 2008).

3.6. Conclusion

The Madagascar mangroves have been deforested over the last fifty years, due to a combination of anthropogenic and environmental causes, but at rates that did not match those of tropical forests (Gade, 1996; Harper *et al.*, 2007b). However, mangrove dynamics vary depending on regions and time period. The last two decades have experienced a significant slowdown and even an increase in mangrove area from 2009 to 2019, and our results indicate that this reversal follows significant efforts to strive for the conservation and preservation of mangrove ecosystems. This confirms a recent trend, as mangrove deforestation slowdown has been observed throughout the tropics (Hamilton & Casey, 2016). Madagascar reflects such tendency, as it features decreasing rates of deforestation in combination with increasing rates of conservation, preservation and reforestation, resulting in mangrove regeneration and expansion. Recent decisions seem to indicate further development of protected mangroves. In August 2020, the mangroves of Ambaro Bay, a major stretch of coast in the Diana region which faced significant deforestation, was designed as a wetland of international importance (Ramsar), thus initiating its protection. The increasing significance of mangrove ecosystems in terms of blue carbon initiatives might even speed up mangrove expansion, as more and more mangrove planting projects are being implemented (Locatelli *et al.*, 2014; Taillardat *et al.*, 2018; Alongi, 2020). Mangroves still face significant threat, and negative changes can happen widely and rapidly (wood harvesting, cyclones and drought damages), however we noticed that they are often able to recover remarkably fast. Nonetheless, we noticed that drastic changes such as intense degradation and clear-cutting, may result in mangroves unable to recover, especially the dryer and less inundated mangroves of the upland fringe.

Natural regeneration and new mangrove settlements also seem to play a significant role in inverting a negative trend. More favorable environmental conditions as well as an increase in sedimentation along the coast have helped mangroves recover and even expand into new habitats. An unexpected consequence of intense tropical forest deforestation appears to be an increasing number of sediments running off into the main bays and estuaries and creating new habitats for mangroves.

Whether positive or negative, these dynamics are happening at a rapid pace, and mangrove habitats can change dramatically within a ten-year timeframe. This is especially true for an island in which local government and stakeholders (NGOs, international organizations) are making important decisions about the status of conservation, reforestation, rehabilitation, and distribution of resources. The aforementioned reasons justify the need for an unbiased and continuous monitoring of the status and change of mangroves in Madagascar. We suggest continuing this work in the future and assessing island-wide dynamics every five to ten years while maintaining a consistent method in order to benefit from the same repeatable process and obtain consistent results which can be compared and analyzed.

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Conclusion

The results and findings of the preceding chapters highlight the importance of not solely relying in broadscale remote sensing, climate and species distribution modeling while understanding and predicting species response to climate change and anthropogenic activity. All chapters have exposed differences based on local conditions, and a certain level of detail would not have been identified through large-scale analysis only.

By coupling thermal tolerance experiments with observational data across multiple range limits for two mangrove species, Chapter 1 revealed species and range-specific differences in thermal niches. The importance of combining experimental data with observational patterns is thus providing a benchmark for integrating physiological tolerance experiments, remotely sensed observations of species' range limit dynamics and distributional modelling to improve our projections of climate change impacts on species distributions. By specifically focusing on Baja California, a unique range limit by its highly challenging environmental conditions, Chapter 2 demonstrated evidence of non-linear relationships between climate variables and mangrove habitat suitability, and emphasized on the importance of the combining effect of environmental stressors. This work also identified the importance of climate-related thresholds in the determination of range dynamics, and on the potential for landscape-scale ecological transitions as the result of environmental changes. Lastly, we saw that although much emphasis is being put on mangrove deforestation, human-driven dynamics play an increasingly significant role. Madagascar is a clear example of not only mangrove deforestation but also resilience, as even in highly degraded areas, mangroves were able to regenerate and regain coverage. We identified that mangrove dynamics varied between regions, population density, and conservation extent, revealing a multitude of factors at play. Such rapidly-evolving dynamics thus emphasize the need for consistent and recurring analysis coverage, that is becoming possible due to increasing availability of geospatial data and computing abilities.

Whether mangroves are responding to climate change or anthropogenic action, this dissertation identifies locally-contrasted dynamics which cannot simply be placed into a single framework of mangroves' worldwide predicted changes. Mangroves are an essential tropical ecosystem for various ecological and societal reasons. Understanding and predicting their dynamics will require multiple tools and various perspectives ranging from landscape-scale to individual-scale.