Forests Under Pressure: A Study on the Vulnerability and Resilience of Panama's Dry Forests to Climate Change

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Abstract

While Tropical dry forests (TDFs) have been underrepresented in the ecological literature, concerns about their vulnerability to climate change are being brought to the forefront by the scientific community. Within the context of Panama, inconsistent and unpredictable changes in rainfall patterns are predicted to occur as a result of a confluence of factors including climate change, El Niño and La Niña oscillation events, and a complex spatiotemporal distribution of deforestation and forest regeneration. This thesis seeks to understand how the climate has already changed in the driest part of Panama, the Azuero peninsula, and if this climatic variability can result in ecosystem adaptive strategies, or in increased vulnerability. It is hoped that such results could support informed adaptation strategies from climate predictions and ecosystems' responses, as well as deepening our understanding of these forests' importance in climate change mitigation. I begin by examining climatic pressures in the Azuero peninsula through times series analysis and the calculation of climate anomaly indices such as Standardized Precipitation-Evapotranspiration Index (SPEI). The analyses unveil a general trend of increasing minimum temperatures by nearly 1°C, and decreasing precipitation averaged to 320 mm across the Azuero peninsula within only 20 years, with a gradient of pressures at a local level that should be further investigated. These results are supported with trends calculated with 57 years' worth of climate data from the WorldClim satellites. The second section of the thesis focuses on how TDFs in Azuero respond to these climatic trends. I adopt the methodology of Esquivel-Muelbert et al. (2018) who compared saplings to trees' drought resistance functional traits in the Amazon Basin. The results evidenced a shift towards drought-tolerant functional traits and species composition in recruits. These findings depict a resilience that these forests have achieved through adaptive strategies to a drier and warmer climate. Nevertheless, studies show that climate predictions within the context of Panama indicate a future shift towards increasing temperatures and precipitations. While these predictions situate Panama in unprecedented climatic conditions, I emphasize the importance of considering climatic trends and subsequent species composition and functional trait shifts to elaborate reforestation, restoration, and conservation efforts and design stronger tactics of climate change mitigation in the face of climate change.

Abrégé

Alors que les forêts tropicales sèches (FTS) ont été sous-représentées dans la littérature écologique, les préoccupations concernant leur vulnérabilité au changement climatique sont portées au premier plan par la communauté scientifique. Ce mémoire cherche à comprendre comment le climat a déjà changé, et si cette variabilité climatique peut entraîner des stratégies d'adaptation des écosystèmes ou une vulnérabilité accrue. De tels résultats pourraient soutenir des stratégies d'adaptation à partir des prévisions climatiques et des réponses des écosystèmes. Le mémoire commence avec une analyse des pressions climatiques dans la péninsule d'Azuero, la région la plus sèche du Panama, à travers de séries chronologiques et d'indices d'anomalies climatiques tels que l'indice normalisé d'évapotranspiration des précipitations (SPEI). Je démontre une tendance générale d'augmentation des températures minimales de près de 1 ° C ainsi qu'une diminution des précipitations moyennes de 320 mm sur la péninsule d'Azuero en 20 ans, avec un gradient de pressions climatiques au niveau local qui devrait être étudié davantage. Ces résultats sont cohérents avec les tendances calculées à partir de 57 années de données climatiques provenant des satellites WorldClim. La deuxième partie du mémoire se concentre sur la façon dont les FTS d'Azuero répondent à ces changements climatiques. J'ai adopté la méthodologie d'Esquivel-Muelbert et al. (2018) qui ont comparé les traits fonctionnels de résistance à la sécheresse des jeunes arbres aux arbres de la canopée dans le bassin amazonien, en Amérique du Sud. Les résultats mettent en évidence une évolution vers des traits fonctionnels tolérants à la sécheresse et la composition des espèces chez les jeunes arbres. Ces résultats suggèrent une résilience des forêts grâce à des stratégies d'adaptation à un climat plus sec et plus chaud. Néanmoins, des études montrent que les prévisions climatiques dans le contexte du Panama évaluent un changement futur vers une augmentation des

températures et des précipitations. Alors que ces prévisions placent le Panama dans des conditions climatiques sans précédent, j’évoque l'importance de prendre en compte les tendances climatiques et les modifications ultérieures de la composition des espèces et des traits fonctionnels dans l'élaboration des efforts de reboisement, de restauration et de conservation pour concevoir des tactiques plus solides face au changement climatique.

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List of Acronyms

ELTI - Environmental Leadership and Training Initiative

ENSO - El Niño and La Niña Southern Oscillation events

CTFS - Center for Tropical Forest Science

CWM – Community Weighted Mean

DBH – Diameter at breast height

IATTC - Achotines Laboratory

LNC – Leaf N content

MANOVA - Multivariate Analysis of Covariance

PCA - Principal Component Analysis

RDA - Redundancy analysis

RWC – Relative water content

SLA – Specific leaf area

STRI – Smithsonian Tropical Research Institute

TDF – Tropical dry forest

TRF – Tropical rainforest

TWF – Tropical wet forest

Chapter 1

Thesis Introduction

Chapter 1 is a review of tropical dry forests in the Neotropics and in Panama. This introduction provides a context of historical land use practices, climate conditions, and forest regeneration trends in Panama's tropical dry forests and Azuero.

Section 1.01 - Tropical dry forests biome

Tropical dry forests used to represent 42% of the world's tropical forests and formed the second largest type of tropical forest on the planet (Murphy and Lugo. 1986; Miles et al. 2006; Dirzo et al. 2011; Tripathi, Srivastava and Singh. 2019). Approximately 550,000 Km^2 of tropical dry forest covered the Pacific coast of Mesoamerica when the Spanish conquistadors arrived (Quesada and Stoner. 2004). These forests have been reduced to nearly 2% of their original cover on account of socioeconomic growth, deforestation, and depletion (Dirzo et al. 2011). Neotropical dry forests now grow from northwestern Mexico to northern Argentina and southwestern Brazil in isolated patterns, leading to separated forest patches varying in size (Miles et al. 2006; Dirzo et al. 2011). With almost 60% of their original extent currently extinct, the remaining forests experience high levels of fragmentation across countries (Sánchez-Azofeifa et al. 2013). TDFs are underrepresented in the literature, potentially leading to a slower recognition of their value in terms of biodiversity, carbon sequestration, and ecosystem services (Dirzo et al. 2011; Sánchez-Azofeifa. 2013; Harvey et al. 2021). The recognition of TDFs' uniqueness in terms of their biodiversity, vegetation dynamics, phenology, and conservation, led researchers to dedicate their work to better understand and describe these forests (Dirzo et al. 2011; Griscom et al. 2011; Sánchez-Azofeifa et al. 2013). With a better understanding of these forests' biological and ecological characteristics, the scientific community brought to the forefront the need to consider the vulnerability of tropical dry forests in the face of climate change (Prieto-Torres et al. 2016; Allen et al. 2017; Castro et al. 2018; Siyum. 2020). TDFs are important for the general wellbeing of communities and could play a role in future climate mitigation strategies established under the 2021 United Nations Climate Change Conference (COP26) goals of reducing deforestation and promoting sustainable forestry, as stated in the *Glasgow Leaders' Declaration on Forests and Land Use, 2021* (Dirzo et al. 2011; COP26. 2021).

Section 1.02 - Putting Panama's tropical dry forests on the map

Panama's TDFs grow along the Dry Corridor of Central America and are primarily found in a region known as the "Arco Seco" in Spanish, or "Dry Arc", in English. This region is located along the Pacific coast of Panama, with a large portion of these forests being in the Azuero peninsula including parts of the provinces of Veraguas, Los Santos, Herrera, and Coclé (See Figure. 1). They occupy about 7% of the national territory, roughly 5,630 Km^2 (Pro Eco Azuero. 2022). TDFs in Panama have been reported to receive <1500mm of precipitation (López, Pérez and Mariscal. 2015), but can have a precipitation range between 700 mm and 2000 mm (Vásquez et al. 2022). They are characterized by seasonally deciduous phenological cycles amongst trees to resist the low rainfall range (Dirzo et al. 2011). This precipitation range falls into Holdridge' life zone classification of the dry tropical forest ecosystem (Holdridge. 1967). The dry season is pronounced, having 5 months out of the year receiving little to no rain (December through March). Rain begins in late April and ends in late November (Griscom et al. 2011). The highest elevations in the peninsula reach 1530.096 m (or 5,020 ft) (Península de Azuero topographic map, elevation, relief. ND), and the peninsula is characterized by its undulating terrains where TDFs are found within elevation from 10 to 100 m (Griscom et al. 2011).

Section 1.03 - A history from forests to cattle farming and from cattle farming to forests

As has been the case across the neotropics, Panama's tropical dry forests along the Pacific coast have been deforested and depleted to replace forested land with cattle ranging lands (Heckadon-Moreno. 1984; Griscom et al. 2011). This shift started in the 16th century with the Spanish colonialist instauration of cattle ranging across TDFs lands which were considered adequate for this use because of the drier weather and the fertile soils that abounded (Murphy and Lugo. 1986; Calvo-Alvarado et al. 2009). These changes in local land use trajectories led to shifts in forest cover, and species composition (Heckadon-Moreno. 1984; Calvo-Alvarado et al. 2009; Griscom et al. 2011). However, between 1947 and the year 2000, cattle farming lands along Panama's Pacific coast experienced a shift in which the forest cover increased due to the agricultural field expansion across other regions of the country and a subsequent abandonment of many exploited lands in the Azuero peninsula (Wright and Samaniego. 2008). In fact, the Dry Arc, which was primarily deforested in 1947 from cattle farming, started to experience an increase in natural regeneration by the year 1992. The total agricultural cover decreased to 38% after a shift from agricultural to forested lands in only eight years, starting with a forest cover of 34% of Panama's Dry Pacific Arc in 1992 which increased by 4.1% annually (Wright and Samaniego. 2008). With the additional impact of active reforestation projects and natural regeneration, Azuero reached a total forest cover averaging 61% by the year 2000 (Griscom et al. 2011). While decreased, cattle farming is still present within the region as cattle provides more financial security to small landowners than investing in agricultural crops vulnerable to droughts and pests, as well as representing a demanded good that could be sold rapidly if needed (Heckadon-Moreno. 1984). In addition to farming, valuable timber species such as *Cedrela odorata*, *Dalbergia retusa*, and *Pachira quinata* started being progressively logged in the early 1900s (Griscom et al. 2011). This practice is maintained today yet is used by the local landowners for personal construction, rather than for the timber market (Griscom et al. 2011). However, the related practice of tree plantation also contributed to the shift from farming to reforested lands, representing 11% of the reduction in agricultural land cover between 1992 and 2000 (Wright and Samaniego. 2008).

Since cattle farming decreased from the year 2000 onward, natural regeneration and active reforestation led to a unique region-based secondary forests increase within Panama (Wright and Samaniego. 2008; Vásquez et al. 2022). While the country's humid forests were undisturbed for the first 50 years of the introduction of cattle farming along the Pacific coast, by the early 2000s Panama's rainforests (forests with high (>25 m), closed evergreen canopies, with annual precipitation greater than ~2000 mm, and little to no dry season) (Pennington at al. 2018) started to experience deforestation (Griscom et al. 2011). The regeneration of TDFs in Panama was instrumental to counterbalance 45 years of net tropical forest loss in the country, through secondary forests' gain that maintained a forest cover balance nationally (Wright and Samaniego. 2008).

Quantifying forest loss from deforestation and degradation provides a tangible value of vulnerable ecosystems in climate change mitigation. This also allows us to better comprehend key forest dynamics such as forest succession, regeneration, adaptation, and resilience in the face of the many challenges that human action and climate change pose on forests. Subsequent to the loss of tropical dry forests in the Azuero peninsula, Panama's TDFs have been subject to an increase in conservation and active reforestation efforts, primarily undertaken and supported by the local community and local researchers. This discontinuity in deforestation in Azuero has also been attributed to a shift of cattle farmers from Azuero to the Darién forests in Panama, expanding cattle farming to the eastern regions of Panama (Cámara-Cabrales. 1999; Perafan et al. 2019). However, local mobilization and mitigation strategies empowered by local knowledge and the increased recognition of these forests at a scientific level expanded alongside the increases in forest cover that have been occurring in the Azuero peninsula.

The local understanding of Azuero's TDFs' importance for water system maintenance, erosion avoidance, and biodiversity conservation has been facilitated and guided through the collaboration between local landowners, non-profit organizations, and research institutions (Vásquez et al. 2022). Local non-profit organizations such as the Pro Eco Azuero, and the Environmental Leadership and Training Initiative (ELTI) play an integral role in environmental outreach, education, and facilitation of reforestation projects with locals invested in forest conservation goals (ELTI. ND; Pro Eco Azuero. 2022; Vásquez et al. 2022). Pro Eco Azuero focuses on the conservation of Azuero's TDFs to restore an ecological corridor of the endemic spider monkey (*Ateles geoffroyi azuerensis*), in addition to supporting sustainable land practices in which the local population can coexist with the forests they protect (Pro Eco Azuero. 2022). ELTI is an initiative of the Yale School of the Environment that focuses on capacity building for conservation and restoration of forests by offering training and support to local communities to implement strategies that improve the environment and local livelihoods in Tropical Asia and the Neotropics (ELTI. ND). In 2014, the government of Panama created ''Alianza por el Millon'' or "Alliance for a Million". This is a government partnership in which multidisciplinary parties, including non-governmental organizations such as Pro Eco Azuero and educational institutions, establish reforestation projects to reach one million reforested hectares (Ministerio de Ambiente. 2019). Some of these reforestation projects already started in Azuero (Pro Eco Azuero. 2022), which indicates that Azuero could continue to impact the country's forest cover increase and carbon offsetting. Scientific and conservation entities such as the Smithsonian Tropical Research - Center for Tropical Forest Science (STRI-CTFS) (CTFS Plot Locations. 2022), IATTC's Achotines Laboratory (IATTC. 2022), and other private reserves in Azuero have been established with the aim of conducting inventories of Panama's TDFs to follow their shift and growth. This shows a growing appreciation of this ecosystem within the scientific and local communities as well as philanthropic groups interested in environmental restoration (Griscom et al. 2011). In other words, regardless of the important deforestation that Panama's TDFs have endured, there is a strong local, scientific, and governmental motivation to contribute to the conservation of these forests that is accompanied with an achieved natural regeneration trajectory that needs to be valued within current goals of climate mitigation strategies and be monitored within the context of other forests in Panama, including the Darién regions.

Section 1.04 - How to predict the impact of climate change in tropical dry forests within a tropical ecosystem gradient

Throughout much of the literature, tropical dry forests are characterized along the continuum of tropical rainforests to savannas. Phenological characteristics of species from TDFs is one of the prevalent identifiers differentiating this ecosystem to rainforests and savannas (Dirzo et al. 2011). Tropical dry forests are often compared to savannas as they experience a drier climate than tropical rainforests, they have more open spaces and light availability through the canopy than tropical rainforests, and they can provide adequate conditions for C_3 herbaceous species to develop in a similar manner to savannas (Meir and Pennington. 2011; Dexter et al. 2018). These characteristics can also be attributed to the historical conversion of forested lands to cattle farming, including the introduction of African grasses (Griscom et al. 2011) and logging, which resulted in high levels of land fragmentation (Drizo. 2011; Meir and Pennington. 2011). Anthropogenic impacts have a strong influence on these forests' vegetation structure and species composition. Therefore, considering these results of anthropogenic pressures as ecosystem dynamics has facilitated blending the classification of TDFs with that of savannas (Fajardo et al. 2005; Dirzo et al. 2011; Dexter et al. 2018).

The impact of fire on TDFs and savannas is quite different. Compared to savannas, which have a higher abundance of C_3 and C_4 grasses, more open spaces, and more frequent fires, TDFs in the Americas experience drier and warmer conditions, yet are not typically considered to be resilient to fires (Dirzo et al. 2011; Ratnam et al. 2011; Sánchez-Azofeifa and Carlos Portillo

Quintero. 2011; Siyum. 2020).

In the tropical regions of Asia and in Malaysia, while the majority of the forest are considered moist forests, drier forests have been recorded. These forests have a high abundance of grasses in the understory which burn regularly and are resilient to reoccurring fires, similarly to savannas. However, it is debated that because of the high presence of these fire-resilient grasses, these ecosystems should rather be considered ‘arid’ dry forests or savannas (Ratnam et al. 2011; Dexter et al. 2018). It is therefore possible that the response of TDFs to climate change and pressures such as fire might not be the same in locations as disparate as Asia, Africa, and the Neotropics; even TDFs within the same regions may differ. Yet, better understanding forests’ fire vulnerability is important for climate mitigation projects.

Tropical dry forests are also often compared with tropical rainforests (TRFs), which have been more thoroughly studied (Dirzo et al. 2011; Dexter et al. 2018; Pennington et al. 2018). TDFs and TRFs share similar vegetation structure with tall woody species (above 10 m), in addition to having tree species in common. Tall woody species grow large in TDFs’ harsh environment because of nutrient-rich soil as compared to savannas and tropical rainforests (Meir and Pennington. 2011; Dexter et al. 2018). A considerable and growing literature devoted to the risks of tropical forests transitioning to savannas or undergoing desertification alongside climate change, points to the fact that TRFs are more at risk of a transition to savannas than TDFs (Dexter et al. 2018). There is also a lack of evidence that TRFs could transition to TDFs, as TDFs species rely on a more fertile soil that is not present on TRF lands (Dexter et al. 2018). This shows that while often being compared along a gradient, the fate of TRFs and TDFs facing climate change could be divergent, and that to have their intended impact, future climate mitigation plans need to consider their unique properties. Considering the forests’ local vegetation structure, species composition, soil mechanisms, the land use history, in addition to the past and predicted climatic pressures at a local level, could be a desirable strategy to plan for the conservation of tropical dry forests.

Section 1.05 - Climate pressures concern in Azuero

Strong El Niño and La Niña Southern Oscillation events (ENSO) during the years 2015 and 2016 brought Azuero's cattle farmers to vocalize and share their concerns about increasing droughts in their region, shedding light on the impact that climate change could have on the region (Vega and Vergara. 2015; Noticias Redacción de TVN. 2016). Echoing the concerns regarding the vulnerability of tropical dry forests to climate change, my M.Sc. thesis research was dedicated to understanding the potential vulnerability and the needed resilience of Panama's TDFs against pressures of climate change. I begin with a climate analysis used to provide information on the behavior of climate change and climate pressures in Azuero. The climate analysis combined geostatistical and time series analyses with the calculation of climate anomaly indices to understand if climate change is visible through climate variable deviations. The second part of my thesis is an analysis of tree species composition and functional traits that may have shifted as a response to these climatic pressures to determine if climate pressures have led to a shift in the forests' species composition. The understanding of functional trait diversity is yet to be deepened in tropical dry biomes, leading to the need for further research to be directed to establishing the value of these systems in carbon storage and production, water cycling and biogeochemical cycling, as well as their resistance and resilience to climate change (Pennington et al. 2018). Functional traits have been increasingly used in the past years to establish a tailored assessment of a forest's resilience and climate adaptation dynamics (Lohbeck et al. 2015). The assessment of forests' responses to climate pressures based on functional traits provides a framework for analysis which is specific to each individual forest, and which can be used to identify the quantifiable strategies which are employed in response to changing pressures. Quantifying the shifts in functional traits which are related to the predicted and observed climatic pressures could help understand the resilience level of forests and facilitate the development of evidence-based policies and reforestation/restoration projects. Esquivel-Muelbert et al. (2018) studied the response of

Amazonian forests to climate change. These authors hypothesized that comparing tree species found in the canopy and tree species found in the understory could indicate if a forest was resilient to climate pressures or if a forest was changing because of these pressures. In this thesis, I aimed to identify increased drought tolerance in saplings versus canopy trees as evidence of a climate change response in TDFs. To interpret the vulnerability/resilience of Azuero's TDFs to climate change, the analyses considered the land use history, the past and predicted climate trends, and climate anomalies to identify resulting shifts between older established canopy trees and recruiting sapling trees. Shifts of interest were shifts in drought-resistance in functional traits, vegetation structure, and species composition. Temporal change of species composition between older canopy trees, established before recent climate change, and recruiting saplings, enduring recent climatic pressures during their establishment, germination, and early growth stages, would suggest that TDFs had the ability to adapt to climate pressures (with future resilience to be further tested).

Chapter 2

Climate Analysis within the Azuero Peninsula, Panama

Chapter 2 is a study in which climate variables and anomaly indices were analyzed within the Azuero peninsula in Panama. This chapter contributes to the understanding of climate change pressures and climate shifts experienced in the Azuero peninsula.

Section 2.01 - Introduction

Tropical forests hold the richest biodiversity amongst the terrestrial ecosystems of our planet (Dirzo et al. 2011). They are vital to our subsistence across the globe through ecosystem services, such as carbon sequestration, regulation of weather patterns and natural disasters, purification of water systems, erosion regulation, and the production of foods, medicines, and other raw materials directly and indirectly contributing to human health (Brandon et al. 2014; Balasubramanian. 2019). We also know that these forests' dynamics are complex enough for any pressure above their threshold of resilience to cause irreversible damages. At the same time, climate change is ongoing, increasingly threatening and there is a prevailing lack of understanding regarding how climate will continue to affect our lives, ecosystems, and biodiversity. Within this reality, we need to further understand: 1. how the climate has already changed, 2. what these changes look like in terms of climatic variability and the resulting ecosystem adaptive strategies and vulnerability, 3. how to predict the way climate pressures will evolve and impact ecosystems in the future, and 4. how to put in place informed mitigation, conservation, and restoration strategies with other multidisciplinary expertise to change the current trajectory our planet faces.

The Sixth Assessment Report of the Intergovernmental Panel on Climate Change (Pörtner et al. 2022), the latest assessment issued to date, provides a myriad of evidence for the impact that climate change has on earth's terrestrial and aquatic ecosystems, as well as human systems. In the case of Central America, the report identifies that all categories of terrestrial and aquatic ecosystems have experienced changes in ecosystem structure and species range shifts attributed to the impact of climate change with a high confidence (Pörtner et al. 2022). Floods and droughts due to climate change have also been strongly correlated to food insecurity and malnutrition increasing in Central and South America. Extreme climatic events have already been reported and forecasted to intensify in both Central and South America (Pörtner et al. 2022) and have increased the potential vulnerability of tropical forests (Murray-Tortarolo et al. 2017). The Neotropics will likely experience warming temperatures, increased frequency and severity in droughts, decreased water availability, sea level rise, coastal erosion, and ocean and lake acidification (Pörtner et al. 2022). While water scarcity is reported in countries such as Brazil, Paraguay and Argentina, regions of Northern South America are expected to be exposed to extreme floods in the future (Pörtner et al. 2022). Considering Central America's Dry Corridor, referred to as the "Dry Arc" or "Arco Seco" in Panama, concerns involve the already extended dry seasons that are predicted to become increasingly inconsistent with unpredictable rainfall patterns (Pörtner et al. 2022).

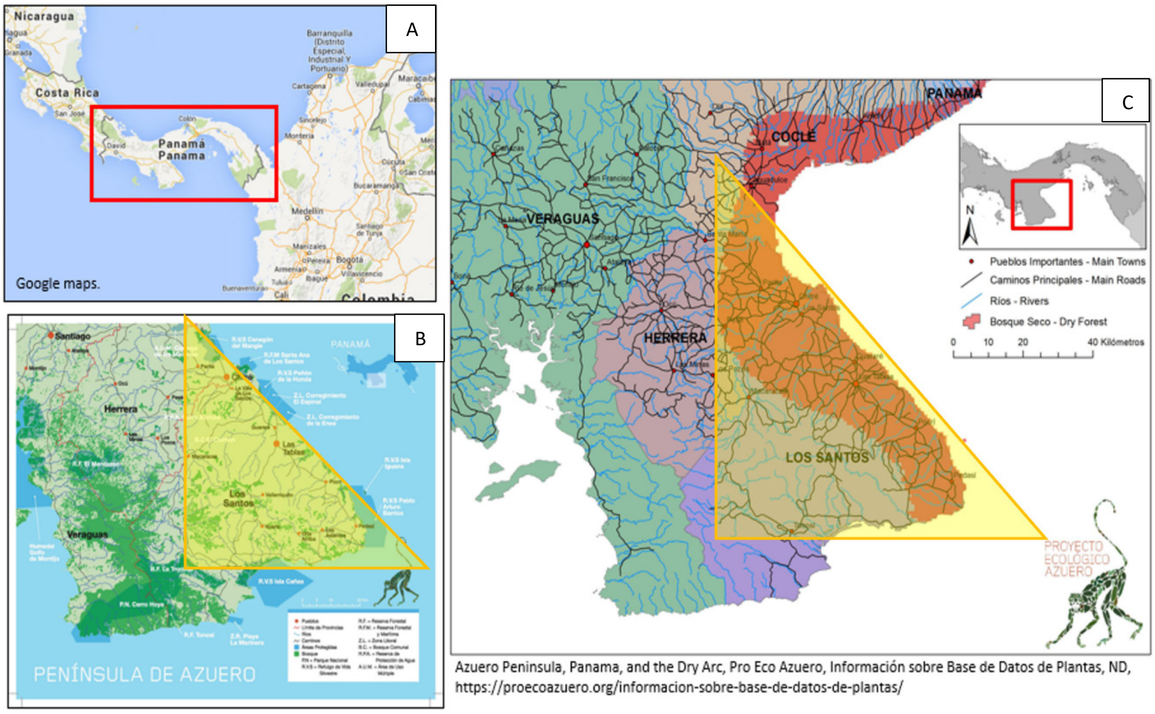
In addition, the report restates the fatal impact that an increase of global atmospheric temperature of 1.5°C would have on ecosystems with low resilience, mostly focusing on ecosystems directly impacted by sea-level rising. The report establishes that a global increase in atmospheric temperature as predicted under different scenarios (1.5°C to 4°C increase) could lead to daily maximum temperatures in Central America ranging from 33°C to 43°C. Temperature increases across Central America reaching 43°C as predicted under the most pessimistic scenario is beyond comprehension of what the future would look like (Pörtner et al. 2022). The IPCC states that recorded and projected impacts indicate that several systems in Central America are already approaching critical thresholds due to current warming levels (Pörtner et al. 2022).

Panama’s tropical dry forests (TDFs) extend along the Pacific Coast of the Azuero peninsula, within the provinces of Veraguas, Los Santos, Herrera, and Coclé. The delimitation for the Azuero peninsula and local TDFs used were provided by Panama’s Ministry of Environment and the Pro Eco Azuero Foundation, an NGO collaborating to this study with maps, shapefiles, and connections to landowners for data collection (Pro Eco Azuero. 2022). A climate analysis was used to provide information on the behavior of climate change and climate pressures in Azuero by combining geostatistical and time series analysis with the calculation of climate anomaly indices.

Section 2.02 - Methodology

Climate analyses have been performed using two sets of data, primarily recorded by local meteorological stations of Empresa De Transmisión Eléctrica, S.A. (ETESA), then using WorldClim satellite data for comparison and support. The data was collected as daily values (ETESA) or monthly values (WorldClim), and was analyzed per year, per season (dry season from December of previous year to March, and wet season from April to November), and considering years that experienced El Niño (2015 and 2016) and La Niña Oscillation events (1998 and 2010) (Hutchison et al. 2018).

The ETESA Panama station network used for climate analysis consists of 442 meteorological stations in Panama, collecting daily data from 1998 to 2018 of climate variables (20 years), from which 88 stations are within provinces situated within the Azuero peninsula (22 stations in Veraguas, 15 stations in Los Santos, 8 stations in Herrera, and 25 stations in Coclé) (ETESA. 2021). Within these 88 stations, the delimitations of the peninsula were the main determinant for either considering or discarding a station for the analysis. Within these stations, the available climate variables were also important for the stations to be considered. Six climate variables were considered: Solar radiation (2 stations), Minimum temperature (15 stations), Maximum temperature (7 stations), Precipitation (22 stations), Wind speed at 2m (3 stations), and Evapotranspiration (16 stations) (ETESA. 2021). ETESA data was downloaded as daily values and was arranged as monthly values. Precipitation and evapotranspiration were summed as accumulative values, while minimum temperatures, maximum temperatures, wind speed at 2m, and solar radiation were averaged as monthly values.



Azuero Peninsula, Panama, and the Dry Arc, Pro Eco Azuero, Información sobre Base de Datos de Plantas, ND, https://proecoazuero.org/informacion-sobre-base-de-datos-de-plantas/

Pro Eco Azuero. PEA Entrega Rompecabezas del Mapa de Azuero a Escuelas Locales. ND, https://proecoazuero.org/2013/06/24/pea-entrega-rompecabezas-del-mapa-de-azuero-a-escuelas-locales/

Figure. 1 Within the context of Panama in (A), the forest cover in the Azuero peninsula (B), and provinces, roads, and rivers within the peninsula and the peninsula's "Dry Arc" shown in red (C). The study area considered for this research is delimited by the yellow triangle in (B) and (C). Maps (B) and (C) were developed by the Pro Eco Azuero organization ©.

The analysis of the ETSA climate patterns was replicated for validation on satellite data from the WorldClim historical monthly weather data between 1960 and 2018, focusing on minimum temperature, maximum temperature, and precipitation for 57 years (*Results in Supplementary Materials Figure. S1-S5*) (WorldClim. https://www.worldclim.org/data/monthlywth.html).

Time series analyses with a nonparametric regression with Mann-Kendall trend test (Mann. 1945; Kendall. 1975; Gilbert. 1987) were used to identify temporal variations for each of the six climate variables considered within the ETESA and WorldClim data. The nonparametric regression Mann-Kendall trend test is commonly used to determine trends in climate data and can handle seasonal patterns data (Gocic and Trajkovic. 2013; Anghileri et al. 2014). Time series were performed considering all the ETESA stations within the Azuero delimitations (and some stations surrounding the delimitations for more accuracy in the climate trend analyses) to determine a regional trend of changes in climate variables (See Figure. 2 - 5). I used the R packages *Kendall* (McLeod. 2022*)* and *trend* (Pohlert. 2019). Time series on WorldClim data can be found in the supplementary materials (*Supplementary Materials Figure. S1-S5)*.

Extreme climate anomalies, such as severe droughts, El Niño and La Niña Oscillation events, as well as anomalies in the duration of seasons, are increasingly recognized as major indicators of climate change and climate pressures on ecosystems (Allen et al. 2017; Aleixo et al. 2019; García et al. 2020). It has been proposed that the severity and abrupt nature of such events could defeat the resilience of forests in the face of climate change and has been related to massive tree mortality (Anderegg et al. 2015) even up to 2 years after the event (Aleixo et al. 2019). A wide range of climate anomaly indices have been developed to analyze specific abnormal climatic events. Some of those respond more precisely to specific climate variables, such as the RAI (Rainfall Anomaly Index) developed by Van Rooy (1965) which exclusively considers abnormal events in precipitation (Haensel et al. 2015; Costa and Rodrigues. 2017; Lins et al. 2017). RAI analyses are available in the supplementary materials (*Supplementary Materials Figure. S7*). Additionally, most indices vary in the technical aspects in which they can analyze time periods, allowing the analysis of years, specified periods, or seasons.

In recent years, Standardized Precipitation Index (SPI) from McKee et al. (1993) (Abdulrazzaq et al. 2019; Bahrami et al. 2019; Kalisa et al. 2020), and Standardized Precipitation Evapotranspiration Index (SPEI) from Vicente-Serrano et al. (2010) have been used to represent abnormal climatic events related to climate change (Haensel et al. 2015; Gao et al. 2017; Miah et al. 2017; Hutchison et al. 2018; Zhang et al. 2018; Wang et al. 2019). SPEI, used in this study, stands out as it allows the consideration of several climate variables: Minimum temperatures, maximum temperatures, precipitation, and evapotranspiration. Unlike SPI, SPEI considers the effects of temperature, which allows the consideration of increased water losses through evapotranspiration (Fung et al. 2020). In addition, SPEI can be used to analyze different timeframes, known as lags (Hutchison et al. 2018). These lags range between monthly, seasonal, and yearly timeframes. This allows a complete interpretation of climate behaviors through time, as well as providing a flexible approach to time-specific scales analyses.

Following the Isbell et al. (2015) classification of SPEI climate anomalies, normal events are represented by SPEI values ranging between -0.67 and 0.67, moderately dry or wet events are represented by SPEI values $\geq \pm 0.67$, and extremely wet or dry events are represented by SPEI values $\geq \pm 1.28$ (Isbell et al. 2015). Negative SPEI values represent dry and warm events, while positive SPEI values represent wet and cold events that surpass the historically established standard weather events. The calculations were performed using the R package *SPEI* (Santiago Beguería and Sergio M. Vicente-Serrano. 2017). The SPEI is measured as follows:

$$SPEI = W - [(C_0 + C_1W + C_2W^2) / (1+d_1W + d_2W^2 + d_3W^3)]$$

where $W = -2\ \ln(P)$ for $P \leq 0.5$ such that $P = 1 - F(x)$ is the probability of being greater than a given value of D (time series time or 12 months). The constants are the following $C_0 = 2.515517$, $C_1 = 0.802853$, $C_2 = 0.010328$, $d_1 = 1.432788$, $d_2 = 0.189269$, and $d_3 = 0.001308$.

The SPEI was calculated for each location where ETESA meteorological stations had the available data for the needed climate variables between 1998 and 2018 in the Azuero peninsula (Figure. 6B). Missing data was not replaced with interpolated data from the geostatistical analysis to avoid the consideration of anomalies that could not be verified. Interpolation has been used by several researchers as an attempt to fill the gaps of missing climate data (e.g., Price et al. 2000; Jeffrey et al. 2001; Hofstra et al. 2008; Mekis and Vincent. 2011; Vincent et al. 2012), however, interpolation methods only result in estimated data, decreasing the statistical robustness of a study (Anderson and Gough. 2018). I used neighboring stations to account for stations with missing data; co-kriging interpolation was used only for support to observe trends through maps (See Figure. 7 and *Supplementary Materials Figure. S6*). Instead, I used a Mann-Kendall regression to aim for a better calculation for the missing data (Lacombe et al. 2012; da Silva et al. 2015; Rahman et al. 2017; Mallick et al. 2021).

Section 2.03 - Results

The central objective of this study was to analyze climate variable trends indicative of climate change and understand their potential impact on Panama's tropical dry forests. With regards to temperatures, results show clear trends of increasing minimum and maximum temperatures between 1998 and 2018 (Figure. 2 and 3 respectively). In addition, decreasing rates of precipitation (Figure. 4) and evapotranspiration (Figure. 5) have also been evidenced. These results have been further explored and confirmed within a larger timeframe from 1961 to 2018 with WorldClim satellites data looking at 57 years' worth of climate data (*Supplementary Materials Figure. S1-S5*). The regional trend in temperatures, and precipitations, unveil increasing climatic pressures in the peninsula that support the literature describing increasing climatic pressures as symptoms of climate change in the tropics (Pinzón et al. 2017; Esquivel-Muelbert et al. 2018; Pörtner et al. 2022). As expected from climate change-related literature, minimum and maximum temperatures increased over the past 20 years, reaching above 1°C of increase from an average 21.6°C to a 22.7°C for the mean minimum temperatures recorded in the region (Figure. 2), and around 0.6℃ increase, from 32.6°C to 33.2°C for the mean maximum temperatures recorded in the region (Figure. 3).

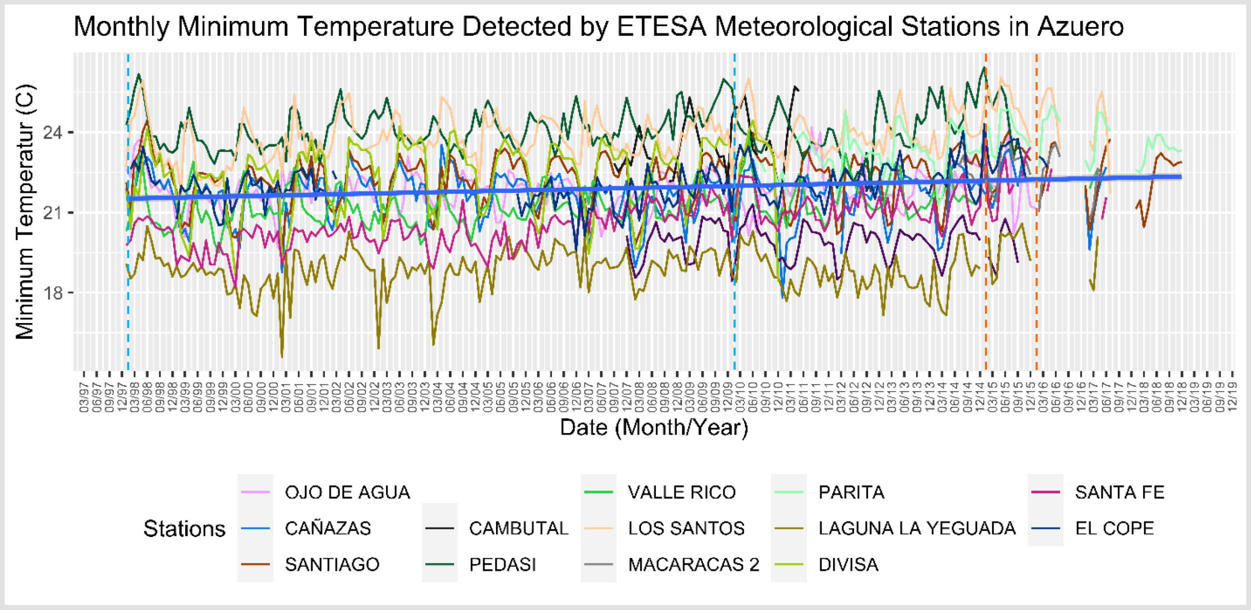


Figure. 2 Time series with a nonparametric regression with Mann-Kendall trend test (blue line) of minimum temperatures (x-axis as 3-month intervals per year, y-axis as minimum temperatures in degree Celsius) from 1998 to 2018 using data from ETESA Panama meteorological stations in the Azuero peninsula. Each colored line corresponds to a ETESA station and their location within the Azuero peninsula, and the minimum temperatures recorded at that location. The vertical blue dotted lines show La Niña years, while the vertical orange dotted lines represent El Niño years. Lines interrupted represent years of missing data.

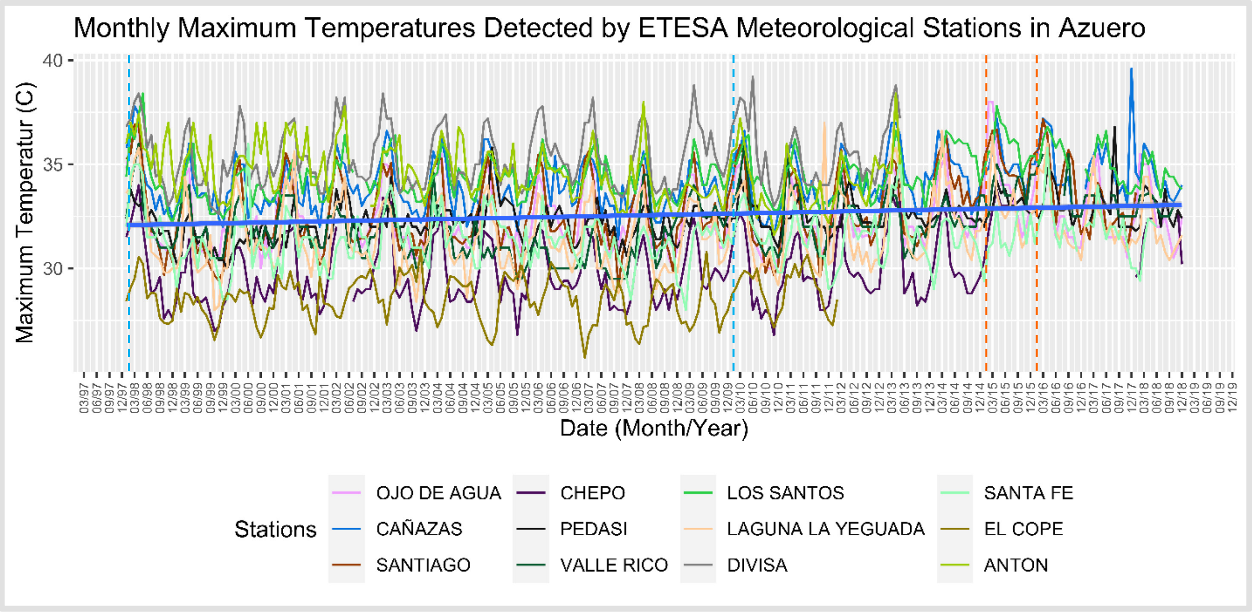


Figure. 3 Time series with a nonparametric regression with Mann-Kendall trend test (blue line) of maximum temperatures (x-axis as 3-month intervals per year, y-axis as maximum temperatures in degree Celsius) from 1998 to 2018 using data from ETESA Panama meteorological stations in the Azuero peninsula. Each colored line corresponds to a ETESA station and their location within the Azuero peninsula, and the maximum temperatures recorded at that location. The vertical blue dotted lines show La Niña years, while the vertical orange dotted lines represent El Niño years. Lines interrupted represent years of missing data.

Nonparametric regression with a Mann-Kendall trend test analyses demonstrate that precipitation in the Azuero peninsula decreased over the past 20 years by an average of 320 mm across the peninsula from 1300 mm to 980 mm (Figure. 4). These important precipitation decreases and temperature increases could have resulted in water stress mirrored by the changing rates of evapotranspiration, as evapotranspiration is sensitive to several climate characteristics, such as temperature, relative humidity, and wind speed (Kundzewicz. 2008). This relationship should be further investigated. Evapotranspiration decreased over the past 20 years, from an average 27mm per month (average of 324mm evapotranspiration per year) to 23mm per month (average of 276mm evapotranspiration per year) (Figure. 5).

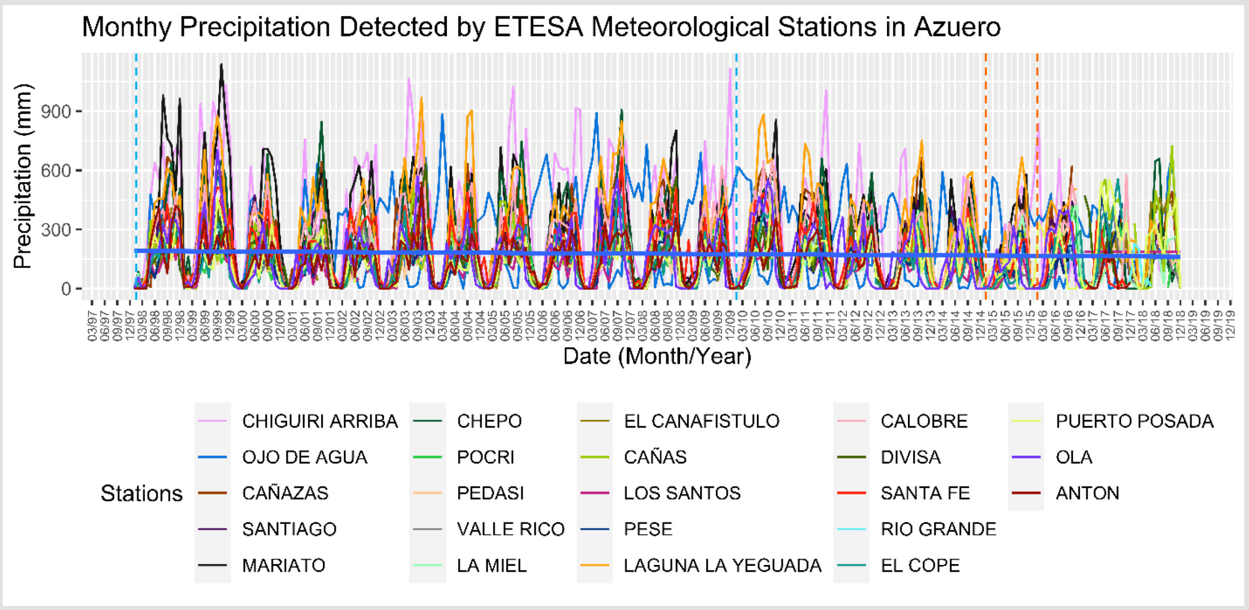


Figure. 4 Time series with a nonparametric regression with Mann-Kendall trend test (blue line) of precipitation (x-axis as 3-month intervals per year, y-axis as precipitation in mm) from 1998 to 2018 using ETESA meteorological stations' data in the Azuero peninsula. The precipitation data was graphed as daily values in mm summed for the dry and rainy seasons between 1998 and 2018. Each colored line corresponds to a ETESA station and their location within the Azuero peninsula, and the precipitation recorded at that location. The vertical blue dotted lines show La Niña years, while the vertical orange dotted lines represent El Niño years. Lines interrupted represent years of missing data.

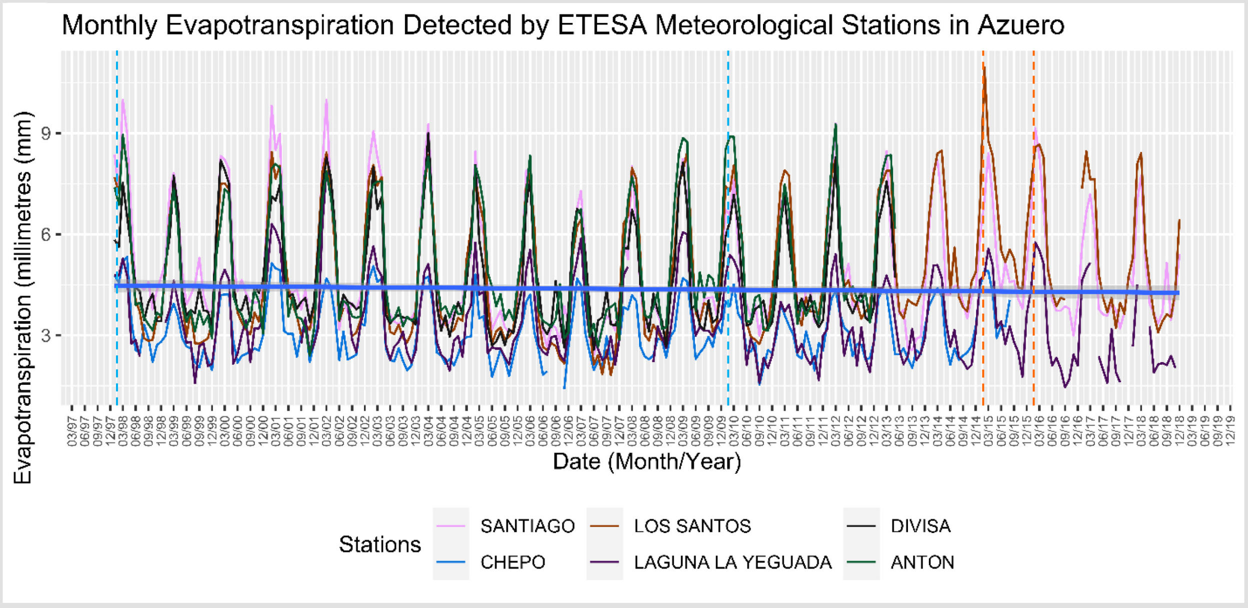


Figure. 5 Time series with a nonparametric regression with Mann-Kendall trend test (blue line) of evapotranspiration (x-axis as 3-month intervals per year, y-axis as evapotranspiration in mm per month) from 1998 to 2018 using ETESA meteorological stations' data in the Azuero peninsula. Each colored line corresponds to a ETESA station and their location within the Azuero peninsula, and the evapotranspiration recorded at that location. The vertical blue dotted lines show La Niña years, while the vertical orange dotted lines represent El Niño years. Lines interrupted represent years of missing data.

Between 1998 and 2018, there have been two occurrences of La Niña events that are present in the data (1998 and 2010), and two years of El Niño events (2015 and 2016) (Hutchison et al. 2018). The SPEI analysis on specific ETESA locations show that there is a concordance between positive SPEI (more humid and cold events) and La Niña events in 1998 and 2010 in some (but not all) locations. There is also concordance between El Niño years and severely dry and warm events (negative SPEI) in 2015 and 2016 for most locations with the exception of locations missing data for these years (Figure. 6). Another interesting result is that regardless of the ambivalent mirroring of SPEI values between extremes and El Niño and La Niña years in some locations, some episodes of extreme climate anomalies are present (e.g. Divisa during La Niña, El Copé, Los Santos and Pedasí, in the early years of the analysis with extremely dry events, and Los Santos, Pedasí, and El Copé with extremely cold and wet years after the 2010 La Niña year, and Divisa before 2010 La Niña event) (Figure. 6B).

Section 2.04 - Discussion

I used the tropical dry forests of the Azuero peninsula located on the Pacific coast of Panama, Central America, as a window from which I could observe the progress and complexity of climate change and extreme weather events in the tropics. Tropical dry forests are underrepresented in tropical forests studies. The results demonstrate that the Azuero peninsula experienced a general trend of increasing minimum temperatures by nearly 1°C and decreasing precipitation averaged to 320 mm across the peninsula within only 20 years, with a gradient of pressures at a local level that should be further investigated. These results have been supported with the use of data from the WorldClim satellite looking at 57 years' worth of climate data in addition to the local meteorological station data from ETESA (*Supplementary Materials Figure. S1-S5*). The SPEI analyses demonstrate that the Azuero peninsula experienced a highly localized range of climate anomalies between 1998 and 2018, with events that fluctuate within the peninsula. However, it is important to mention that in the SPEI analysis, missing data from the ETESA stations represented a difficulty in the determination of trends, having years that could not be represented in the analysis. For this reason, the SPEI results should be considered with the regional time series analysis of the same timeframe.

The IPCC 6th Assessment Report analyses projections of Global Warming Levels (GWL), as well as projected continental warming levels under the predicted GWL increase between 1.5°C to 4C° (Pörtner et al. 2022). The report depicts in Central and South America possible increases of mean daily minimum temperatures that range from 17°C to 21°C (under a forecasted GWL increase of 1.5°C to 2°C), 19°C to 22°C (under a predicted GWL increase of 3°C), and 19°C to 24°C (under a projected GWL increase of 4°C). The results found in the Azuero peninsula for the mean daily minimum temperatures between 1998 and 2018 show an averaged 1°C increase from 21.6°C to a 22.7°C at the local level. These minimum temperatures exceed the IPCC's predicted mean daily minimum temperatures that would be reached locally as a result of increased GWL of 3°C within the end of the century, estimated between 19°C and 22°C (Pörtner et al. 2022). This could indicate that the local climate analysis in Panama's Azuero peninsula is revealing signs of an undesirable GWL trajectory that should demand our attention, understanding that additional research would be needed.

Maximum temperatures have been predicted by the IPCC 6th Assessment Report to increase in Central and South America from 25°C to 30°C (under a GWL increase of 1.5°C), from 26°C to 31°C (under a GWL increase of 2°C), and from 27°C to 32°C (under a GWL increase of 3°C to 4°C). The mean maximum daily temperatures recorded in the Azuero peninsula in the results show a 0.6°C increase over the past 20 years from an averaged 32.6°C to 33.2°C. These temperatures exceed the IPCC's predicted increased mean maximum daily temperatures that Central and South America could reach under a projected GWL increase of 3°C to 4°C (Pörtner et al. 2022).

Lastly, the IPCC's 6th Assessment Report compared predictions related to drought and precipitation levels globally and at a continental level (Pörtner et al. 2022). The report shows that by considering future scenarios of increasing GWL between 1.5°C to 4°C, the maximum 1-day precipitation amount, and the maximum 5-day precipitation amount would experience a slight increase from the least to the most pessimistic scenario of GWL increase (Pörtner et al. 2022). However, the consecutive dry days (precipitation < 1 mm per day) is expected to increase as the GWL increases. This could indicate that in Central and South America, minimum and maximum temperatures could increase under each GWL scenario of roughly 3°C to 5°C locally, precipitation is expected to increase in Central and South America, and the duration of droughts is also predicted to increase from the lowest to the most pessimistic scenario (Pörtner et al. 2022). The averaged ranges of temperatures for Central and South America provided by the IPCC should be considered at a different scale to my results in Azuero, and would demand a scale-comparable analysis for further conclusions. The comparison of the increases of temperatures that we can see in Azuero to IPCC's predictions that look into future scenarios resulting from GWL increases, shows that Azuero has been undergoing a strong pressure from climate variables quite rapidly, and propose that future increases in temperatures could be worrying and exceeding our expectations even under pessimistic scenarios as the ones analyzed by the IPCC.

As a result, according to the IPCC, it is predicted that Central and South America could experience increasingly warmer temperatures, and higher precipitations, with longer periods of droughts. This means that local forests would experience pressures to adapt, not only to general trends of increasing temperatures and precipitation, yet also recruit species that can survive longer periods of water scarcity. My results in the Azuero peninsula partially support these predictions, as my temporal data analysis shows increasing temperatures, but rather a decline in precipitations over the past 20 years. For this reason, my results show that local TDFs have had to adapt to a general increase in temperatures and an increasingly dry weather, yet their chances of resilience or adaptation in the future should rather be based on climate predictions. On the other hand, other predictions raise the concern for a drier climate resulting from decreasing precipitation in both, Central and South America (Esquivel-Muelbert et al. 2018, Pinzón et al. 2017). These have been primarily supported looking at climate shifts in the Amazon Basin's tropical rainforests (Esquivel-Muelbert et al. 2018), while others considered a sub-continental approach in which most cities of Central America will become drier in the future (Pinzón et al. 2017). As a result, while the temporal climate analysis shows that local TDFs have been able to adapt to increasingly dry weather, their capacity to continue to adapt will be influenced by experiencing either increased precipitation and longer drought periods or a drier and warmer climate. While general trends will primarily dictate how forests will react to climate pressures in the future, short and acute climatic episodes of drought and extreme weather events could also pose a threat to their survival. Some irregular weather events are better understood than others, such as El Niño and La Niña Southern Oscillation events (ENSO), which are considered under a cyclical approach expected to occur and can be predicted quite accurately. In the Azuero peninsula, ENSO episodes such as the 2014-2015 ENSO, have shown the severity that extreme weather events can represent in terms of water stress for forests. While the mean precipitation for the peninsula was estimated to roughly 1100mm in 2014 and 1000mm in 2015, the locations with the highest precipitation levels during the 2014 and 2015 wet seasons had 2500mm. However, locations with the lowest precipitations experienced precipitation levels averaging 500mm for the entire wet season of 2014 and 2015. Within the 20-year analysis, it was established that the driest location would have a wet season that would at least closely reach the mean precipitation levels for the Azuero region. However, 2014 and 2015 are drastically drier in comparison, showing precipitation levels under the mean precipitation levels by nearly 500mm. On the other hand, La Niña years such as 1998 and 2010 have precipitation levels in the driest locations of the peninsula that exceed the mean precipitation for the entire region (the driest location exceeding the mean precipitation by nearly 400mm in 2011). As a result, considering that the Dry Arc of Panama, where Azuero's TDFs grow, receive <1,500 mm yearly (López, Pérez, and Mariscal. 2015), abrupt changes in precipitation levels that El Niño and La Niña events engender need to be considered as extreme influences on vegetation. These will add pressure with ongoing general increasing temperatures and precipitation changes rooted from climate change.

While this study demonstrated an increasingly warmer and drier climate pressuring the TDFs in Panama, more is left to unveil regarding the future of these forests with climate predictions. This is true at a global level, considering analyses presented by bodies as the IPCC, as well as at a national and regional level, and variations are frequently encountered due to the complicated nature of the matter. I looked at studies that focused on the impact of climate change in the Neotropics, and these revealed some surprising results regarding the conditions that Panama's forests will be facing in the future. Pinzón et al. (2017) used climate analogues to relate the climatic pressure of seven capitals in Central America to climates anywhere in the planet that we experience in the present. Climate analogues allow a firsthand comprehension of future climate by identifying future-resembling climate analogues. Pinzón et al.'s predictions for 2075 to 2099 point to increasing temperatures and decreasing precipitation across Central America. A climate analogue was found for all capitals with the exception of Panama. Panama is thus expected to have a "*novel climate during the later 21st century*" with increasing precipitations and warmer surface air temperatures and ocean surface temperatures (Pinzón et al. 2017). These predictions considered several factors of importance for the case of Panama, including its location between the Pacific and the Atlantic oceans, the intertropical conversion zone, the effects of ENSO, and how oceans' surface temperatures could affect precipitation at a regional level.

However, since climate pressures can vary at a regional scale (due to topography, winds, land use, proximity to oceans, vegetation, etc.), it is important to consider a regional scale and ecosystem-specific analyses within countries. Another study by García, Del Castillo and Saavedra (2020) predicts future climatic pressures in the La Villa watershed within the Azuero peninsula in Panama. Using both ETESA meteorological stations and WorldClim satellite data (as I did), their results suggest that between 2050 and 2070 this watershed will experience higher rates of precipitation and increasing temperatures (García et al. 2020). This supports Pinzón et al. (2017)'s predictions for Panama at the regional level for Azuero. This indicates that past climate tendencies showing a drier and warmer climate within the Azuero peninsula could shift, requiring TDFs to adapt to wetter conditions, and continually increasing temperatures. This analysis did not consider shorter extreme weather events, meaning that we also need to consider the added pressure from severe weather events such as sporadic droughts, as mentioned in the previous section.

There is a great variability in the way climate change impacts ecosystems at both large and small scale. It was established that there are variations in what is called the mid-summer drought (MSD) timing, as well as the amount of rainfall during the rainy season, the number of consecutive and total dry days, and the frequency and severity of extreme wet events at the local scale since the 1980s (Anderson et al. 2019; Pörtner et al. 2022). For Central America, a positive trend in the duration of the MSD was found, yet not for the severity of MSD (Anderson et al. 2019; Pörtner et al. 2022). In fact, projections show that the rainy season in Central America could be prone to more noticeable MSDs by the end of the century (Maurer et al. 2017). Central America should be further prioritized as a hotspot for climate action and conservation in the face of climate change considering the intensity of rainfall variation occurring and that will continue to experience (Imbach. 2017; Pörtner et al. 2022). A question that arises amongst many other questions is: What will be the fate of Azuero's TDFs by the end of the century if, after showing resilience mechanisms to survive drier and warmer climatic pressures in the past years, these face future climatic pressures involving increasing precipitation, more increases in temperatures and longer droughts? This uncertainty remains a difficulty in the identification of climate predictions that will, in fact, be experienced by these forests.

Section 2.05 - Conclusion

It is projected that future climate change impacts will include higher mean temperatures, higher water scarcity from decreasing precipitations and/or from an increased duration of droughts, and more intense El Niño-Southern Oscillation events, and we still need to understand how ecosystems will respond to these extreme weather events (Hutchison et al. 2018). These extreme weather events represent a risk to these forests as they are a shift of climate conditions from a baseline of normal years (Hutchison et al. 2018). In this study, I calculated the SPEI within years and seasons from 1998 to 2018. In their study, Hutchison et al. (2018) used SPEI calculations to understand if systems in the tropics have the ability to adapt to change, developing resistance and resilience to extreme weather events related to climate change. Results found from a tropical tree monoculture and mixed plantation experiment in Sardinilla, Panama (TreeDivNet. 2011; Müller et al. 2022) showed that considering data from 1995 to 2016, extreme climate events occurred roughly in 20% of the analyzed years, moderate dry and wet events each occurred 25% of the analyzed years, and normal conditions represented 30% of the analyzed years in the data (Hutchison et al. 2018). Between 2006 and 2016 monocultures exhibited greater sensitivity to extreme conditions than mixed-species plantations, suggesting a positive relationship between diversity stability and a species richness on growth and mortality as a response to stress (Hutchison et al. 2018). Climate pressures will continue to impact forests through general trends and climate anomalies, and little is known about the reaction of tropical (and tropical dry forests) to these pressures.

Chapter 3

Response of Tropical Dry Forests in Azuero to Past Climatic Pressures

Chapter 3 is a study looking at the response of tropical dry forests in the Azuero peninsula in Panama to the previously identified climatic pressures. This chapter contributes to the understanding of Panama's tropical dry forests responses to increasingly dry and warm climatic conditions, resulting in species composition and functional traits shifts towards a greater drought resistance and resilience to climate pressures.

Section 3.01 - Introduction

Whether considering large scale climate predictions such as the ones provided by the IPCC, or regional and small-scale predictions in Panama as the ones described by García et al. (2020), Hutchinson et al. (2018), and Pinzón et al. (2017), the climate forecasts for 2100 suggest temperature increases and increases in extreme weather events frequency and severity (Pinzón et al. 2017; Hutchison et al. 2018; García et al. 2020; Pörtner et al. 2022). By the mid-20th century, extremely warm temperatures would be reached while temperatures considered 'extreme cold temperatures' decreased in Central America (Seneviratne et al. 2021; Pörtner et al. 2022). Massive heat waves and an increased incidence of warm extremes are projected at the end of the 21st century in Central America. Comparing 2°C with 1.5°C GWL, the longest heat waves are projected to extend over 60 days (Taylor et al. 2018). The results of Chapter 2 however, tend to support IPCC's forecasts showing decreased precipitation and increased temperature in the past 20 and 57 years (Figure 2 – 5; *Supplementary Materials Figure. S1-S5)*.

Predictions of precipitation regimes largely determine outputs of future climate scenarios in the neotropics. The connection to drought episodes is well-established as a high cause of risk for tropical rainforests of South America, such as those established by several studies including Esquivel-Muelbert et al. (2018). The IPCC's 5th and 6th Assessment Report also describe that drought conditions in Central America and the Caribbean have increased following climate model predictions that have been previously considered (Pörtner et al. 2022). Increases MSD duration identified in Central America by the end of the century could also represent further vulnerability to climate change (Anderson et al. 2019; Pörtner et al. 2022). This would result in reduced minimum precipitations (Fuentes-Franco et al. 2015; Maurer et al. 2017; Imbach et al. 2018; Naumann et al. 2018; Ribalaygua et al. 2018; Corrales-Suastegui et al. 2020; Pörtner et al. 2022). However, it is stated that more incoherencies with regards to drought-related extremes are found in contrast with precipitation extremes (Seneviratne et al. 2021; Pörtner et al. 2022). For Central America, the general trend predicted is one of a decreased magnitude of heavy precipitations events if reaching 1.5ºC GWL projections (Chou et al. 2014; Giorgi et al. 2014) but an increased incidence of extreme precipitation if reaching 2ºC and 4ºC GWL (Imbach et al. 2018; Pörtner et al. 2022). Substantial increases in the intensification of tropical cyclones across the Atlantic basin have also been evidenced (Bhatia et al. 2019; Pörtner et al. 2022). Tropical cyclones contribute with nearly 10% of the annual precipitation in this region (Khouakhi et al. 2017; Pörtner et al. 2022). In addition to several sub-continental interpretations of climate predictions, local studies of future climate suggest that Panama and the Azuero peninsula will experience a completely different climate trajectory by the end of the 21st century in comparison to the rest of Central America (Christensen et al. 2007; Pinzón et al. 2017; Pörtner et al. 2022).

To understand how TDFs in Azuero respond to recent past climate change, I adopted the methodology of Esquivel-Muelbert et al. (2018) who compared saplings to trees' drought resistance functional traits in the Amazon Basin, South America. This study was the first Amazon-wide report on temporal trends in functional and floristic composition of lowland tree communities from inventory plots considering over three decades (Esquivel-Muelbert et al.

2018). Their study was motivated by an intensified drought during the dry season in the Amazon Basin and aimed to understand and quantify the shifts of the species composition of Amazonian tree communities due to the recent climatic pressures (Esquivel-Muelbert et al. 2018). The authors documented a shift towards a floristic composition that is affiliated with drought resistance strategies, including high wood density and decreases in tree size (Esquivel- Muelbertet al. 2018). This study showed that under climatic pressures including stronger and more frequent droughts and increasing temperatures, neotropical rainforests are at risk of experiencing a strong shift in species composition. Hypothesizing that the Azuero tropical dry forests experienced increases in temperatures and drought as well, I aimed to test a potential shift towards drought-tolerant functional traits and species composition, which my results have evidenced. This supports the concerns shared amongst researchers dedicated to the Neotropics that the predicted temperatures and rain fluctuations will have an unprecedented impact on neotropical ecosystems.

Section 3.02 - Methodology

(a) Field work sites selection

Land tenure within the Azuero peninsula varies from private lands which can be developed or forested, national parks, and reserves. Private developed lands are mostly used for settlement, cattle farming, and agriculture. For the field work, I selected forest sites both private and public. I aimed to choose sites in tropical dry forests that passed the early succession stages in which recruitment is high and mostly favors pioneer species establishment until reaching the first 10 years of regeneration (Lebrija-Trejos et al. 2010). Stages beyond that period allows a mixed pattern between high recruitment and fast growth of pioneer species, with the gradual recruitment and slower growth of larger mature forest species (2010). In TDFs, patterns for the mature species communities can appear shortly between 15 and 18 years (Lebrija-Trejos et al. 2010).

In fact, shifts in dominance from pioneers to mature species have been recorded between 17 - 39 years of natural regeneration with a 95% confidence (2010). As Powers and Tiffin (2010) provided evidence that TDFs between 10 and 35 years-old forests can be considered young secondary forest, I expected to collect data from a range of young to old secondary TDFs. This mixture of pioneer with mature species communities was considered adequate to provide interesting insights on species composition shifts from climate pressures. The recruiting species that are found in my studies will likely become the future canopy trees representative of the forest, which can provide a prediction of a potential change of the local TDFs as we know them presently. Site selection for field work was performed considering the climatic pressures analysis, the location of local tropical dry forests, and the current land use and land tenure within the peninsula. In the climate pressure analysis, a first attempt to classify the intensity and severity of climatic pressures within the Azuero peninsula (Figure. 6A) was undertaken by considering station-specific climate anomaly indices (SPEI) (Figure. 6B). I also looked at the regional trend of increasing climatic pressures with temperature and precipitation changes (Figure. 6C).

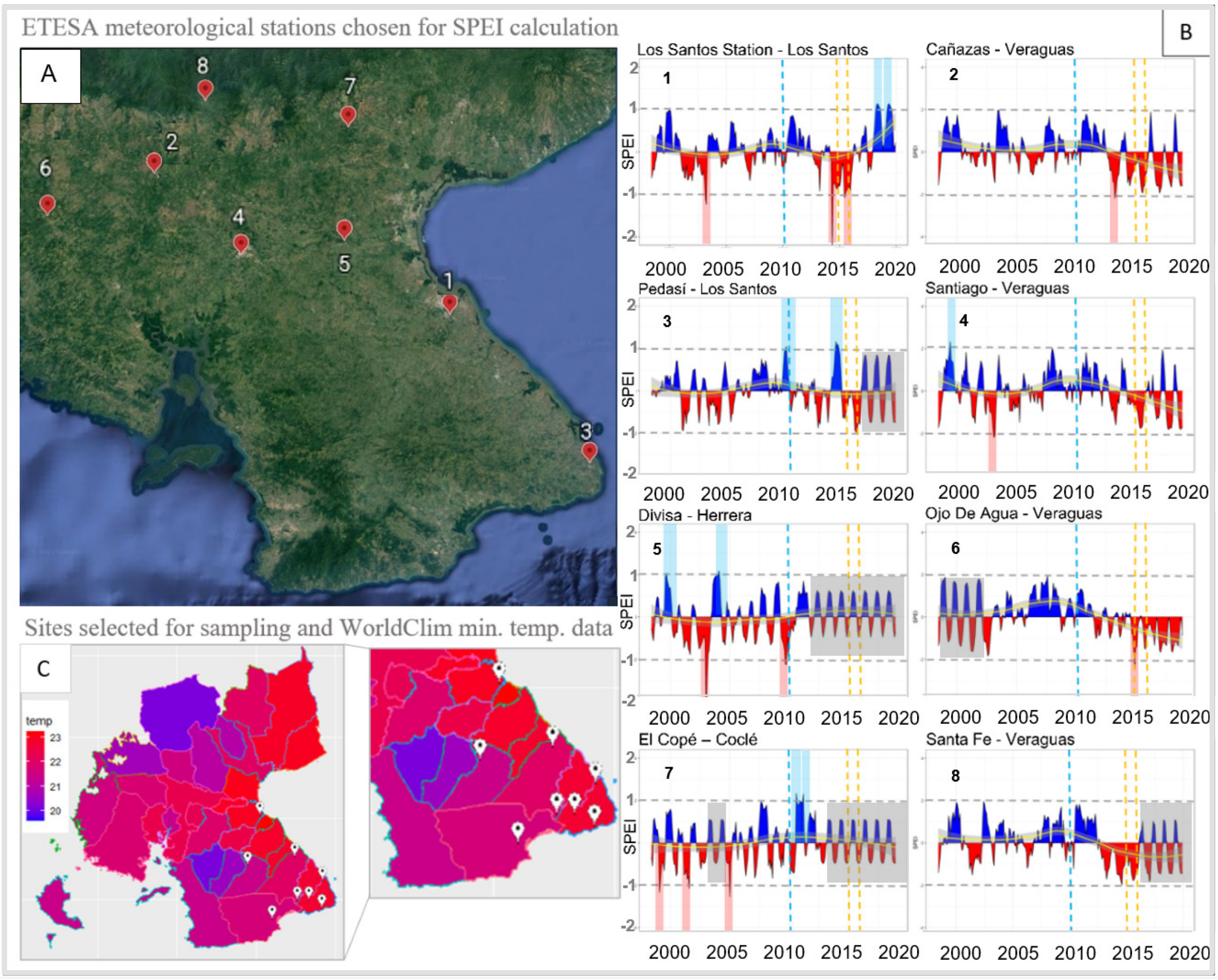


Figure. 6 Using ETESA meteorological stations (locations shown as red pins) with climate information from 1998 to 2018 in (A), I calculated SPEI values in (B). From eight locations of the chosen ETES stations (red pins in (A)), eight sampling sites for field work have been selected (white pins in (C)) with the consideration of the climate and SPEI analysis (B), the extend of TDFs, and climate variable mean values in 2018 (C). In (B), negative (drier) climatic values are represented in red and under the standard values, while positive (wetter) climatic values are represented in blue and above the standard values. Sections highlighted in grey represent years with missing values in which the SPEI could not be properly calculated. The x-axis represents the years, and the y-axis represents the negative and positive CWB values from the SPEI calculation. Colors on map (C). stand for the mean minimum temperatures in 2018 in °C at the district level. Warmer temperatures are represented by warmer (red) colors, while cooler temperatures are represented by cold (blue) colors.

The SPEI time series lag-12 (considering monthly values) of positive and negative climate weather balance values (CWB), was calculated with the ts, SPI and *SPEI* R packages between 1998 to 2018 in the Azuero peninsula using ETESA meteorological station data. Using the Hargreaves method, the CWB calculation considers the minimum temperatures, the maximum temperatures, precipitation, and the evapotranspiration, to determine abnormally dry months and years (as red) and abnormally wet months and years (as blue). Values of higher extreme climate anomalies are farther away from the x-axis, for which 0 would be equal to normal events. The yellow line shows the trend of climate anomalies in the site of the station. The gray dotted lines on the graphs show the wet or dry events are represented by SPEI values ≥ ± 0.67, and extremely wet or dry events are represented by SPEI values ≥ ±1.28 within a range from -2 to 2 on the graph (Isbell et al. 2015), while the blue dotted lines show the La Niña years, and the yellow dotted lines show the El Niño years. Colors on map C. stand for the mean minimum temperatures in 2018 in °C at the district level. Warmer temperatures are represented by warmer (red) colors, while cooler temperatures are represented by cold (blue) colors. Sections highlighted in grey represent years with missing values in which the SPEI could not be properly calculated.

While I aimed to select sites by considering all four datasets together (time series analyses, SPEI analyses, presence of TDFs and land use), the data available for the time series analyses and for the SPEI calculations were rather complementary instead of matching or corresponding by location. This is because while the time series analyses only require one climate variable to be analyzed individually, allowing more stations to be considered within the peninsula and close to the areas of TDFs growth, the SPEI calculations were restricted to stations having all the required variables. Therefore, most of the stations used for the SPEI calculations were located in the north of the Azuero peninsula, with only few having the required data located near TDFs' growth (e.g., stations of Los Santos, Pedasi, and Divisa).

In addition, an interpretation of the SPEI indices was difficult due to missing data, as missing data in any of the variables needed for its calculation would result in unknown SPEI. Unknown SPEI calculation tended to prevail in the last years of the analyses due to this barrier, which made the last years' anomalies difficult to identify. As a result, while the time series analyses unequivocally demonstrate changes in the climate through time, the interpretation of climate anomalies could only be interpreted sporadically and were mostly contrasted with expected climate anomalies due to El Niño and La Niña. This juxtaposition with these events shows additional irregularities with extreme climatic events within the data available. While I first aimed to establish a clear classification pattern between more and less impacted locations which would indicate more to less vulnerable TDFs to climate anomalies, I consider that different intensities of climatic pressures have occurred along a spectrum from most to least extreme climatic pressures within a clear trend of climate shift. Further research should be conducted to better understand and identify SPEI climate anomalies in the region.

The second step used to select sampling sites was to locate the TDFs with their current extent. To that end, data from Panama's Ministry of Environment (MiAmbiente), including the most recent land cover and land use map, was used (MiAmbiente, 2012) (See Figure. 7). A MiAmbiente land cover map from 2016 was under revisions and was not available for use during the time of the research. The criteria to classify TDFs using this data was to identify forest cover which included secondary to primary forests, avoiding forest fragments, and excluding lands used for agriculture or cattle farming. In Azuero, forested lands are often found as forest fragments, and share their boundaries with agricultural and cattle farming lands. Due to the scarcity of old-growth TDFs, this study considered both old growth forests and secondary forests as established by MiAmbiente's data. The presence of forest at selected sites was verified by field visits. In addition, because the Azuero peninsula harbors TDFs and humid forests, the later forests were excluded from the study using the Global Ecological Zones and Terrestrial Ecoregions classification (Olson et al. 2001). Classification of the selected field sites as TDFs was confirmed in the field through the assessment of vegetation primarily including species pertaining to the *Rubiaceae, Fabaceae, Apocynaceae, Malvaceae, Burseraceae,* and *Myrtaceae* families (Sánchez-Azofeifa et al. 2013; López, Pérez and Mariscal. 2015).

The final step taken to select sampling sites in Azuero's TDFs, was to identify locations of interest as either private lands, reserves, or national parks, and establish contact with landowners to ask for the possibility of collecting data on their lands for this study. To do so, information on land tenure (private to non-private lands) was shared by "Autoridad Nacional de Administración de Tierras" (ANATI) or the "National Land Administration Authority" in English (Autoridad Nacional de Administración de Tierras – ANATI. 2015). Afterwards, information on owners of forested private lands previously collaborating with the Pro Eco Azuero Project was shared, allowing the visit and exchange with local landowners. The process to select sampling sites is shown in Figure. 7, including locations at private lands or reserves and parks of: Las Tablas at the "Centro Regional Universitario de Las Tablas", Tonosí at the "Instituto Profesional y Técnico Agropecuario de Tonosí" (IPTA), a private forested land at Los Asientos, Pedasí at the PANAMAES private reserve, a private forested land at Oria Arriba, Parita at the National Park Sarigua, Macaracas at the National Park El Colmón, and a private forested land at Mariabé.

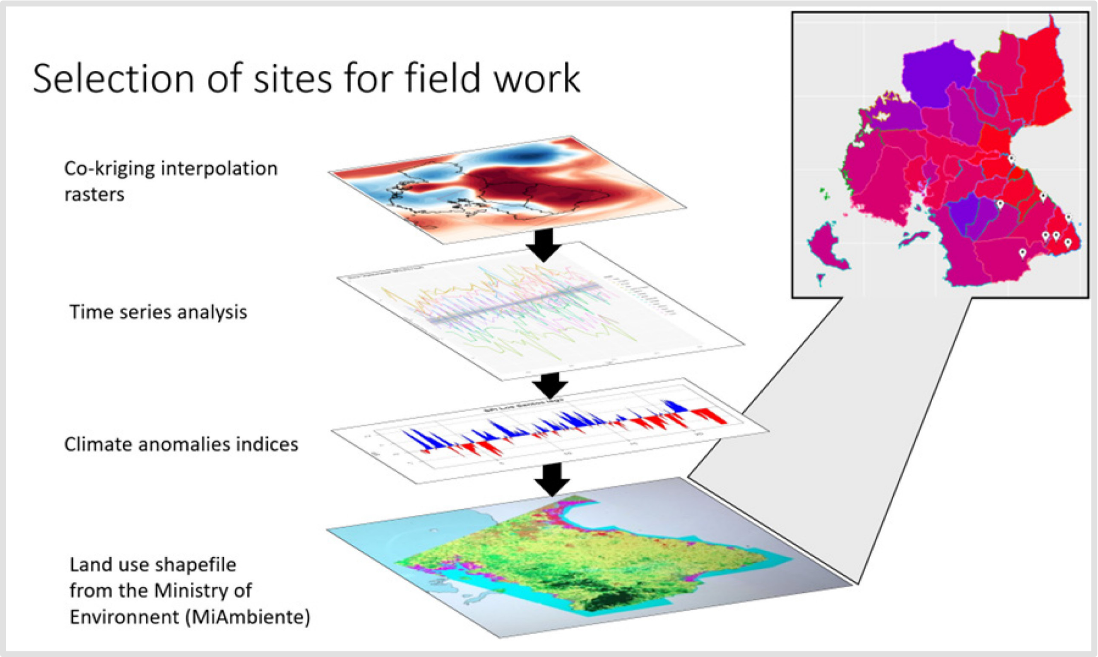


Figure. 7 Process and analyses used to select sampling sites within TDFs' presence in MiAmbiente's (2012) shapefile of land use and forest cover in the Azuero Peninsula. Sampling sites are indicated with white pins on the Azuero peninsula map on the upper right corner.

Field work focused on the response of TDFs to climate pressures at the level of species composition and functional traits comparing trees from the canopy to the recruiting saplings in the understory. This approach follows Esquivel-Muelbertet al.'s comparison between the canopy and recruits' response to climate change in the tropical rainforests of the Amazon Basin (2018). In my study, field work was conducted during the month of August (rainy season), when TDF trees have not yet shed their leaves, allowing an easier identification of the species and leaf functional trait measurement (Dirzo, et al. 2011; Allen et al. 2017).

The field plots used for the data collection were Modified Gentry plots (Figure. 8) designed to conduct time-efficient floristic inventory (Phillips et al. 2003). Adjustments were made from Phillips et al. (2003)'s model to collect data on canopy trees and saplings rather than herbs, as originally sampled within 1m x 1m subplots at the edges and halfway points of the plots' transects (See Figure. 8 and Figure. 9). Phillips et al. (2003)'s Modified Gentry plot (Figure. 8) consists of a 180m-long central belt, from which ten 50m long perpendicular transects start within every 20m along the belt. The first five transects unfold towards one direction from the central belt, while the remaining five transects are directed to the opposite direction from the belt. This maximizes the coverage of the sampled area, having a total plot area covering 180m x 100m (Phillips et al. 2003). Instead of using 50 1m^2 subplots as in this design, I deployed 30 subplots per site, three 4m^2 subplots per transect were used to sample data on recruiting saplings, two on each side of the transects, and the one in the middle varying sides. This led us to have a total of 240 subplots where species composition and functional traits data were collected (See Figure. 9).

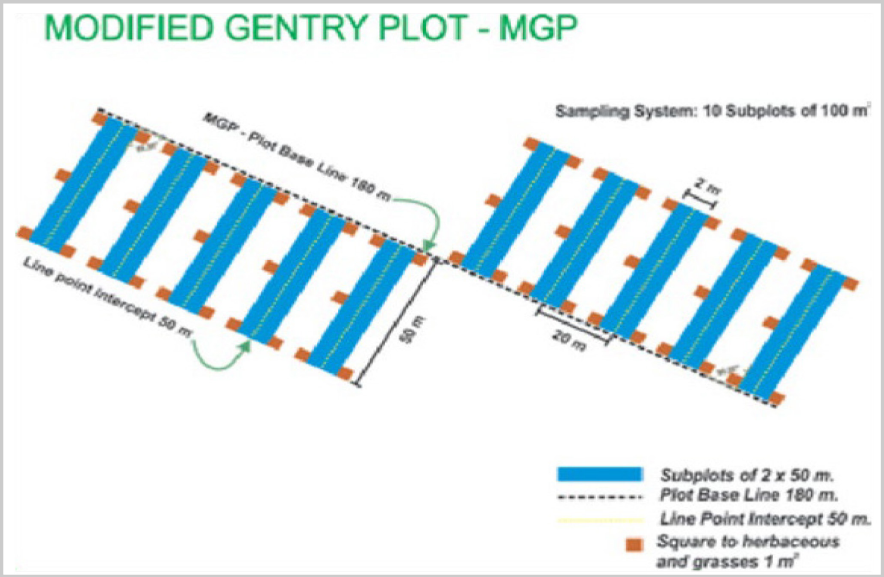


Figure. 8 Sampling design adapting Phillips et al. (2003) Modified Gentry plots to the study conducted in Azuero.

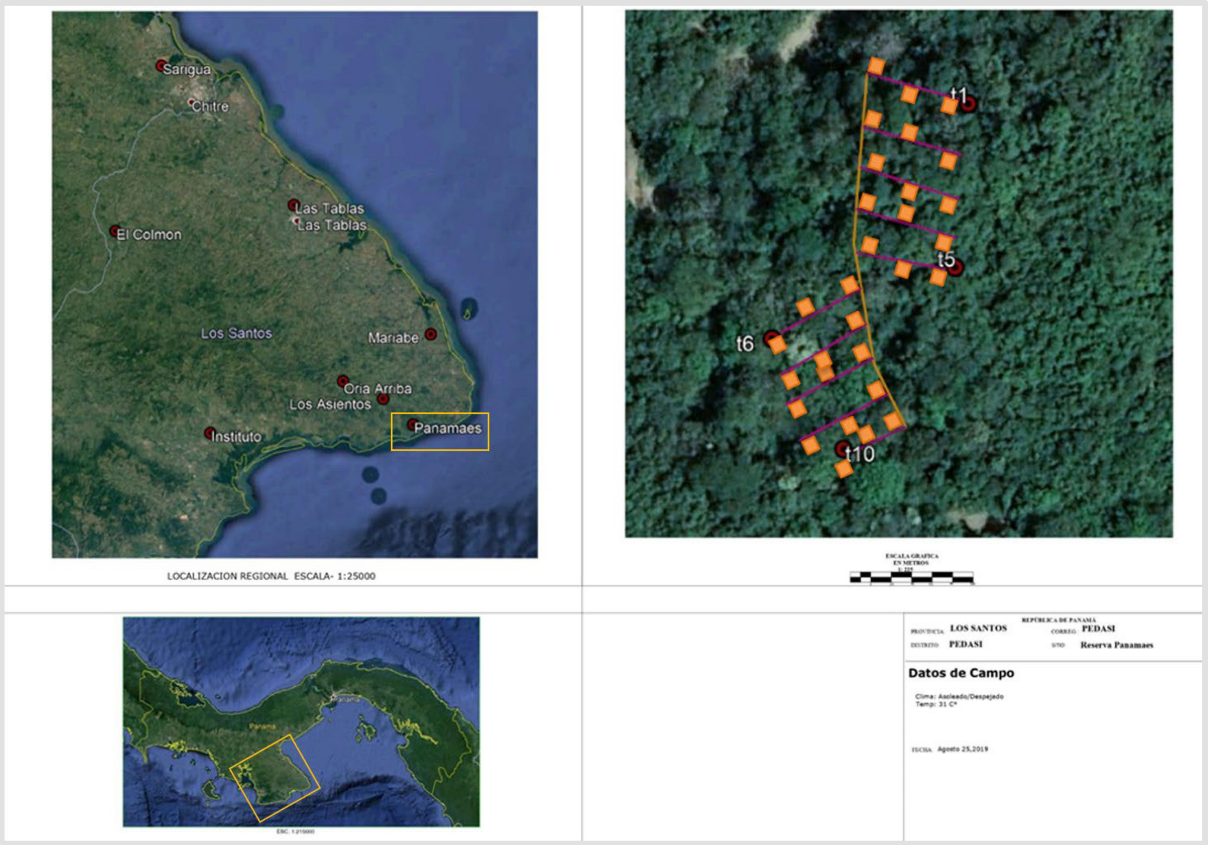


Figure. 9 Map with aerial photography from Google Earth showing PANAMAES sampling site with satellite imagery. The plot is modified from Phillips et al.’s (2003) design, having a total of 30 sublots where data on samplings were collected. Data on trees was collected along the plot (beyond the limits of the subplots). 4m^2 subplots are depicted in the map as orange squares. The plot’s delimitations and transects were defined with UTM GPS points (red circles) taken on site in the field. The map was developed in 2018 by Miguel Cañizales.

Following Phillips et al. (2003)’s plot design, data was collected to analyze species composition and functional traits between two layers of the forest. Trees and saplings have grown at different times and under different climate conditions. Hence, I considered the species of canopy trees and saplings separated in three categories: 1. Tree species found uniquely in the canopy, 2. Tree species found uniquely recruiting the understory as saplings, and 3. Reoccurring tree species found in both the canopy and recruiting the understory as saplings (See Figure. 10).

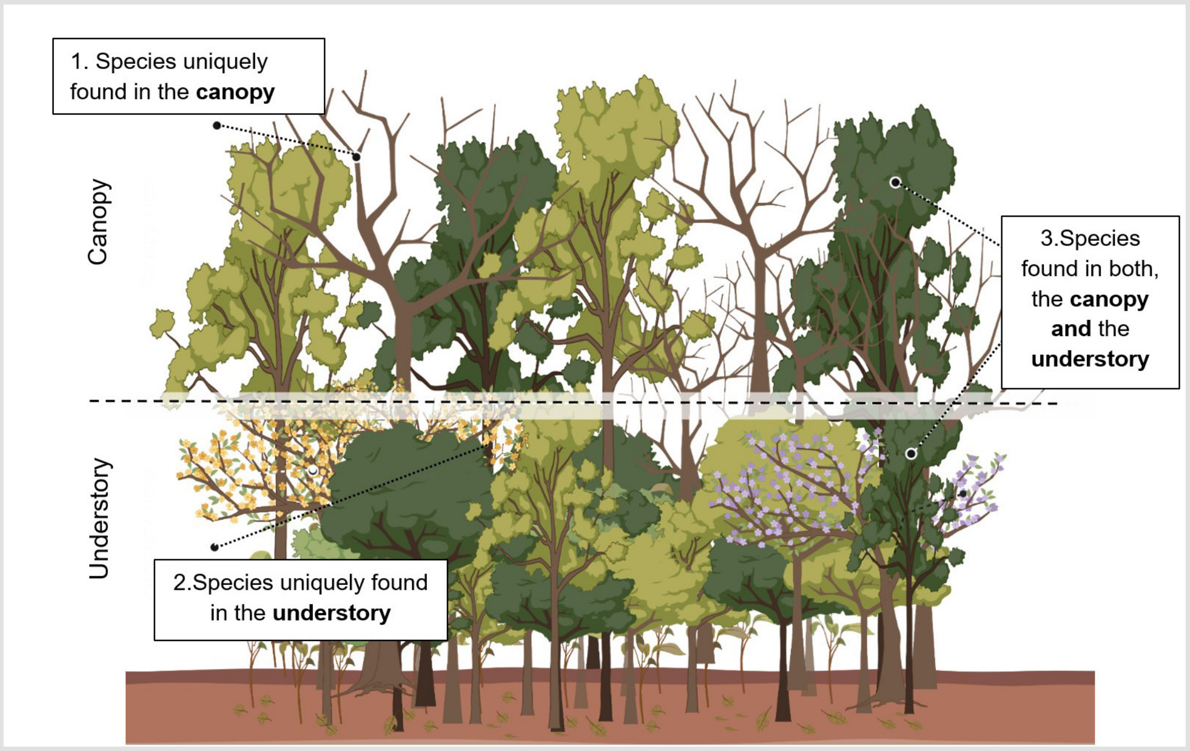


Figure. 10 Depiction of field plot with samples characterized under three strata: Species uniquely found in the canopy, species uniquely found in the understory, and species found in both, the canopy and the understory. These strata will allow the comparison of species composition and functional traits of established canopy trees to the species composition and functional traits of recruiting species.

The collected traits and samples would differ between saplings and trees. Every tree within 2m on each side of the transects (Phillips et al. 2003) having ≥ 20cm diameter (Cannon et al. 1998; Clark and Clark. 2001; Shahabuddin and Kumar. 2006) was collected for identification. In some cases, species identification occurred on site. Otherwise, unknown species were identified by botanical students from the University of Panama, as well as STRI botanists. Some canopy trees attained a height that was out of reach for leaf-based identification, so that the identification of the species was facilitated with photographs of the individuals' particular characteristics, trunk, leaves, and crown. When leaf-collection was possible regardless of height limitations, vouchers were prepared and saved at the University of Panama herbarium. Tree species abundance was also considered per plot. Species composition for saplings was collected within three 4m x 4m quadrants, two quadrants located at each end of the transect, and one additional quadrant located at halfway point of the transect (30 subplots per plot in total). The criteria to select saplings was to only consider woody species of recruiting trees having one trunk (to exclude shrubs and lianas) measuring between 1m and 3m of height (King. 1990; Chaturvedi et al. 2014; Ahrens et al. 2020). Repetition in species was considered to account for abundance. Saplings were considered as recruiting trees rather than newly germinated individuals to consider individuals that survived through germination and establishment under the present climate conditions (Esquivel-Muelbert et al. 2018).

(b) Drought-related functional trait measurements

Functional traits highly correlated with drought resistance have been used to identify climate-related functional trait shifts. Based on previous literature that established functional traits significantly related to climate and drought, the functional traits considered in this study are: Wood density, Specific Leaf Area (SLA), Deciduousness, Relative Water Content (RWC), Leaf Nitrogen Content (LNC), Leaf Pubescence, Leaf Thickness, and Tree Vegetative Height (Powers and Tiffin. 2010; Pérez-Harguindeguy et al. 2013; Lohbeck et al. 2015; Raymundo et al. 2018; Ahrens et al. 2020). Functional traits were either collected in the field or retrieved from the TRY Database (https://www.try-db.org) (Fraser. 2020) and the STRI database (https://stricollections.org/portal/) (STRI Research Portal Home. ND). For trees, data collection in the field included coring trees to calculate wood density, measuring the diameter at breast height (DBH) and collecting leaves whenever possible, to measure functional traits related to drought resistance. Field data collection on saplings was performed solely on leaves. In the case of saplings, ideal leaves selected for the measurement of functional traits should be on a sun-lit branch, with no or few parasitic and herbivorous predation (Cornelissen et al. 2003; Lohbeck et al. 2015). However, collecting solely sun-lit leaves was not always possible as many saplings were under the shadow of the canopy. This is a common difficulty encountered in the field for the calculation of leaf-specific functional traits of understory and recruiting individuals (Cornelissen et al. 2003). In the case of canopy trees, collecting leaves above 10m was not possible, leading us to retrieve some functional traits from databases and additional resources. If able to obtain leaves in the field for either saplings or trees, a branch with several leaves attached would be collected to increase the durability and freshness of the leaves, until reaching the research base for functional trait measuring (Cornelissen et al. 2003; Maréchaux et al. 2015). These were kept in a black plastic bag, itself in an empty cooler to avoid evapotranspiration from increased temperatures and sunlight during data collection and transportation (Cornelissen et al. 2003; Maréchaux et al. 2015).

The leaves collected in the field were used to measure Relative Water Content (RWC) from one relative mid-sized leaf for each sample (each sample being an individual per species found per subplot (samplings) and per plot (trees)), with no or minimal parasitic and herbivorous marks. Leaves were first weighted at their collected biomass (leaf fresh biomass), and then placed after each data collection day in a Ziplock containing water, with the stem emerging in the water for 48 hours (to allow alternation between field work and functional trait measurements). Leaves would then be weighed again at their full water uptake to measure the leaf turgid weight. Afterwards, the leaves were left to fully dry in a customized drying chamber at the research station, which was a sealed room with two dehumidifiers that would remove air humidity and produce dry warm air continuously. Leaves were left in a wood press to dry in the chamber until their biomass would no longer change (72 hours or more to get the leaf dry weight). The RWC was calculated as:

$$[(W-DW) / (TW-DW)] \times 100.$$

(González and González-Vilar. 2001)

Functional traits needing leaves that could not be collected due to height (trees higher than 10m) were taken from the TRY Database and the STRI database. These traits include Specific Leaf Area, Deciduousness, Leaf Nitrogen Content, Leaf Pubescence, Tree Vegetative Height, and Leaf Thickness. These have been compared to the field collected trait measurements with a paired T-test (Kendall), and all except for Specific Leaf Area, had no significative differences. This was performed at the species level and at the sapling versus tree level (*See Figure. S14-S18 in Supplementary Materials*). Consequently, SLA values were taken for all species of trees and saplings from the TRY Database.

Wood density was estimated for every tree found within 2m from each transect with a diameter of ≥ 20cm (Cannon et al. 1998; Clark and Clark. 2001; Phillips et al. 2003; Shahabuddin and Kumar. 2006). For each tree, one wood core sample was collected with an increment borer of 16'' and 5.10mm of inner diameter (Chave. 2006) at 1.30m height (Powers and Tiffin, 2010; Chave. 2006). Once the wood samples were collected, they were carefully placed inside a plastic straw, labeled with the site code and tree number, and both ends of the straw were folded and closed to avoid losing samples and minimizing the wood drying until reaching the station (Chave. 2006). Once reaching the station at the end of every day, the wood samples were taken out of the straws and weighed to calculate the sample fresh weight (Chave. 2006). At the end of the field work period, these samples were transported in sealed bags to Panama City and were left to dry completely in a drying oven located at the Smithsonian Tropical Research Institute, Panama for 72 hours. Each sample was immediately weighed from the Smithsonian Tropical Research Institute once taken out of the oven to avoid humidity to be absorbed and misleading weight calculations (Chave. 2006).

Once all the functional trait values were collected with field work and use of external databases, I performed a correlation test to identify functional traits that were highly correlated, based on significant (≤ 0.05) p-values of the coefficient values (See Table. 2). I then used a log-transformation to correct outliers' effect and analyzed through PCAs (Principal Component Analysis) to understand how the position in the strata explains species associations with different functional traits (Figure. 14). This was followed by a Redundancy Analysis (RDA) considering all species recorded across sites found, either as trees, recruits, or found in both strata (Figure. 15). Functional traits distribution was also analyzed within the considered strata to explore shifts within species found exclusively in the canopy, exclusively found in the understory and repeated species found in the canopy and the understory (Figure. 16). The results of these shifts are further illustrated on Figure. 17. I then proceeded by calculating the CWMs (Community Weighted Means) of the functional traits using a Multivariate Analysis of Covariance (MANOVA) using a Pillai's test (See CWM table in *Supplementary Materials Table S8)*. I used Pillai's test because it is usually difficult to assume normality with functional trait values, and Pillai's test provides the most robust results when that assumption cannot be made. I did not calculate the CWM on categorical values, such as leaf pubescence. For this reason, categorical variables will not be represented through CWM analyses. Additional PCAs were performed with CWMs per stratum considering all the sites (*Supplementary Materials Figures S19 – S26).*

Section 3.03 - Results

(a) Species composition shifts in tropical dry forests

In this study, species composition was considered to identify potential shifts between older established trees found in the canopy and recruits. To this end, analyses were conducted on the species richness and abundance for species found uniquely in the canopy, species uniquely found in the understory and species found in both strata. I also assessed the relative percentage of species found per stratum and used a two-way ANOVA to quantify the significance of the variation between the species found in these strata.

Looking at the species richness and abundance per stratum at each site and throughout the region supports the common notion that the understory of tropical forests is highly dynamic in terms of species composition and recruitment, showing a larger richness and abundance of species than in the canopy (Figure. 11 and Table. 1). The richness and abundance of species tends to be unmistakably higher within species uniquely recruiting the forest understory and species found in both strata, in comparison to species found uniquely in the canopy (Figure. 11).

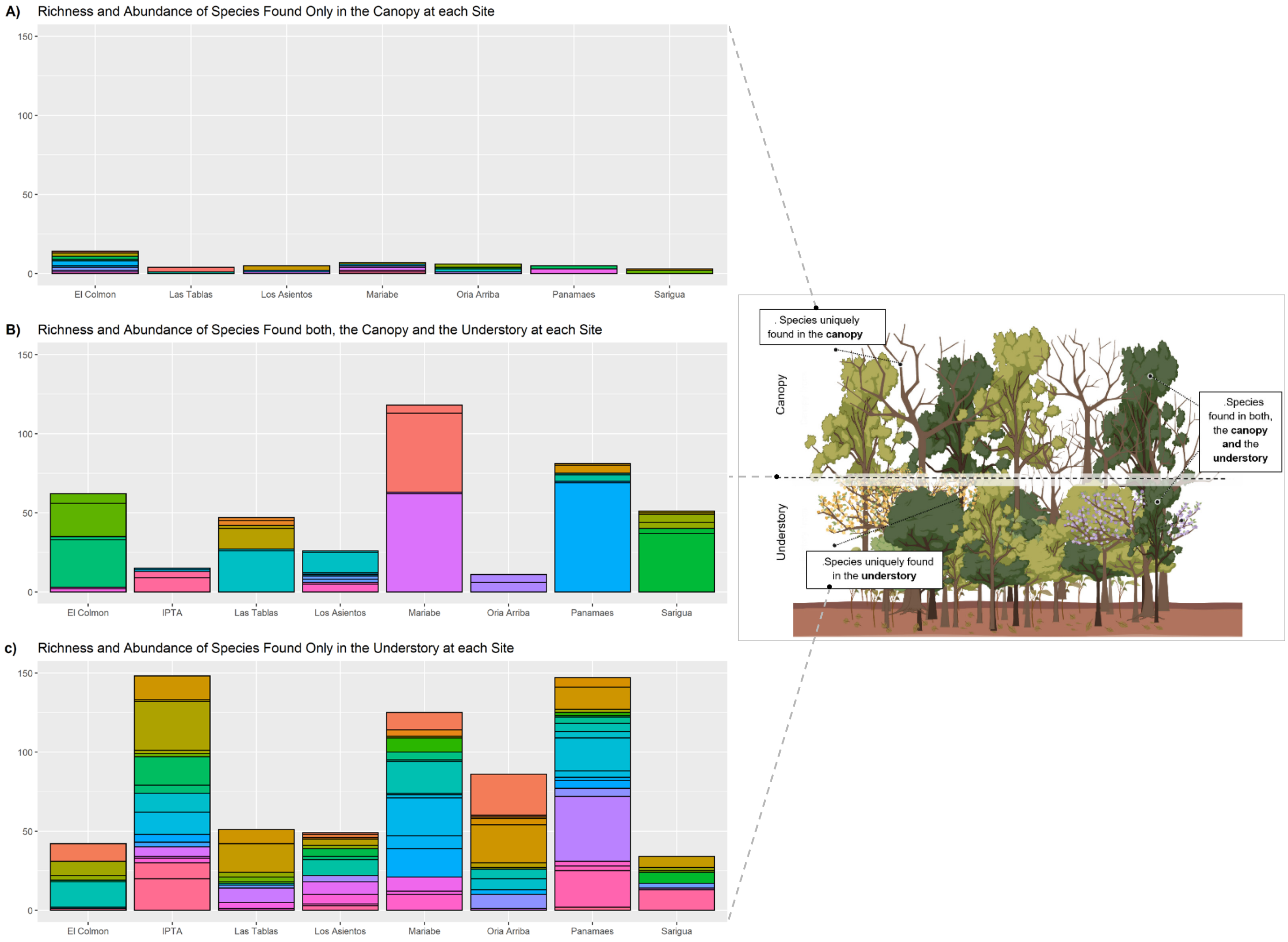
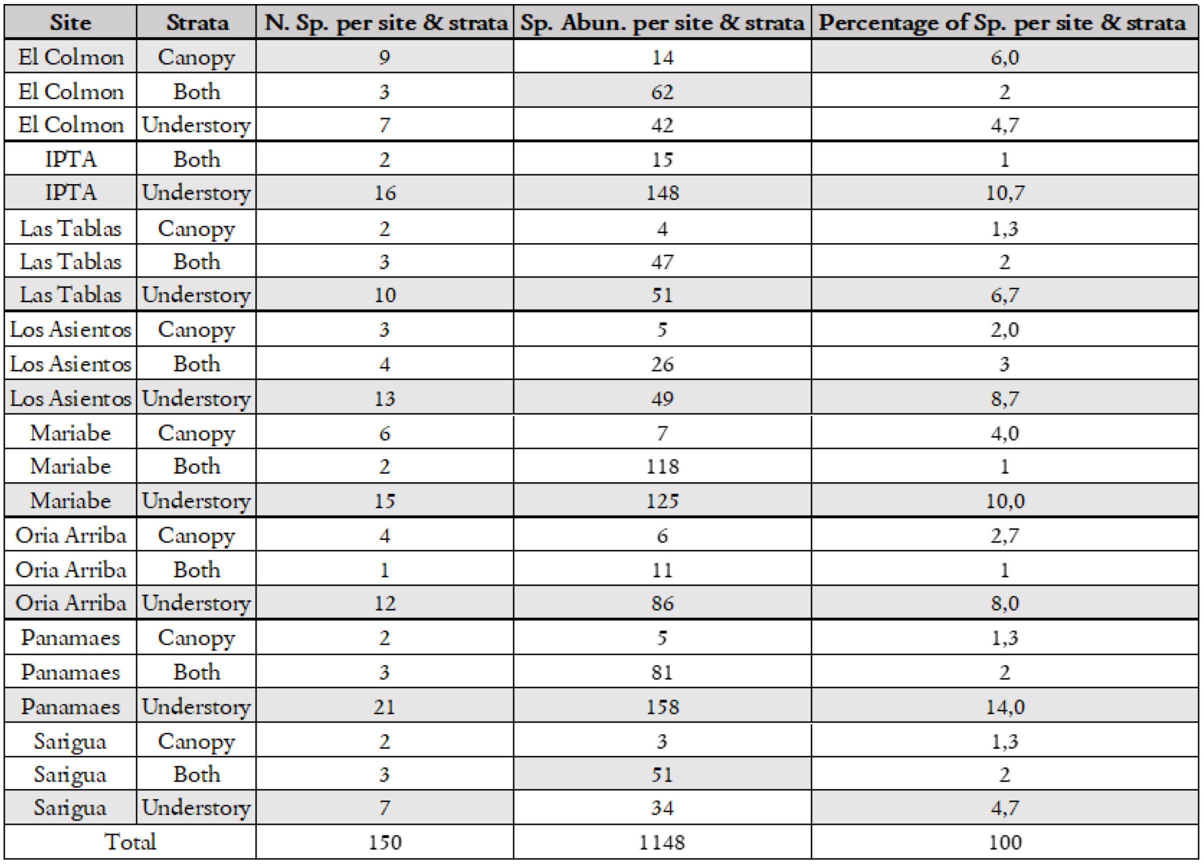


Figure. 11 Species richness found exclusively A) in the canopy, B) in both, the canopy and the understory, or C) in the understory of tropical dry forests of Azuero, classified by abundance (y-axis). The colors within the bars of A) to C) do not show coinciding species between the different strata, but rather are used to show the species richness within each independent stratum. A) Shows the abundance of each species exclusively found in the canopy of each site. The x-axis specifies the sampling sites, and the y-axis shows the abundance of each species found. From the eight sites, one of them (IPTA) did not have any species of trees exclusively found in the canopy and is not shown in the figure. B) Shows the abundance of recurring species found in the canopy and the understory of each site. The x-axis specifies the sampling sites, and the y-axis shows the abundance of each species found that are exclusively shared between the canopy and the understory. C) Shows the abundance of each species exclusively found in the understory of each site. The x-axis specifies

the sampling sites, and the y-axis shows the abundance of each species found. D) Figure that describes the diversity within TDFs based on the species richness data from A) to C).

From 1,148 individuals of 66 unique species collected throughout Azuero and a total of 150 site-specific species, the highest percentage of species primarily lies within TDF's recruiting saplings in the understory. At each site, an analysis on the percentage of species found within strata (Table.1) was performed with a Two-way ANOVA. This analysis provided highly significative results at the strata level (Pr(>F) = 0.0001 ***) and less significant results considering the sites (Pr(>F) = 0.8). The highest proportion of species is repeatedly found in the understory recruiting the forest, with the exception of the site "El Colmón" (Table. 1). Considering the region all together, over 67% of the species are recorded as uniquely found in the understory, while species uniquely found in the canopy accounts for 19% of the species recorded and 14% of the species are found shared between the canopy and the understory (Figure. 12 and 13). The highest abundance of species per site is also primarily found in the understory except for two sites where the highest species abundance is found as shared species between the canopy and the understory. Except for one site, the highest variation of species is found in the understory. In total there are 66 unique species collected amongst all sites and 150 considering the sites independently with 1148 individuals.



Site	Strata	N. Sp. per site & strata	Sp. Abun. per site & strata	Percentage of Sp. per site & strata
El Colmon	Canopy	9	14	6,0
El Colmon	Both	3	62	2
El Colmon	Understory	7	42	4,7
IPTA	Both	2	15	1
IPTA	Understory	16	148	10,7
Las Tablas	Canopy	2	4	1,3
Las Tablas	Both	3	47	2
Las Tablas	Understory	10	51	6,7
Los Asientos	Canopy	3	5	2,0
Los Asientos	Both	4	26	3
Los Asientos	Understory	13	49	8,7
Mariabe	Canopy	6	7	4,0
Mariabe	Both	2	118	1
Mariabe	Understory	15	125	10,0
Oria Arriba	Canopy	4	6	2,7
Oria Arriba	Both	1	11	1
Oria Arriba	Understory	12	86	8,0
Panamaes	Canopy	2	5	1,3
Panamaes	Both	3	81	2
Panamaes	Understory	21	158	14,0
Sarigua	Canopy	2	3	1,3
Sarigua	Both	3	51	2
Sarigua	Understory	7	34	4,7
Total		150	1148	100

Table 1 Percentage of species found between the three strata at each site. The highest values of species number per site's strata, species abundance per site's strata, and percentage of species found per site's strata are highlighted in light gray. Except for one site (El Colmon), the highest variation of species is found in the understory. In total there are 66 unique species collected amongst all sites and 150 considering the sites independently with 1148 individuals.

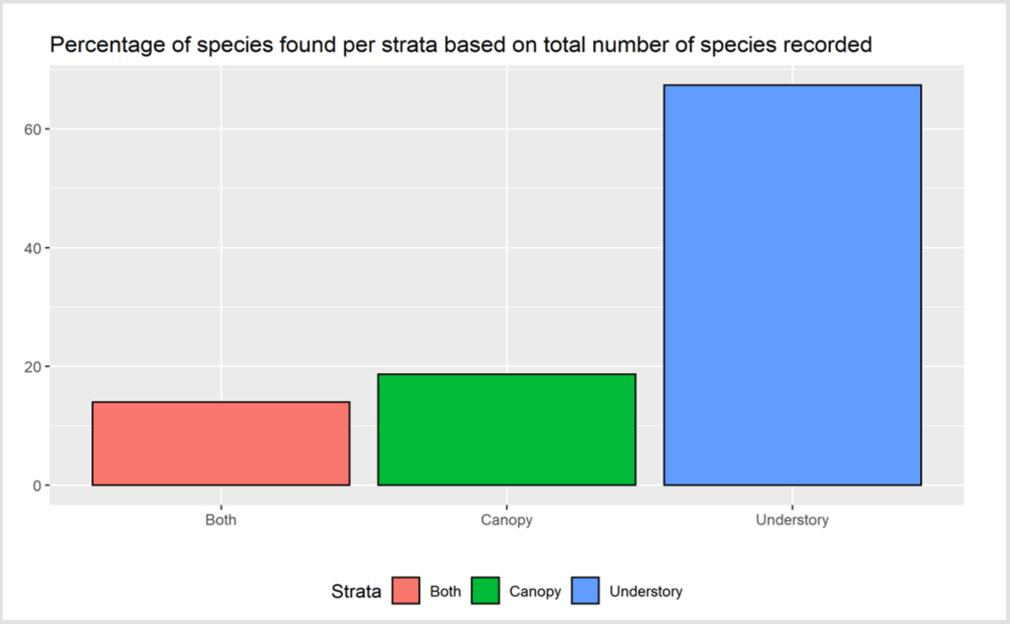


Figure. 12 Percentage of species found in the three strata considering all sites together, based on the total 150 species recorded amongst sites. The y-axis is the percentage of species found per stratum while the x-axis shows the three strata where the species were found.

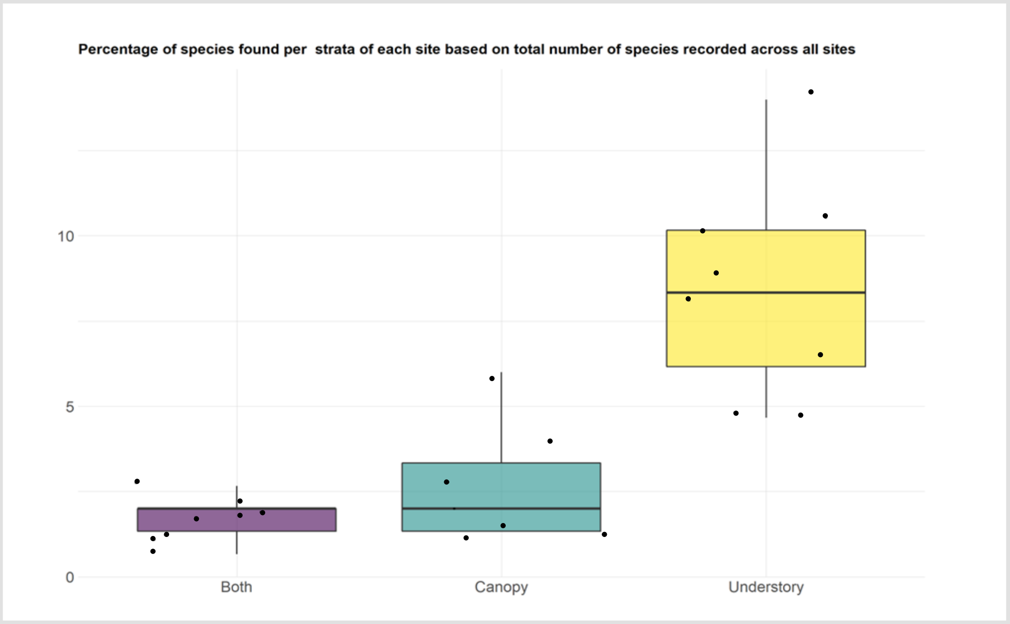


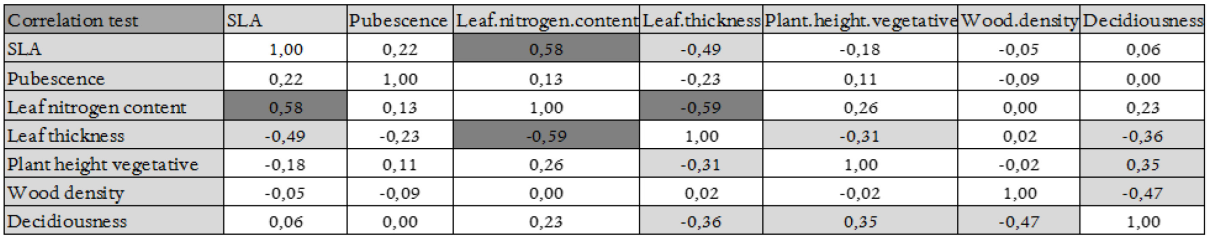
Figure. 13 Percentage of species found per stratum of each site (plotted individually) based on total number of species recorded across all sites (150 species). The y-axis corresponds to the

percentage of species found per site stratum, while the x-axis corresponds to the three strata where the species were found. The boxplot distribution corresponds to the range of species percentage found per stratum considering each site separately.

A closer look at the species found per site and stratum shows that the predominant species throughout the study area are *Genipa Americana, Bursera simaruba, Calycophyllum candidissimum, Hura crepitans, Melicoccus bijugatus, Gustavia superba,* and *Anacardium excelsum*. I observed that 12 species of recruiting trees are becoming established without having a parent at the same site. These are: *Astronium graveolens, Allophylus psilospermus, Calycophyllum candidissimum, Azadirachta indica, Hamelia patens, Licania arborea, Manilkara zapota, Trichilia hirta, Bursera simaruba, Zanthoxylum setulosum, Heisteria concinna* and *Hura crepitans*. Some of these happen to also be the most abundant and most recorded species throughout the region of Azuero considering all the sites together. Additional information on species composition, abundance and diversity can be found in supplementary materials (*Supplementary Materials Figure. S8-S13 and Table S1*). PCAs were performed considering species classified as species mostly found in dry forest, species mostly found in humid forest, species found near open spaces/roads/farming, species found in secondary forest, and species found in old growth forest (*Supplementary Materials Figure. S27 and S28*).

(b) Shifts in functional traits unveil climate-sensitive changes in tropical dry forests

To understand if drought-resistant functional traits are becoming increasingly selected within Panama's tropical dry forests as a response to climate pressures, a shift in functional traits between the canopy and the understory within Azuero's TDFs was hypothesized. I used species for which we collected a minimum of four samples per functional trait measured in the field. Leaf area per leaf dry mass (specific leaf area, SLA or 1/LMA): petiole included, Wood density (stem dry mass per stem fresh volume), Relative Water Content, Leaf Water Content have been measured using this method (See *Supplementary Materials Table S2*). I first performed paired t-tests to establish if field data functional trait values from trees and saplings differed significantly with functional trait values from the TRY database (See *Supplementary Materials Table S3-S7 and Figures. S14-S18*). Analyses started with the comparison of functional traits per site and stratum through PCAs (Principal component analysis) (Figure. 14). Next, after performing a forward selection of the explanatory variables (functional trait values per species and strata) to the species found across the study area, an RDA using forward selection was used to explore the functional traits potential shift (Figure. 15). Next, the distribution of functional traits values at the species level between strata was plotted to observe changes between the strata's distributions (Figure. 16 and 17). Lastly, I calculated the traits' Community Weighted Means (CWMs) and performed MANOVAs between CWMs per stratum considering functional traits and dispersal mechanisms per stratum and site (Lohbeck et al. 2015; Raymundo et al. 2018). A Kendall correlation test was performed to identify functional traits that were highly correlated (Table. 2). The criteria for the correlation test and exclusion of traits in later analysis was based on significant (≤ 0.05) p-values of the coefficient values. The only significant correlations identified were leaf N content with SLA and with leaf thickness (Table. 2). Even though SLA was correlated with leaf N content I chose to keep this functional trait because of the documented correlation to drought-resistance in the literature (Poorter and Markesteijn. 2008; Lohbeck. 2015; Chaturvedi et al. 2021). Thus, the final traits considered are SLA, leaf pubescence, leaf nitrogen content, plant vegetative height, and wood density. Although I chose to disregard the most correlated traits, the weak correlations amongst them indicate that strategies within the level of the leaf vary enough to not be significantly correlated and provide valuable information on the plant's response to climatic pressures.



Correlation test	SLA	Pubescence	Leaf.nitrogen.content	Leaf.thickness	Plant.height.vegetative	Wood.density	Decidiousness
SLA	1,00	0,22	0,58	-0,49	-0,18	-0,05	0,06
Pubescence	0,22	1,00	0,13	-0,23	0,11	-0,09	0,00
Leaf nitrogen content	0,58	0,13	1,00	-0,59	0,26	0,00	0,23
Leaf thickness	-0,49	-0,23	-0,59	1,00	-0,31	0,02	-0,36
Plant height vegetative	-0,18	0,11	0,26	-0,31	1,00	-0,02	0,35
Wood density	-0,05	-0,09	0,00	0,02	-0,02	1,00	-0,47
Decidiousness	0,06	0,00	0,23	-0,36	0,35	-0,47	1,00

Table 2 Correlation (Kendall) between the functional traits considered amongst all trees and saplings. The functional traits considered are SLA, Pubescence, Leaf nitrogen content, Leaf thickness, Plant height vegetative, Wood density, Deciduousness. The values highlighted in light gray are correlation of moderate degree or medium correlation (coefficient value between ± 0.30 and ± 0.49), and in dark gray are correlation of high degree or strong correlations, and most significative correlations (coefficient value between ± 0.50 and ± 1, p-value ≤ 0.05).

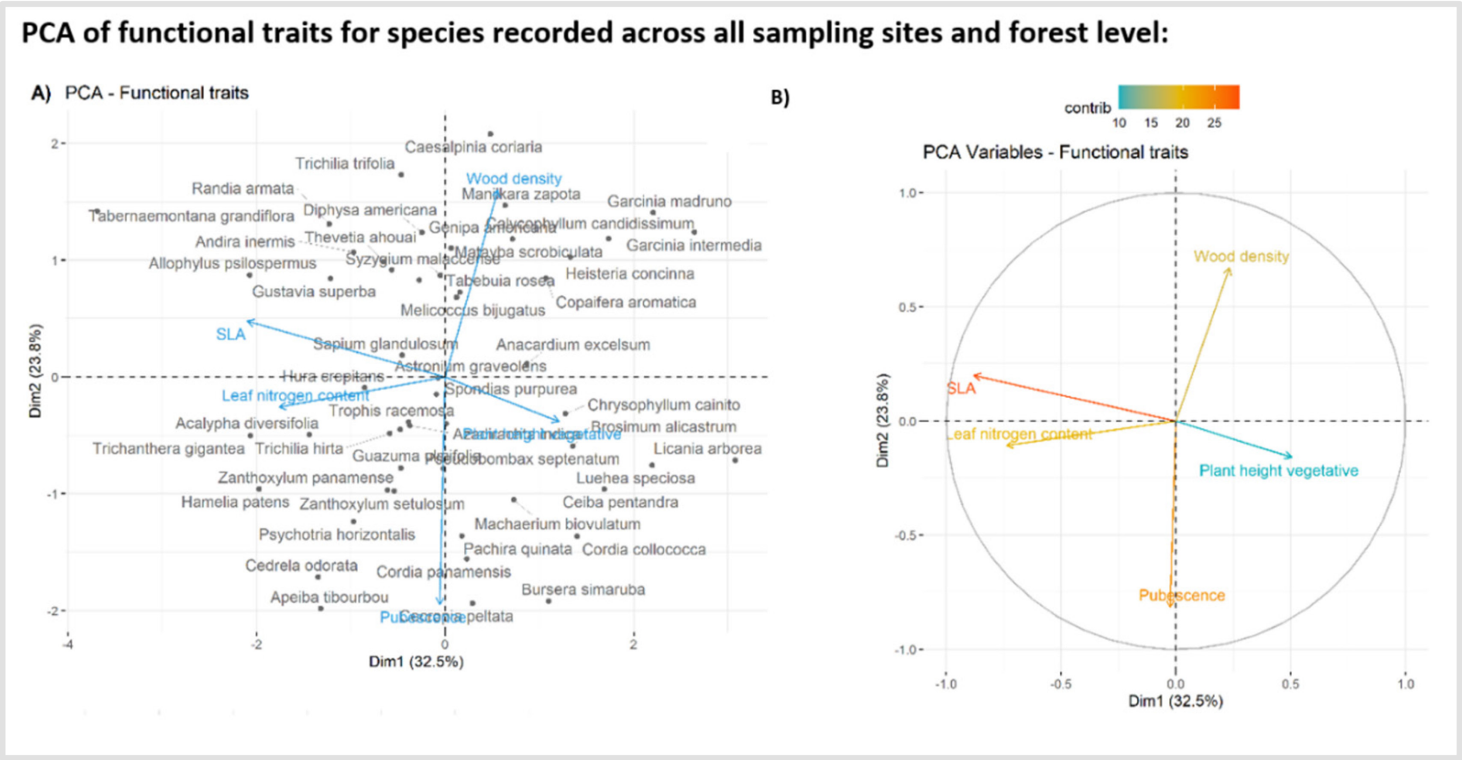


Figure. 14 A) PCA biplot of species found across sampling sites (in gray) and functional traits (in blue with arrows), and B) variables PCA showing positively correlated functional traits pointing to the same side of the plot, and negatively correlated functional traits pointing to opposite sides of the graph. The functional traits are related to leaf, wood, and plant characteristics (SLA, Leaf nitrogen content, Pubescence, Plant height vegetative, and Wood density). While B) shows the direction and contribution of each functional trait, A) shows the overall influence of functional traits on the entirety of the species recorded along all the sampling sites (total 66 species of trees and sapling). Values have been log-transformed prior to the PCA, to correct outliers' effects.

This was followed by a Redundancy Analysis (RDA) considering all the species recorded across all sites that have been found, either as trees, recruits, or found in both strata (Figure. 15). A forward selection was used to select the most significant variables. Plant vegetative height was recorded as the most significative variable (ancova test with 999 permutations = 0.004 **). RDA1 is also highly significative (0.001 ***), while RDA 2 and RDA 3 are less significant. The model's R^2adj = 0.160. Because the model is highly significant, we can conclude that the correlation between species to the selected functional traits is highly significant. In fact, wood density, plant vegetative height and leaf nitrogen content, have the strongest effect on the data.

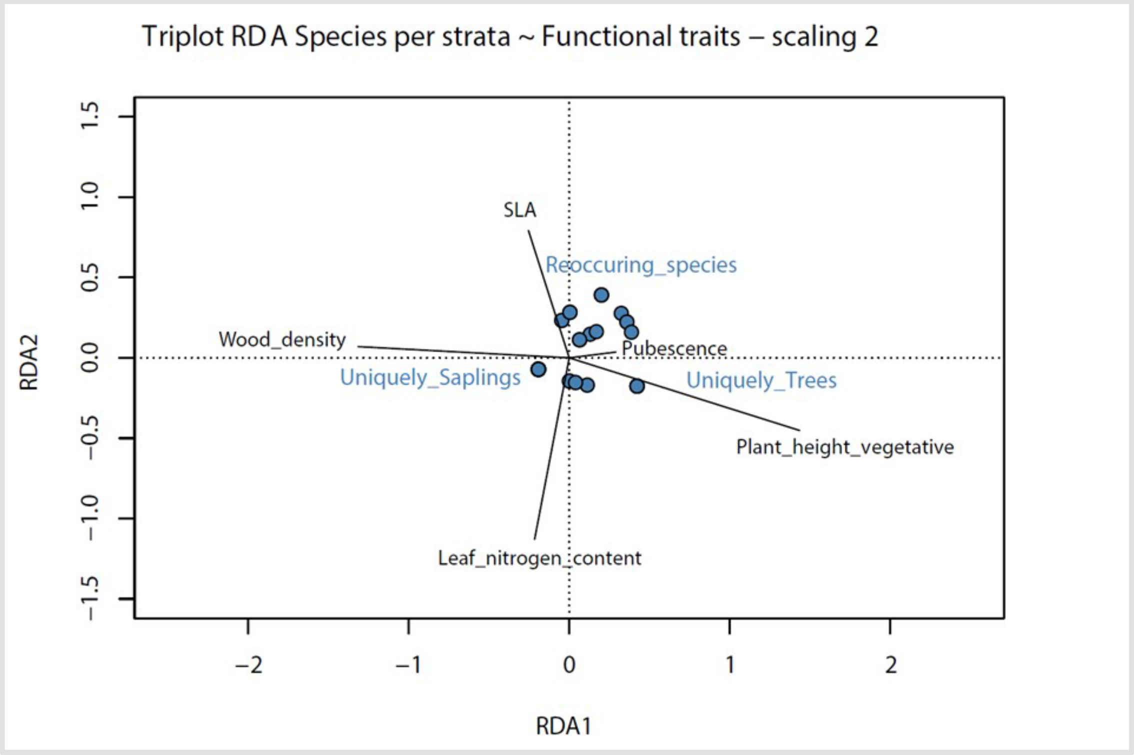


Figure. 15 RDA considering all the species (blue dots; some agglomerated) recorded across all sites that are recorded either as canopy species, understory species, or species found in both strata.

The distribution of functional traits per stratum was also analyzed to identify possible shifts between trees and saplings (See Figure. 16). The results demonstrate shifts from which SLA, leaf nitrogen content, and wood density are widening their range of distribution within the recruiting species (Figure. 16). Leaf pubescence seems to be showing less significant results in terms of shifts, and results on plant vegetative height demonstrate that recruiting species are decreasing in height as a response to climate pressures. Interestingly, species found in both strata, canopy and understory, show a rather subtle response in most of the cases. In other words, the recruiting species found in the understory have higher wood density, higher leaf nitrogen contents, are shorter, and have a slightly decreasing SLA (compared to some high SLA canopy species) or remain intermediate (compared to some canopy species that have a lower SLA) (Figure. 16). These results are associated with a greater drought resistance based on the literature, except for SLA, which was expected to strongly decrease instead of fluctuating between an overall decrease and intermediate values compared to some canopy species (Khurana and Singh. 2004; Pinho et al. 2019). A literature review posterior to these analyses, showed that these results are in fact supporting a range of research stating that generally evergreen species can have a lower SLA, photosynthetic capacity and leaf N content per unit leaf area compared to drought-deciduous species (Eamus and Prichard. 1998; Vico et al. 2015; Van der Sande et al. 2016; Vico et al. 2017), which allows evergreens to achieve a higher LAI (Leaf Area Index) for a given N supply compared to drought-deciduous species (Vico et al. 2017). Leaf pubescence is more difficult to assess in the case of recruiting species, showing a close to equal number of species with and without leaf pubescence. Species found in both the canopy and recruiting the forest have a lower leaf pubescence, low leaf nitrogen contents, and intermediate wood density, plant height and SLA. Finally, species found as established trees in the canopy have higher rates of leaf pubescence, higher plant height, a higher or lower SLA values compared to understory species, while having low wood density, most associated with a weaker drought resistance based on the literature, except for the observed higher rates of leaf pubescence and some of the lower SLA values (Figure. 16 and 17).

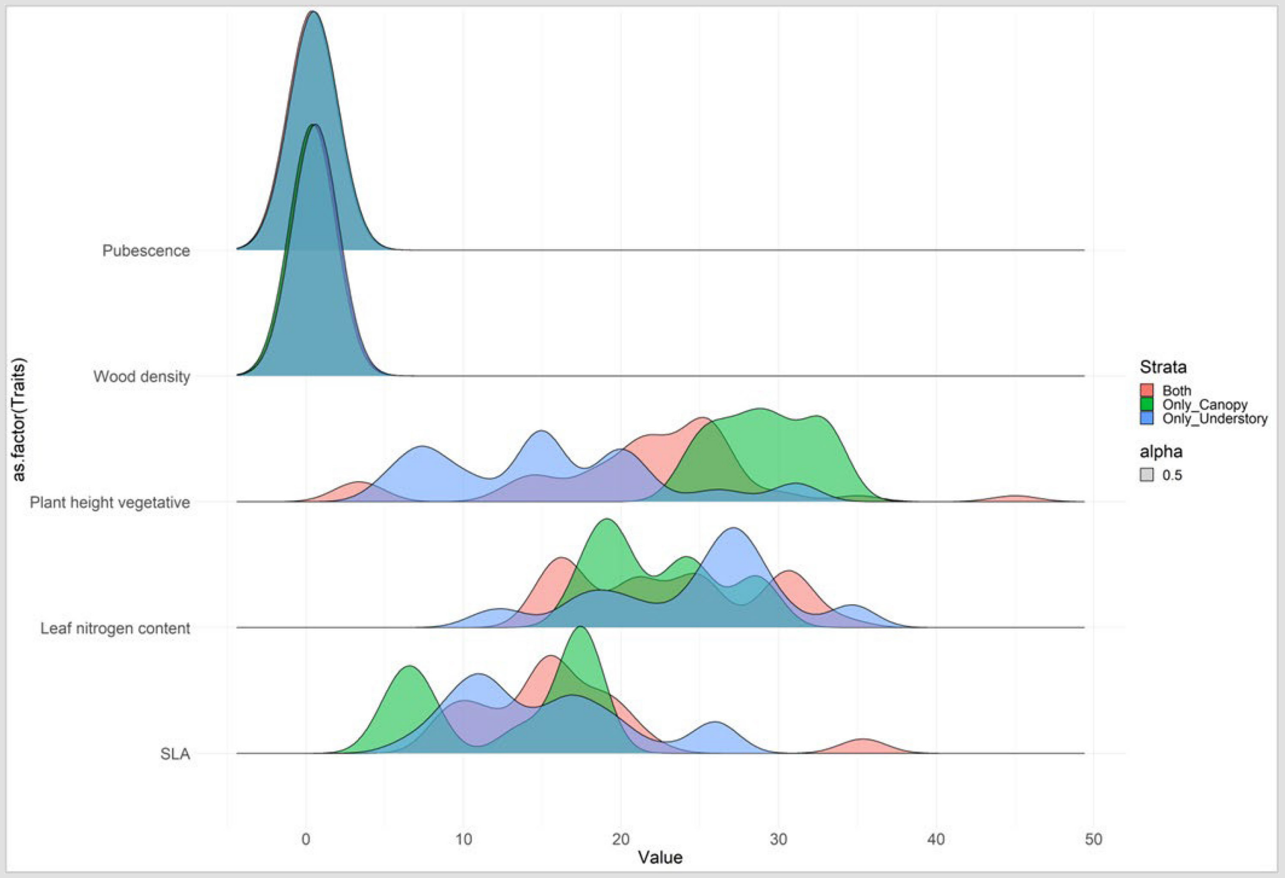


Figure. 16 Distribution of functional traits' measurements by species found uniquely in the canopy (green), species found uniquely in the understory (blue), or species found in both stratum (red), and having a minimum of four measurements per functional trait for a total of 53 species (21 species with at least four trait measurement per species found in both stratum, 5 species with at least four trait measurement uniquely found in the canopy , and 27 species with at least four trait measurement uniquely found in the understory).

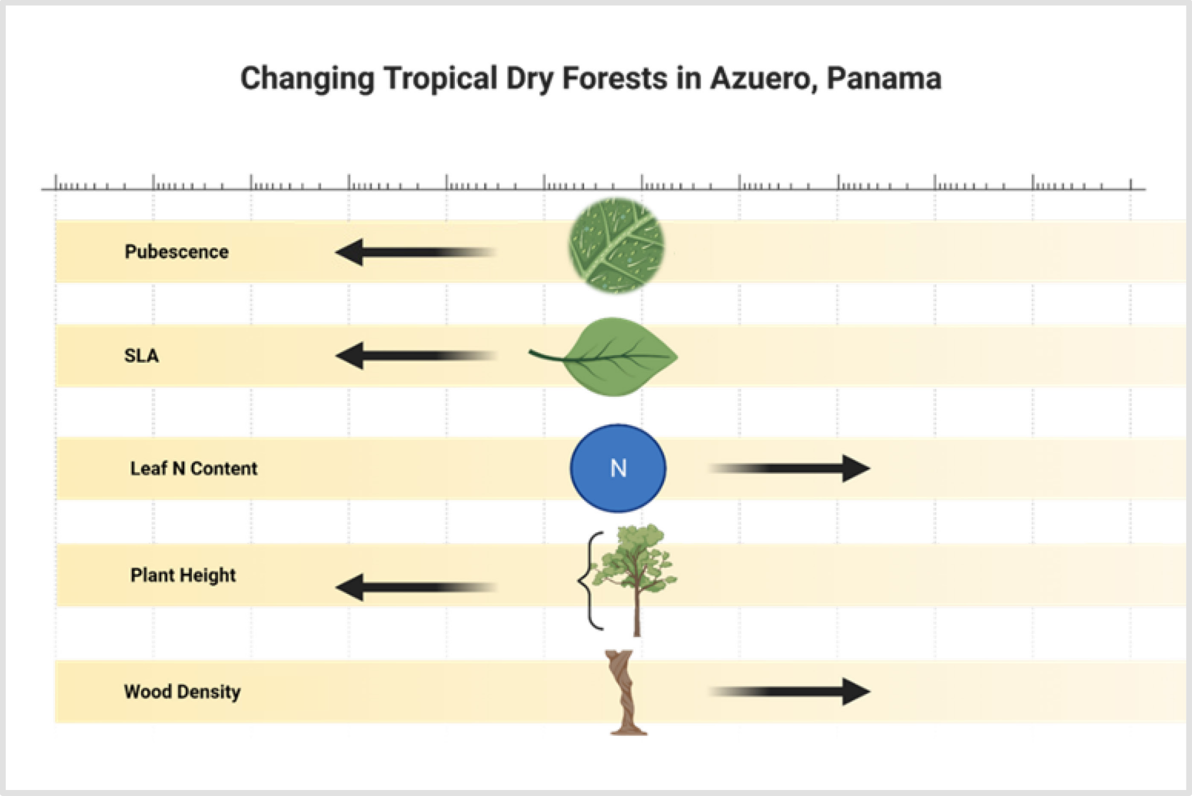


Figure. 17 Figure depicting the functional trait shifts observed in the study. We observed in recruiting species a higher, leaf N content, wood density, and a shift towards a lower SLA, pubescence and height.

Another way to analyze shifts in functional traits is through the comparison of CWMs (Community Weighted Means). CWMs for each functional trait were estimated per stratum across all sites and analyzed by a Multivariate Analysis of Covariance (MANOVA). Performing a MANOVA on both, considering CWMs per site and stratum, to avoid having a saturated model by only considering strata, and considering the functional trait values per species found per site and stratum, the results were significant. The MANOVA using a Pillai's test, demonstrates a significant difference between strata considering the CWM of functional traits per site, especially for wood density. These provide a significant p-value from the MANOVA of 5.352e-16 *** intercept and 0.003385 ** between strata and sites.

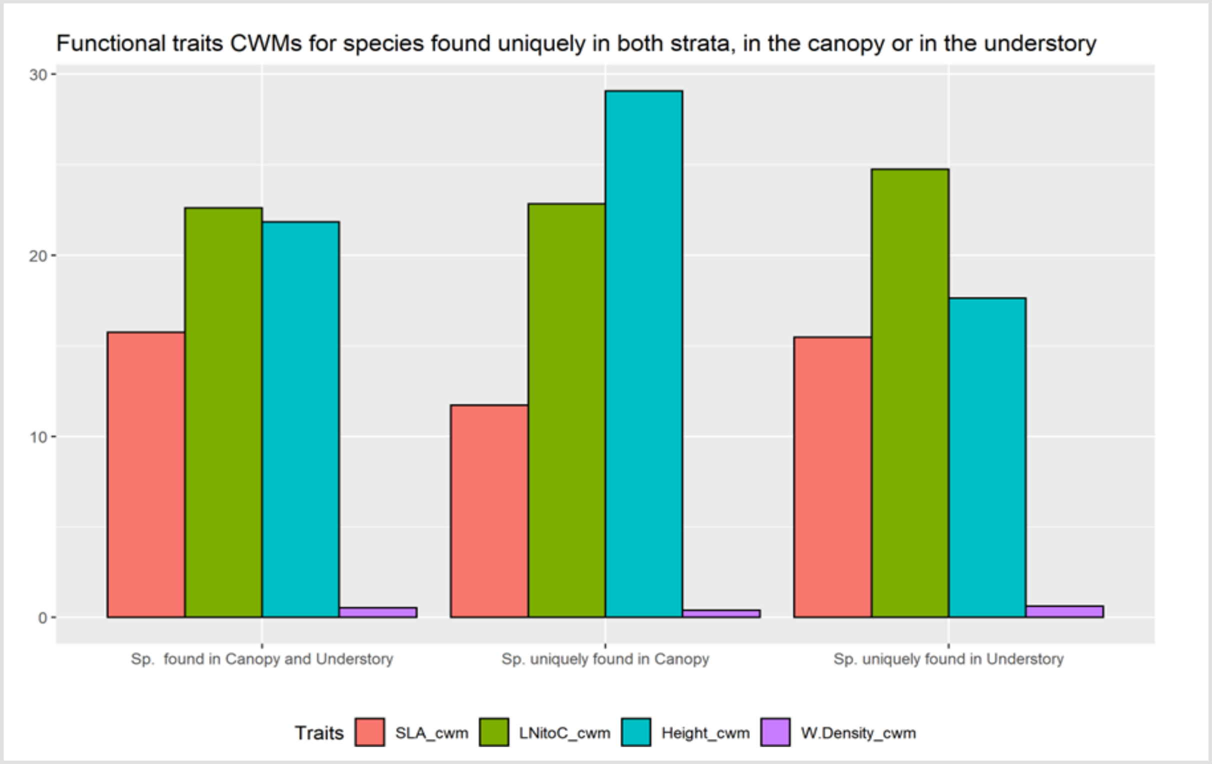


Figure. 18 Bar colors refer to functional traits' CWMs (SLA, LNC, height, wood density). Bars are arranged by stratum (on the x-axis) and values of traits' CWMs are shown on the y-axis.

(c) Tropical dry forests' seed dispersal mechanisms

The MANOVA results previously discussed reveal a significant difference between the strata in terms of tree species richness and abundance. Because recruitment success depends heavily on dispersal mechanisms' efficiency (Nathan and Muller-Landau. 2000; Khurana and Singh. 2004), seed dispersal mechanisms in recruiting species were examined. The literature indicates that in tropical dry forests (using Caatinga as an example) the three most important dispersal modes are dispersal by animals (36%), wind dispersal (33%), and ballistic dispersal (19%) along with barochory (12%) (Griz and Machado. 2001), which is considered in my study as 'fruit opening seed dispersal' (representing 21% considered together), to differentiate these dispersal mechanisms with the ones influenced either by animals or by wind. Here, species are found to be dependent on all three mechanisms of seed dispersal, yet show a higher reliance on animal dispersal as the forests replace themselves with new recruiting species (Figure. 19). This means that local animal species play an important role in the regeneration of these forests. A PCA was performed using the CWM values of functional traits and dispersal mechanisms (*Supplementary Materials Figure 31*).

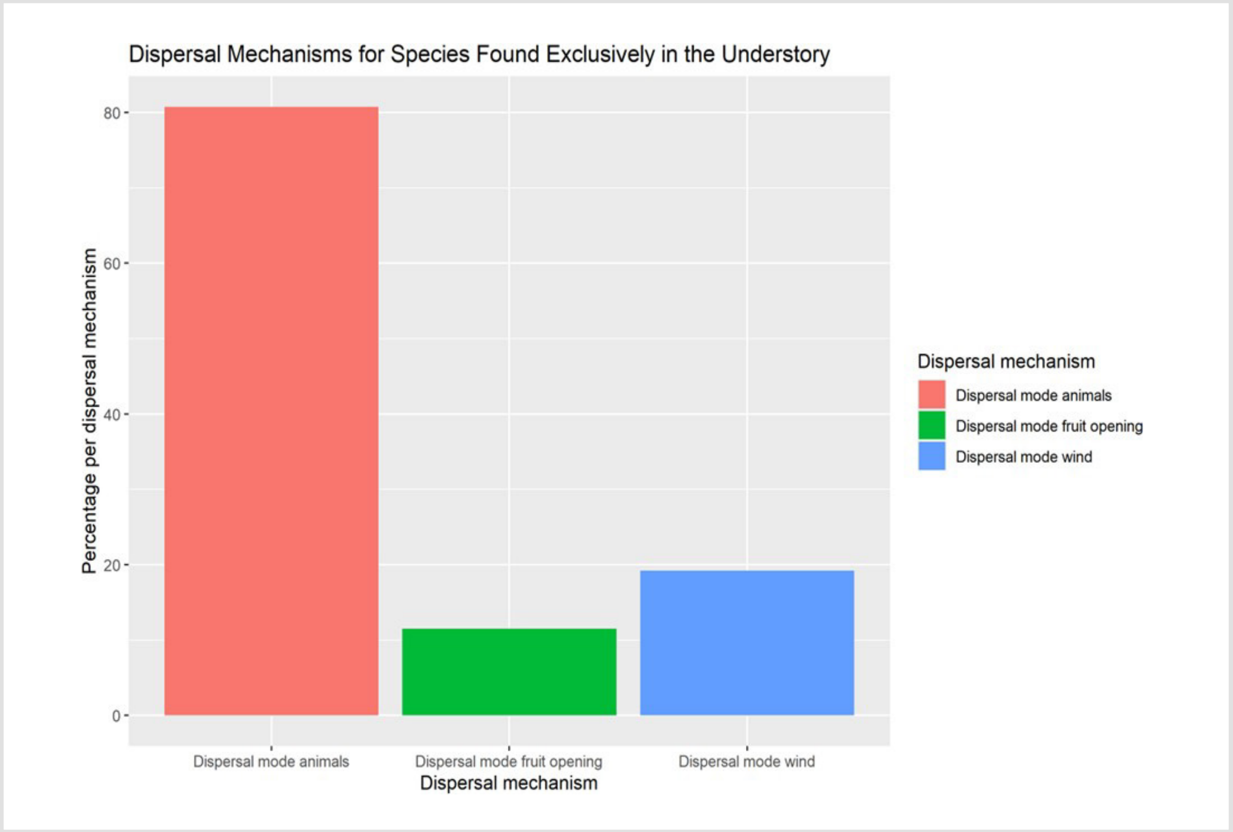


Figure. 19 Seed dispersal mechanism percentage from species found across all sites uniquely in the understory. Bars correspond to the three most prevalent modes of dispersal in TDFs. This information was retrieved from the TRY Database and the STRI database.

Section 3.04 - Discussion

Using functional traits to assess the response of TDFs to climate change builds on multiple papers that aim to understand the future of tropical forests (Anderegg et al. 2015; Lohbeck et al. 2015; Kimball et al. 2018; Allen et al. 2017; Esquivel-Muelbert et al. 2018; Raymundo et al. 2018; Anderegga. 2019; Stan and Sánchez-Azofeifa. 2019). Functional traits have been used to calculate changes in plant population abundance facing climate change (Soudzilovskaia et al. 2013; Anderegg et al. 2015), and were identified as a crucial component to model the complexity of the vulnerability and response of ecosystems to drought and other climatic pressures (Anderegg et al. 2015; Raymundo et al. 2018). They portray the ecological strategies that plants use to avoid stress and to use resources efficiently while enduring biotic or abiotic pressures through time. In this research, the use of functional traits related to drought resilience was used to compare the vulnerability and resiliency of Azuero's tropical dry forests facing the last 57 to 20 years' climatic pressures. The resilience of TDFs in Azuero was suggested by the shift of drought-resistant functional traits as the forest replaces itself. The Community-Weighted Mean (CWM) calculations of the plant strategies show that throughout the Azuero peninsula's TDFs, the forest is changing in species composition with species that are more resistant to droughts through higher leaf nitrogen content, a lower plant vegetative height, and a higher wood density.

Lohbeck et al. (2015) conducted a similar study in Mexico describing the variations in the functional traits and strategies used by tropical dry forests (TDFs) and tropical wet forests (TWFs) from an early succession stage to a late succession stage. Their results show that, while secondary TDFs and TWFs will use a similar spectrum of functional traits for survival, these forests will differ in the use of functional trait strategies and will also change within the forest as succession advances (Lohbeck et al. 2015). These strategies were characterized as either acquisitive strategies or conservative strategies. Acquisitive strategies are used by plants investing in traits designed to acquire needed resources for growth, while conservative strategies are more commonly found in plants investing in functional traits to maintain optimal conditions when the forest is at a later life stage, once that competition decreases (Lohbeck et al. 2015). Some of the traits that they considered are reflected in my research and, together, show an interesting transition in tropical dry forests. The shifts in traits and strategies which have been identified by Lohbeck et al. (2015) and which are relevant to the understanding of Azuero's TDFs' shifts through time include SLA, wood density, leaf nitrogen content, tree size, and seed dispersal mechanisms. The results evidence an increase in SLA, wood density, leaf nitrogen content, a decrease in tree size, and a shift from wind dispersal seed mechanisms to animal seed dispersal mechanisms.

I expected to see a decrease in SLA (Esquivel-Muelbert et al. 2018) (See Figure. 20), indicating that leaves are decreasing in size as a conservative strategy to reduce the sun exposure, the exchange of gases, and the evapotranspiration from increasing temperatures and drought (Dirzo et al. 2011). Contrary to the hypothesized decrease in SLA, the results partly supported those of Lohbeck et al. (2015), which establish that TDFs experienced a shift towards increasing SLA and that this shift was related to the progression of the forests' succession stage (Lohbeck et al. 2015).

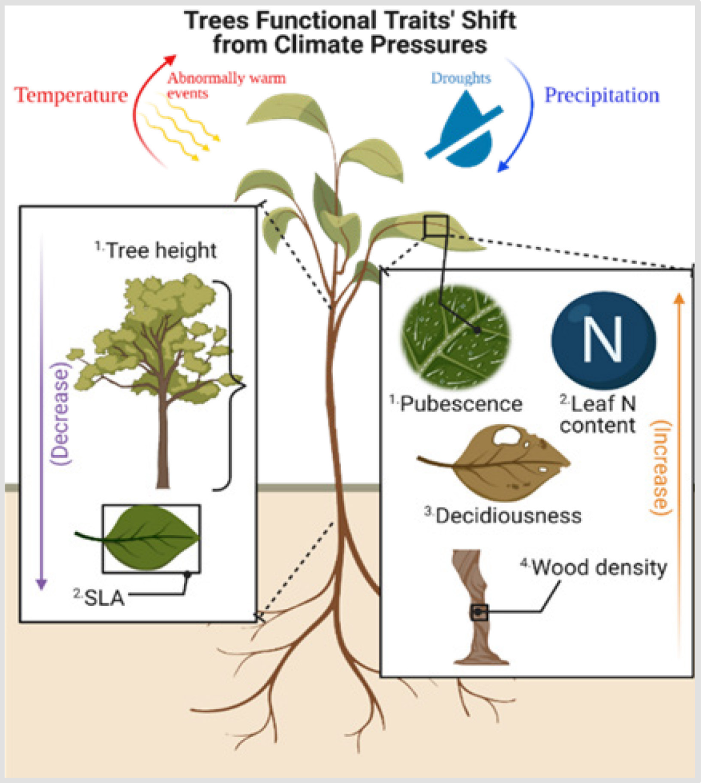


Figure. 20 Expected results from drought-related functional trait shifts from established TDFs canopy trees to recruiting saplings. All traits shifted as hypothesized with the exception of SLA and pubescence fluctuations.

Lohbeck et al.'s findings suggest that TDFs invest in larger leaves (including having more compound leaf species in the forest) as an acquisitive strategy used towards late succession stages of the forest (Lohbeck et al. 2015). This is particularly relevant considering Azuero's TDFs because, while Panama suffers from important forest depletion and deforestation, the regeneration of Azuero's forests resulted in an overall gain of secondary forests and a stable forest cover, as 1992–2000 forest-cover change was evidenced as positive in Azuero (amongst other regions) which were largely deforested in 1947 (Wright and Samaniego. 2008). Lohbeck et al. argued that high SLA "*enhances light capture, leaf cooling and gas exchange and enables high photosynthetic capacity (allows the plant to avoid high insolation, high temperatures and excessive evaporation* *by folding their leaflets at noon or during the dry season and controlling water loss) and growth rates*" (2015). The observed shift in SLA in Azuero's recruiting species could demonstrate that some of the forests I analyzed are in a late succession stage (Lohbeck et al. 2015). Allen et al. (2017) and Paz et al. (2015) argue that the succession stage may be crucial to explain TDFs' trade-off from vertical foraging to water storage during secondary succession, which would mean that species differ in their belowground vulnerability to drought at early life stages (Paz et al. 2015; Allen et al. 2017).

I also reported a shift in recruiting saplings having a higher wood density and a shorter tree height. Both shifts can be attributed to a conservative trait strategy, wherein an increase in wood density can provide a more efficient transport of water. This strategy is associated with thin and short xylem vessels, thicker cell walls, smaller pores, and reduced lumen area, making species with a higher wood density more resistant to xylem cavitation (Guillemot et at. 2022), which is a frequent cause of tree death. Similarly, a shorter stature in trees reduces the risk of embolism in trees when water is scarce (Hacke et al. 2001; Meinzer et al. 2008; Lohbeck et al. 2015; Rowland et al. 2015; Guillemot et at. 2022; Esquivel. 2018; McDowell et al. 2018; Olson et al. 2018). High wood density is related to a reduced risk of breakage in storms and stem deterioration from pathogens (Lohbeck et al. 2015). Besides increases in temperatures, climate change is expected to cause increases in the frequency and severity of natural disasters, the number of pests and pathogens. Climate projections suggest an increased frequency of intense cyclones (Pörtner et al. 2022). High wood density could provide some positive indication of future resilience to these risks (Lohbeck et al. 2015).

Additionally to the analysis directed to functional traits, I investigated seed dispersal to understand the mechanisms used in the understory and canopy of these forests. While TDFs are usually characterized by using wind dispersal mechanisms, producing small seeds that can also endure a longer time of dormancy and germinate with limited soil moisture; animal dispersal occurs with larger fruits and are more common in evergreen species (Lohbeck et al. 2015).

However, Lohbeck et al. reported that while TDFs will often invest in trait values related to drought tolerance and optimal light acquisition during the early stages of succession, in their late successional stages TDFs are more likely to invest in larger seeds that are mostly animal dispersed (Lohbeck et al. 2015). This means that while tropical dry forests may invest during their early successional stages in traits related to drought tolerance and optimal light acquisition, in their late successional stages TDFs are more likely to invest in traits related to large seeds and biotic dispersal (Lohbeck et al. 2015). They related this result with larger seeds being able to colonize shaded sites, which become more common during late forest succession. The results demonstrate that most understory species rely on animal seed dispersal as a reproductive effort strategy, supporting the argument that most of the sampled forests are at a late succession stage.

The gradient of succession in the forests that were sampled in my study results from the forest fragmentation that most forested lands experience in Azuero. I aimed to sample forests instead of forest fragments, resulting in a sample pool of forests ranging between early and late successional stages. I still attempted to consider mostly old growth and old secondary forests, which is why the results mostly mirror responses from late succession forests. This becomes important when considering the response of forests to climate variability. While Amazonian forests have been recorded as adapting and becoming more resistant to increased temperatures and droughts (Esquivel-Muelbert et al. 2018), there’s evidence of intact Amazonian forests being more resistant to short-term climate anomalies compared to human-impacted forests (Saleska et al. 2007). I therefore aimed to collect samples from more intact forests that would better portray TDFs’ responses to climate change pressures. We can interpret the results as showing that Azuero’s TDFs have a reasonably closed canopy which occurs as the forest matures. In addition, it is possible that with a steady succession, seed-dispersing animals would more frequently find refuge in sites that have become safer (i.e. less fragmented and more separated to human activities) (Lohbeck et al. 2015). This change of trait, just as the change of specific leaf area, can be considered a functional trait shift to improve acquisitive strategies. In this research, seed sizes were not considered, and I suggest further research considering this shift in the future. Lohbeck et al. (2015)'s study shows that species in TDFs and TWFs face different pressures and invest in different trait strategies. In other words, Lohbeck et al.'s results demonstrate the divergent succession strategies used by tropical dry forests versus tropical wet forests, and in doing so emphasize the importance of aiming for a clearer understanding of TDFs through rigorous criteria to understand succession of tropical forests and to plan for successful restoration and reforestation projects.

My results demonstrate a higher LNC in recruiting saplings in Azuero's forests which also provides evidence of an adaptive strategy intended to avoid water stress through time (Lohbeck et al. 2015). In TDFs, nutrient cycles (including the input, use, and output of nitrogen) are complex and highly influenced by rainfall seasonality as well as the historical land use in which the forest grows. There is evidence that dryland plants often show higher leaf nitrogen contents than species from wetter ecosystems (Wright et al. 2001; Wright et al. 2003). This higher concentration has been linked to plants in low-rainfall environments increasing their N content per unit leaf area to save water while maintaining stable photosynthetic rates (Wright et al. 2001), which may be accounted for by the 70% of the total N contained in plant leaves being allocated to rubisco and other enzymes and proteins involved in photosynthesis (Evans. 1989; Onoda et al. 2017; Evans and Clarke. 2018). Therefore, a higher investment in N uptake and allocation to leaves enhances CO_2 fixation and reduces CO_2 concentration. This is achieved by optimizing carboxylation and carbon assimilation capacity from the high leaf N area, while at the same time reducing stomatal conductance and transpiration rates to minimize water loss and maintain supply of CO_2 in leaves (Querejeta et al. 2022).

There has also been evidence of a shift from vascular species with low leaf N content at low soil N availability towards species that would have high leaf N content at high soil N availability, showing a relationship between plant leaf traits and soil nutrient fertility (Ordoñez et al. 2009; Du et al. 2017). Under normal circumstances, we expect to see a higher presence of dry land legume species (*Fabaceae*) in TDFs than in tropical rainforests. The *Fabaceae* family is one of the most abundant and species-rich families in neotropical TDFs (Gei and Powers. 2013; Vargas et al. 2015). These species would present higher leaf N mass, higher SLA and thinner leaves compared with nonlegume species (Querejeta et al. 2022). Specifically amongst legume species, a higher leaf nitrogen content would also be correlated with thinner leaves. However, compared with nonlegume deciduous species, deciduous legume plant species have lower predawn water potentials, which can be attributed to a "*colonization of drier microsites, and the use of shallower, more evaporatively enriched soil water sources by deciduous legumes*" (Querejeta et al. 2022). This demonstrates that the acquisition of N and water is mutually interchangeable, allowing plants to attain photosynthetic carbon gain when one of these resources is scarce by compensating with the other (Wright et al. 2001; Wright et al. 2003; Prentice et al. 2014).

On the other hand, it can be expected that due to the high abundance of nitrogen-fixing species and species with high LNC in a deciduous forest, that a lot of the leaf litter could contribute to the soil's fertility. While it has previously been suggested that 28% to 88% of the N content of legume species comes from fixation, and that the remaining N content would come from mineral N in the soil (Freitas et al. 2010), it has also been shown that N fixation contributes to the accumulation of N in the soil and ecosystem as the succession of tropical forests progresses (Pearson and Vitousek. 2001; Gei and Powers. 2013). This happens with rain soluble organic matter from leaf litter used in microbial activity, which promotes N mineralization (Anaya et al. 2007; Gei and Powers, 2013).

Nitrogen cycling variations are not only due to biotic factors. Several studies experimenting with the impact of soil N deposition on LNC indicate a direct increase in LNC plant species with N enrichment through the soil (Du and Fang. 2014; Zhang et al. 2015). We know that inputs of N are increasing both globally (Gruber and Galloway. 2008) and regionally within the tropics (Hietz et al. 2011) because of human activities and land use change from forest to agricultural lands (Gei and Powers. 2013). The land use change from TDFs into pastures and fields, as well as the secondary forest succession that would follow, have an impact on N cycling (Gei and Powers. 2013). A large input of N in the soil and increase in the vegetation N pools can come from livestock manure in silvopastoral systems (Gei and Powers. 2013). As is common in TDFs that are fragmented by pasture, livestock often shelter under large trees for shade, and they can provide animal-originating nitrogen through manure. This can be further incentivised with the presence of N-fixing trees that produce pods that are attractive to cattle (Querejeta et al. 2022). In Azueros' TDFs, the high LNC could be indicative of trees developing strategies for more efficient water conservation (higher LNC) as temperatures increase with a higher acquisition of light for photosynthesis (higher SLA). This also indicates that the high content of LNC in these forests, while common for a TDF, could show an increasing recruitment of *Fabaceae*, in addition to forest dynamics that are proper for a TDF undergoing a late succession stage.

Research indicates positive feedback of TDF late succession after land use change for cattle farming and the exponential release of Nitrogen oxide emissions from the soil system, resulting in increasing GHGs emissions from TDFs (Craine et al. 2008; Gei and Powers. 2013; Ruiz-Navarro et al. 2016; Querejeta. 2022). This, rather than being a reason to believe that TDFs could be the source of more emissions than they could intake, shows once again the regressive effect that forest depletion and deforestation have on the ecosystem services that forests offer, even if we think that the damage is "restored" by natural regeneration and reforestation post land use. We know as well that in addition to the disruption of soil habitats, indicating the need to further study the microbial soil populations of TDFs, (Dirzo et al. 2011), climate change pressures mostly related to instability in rain, will have an impact on nutrient cycles, including P and N fluxes (Gei and Powers. 2013).

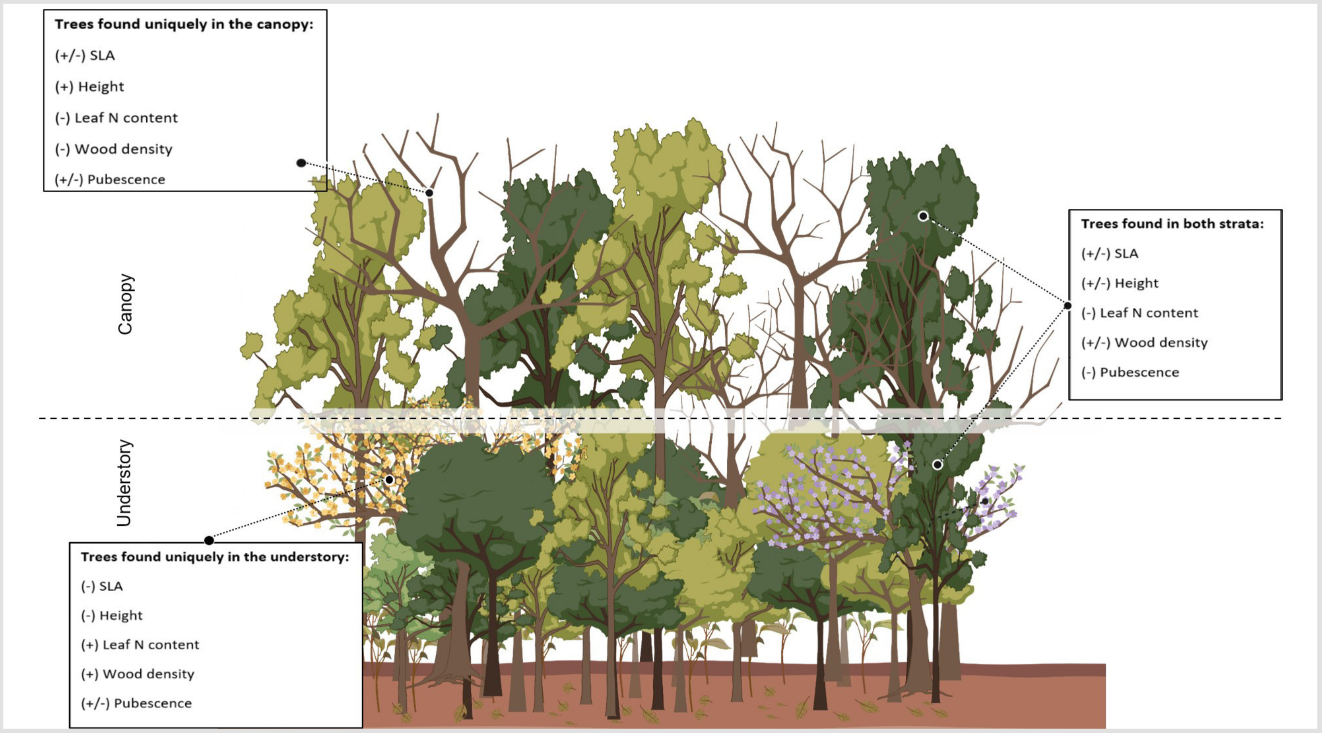


Figure. 21 Observed functional traits' shifts from this study from species found uniquely in the canopy, uniquely found in the understory, or found in both strata to Azuero's TDFs.

Section 3.05 - Conclusion

The functional traits differences between canopy trees and saplings reveal a level of drought resistance that allowed tropical dry forests in Azuero to cope with the fairly recent climatic pressures. However, as these results tend to demonstrate a shift in functional trait values between canopy and understory species, we must recognize one of the limitations encountered with the use of functional trait measurements from both the field and the TRY Database, as research shows that traits can vary considerably within same species individuals due to genetic and environmental factors, as well as considering variances in measurement methods and regions where the data is collected. There is still a lot of research that could be dedicated to collecting more functional traits data to counteract this difficulty and support future studies on forest functional shifts from pressures. The changes in functional traits observed in these forests should still be further studied to solidify the claim that the tropical dry forests of the Azuero peninsula are showing signs of adaptation to climate change. The differences between canopy and understory species may also be related to differences in succession stages. Succession could influence the response and ability of Azuero's TDFs to adapt and be resilient to climate change. While paleo-studies have shown that TDFs are drought tolerant (Meir and Pennington. 2011; Allen et al. 2017), the risk of either overpassing a drought threshold or a sudden shift to increasing temperatures and precipitation cannot be ruled out. However, the signs of drought resilience that I have shown in these forests provides some positive insights for forest plasticity to adapt to drier and warmer climates based on species composition and functional strategies.

Recent models suggest that increased precipitations may be expected in Panama as well as Panama's Azuero peninsula, while strong declines in mean daily rainfall are projected for most of Central America (Pinzón et al. 2017; Stennett-Brown et al. 2017; García et al. 2020; Seneviratne et al. 2021; Pörtner et al. 2022). This could be attributed to the impact of higher temperatures leading to a higher evapotranspiration, resulting in higher rates of rainfall in Azuero (Larsen. 2019). However, the variations between Panama and the rest of Central America shows some contradictions in this regard. While several studies conducted in the Amazon Basin now indicate with medium confidence a consequential transition from tropical rainforest to tropical dry forests or savannas from climate change, little is known for other systems such as TDFs for either of these impacts. While there is still a lot of uncertainty, predictions indicate that the Azuero peninsula and its TDFs might need to adapt to not only increasing temperatures but also to heavier rains that will be interrupted by sporadic longer droughts (Pinzón et al. 2017; Stennett-Brown et al. 2017; García et al. 2020; Seneviratne et al. 2021; Pörtner et al. 2022). If a shift towards stronger precipitation is to occur, it would be critical for TDFs to be able to adapt rapidly to these changes. A study from Raymundo et al. (2018), aimed to understand the impact of increased water availability (from a reservoir flooding) in two tropical dry forests in the Minas Gerais, Southeastern Brazil. Their results showed that plots that were closer to the water's edges experienced an increase in species and functional diversity. However, they also evidenced a shift towards species with traits that are associated with low resistance to drought due to the increase of water availability, and stated that shifts amongst the recruiting species were distant and important enough to show the overall changes in the community (Raymundo et al. 2018). This would indicate that TDFs could react quite quickly once again to a change in the precipitation regime. This provides some hopeful signs of future species composition and functional strategies adaptation and resilience in Azuero's tropical dry forests if precipitation increases as predicted, as a unique case within Central America.

Chapter 4

Thesis Conclusion

Chapter 4 provides a review of the results found in Chapter 2 and 3, and aims to contribute with reflections and suggestions in which these findings could be applied in climate-conscious reforestation and conservation projects in Panama's tropical dry forests in the face of climate change. Considering the results found from past climatic pressures and a thorough literature review of climate predictions in Azuero, Panama and Central America, this chapter also establishes questions to consider in future research.

With each new study released, each methodology accounting for previous limitations, and each new technological innovation that improves the analysis of climatic variations and biodiversity responses, research deepens our understanding of the behavior and prognostics of climatic pressures on Earth's ecosystems. While technology, innovation, and a reframing of our approach to resilience facing climate change are required, the unmatched climate mitigation contributions from forests need to be placed in the forefront of our climate mitigation strategies. The last section of this thesis is a conclusion intended to reframe my results within the context of the impact that tropical dry forests could have in climate mitigation strategies in Panama, incorporating relevant literature. I review a series of considerations and potential applications for this study on the past climatic variations in the Azuero peninsula and the behaviors of tropical dry forests of Panama facing climatic pressures. This conclusion is separated into sections that discuss: 1. A recapitulation of my results including initial analyses on the anthropogenic impact of land use on Azuero's TDFs in the study sites, 2. The potential carbon sequestration contribution of TDFs for climate change mitigation, and 3. The prospective applications of my results in reforestation and conservation projects in Panama's tropical dry forests.

Section 4.01 - Land use practices' impact on Azuero's tropical dry forests

Tropical dry forests represent some of the least protected and most threatened tropical terrestrial ecosystems from anthropogenic pressures causing deforestation and forest degradation (Portillo-Quintero and Sánchez-Azofeifa. 2010; Portillo-Quintero et al. 2015; Powers et al. 2018; Stan and Sánchez-Azofeifa. 2019; Reyes-Palomeque et al. 2021). TDFs are extensively repurposed by communities because of the fertile soils they grow on, their growth commonly happening on flat terrains, and their vegetation structure being considered easier for land conversion than more humid forests (Portillo- Quintero et al. 2015; Powers et al. 2018; Reyes-Palomeque et al. 2021) This deforestation trend has led tropical dry forests to split into a mosaic of secondary vegetation between previously used and subsequently abandoned lands, remnants of primary forests, and lands converted to agriculture, cattle farming, and human settlements (De la Barreda-Bautista et al. 2011; Reyes-Palomeque et al. 2021). Within the context of Panama, this study highlights the combination of land uses with the studied forested lands ranging from early to late succession secondary forests. However, because the anthropogenic impact is evident within the Azuero peninsula, while land abandonment and reforestation efforts led to an increase in forested lands, land conversion could have had a strong influence on the growth of these forests and the species that recruit these lands. It was important to compare the influence observed from climatic variability through time with the anthropogenic pressures of land use on the forests that were studied in the Azuero peninsula to understand if the change of species and functional traits was associated more with land use practices or with climatic changes. To account for historical land use pressures, the most common land use practices used in the past were considered both inside the land that is now forested, as well as the past and present activities of neighboring lands. I also considered present practices that could currently take place inside the forested land. The impacts considered for each site were: Previous uses (finca, cattle farming, agriculture, timber), present uses (finca, cattle farming, agriculture, timber), neighboring activities (finca, cattle farming, agriculture, timber, '*pasto mejorado*'/ introduction of African grasses). The results provide evidence that climate pressures are more strongly correlated than land use practices with impact on the species composition and functional traits shifts that these forests experienced. Figure 22 shows a non-significant RDA correlation between CWM values of functional traits, dispersal mechanisms, and land use practices per stratum and site. While land use practices seem to be less correlated with the shifts in the CWM of functional traits than climatic pressures in this study, it would be beneficial to have more studies compare the impact of climatic pressures and land use practices in tropical dry forests. The eigenvalues for constrained axes are RDA1 explains 13.5% and RDA2 explains 6% of the RDA. The eigenvalues for unconstrained axes are PCA1 explains 32.5%, PCA2 explains 13%, PCA3 explains 4.6%. The total inertia is 71.7%, from which 21.5% is constrained and 50.2% is unconstrained. Some constraints were aliased because they were collinear (redundant). R adjusted is -0.077. Pr(>F) is 0.725. The anova.cca test for the entire model with 999 permutations was not significant (Pr(>F) 0.725). The anova.cca test for the significance of axes provided the following Pr(>F) results: RDA1 0.685, RDA2 0.945, RDA3 0.999, showing that the RDA model is not significant (p=0.001) as well as all three canonical axes.

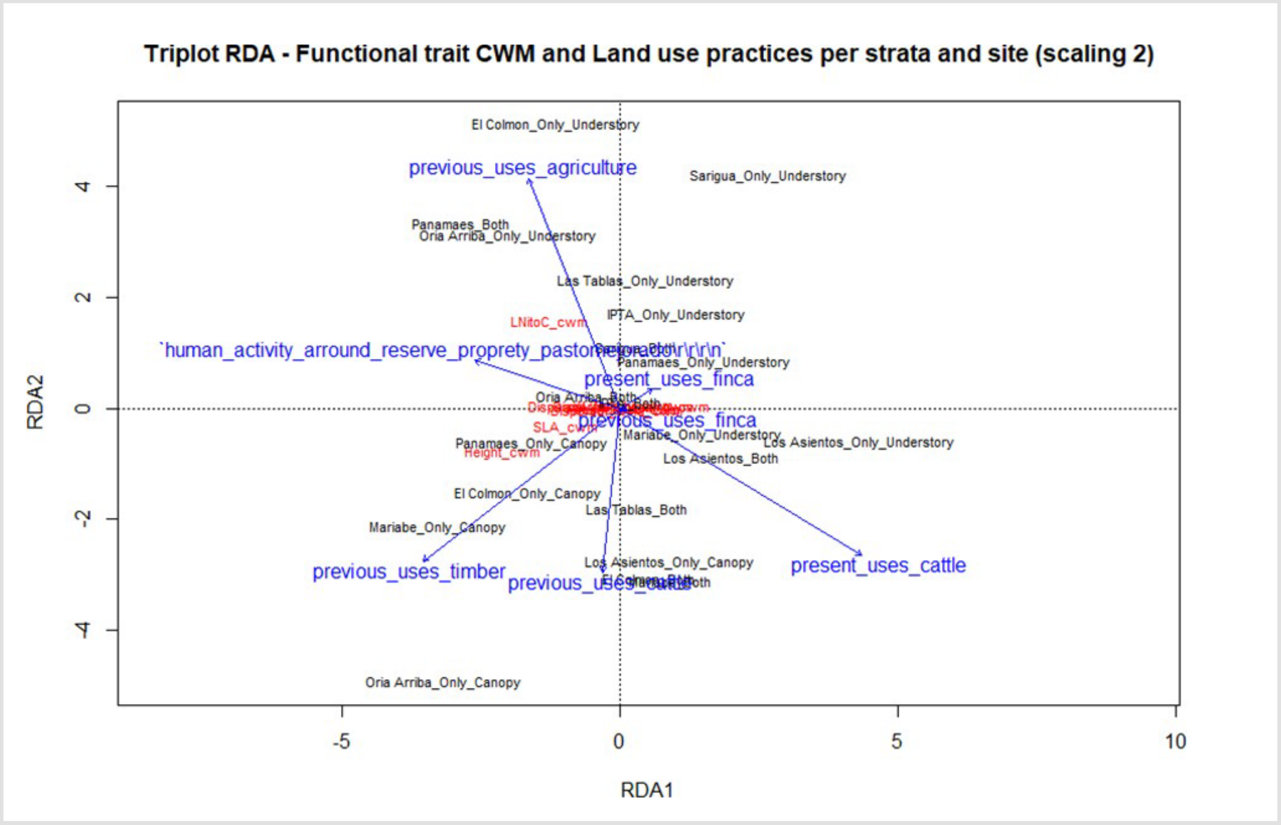


Figure. 22 RDA triplot of CWM values of functional traits and dispersal mechanisms (in red), and land use practices (in blue) per stratum and site (in black).

It is established that tropical tree species can be affected by slight climate changes (Pinzón et al. 2017). As the tropics are expected to be strongly susceptible to pressures from climate change, this study provides evidence of the impact that climate pressures can have on tropical dry forests. While Panama's TDFs have experienced drier and warmer conditions, the studies mentioned in this thesis and the IPCC 6th report indicates that Panama is expected to have a unique trajectory within the context of Central America with increasing precipitations and still warmer temperatures, potentially leading Panama to experience an unparalleled climate (Pinzón et al. 2017; García et al. 2020; Seneviratne et al. 2021; Pörtner et al. 2022).

Between my results that show a past trend of increasing temperatures and decreasing precipitation within the Azuero peninsula, and climate predictions that forecast future increases in precipitation, it can be reasoned that drastic climatic changes and extreme pressures can surge over a short period of time with no clear indication of how forests will react. While the present work demonstrates past aggravated droughts and increases in temperature in Panama, other studies predict increasing precipitation in Panama while Central America becomes drier (Pinzón et al. 2017; García et al. 2020; Seneviratne et al. 2021; Pörtner et al. 2022). With increasing precipitation, the impact of rising temperatures in the Azuero Peninsula will pose a great challenge in predicting the shifts likely to happen in Panama's tropical dry forests. The need to predict and plan ahead in order to protect forests with increasing pressures from climate change and extreme weather events is a challenge that we need to find solutions for within an immense range of uncertainty. Considering this uncertainty, one reasonable hypothesis that can be postulated is that the more forest systems can regenerate and be supported by scientifically based projects, the less vulnerable these systems will be to pressures. Following the *Glasgow Leaders' Declaration on Forests and Land Use, 2021*, stopping forest conversion and maintaining forested lands remains crucial to the mitigation of predicted extreme events (COP26. 2021).

Section 4.02 - Tropical dry forests and climate change mitigation

Panama's tropical dry forests contributed to a national gain of secondary forests and offset the loss of primary forests (Wright and Samaniego. 2008). This demonstrates both that Panama's TDFs have taken a considerably different trajectory than most tropical dry forests, potentially because of local reforestation and conservation efforts or a shift from farming to other sectors, and that TDFs in Panama could have a considerable impact in climate mitigation strategies because of their current regeneration trend. It is clear that a central strategy for climate change mitigation in international agreements such as COP26 revolves around stopping deforestation, better accounting for local and Indigenous knowledge in forest conservation, and increasing well-informed reforestation projects (COP26. 2021).

However, climatic pressures such as drought severity and water scarcity have an important impact on carbon fluxes in tropical forests. Castro et al. (2018) establish in their study on the effects of drought on productivity in a tropical dry forest in the Santa Rosa National Park, Costa Rica, that decreased precipitation rates during the 2014 and 2015 years led to a reduction in net ecosystem CO_2 exchange (NEE), and total ecosystem respiration (Reco) (Castro et al. 2018). In fact, this tropical dry forest showed vulnerability to precipitation anomalies, during El Niño severe drought events. They argue that this ecosystem, being a secondary tropical dry forest, still acted as a mean carbon sink, even during severe droughts. Considering the functional convergence theory (Bloom et al. 1985; Solbrig et al. 1979) which states that resource availability will lead to variations in the investment on CO_2 fixation, with productivity being shortened with limited resource availability, (Castro et al. 2018) it is legitimate to be concerned about the positive feedback effect that increasing climatic pressures will have on the carbon sequestration capacity of tropical dry forests. The conversion of forested areas to agricultural and cattle farming lands or human settlements is one of the main activities affecting TDFs and is the second largest source of CO_2 emissions to the atmosphere (Reyes-Palomeque et al. 2021). It is a shared perspective amongst several scientists specializing in tropical dry forests that analyzing secondary forest succession is crucial to understanding the recovery of vegetation structure, species richness, and species composition of forests over time, as well as carbon accumulation within these systems (Chazdon. 2014; Stan and Sánchez-Azofeifa. 2019). While primary forests are often attributed a high value in carbon sequestration and biodiversity conservation, secondary forests have been recorded to provide key ecosystem services varying within a successional age gradient (Chazdon, 2014*;* Chazdon et al. 2016; Poorter et al. 2016). Reyes-Palomeque et al. (2021) show that amongst four forest age classes they studied (class 1: 3–8 years; class 2: 9–16 years, class 3: 17–50 years; class 4: >50 years), some tropical forest plant attributes, including biomass, basal area and species richness saturate through time. They found high rates of increase in these values in tropical dry forests during the first 15 to 20 years, with a slower rate at older ages (Reyes-Palomeque et al. 2021). A similar increase within that approximate stand age was also found by other researchers (Marín-Spiotta et al. 2007; Poorter et al. 2016). There are still strong controversies in determining which forest succession stage contributes the most for carbon sequestration purposes. Considering that Panama's TDFs started a regeneration process from agricultural land abandonment starting in 1992 (Wright and Samaniego. 2008), it would be of interest to further analyze and quantify the carbon sequestration service of Panama's tropical dry forests. López, Pérez, and Mariscal (2015) comment that forest fragments and species commonly found within Panama's TDFs, especially large species such as *A. excelsum* and *C. aromatica* could play an important role in mitigation efforts (López, Pérez and Mariscal. 2015). Forest fragments are recognized for their potential contribution in carbon and biodiversity cobenefits (Matos et al. 2020). Research efforts to account for the carbon sequestration contribution of these forests would also support the planning of more reforestation and conservation projects within the area and provide important information on the carbon sequestration contribution of tropical forests.

Section 4.03 - Possibilities in climate-conscious reforestation and conservation programs

The results of my studies show the important pressure that climate variability and extreme weather events have on tropical dry forests within the Azuero peninsula in Panama. It is likely that the observed shift of species and climate pressure resilience is taking place within other TDFs and other tropical forests because of climate change. As the forests studied in Azuero show some signs of resilience within the past and current climatic pressures, the shift in species composition and CWMs demonstrate the fitness of some species over species that are no longer recruiting the forests' understory. Reforestation efforts are commonly used as a solution to deforestation and rehabilitation of vulnerable biodiversity habitats, and have been used in Azuero. These efforts are however costly, demand efforts of a large number of people, and often experience a low level of success with high tree mortality. As climate change impacts our forests, it is imperative to plan forward-thinking reforestation and conservation projects that consider the forests' response to climate pressures. Within this lens, aspects that become important to consider are the climate trends observed in the area, abundant recruiting sapling species, and the prevalent dispersal mechanisms. While these suggestions come from my results rather than a more in-depth literature review, this study shows the importance of supporting resilient species to reinforce the fitness of the forest within the context of climate change. It is contested in the literature that the approach to tropical dry forest restoration needs to be tailored for the ecosystem itself instead of following methods utilized for tropical rainforests (Vieira and Scariot. 2006). This supports the claim that reforestation programs could become instrumental in a higher success of forest resilience to climate change through the assisted recruitment of local (naturally growing) climate resilient species. Considering functional traits as an important factor in establishing the resilience to current climatic conditions could help make informed decisions in restoration and reforestation. The findings show a higher recruitment of species using animal dispersal mechanisms, which suggest the importance of local seed dispersers for natural regeneration strategies. In Azuero, organizations such as the Pro Eco Azuero aim to strengthen an ecological corridor for the restoration of tropical dry forests and the conservation of the endemic Azuero spider monkey *Ateles geoffroyi azuerensis* (Pro Eco Azuero. 2022). My results indicate further reasons to support this and other similar projects that support seed dispersal species. While the capacity of carbon sequestration is still contested between forest succession stages, it is well established that biodiversity and vegetation structure increase as the forest ages. Reyes-Palomeque et al. (2021) demonstrated a strong correlation between forest succession age and species composition, vegetation structure and richness in tropical dry forests of Yucatan, Mexico (Reyes-Palomeque et al. 2021). This indicates that the stage of a forest in succession is highly determinant of the ecosystem's capacity to recover from land use affecting biodiversity and forest structure and composition.

It is difficult to know what the future holds for Panama's tropical dry forests as a drier climate could shift into wetter climate conditions if following the predictions mentioned. This study shows that TDFs in Azuero have been able to adapt and show resilience to drier and warmer conditions experienced in the past with recruiting species being fit for these conditions. I encourage more studies to be conducted on tropical dry forests as climate change continues to impact this ecosystem, and to plan for local and regional climatic scenarios to support these forests that will continue to be under climatic pressures from climate change.

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Appendices

Supplementary Materials

Section 5.01- Chapter 2: Climate time series and climate anomalies analyses

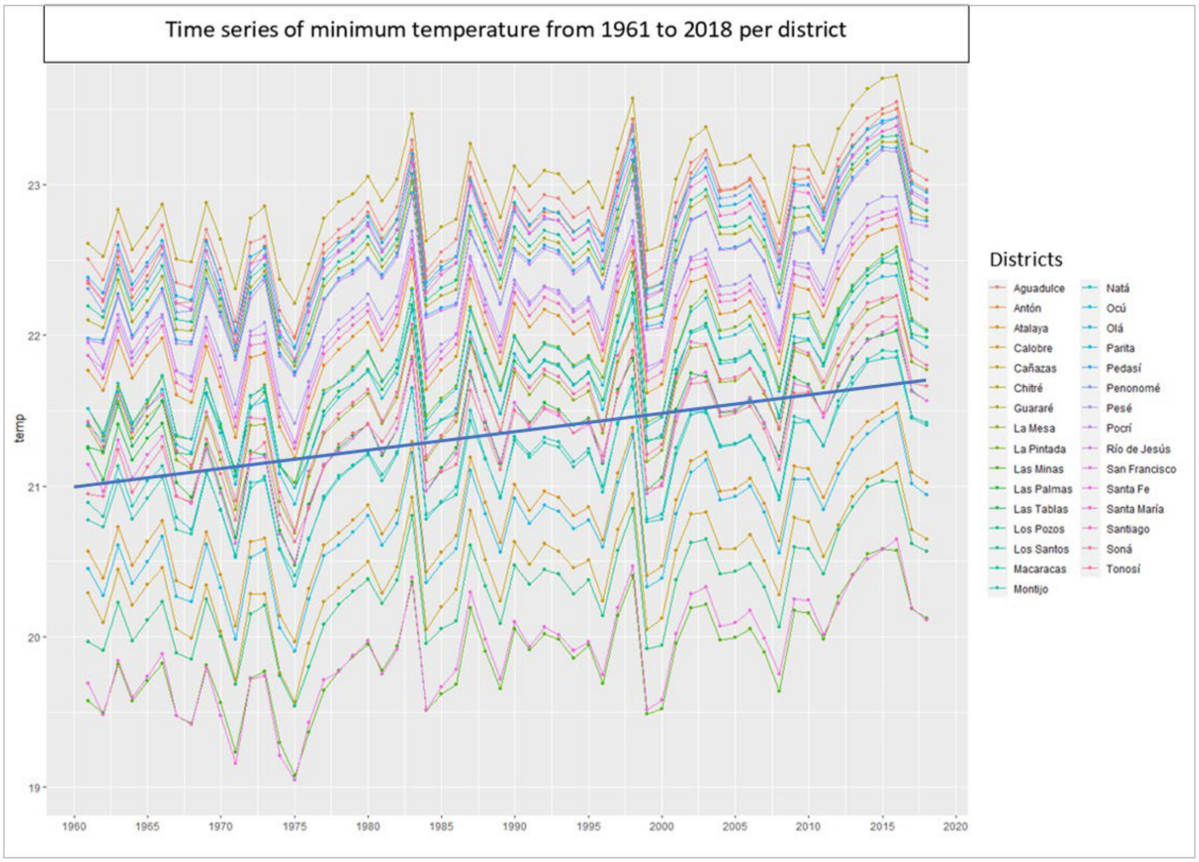


Figure. S1 Time series analysis from 1961 to 2018 of the minimum temperatures at the district level from the WorldClim data. The x-axis shows the yearly change of minimum temperature on the y-axis in degree Celsius. Each line on the graph represents the temporal change of minimum temperatures as a yearly mean (not considering differences in seasonality), for the 31 districts of the Azuero peninsula from the figure legend. Figure. The districts are represented in the map's legend. The mean increase of temperature for the peninsula is 0.7 °C, using the WorldClim data.

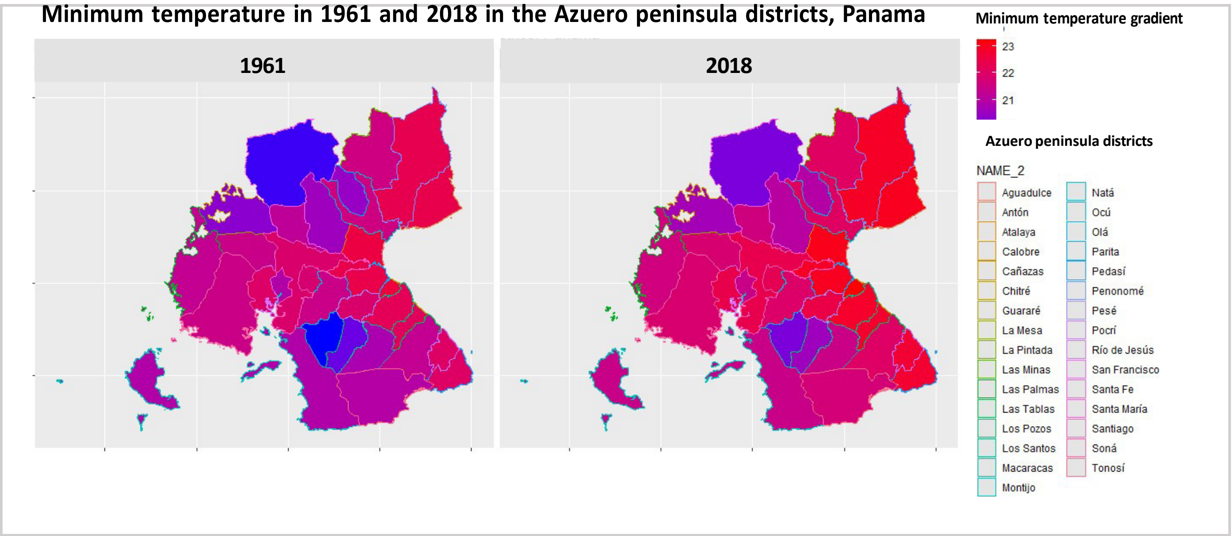


Figure. S2 Maps of the first year (1961) and last year (2018) considered from the dataset of minimum temperatures from the WorldClim dataset at the district level from the legend Azuero peninsula districts. Colors of the maps represent minimum temperatures from the gradient from 19.5C to 23 C, while districts' contours match the Azuero peninsula district legend.

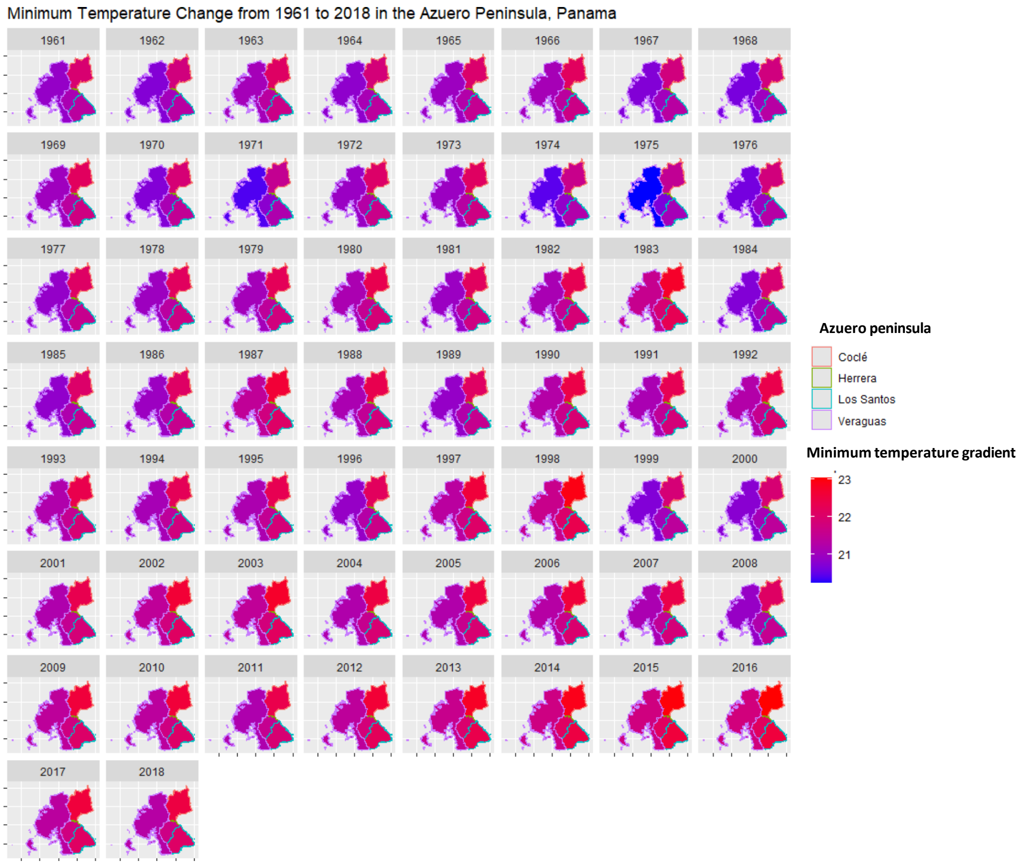


Figure. S3 Maps showing the change in minimum temperature in the Azuero peninsula from 1961 to 2018 at the provincial level. The provinces as shown under the Azuero peninsula provinces legend, matching the province's border with the legend. Years are shown above each map. Temperatures in the maps represent the temperatures between 20°C and 23°C. Years with climate anomalies such as El Niño years (1998, 2015 and 2016) are easily observable. A trend towards increasing temperatures is shown all four provinces.

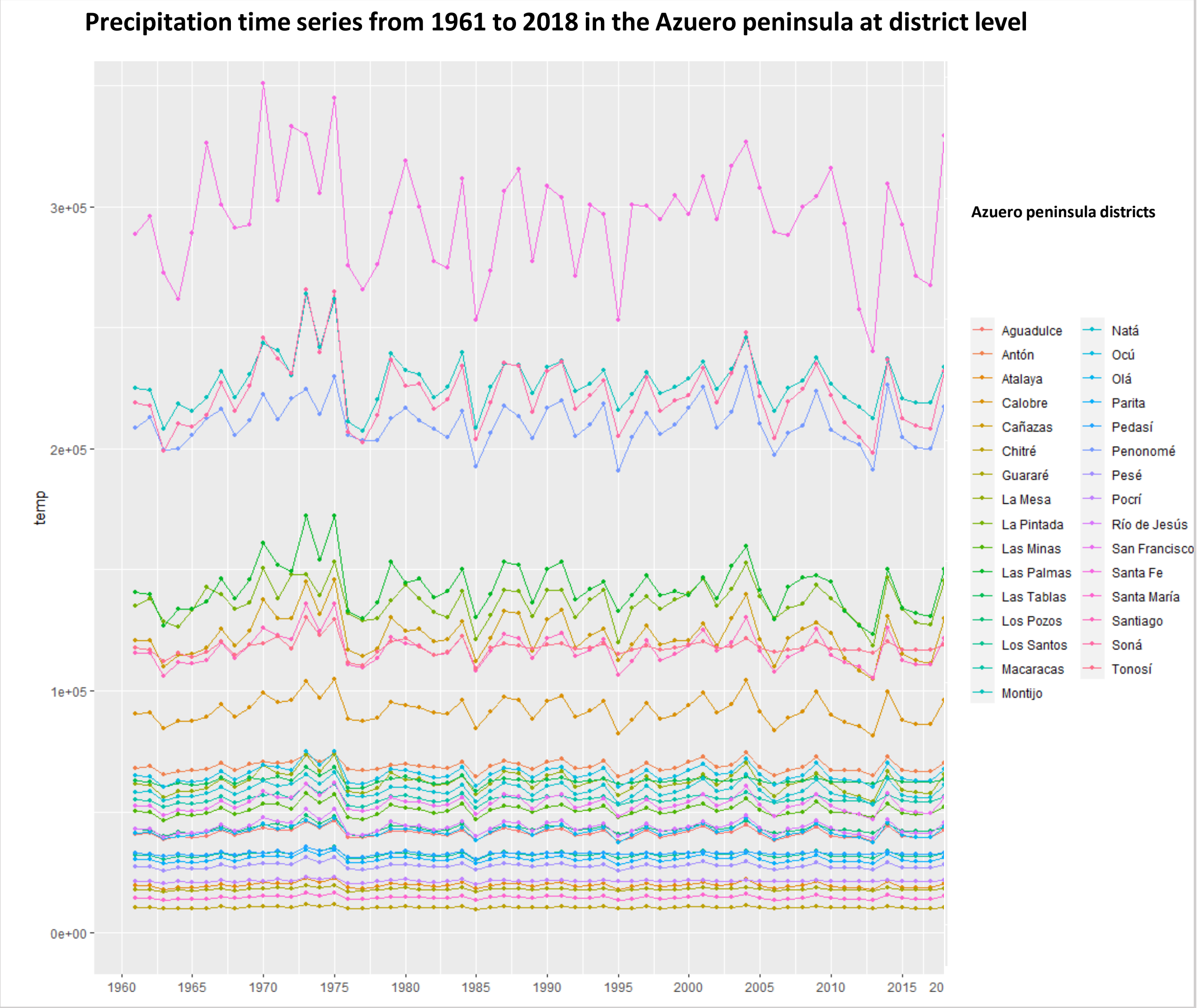


Figure. S4 Precipitation time series as yearly values in mm (x-axis years from 1961 to 2018, y-axis precipitation in mm) per district in the Azuero peninsula. The districts are represented on the map by a different line with the color represented from the legend Azuero peninsula district.

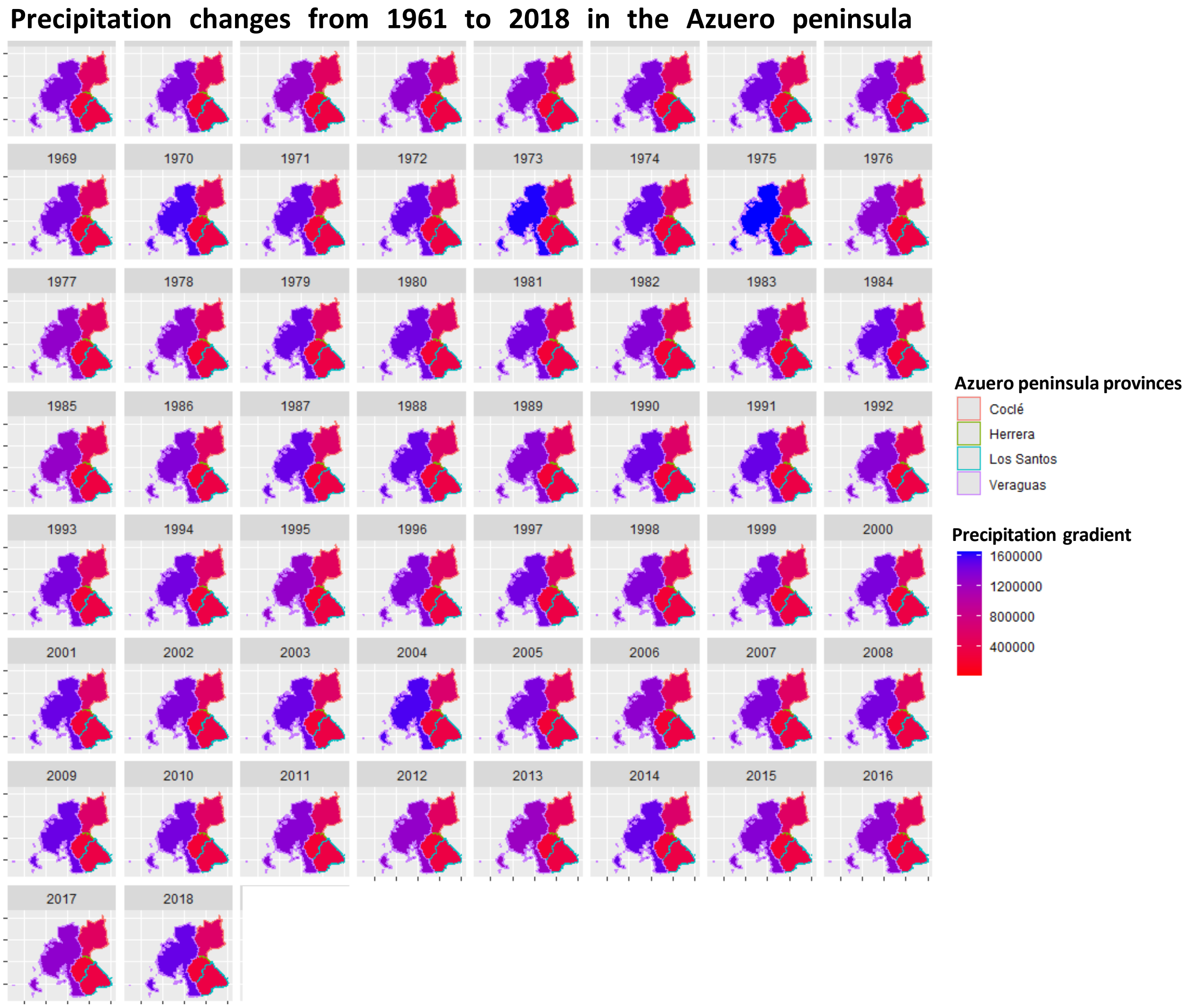


Figure. S5 Maps showing the change in precipitation as yearly values in mm in the Azuero peninsula from 1961 to 2018 at the provincial level, provinces as shown under the Azuero peninsula provinces legend, matching the province's border with the legend. Years are shown above each map. Precipitation in the maps represent yearly precipitation between 100,000 C and 1600,000 mm. Years with climate anomalies such as El Niño and La Niña year can be identified, but it is more difficult to identify a general trend across the peninsula.

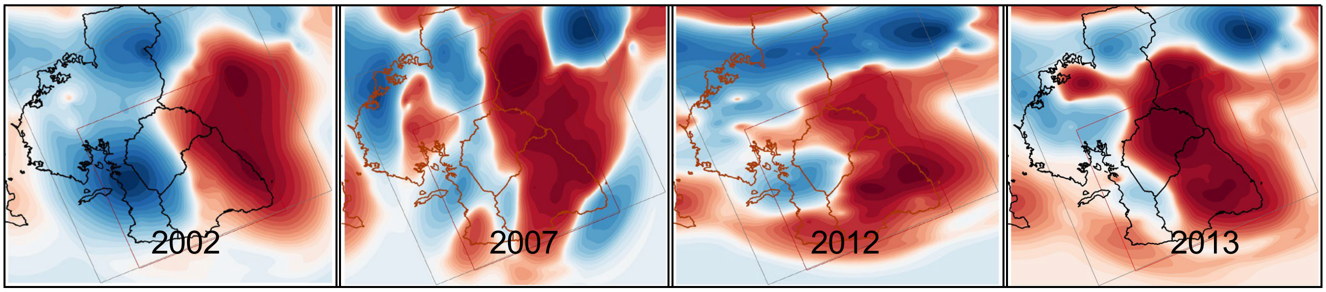
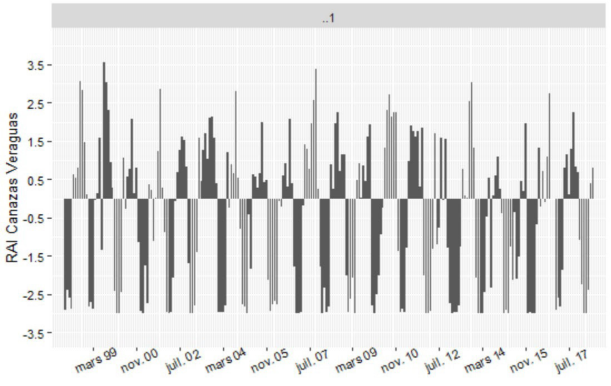


Figure. S6 Co-kriging interpolation maps showing the precipitation during the dry season (December to March) of every five years between 2002 and 2013. Red zones represent regions with the least amount of rain in mm, blue zones are the zones with the highest amount of rain in mm. While the entire peninsula (peninsula delimitations in orange and black) is considered (within the larger grey square), the study area is within the red (smaller square).

The general pattern from drier conditions during the dry season in the coastal regions is clearly represented, indicating a significant change towards drier conditions in the central/Northern regions of the peninsula.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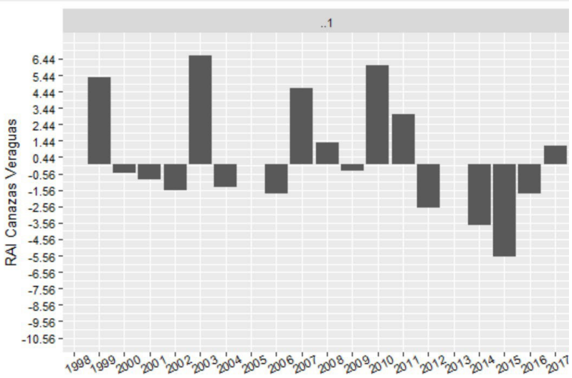
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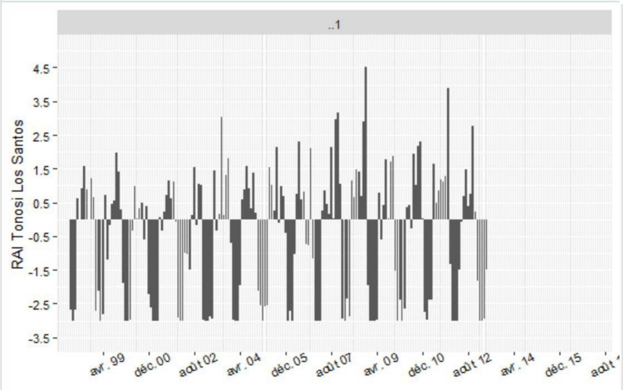
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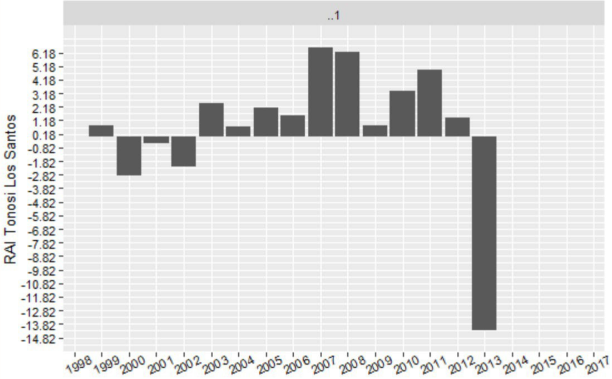
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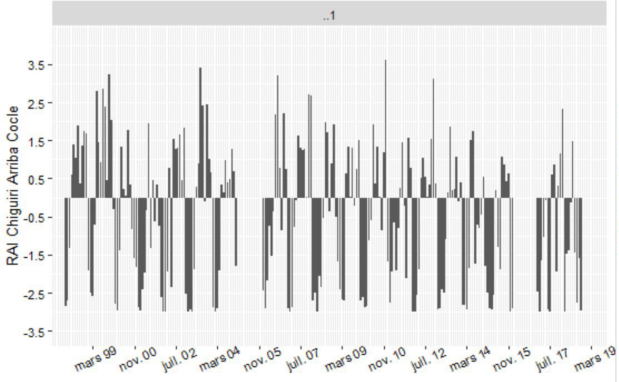
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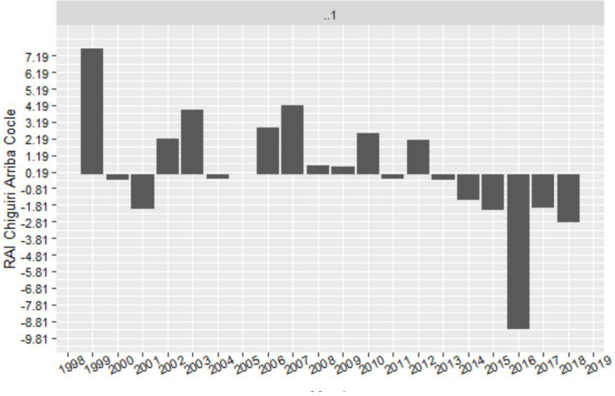
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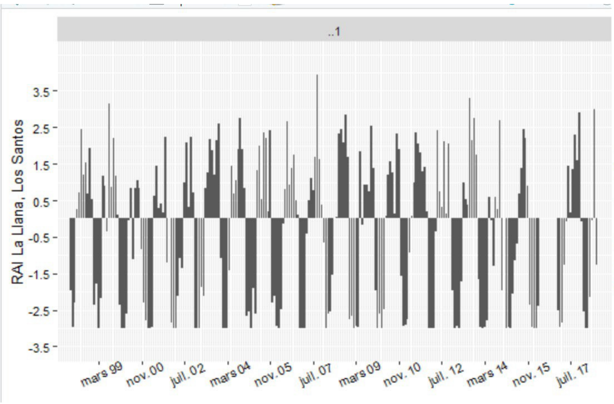
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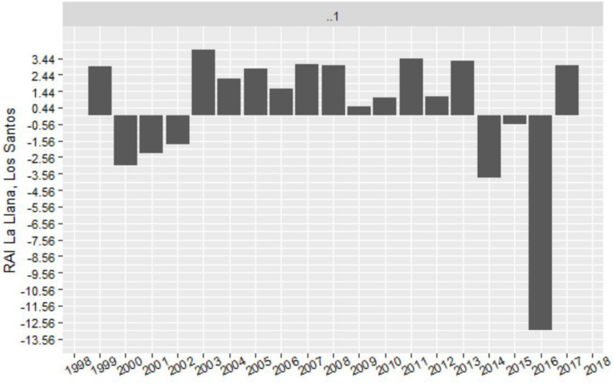
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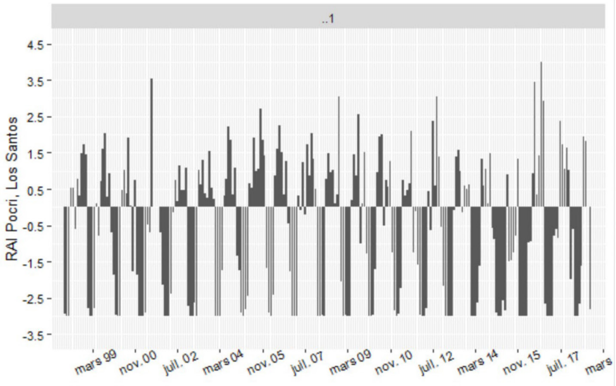
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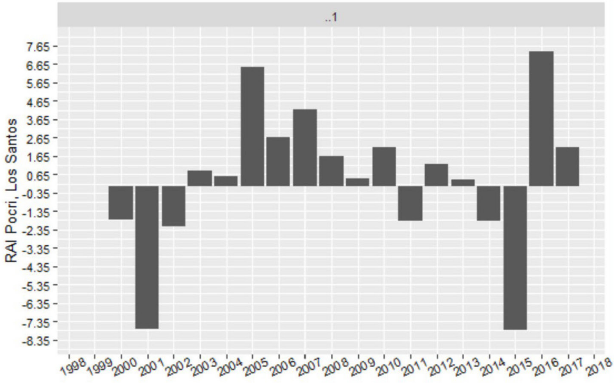
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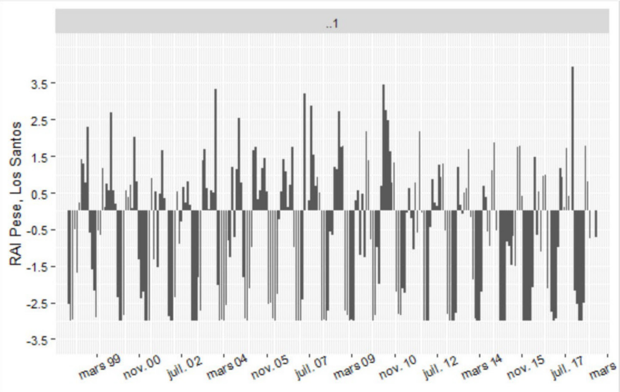
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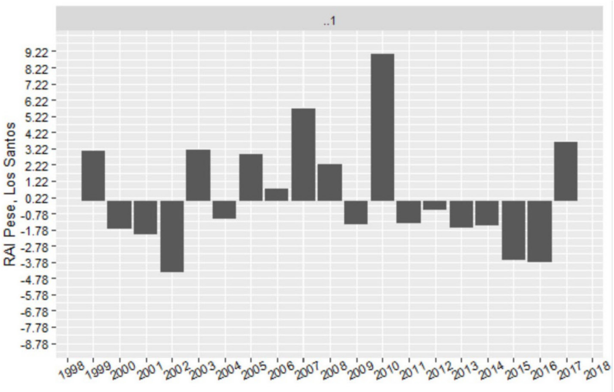
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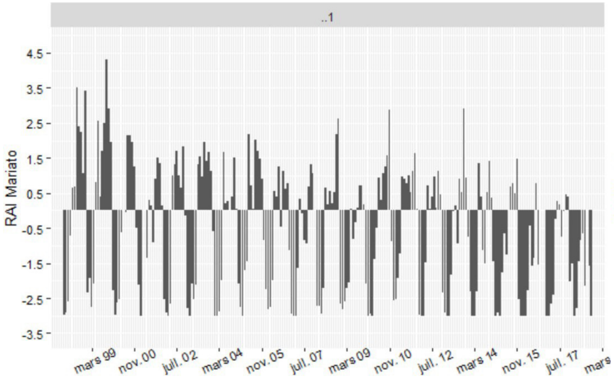
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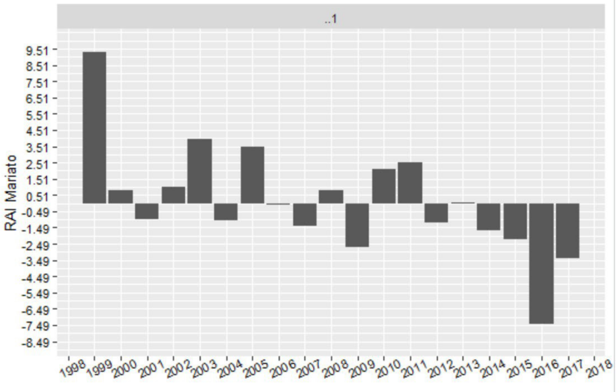
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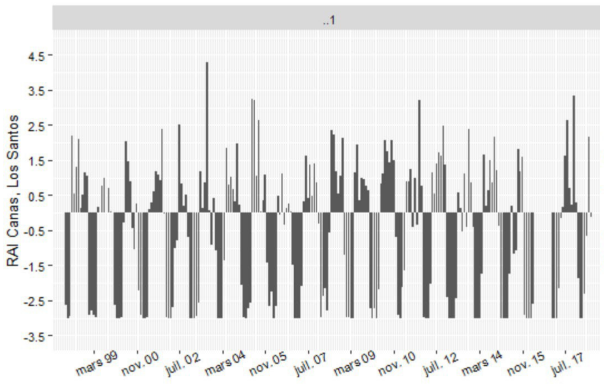
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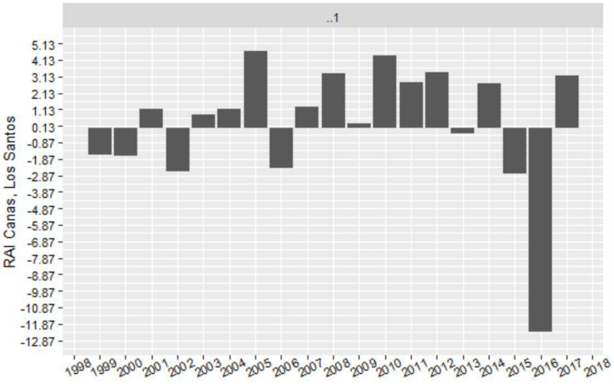
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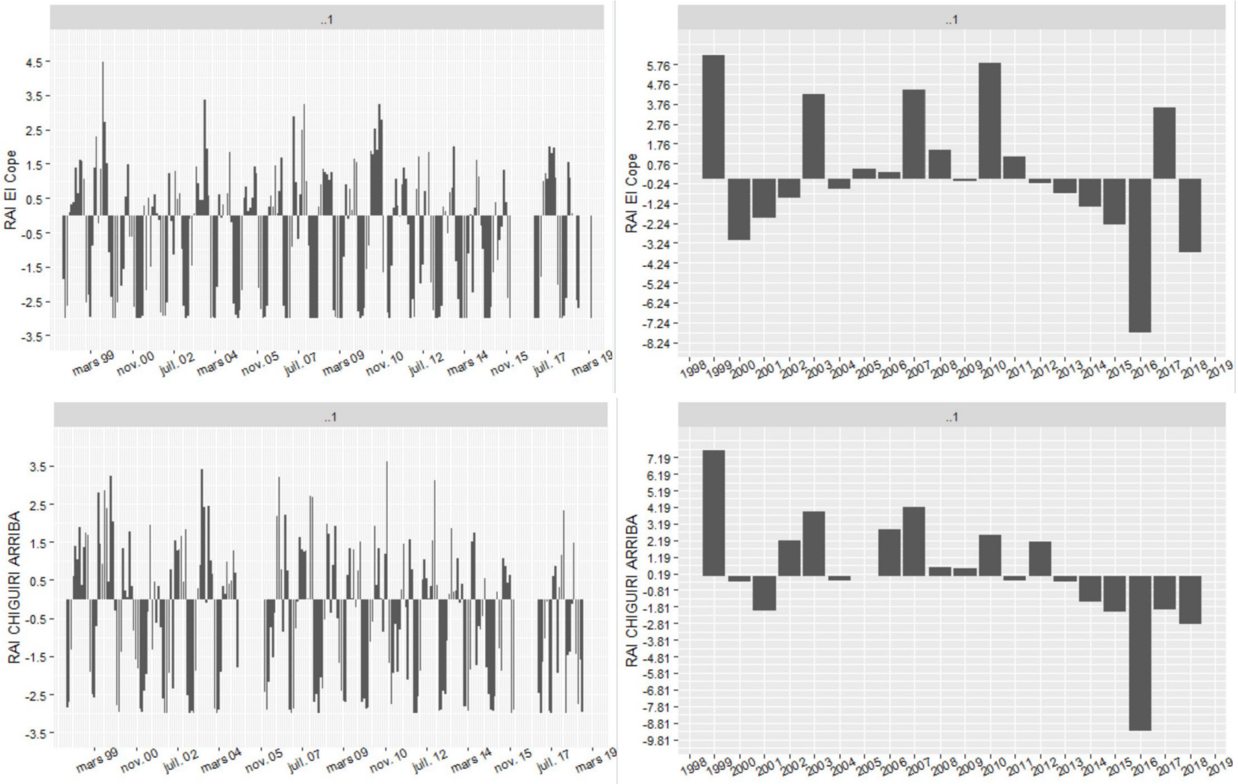

Figure. S7 Rainfall Anomaly Index (RAI) time series lag- 3 and 12 (considering monthly values) of normalized precipitation of normalized precipitation values based upon the station history of a location (using latitude). Comparison to the current period puts the output into a historical perspective. The x-axis represents the months or years, and the y-axis represents the negative and positive RAI values. Values of higher extreme precipitation anomalies will be farther away from the x-axis.

Section 5.02 - Chapter 3: Response of Tropical Dry Forests in Azuero to Past Climatic Pressures

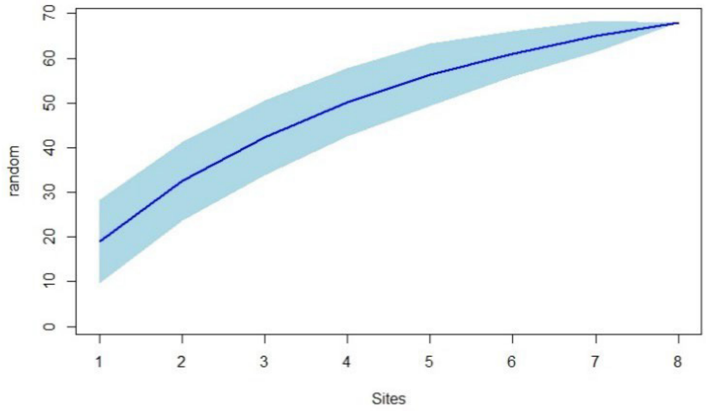

Figure. S8 Species accumulation curve showing the cumulative number of species recorded in at all sites, using the package *vegan* in R, the weighted "random" method as a function of the cumulative effort in sampling, considering trees and saplings together.

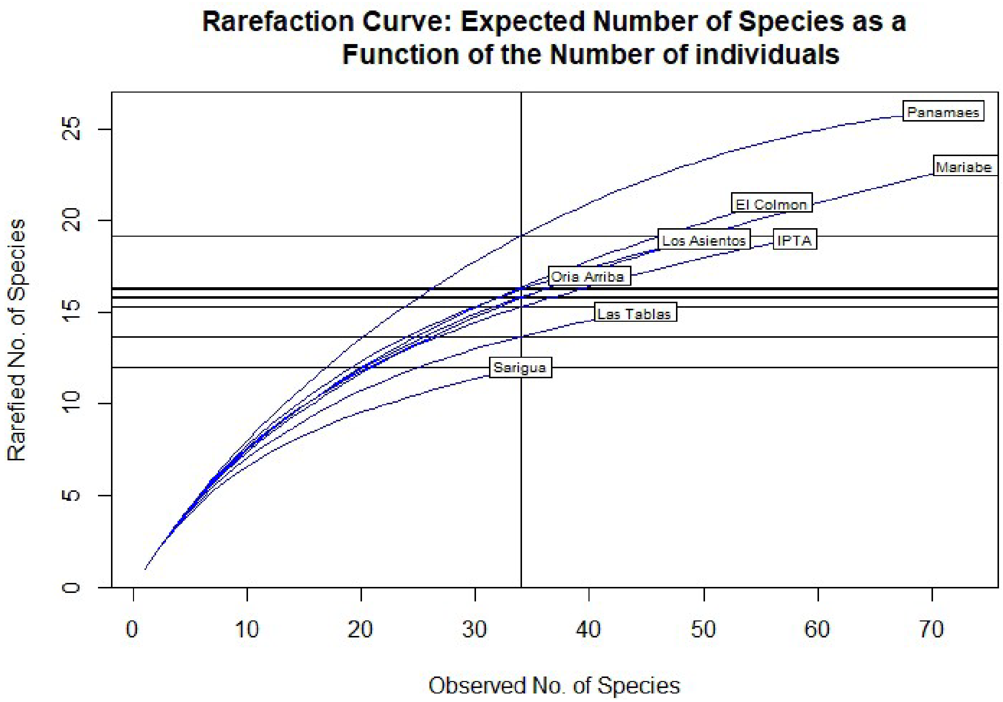

Figure. S9 Rarefaction curve per site showing on x-axis the observed number of species and on the y-axis the rarefied number of species. In sites such as Panamaes and Mariabé, the most common species are found, and the curve plateau as only the rarest species remain to be sampled. Sites such as Sarigua and Oria Arriba might show that more species should have been found.

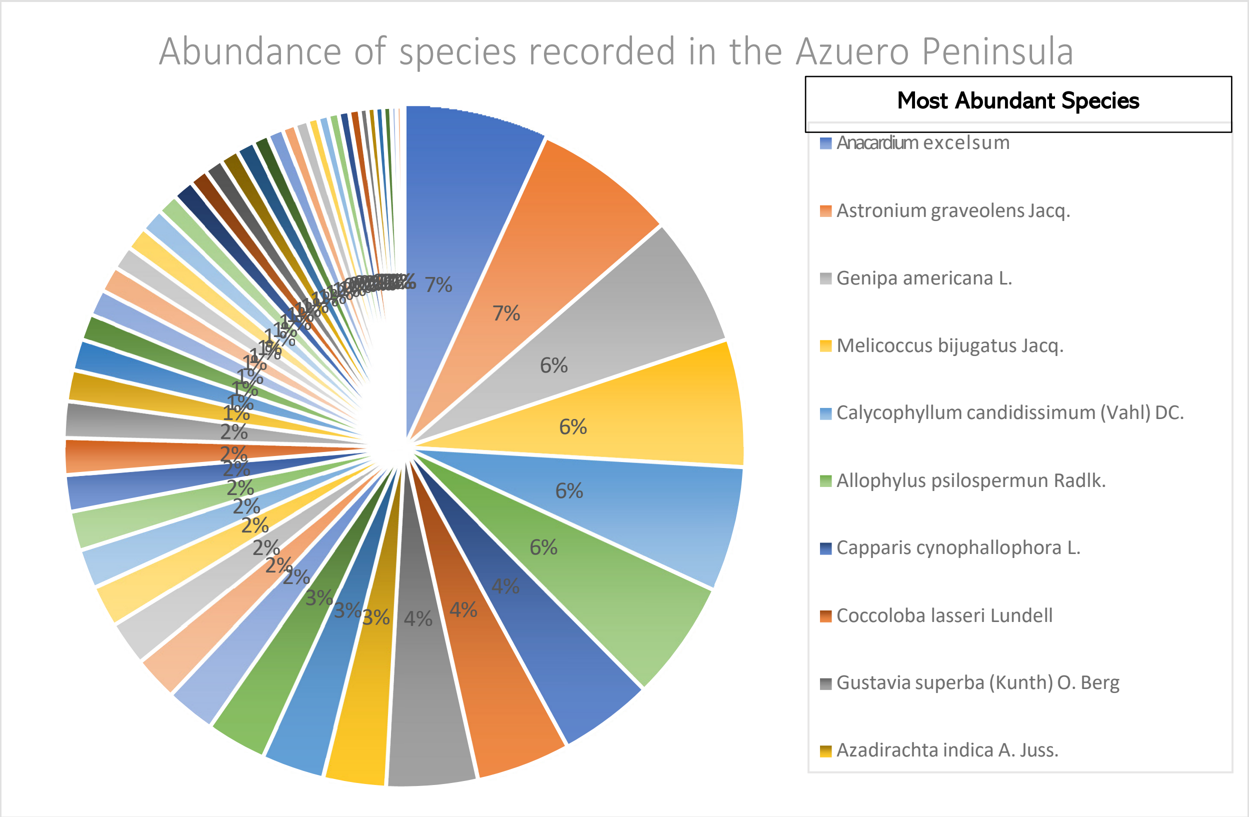

Figure. S10 Pie chart showing the abundance of species of saplings and trees found at the eight sites as a percentage from a total of 63 species throughout the sampling. The species with the highest abundance are shown in the figure legend “Most abundant species”, representing from 7% to 3% of the recorded species with their respective color from the pie chart.

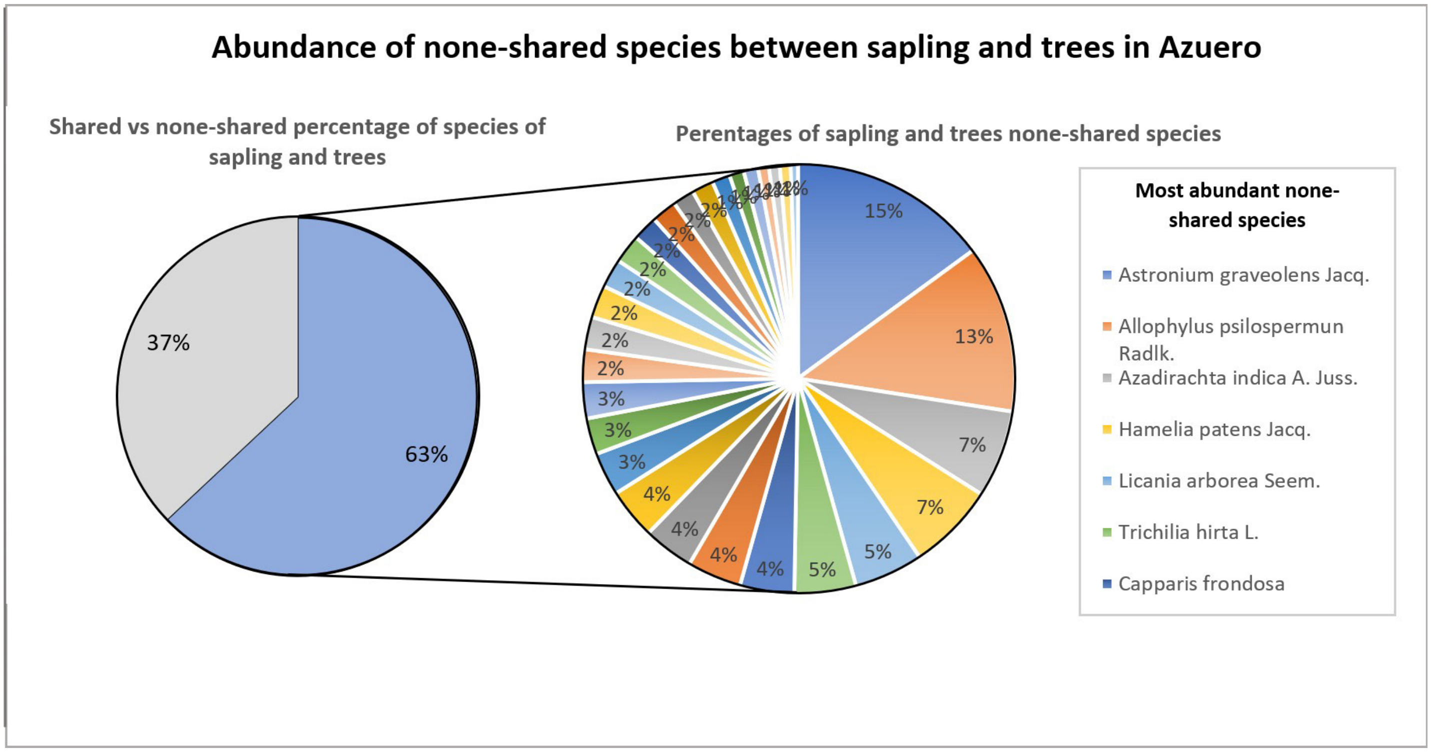

Figure. S11 Pie charts showing the percentages of shared to none-shared species between recruits and established trees, having a 37% of species shared between trees and saplings throughout the region, and a 63% of the species are not shared from a total of 63 species throughout the sampling (left pie chart). From the 63% of none-shared species, the most abundant species are represented by pie chart on the right of the figure, showing on the legend species with the highest abundance (from a 15% to a 4%) of the species abundance from the sampling.

Sites	**Number of Saplings**	**Number of Trees**
El Colmón	32	24
IPTA	51	7
Las Tablas	35	9
Los Asientos	41	9
Mariabé	60	13
Oria Arriba	29	11
Panamaes	63	8
Sarigua	22	12
All sites (Total)	333	93

Table S1. Shows the number of saplings and trees recorded per site using a modified gentry plot.

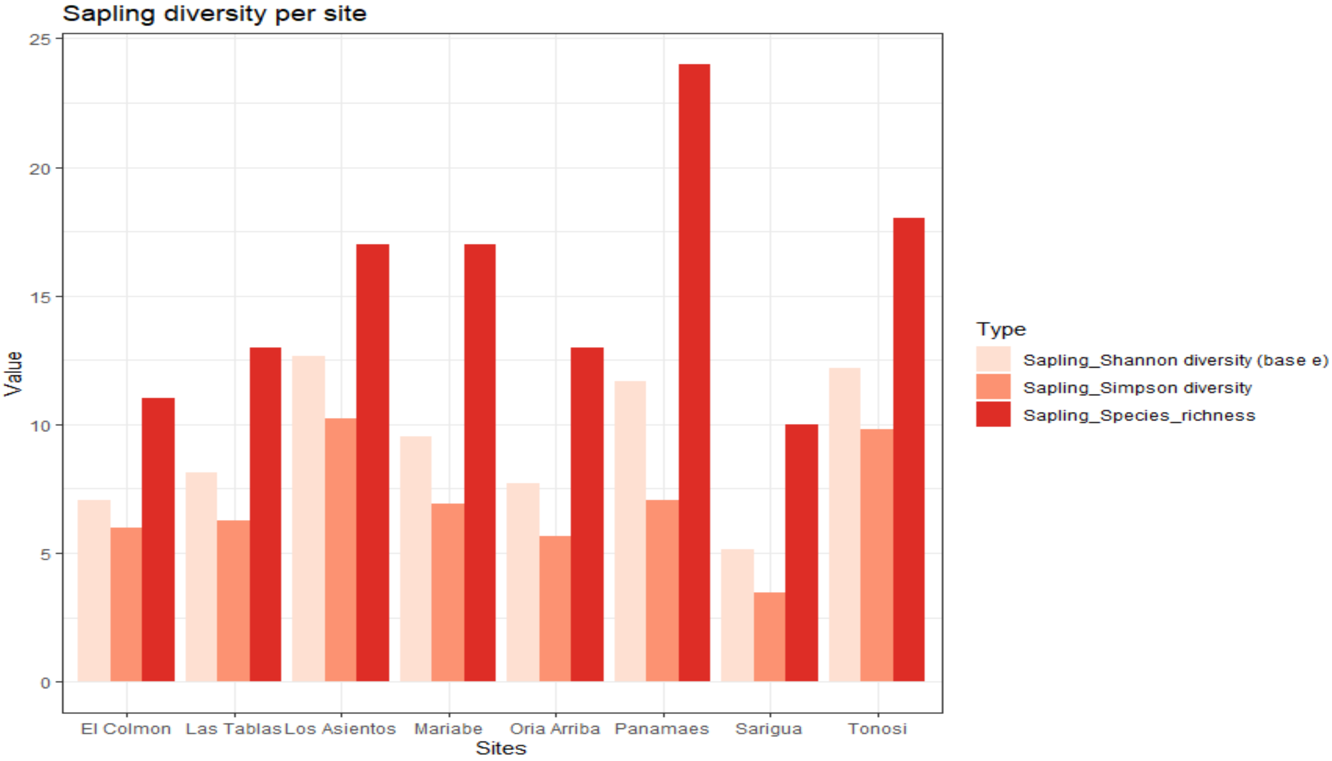

Figure. S12 Sapling Shannon and Simpson diversity indices and richness per site, showing on the x-axis each sampling site and on the y-axis the values for each site’s Shannon, Simpson diversity and richness.

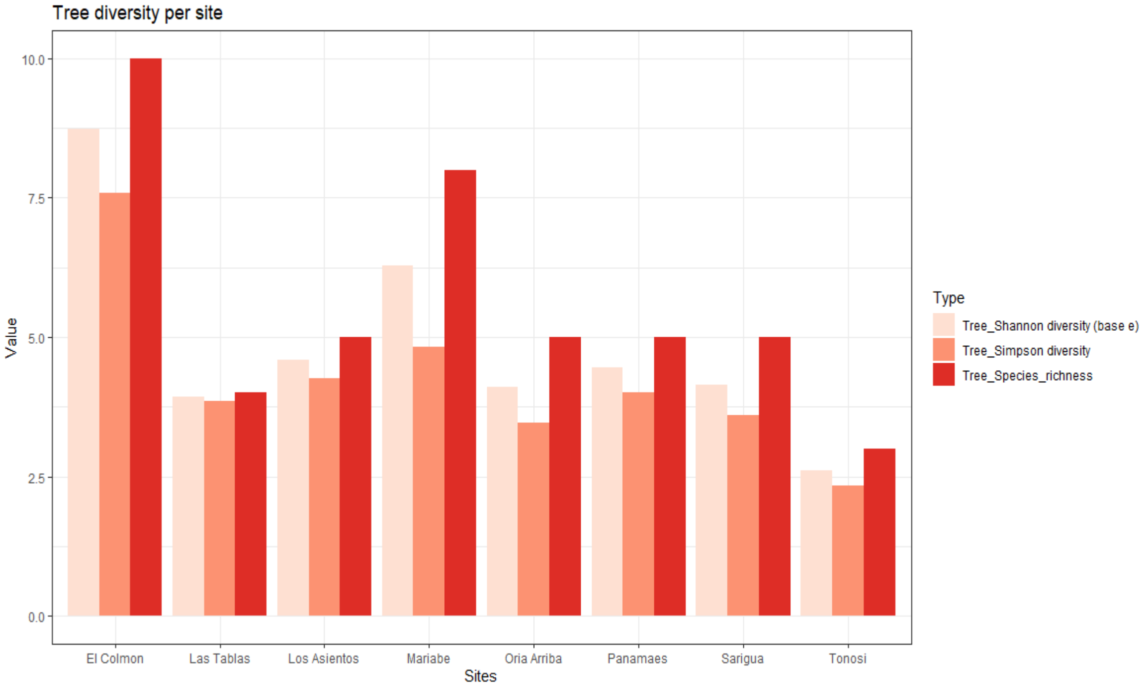

Figure. S13 Tree Shannon and Simpson diversity indices and richness per site, showing on the x-axis each sampling site and on the y-axis the values for each site’s Shannon, Simpson diversity and richness

(a) List of species having four or more samples collected and their ratio of saplings to trees:

	Species	**Presence**	**Abundance**	**Trees**	**Saplings**
1	*Genipa americana L.*	42	58	2	40
2	*Bursera simaruba (L.) Sarg.*	21	28	6	15
3	*Calycophyllum candidissimum (Vahl) DC.*	18	36	8	10
4	*Hura crepitans L.*	18	28	8	10
5	*Melicoccus bijugatus Jacq.*	16	62	1	15
6	*Gustavia superba (Kunth) O. Berg*	14	68	1	13
7	*Anacardium excelsum (Bert. & Balb. ex Kunth) Skeels*	10	57	6	4
8	*Zanthoxylum setulosum P. Wilson*	9	16	1	8
9	*Andira inermis (W. Wright) Kunth ex DC.*	8	15	3	5
10	*Capparis cynophallophora L.*	7	20	3	4
11	*Coccoloba lasseri Lundell*	7	37	2	5
12	*Syzygium malaccense (L.) Merr. & L.M. Perry*	7	13	4	3
13	*Caesalpinia coriaria (Jacq.) Willd.*	6	9	5	1
14	*Cordia panamensis L. Riley*	6	9	1	5
15	*Guazuma ulmifolia Lam.*	6	6	4	2
16	*Pittoniotis trichantha Griseb.*	5	3	1	4
17	*Sapium glandulosum (L.) Morong*	5	10	3	2
18	*Apeiba tibourbou Aubl.*	4	4	3	1
19	*Hirtella latifolia Prance*	4	3	3	1
20	*Psychotria horizontalis*	4	8	3	1
21	*Tabernaemontana grandiflora Jacq.*	4	11	1	3
	Total	**221**	**501**	**69**	**152**

Table S2. Table shows the species from the study area from which at least four samples for the four field-collected functional traits (Leaf area per leaf dry mass (specific leaf area, SLA or 1/LMA): petiole included, Wood density (stem dry mass per stem fresh volume), Relative Water Content, Leaf Water

Content) have been measured. The table indicates per species the presence (number of recorded time), the abundance, and the number of trees and saplings for the species recorded.

(b) Comparing field measurements of functional traits between sapling and trees

Leaf water content (LWC)

	Species	Mean Sapling LWC	Mean Tree LWC
1	*Anacardium excelsum (Bertero & Balb. ex Kunth) Skeels*	72,15	74,94
2	*Andira inermis (W. Wright) Kunth ex DC.*	72,48	62,32
3	*Apeiba tibourbou Aubl.*	77,43	79,06
4	*Caesalpinia coriaria (Jacq.) Willd.*	100,00	62,96
5	*Capparis cynophallophora L.*	62,50	52,00
6	*Cedrela odorata L.*	83,56	74,46
7	*Coccoloba lasseri Lundell*	68,37	76,67
8	*Copaifera aromatica Dwyer*	60,98	52,38
9	*Cordia panamensis L. Riley*	78,06	66,54
10	*Genipa americana L.*	79,96	75,57
11	*Guazuma ulmifolia Lam.*	79,25	78,77
12	*Gustavia superba (Kunth) O. Berg*	73,28	73,05
13	*Hura crepitans*	77,86	83,10
14	*Melicoccus bijugatus Jacq.*	49,34	59,30
15	*Pittoniotis trichantha Griseb*	86,98	81,40
16	*Psychotria horizontalis Sw.*	81,33	78,95
17	*Tabernaemontana grandiflora Jacq.*	89,62	86,36
18	*Zanthoxylum setulosum P. Wilson*	75,46	76,15

Table S3. Mean sapling and tree leaf water content (LWC) measurements taken in the field per species.

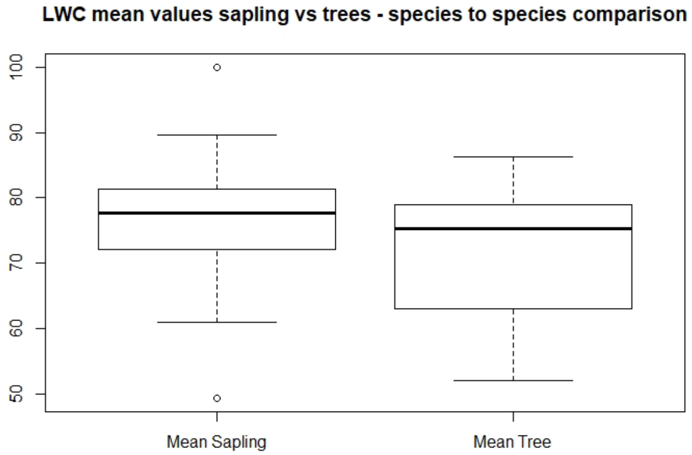

Figure. S14 Boxplot showing the non-significative (paired t-test, p-value = 0.11) difference between sapling and tree (y-axis) LWC mean values per species (x-axis).

(c) Comparing field measurements of functional traits between sapling and trees per site

	Site_Species	Mean Sapling	Mean Tree
1	*Mariabe_Anacardium excelsum (Bertero & Balb. ex Kunth) Skeels*	71,85	74,94
2	*Las Tablas_Andira inermis (W. Wright) Kunth ex DC.*	78,57	72,00
3	*Sarigua_Caesalpinia coriaria (Jacq.) Willd.*	100,00	62,96
4	*Sarigua_Capparis cynophallophora L.*	62,50	52,00
5	*Las Tablas_Genipa americana L.*	72,98	73,96
6	*Los Asientos_Genipa americana L.*	80,52	77,18
7	*Los Asientos_Guazuma ulmifolia Lam.*	84,38	78,77
8	*Panamaes_Gustavia superba (Kunth) O. Berg*	73,28	73,05
9	*Oria Arriba_Hura crepitans*	93,07	83,10
10	*El Comlon_Pittoniotis trichantha Griseb*	88,89	81,40

Table S4. Mean sapling and tree leaf water content (LWC) per species and site.

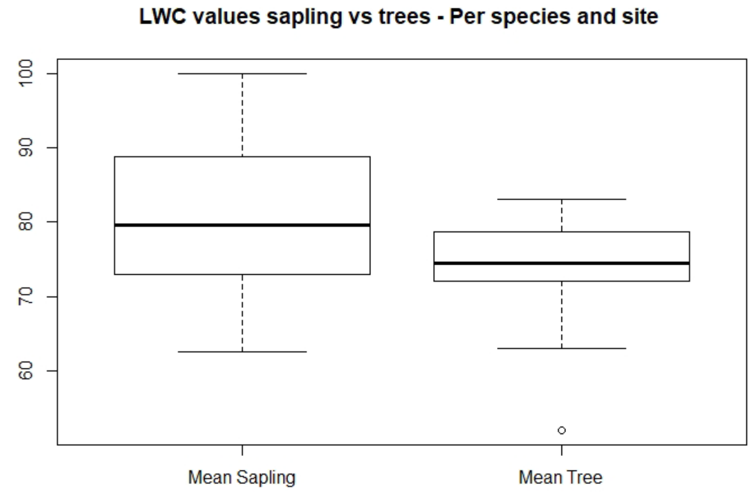

Figure. S15 Boxplot showing the non-significative difference (paired T-test, p-value = 0.060) between sapling and tree LWC mean values per species per site.

(d) RWC: Relative water content

	Species	**MeanSapling**	**MeanTrees**
1	*Anacardium excelsum (Bertero & Balb. ex Kunth) Skeels*	103,54	96,06
2	*Andira inermis (W. Wright) Kunth ex DC.*	99,27	72,78
3	*Apeiba tibourbou Aubl.*	85,78	99,75
4	*Caesalpinia coriaria (Jacq.) Willd.*	20,00	68,00
5	*Capparis cynophallophora L.*	85,37	69,64
6	*Cedrela odorata L.*	87,98	84,45
7	*Coccoloba lasseri Lundell*	53,17	85,98
8	*Copaifera aromatica Dwyer*	96,15	61,11
9	*Cordia panamensis L. Riley*	78,67	77,38
10	*Genipa americana L.*	95,99	82,15
11	*Guazuma ulmifolia Lam.*	52,36	93,86
12	*Gustavia superba (Kunth) O. Berg*	64,41	99,60
13	*Hirtella latifolia Prance*	81,15	87,40
14	*Hura crepitans*	84,94	83,10
15	*Melicoccus bijugatus Jacq.*	88,57	100,00
16	*Pittoniotis trichantha Griseb*	94,82	70,00
17	*Psychotria horizontalis Sw.*	98,39	93,75
18	*Tabernaemontana grandiflora Jacq.*	89,52	86,36
19	*Zanthoxylum setulosum P.Wilson*	81,57	89,66

Table S5. Mean sapling and tree relative water content (RWC) per species.

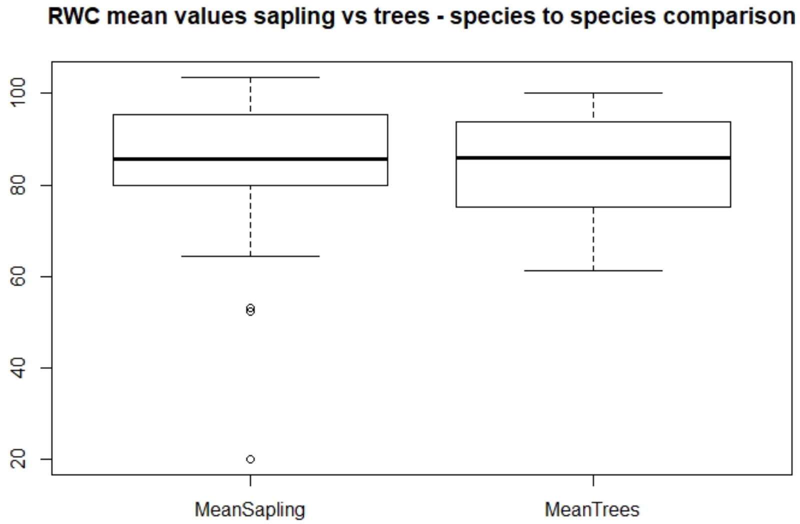

Figure. S16 Boxplot showing the non-significative difference (paired T-test, p-value = 0.56) between sapling and tree RWC mean values per species.

	Site_Species	**MeanSapling**	**MeanTrees**
1	*Sarigua_Caesalpinia coriaria (Jacq.) Willd.*	20,00	68,00
2	*Sarigua_Capparis cynophallophora L.*	85,37	69,64
3	*Las Tablas_Genipa americana L.*	80,86	81,92
4	*Los Asientos_Genipa americana L.*	89,79	82,37
5	*Los Asientos_Guazuma ulmifolia Lam.*	81,82	111,02
6	*Panamaes_Gustavia superba (Kunth) O. Berg*	64,41	99,60
7	*Oria Arriba_Hura crepitans*	95,13	83,10
8	*El Comlon_Pittoniotis trichantha Griseb*	86,49	70,00

Table S6. Mean sapling and tree relative water content per species per site.

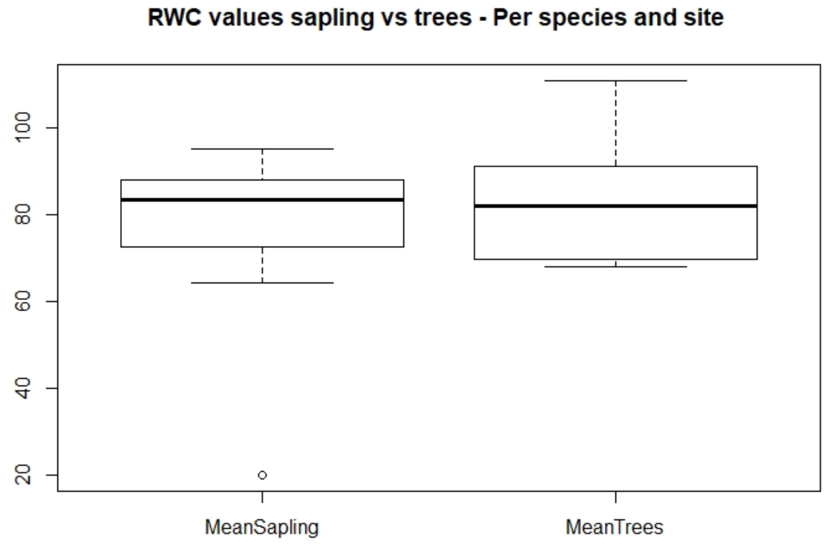

Figure. S17 Boxplot showing the non-significative difference (paired T-test, p-value = 0.42) between sapling and tree RWC mean values per species per site.

(e) Wood Density

Site	Codes	Species	Code	Wood_Density	TRY_Wood_Density
Mariabe	Mariabe T4A1	*Anacardium excelsum (Bert. & Balb. ex Kunth) Skeels*	P6 t4 A1	0.75	0.42
Mariabe	Mariabe T2A1	*Anacardium excelsum (Bert. & Balb. ex Kunth) Skeels*	P6 t2 A1	0.43	0.42
Las Tablas	Las Tablas T9-A1	*Andira inermis (W. Wright) Kunth ex DC.*	P8 t9 A1	0.81	0.64
Las Tablas	Las Tablas T10A1	*Bursera simaruba (L.) Sarg.*	P8 T10 A1	0.54	0.43
El Colmón	El Colmón T3A1	*Bursera simaruba (L.) Sarg.*	P2 T3 A2	0.61	0.43
Mariabe	Mariabe T8A1	*Bursera simaruba (L.) Sarg.*	Pb t8 A1	0.40	0.43
Sarigua	Sarigua T2A1	*Bursera simaruba (L.) Sarg.*	P3 T2 A1	0.28	0.43
El Colmón	El Colmón T3A1	*Bursera simaruba (L.) Sarg.*	p2 t3 A1	0.73	0.43
Sarigua	Sarigua T1A2	*Caesalpinia coriaria (Jacq.) Willd.*	P3T2 A2	0.56	1.03
Sarigua	Sarigua T1A3	*Caesalpinia coriaria (Jacq.) Willd.*	T2 A3 P3	0.59	1.03
Las Tablas	Las Tablas T9-A3	*Cordia panamensis L. Riley*	P8 t9 A3	0.76	0.4
Las Tablas	Las Tablas T4A1	*Genipa americana L.*	P8 t4 A1	0.89	0.65
Panamaes	Panamaes T8A1	*Gustavia superba (Kunth) O. Berg*	P7 T8 A1	0.59	0.6
Panamaes	Panamaes T2A1	*Sapium glandulosum (L.) Morong*	P7 t2 A1	0.76	0.52
Panamaes	Panamaes T1A1	*Spondias radlkoferi*	P7 T1 A1	0.50	0.4
IPTA	IPTA T1A2	*Syzygium malaccense (L.) Merr. & L.M. Perry*	ENVIRON P9 T1 A2	0.61	0.6
El Colmón	El Colmón T6-A3	*Tabernaemontana grandiflora Jacq.*	T6A3	0.63	0.49

Table S7. Comparative table between the measurements of wood density collected in the field and from the TRY Database at the species level per site. Codes and Code column refer to codes given to samples collected on site, while the column Wood_Density shows results from field-collected measurements and the TRY_Wood_Density column shows the values from the TRY Database.

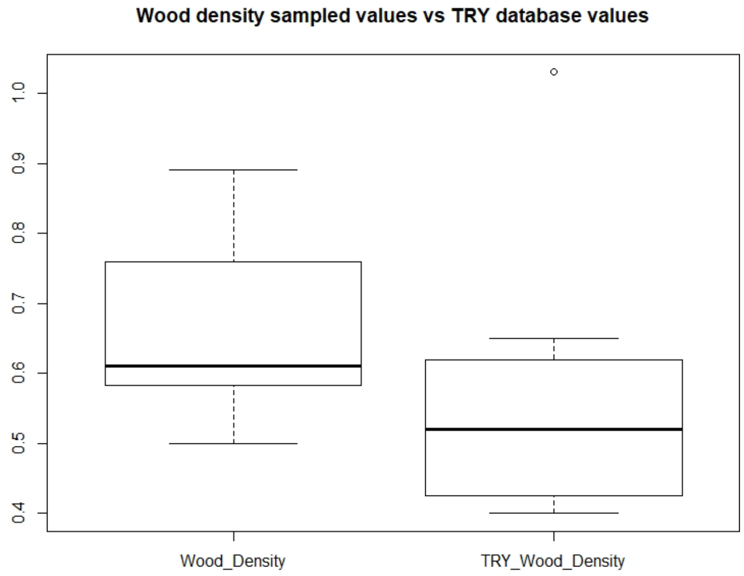

Figure. S18 Boxplot showing the non-significative difference (paired t-test, p-value = 0.166) between the collected samples' measurements for wood density, and the TRY database measurements for the same species.

Site	Strata	SLA_cwm	LNitoC_cwm	Height_cwm	W.Density_cwm
El Colmon	Both	13.747181	17.85682	23.43123	0.6224283
El Colmon	Only_Canopy	11.596282	23.12586	28.42151	0.4047591
El Colmon	Only_Understory	22.891909	32.65366	15.92424	0.5438182
IPTA	Both	13.995384	23.24800	21.19464	0.5406951
IPTA	Only_Understory	12.721706	24.69795	18.11327	0.5698618
Las Tablas	Both	14.697395	20.04125	22.32331	0.5310323
Las Tablas	Only_Understory	15.863420	26.24906	17.51662	0.6483915
Los Asientos	Both	18.180573	19.48694	16.02147	0.4841100
Los Asientos	Only_Canopy	7.354241	17.98329	25.00000	0.6353143
Los Asientos	Only_Understory	11.557814	16.82334	12.38354	0.7033199
Mariabe	Both	15.655424	17.22507	21.60837	0.4433801
Mariabe	Only_Canopy	17.434407	24.13704	30.56318	0.3741539
Mariabe	Only_Understory	13.150179	20.68164	18.79045	0.6075527
Oria Arriba	Both	14.984159	24.36652	22.60067	0.4542242
Oria Arriba	Only_Canopy	17.533518	19.66323	32.89575	0.2418060
Oria Arriba	Only_Understory	21.477080	30.64189	20.57895	0.6422112
Panamaes	Both	17.906797	32.10483	24.23998	0.5845057
Panamaes	Only_Canopy	5.778261	24.55040	30.00000	0.3076851
Panamaes	Only_Understory	14.451110	22.66299	16.88042	0.6368531
Sarigua	Both	12.668475	24.65953	20.60562	0.9629908
Sarigua	Only_Understory	15.054297	26.37969	10.48208	0.7326678

Table S8 shows the community weighted mean values for the chosen functional traits per sampling site and strata.

(f) PCA of functional traits and species matrix organized by stratum

1) Canopy:

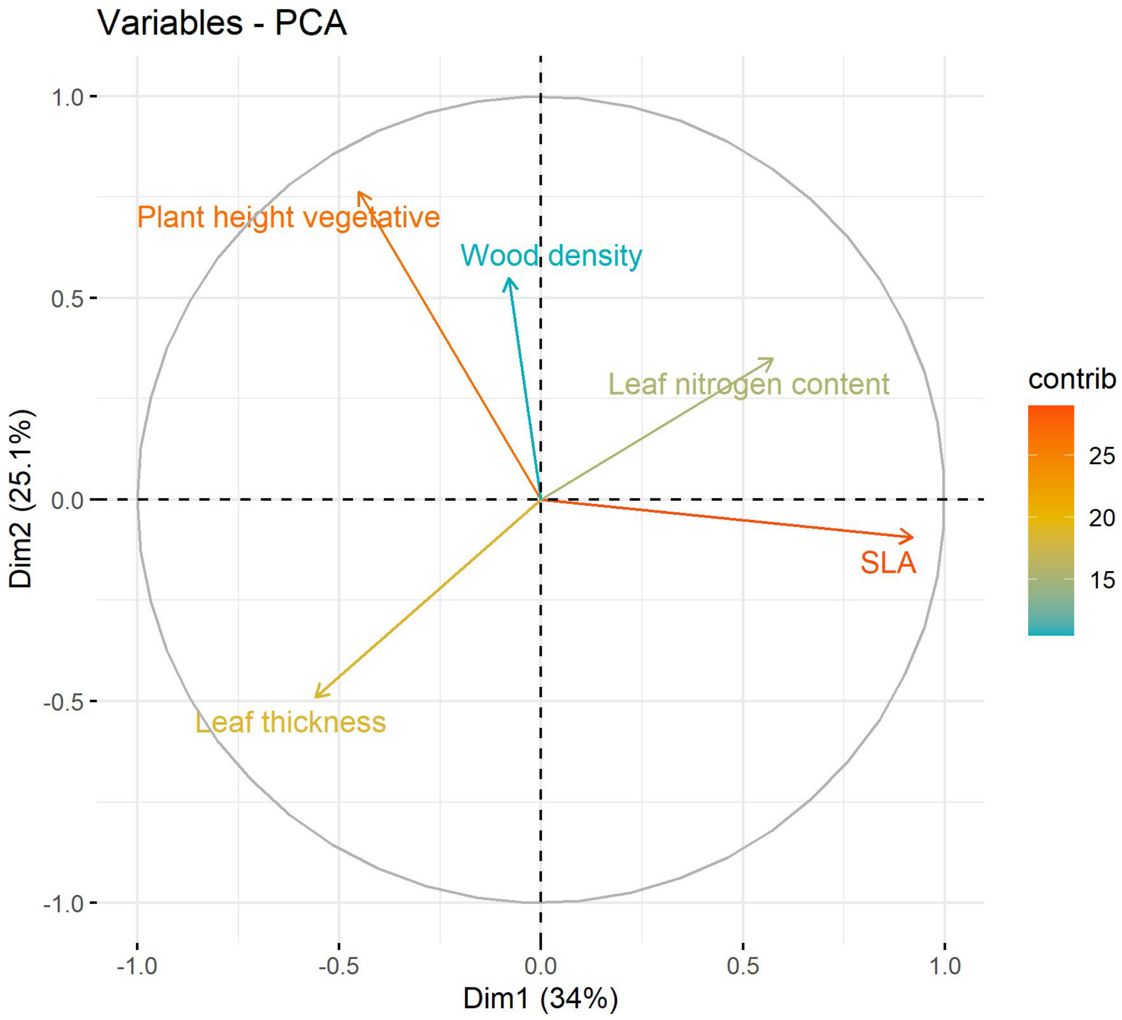

Figure. S19 Variables PCA, showing positively correlated variables pointing to the same side of the plot, and negatively correlated variables pointing to opposite sides of the graph for species found in exclusively in the canopy. These considers the functional traits: SLA, Leaf nitrogen content, Leaf thickness, Plant height vegetative, and Wood density. Traits' contributions are shown by arrow's length and color as shown on the legend, going from a lesser contribution (towards blue), to a stronger contribution (towards red).

Figure. S20 PCA biplot of species exclusively found in the canopy (in grey) and functional traits (in blue and with arrows). Values of the functional traits have been log-transformed prior to the PCA, to correct outliers' effect. All values considered are numeric values, considering SLA, leaf thickness, leaf nitrogen content, wood density, and plant vegetative height. There are no binary values.

2) Understory:

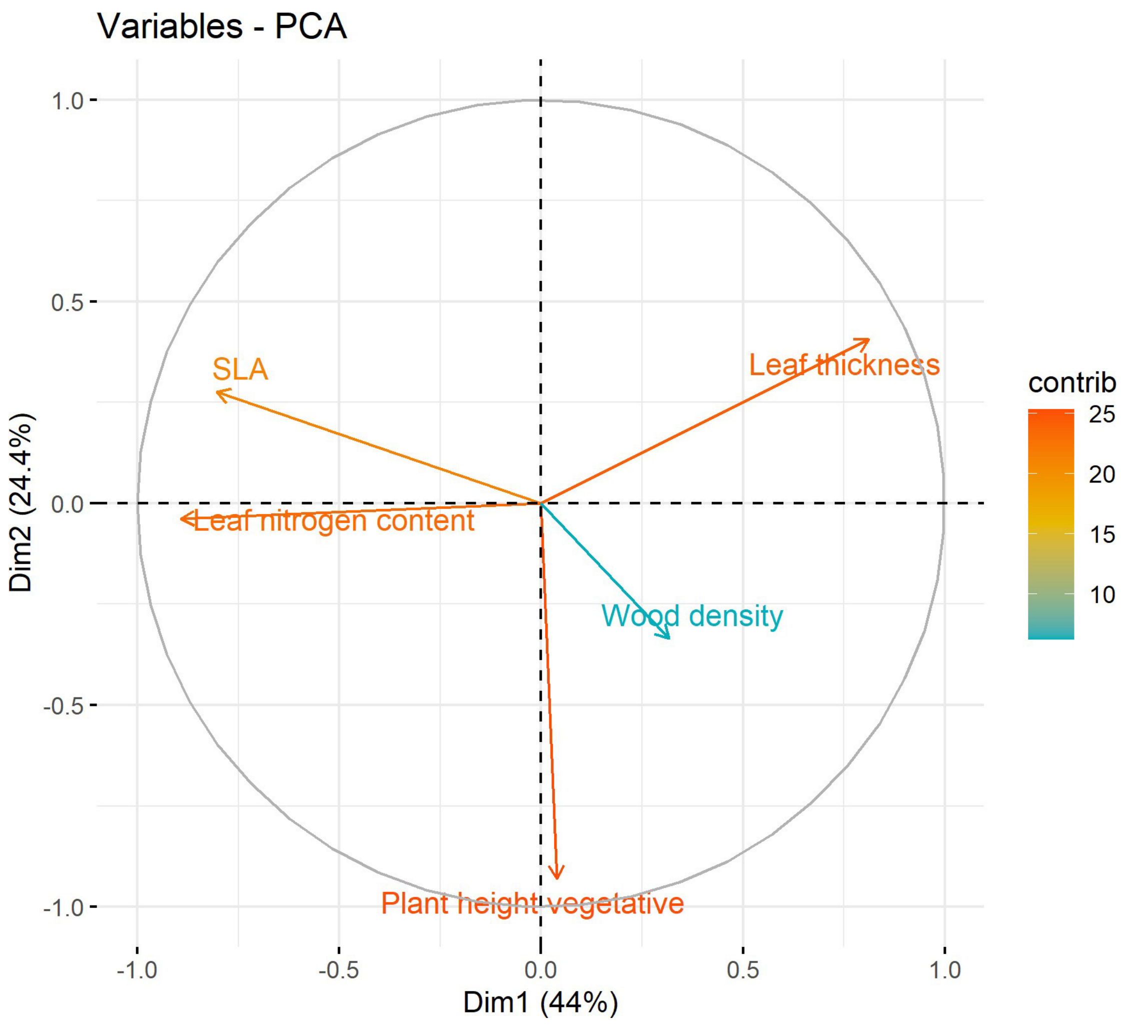

Figure. S21 Variables PCA, showing positively correlated variables pointing to the same side of the plot, and negatively correlated variables pointing to opposite sides of the graph for species found exclusively in the canopy and the understory. These considers the functional traits: SLA, Leaf nitrogen content, Leaf thickness, Plant height vegetative, and Wood density. Traits' contributions are shown by arrow's length and color as shown on the legend, going from a lesser contribution (towards blue), to a stronger contribution (towards red).

Figure. S22 PCA biplot of species exclusively found in the understory (in grey) and functional traits (in blue and with arrows). Values of the functional traits have been log-transformed prior to the PCA, to correct outliers' effect. All values considered are numeric values, considering SLA, leaf thickness, leaf nitrogen content, wood density, and plant vegetative height. There are no binary values.

3) Both, canopy and understory:

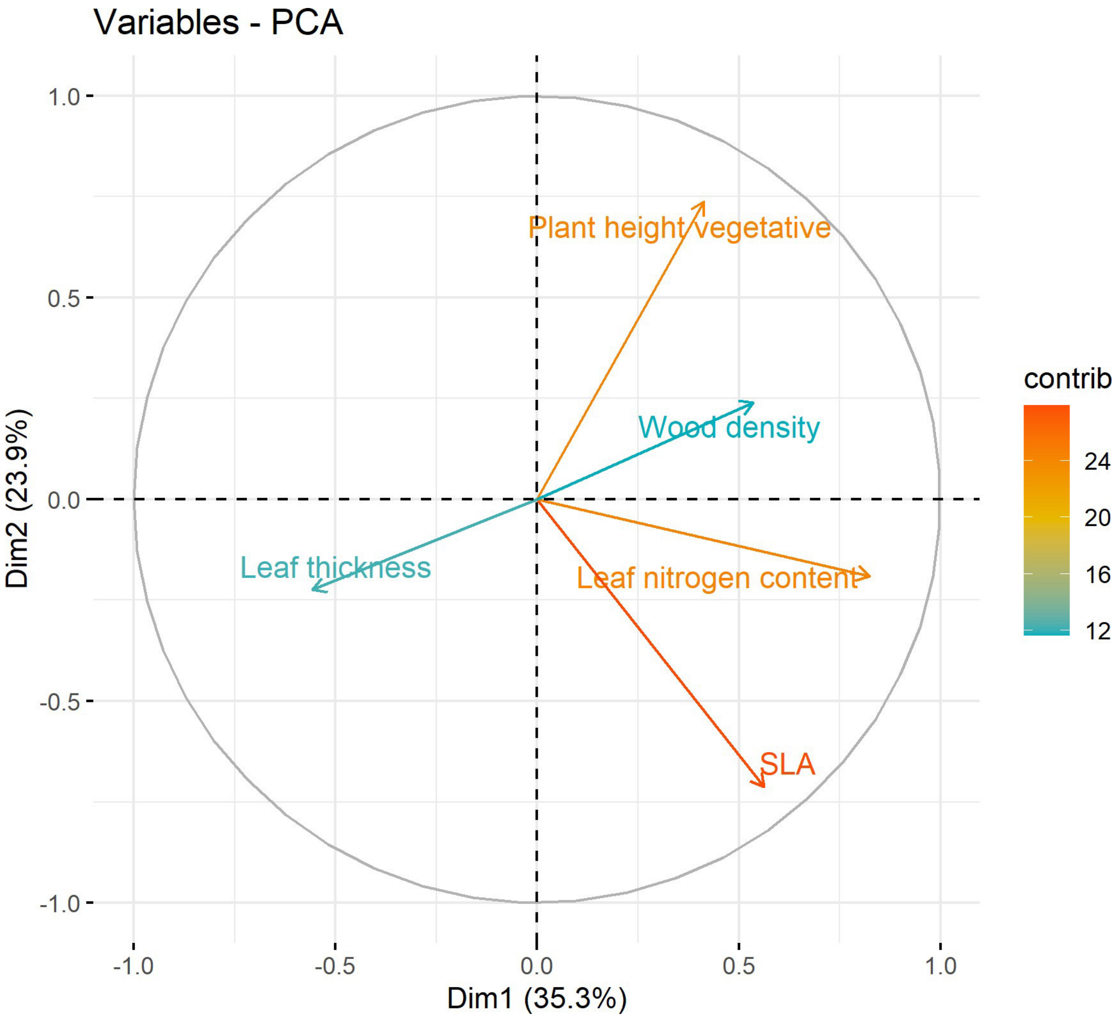

Figure. S23 Variables PCA, showing positively correlated variables pointing to the same side of the plot, and negatively correlated variables pointing to opposite sides of the graph for species found in both, the canopy and the understory. These considers the functional traits: SLA, Leaf nitrogen content, Leaf thickness, Plant height vegetative, and Wood density. Traits' contributions are shown by arrow's length and color as shown on the legend, going from a lesser contribution (towards blue), to a stronger contribution (towards red).

Figure. S24 PCA biplot of species exclusively found in both, the canopy and the understory (in grey) and functional traits (in blue and with arrows). Values of the functional traits have been log-transformed prior to the PCA, to correct outliers' effect. All values considered are numeric values, considering SLA, leaf thickness, leaf nitrogen content, wood density, and plant vegetative height. There are no binary values.

PCA of all species found in Azuero plotted to all traits organized by matrix of traits in A) non-binary data, B) traits in binary data, and C) binary data of species distribution

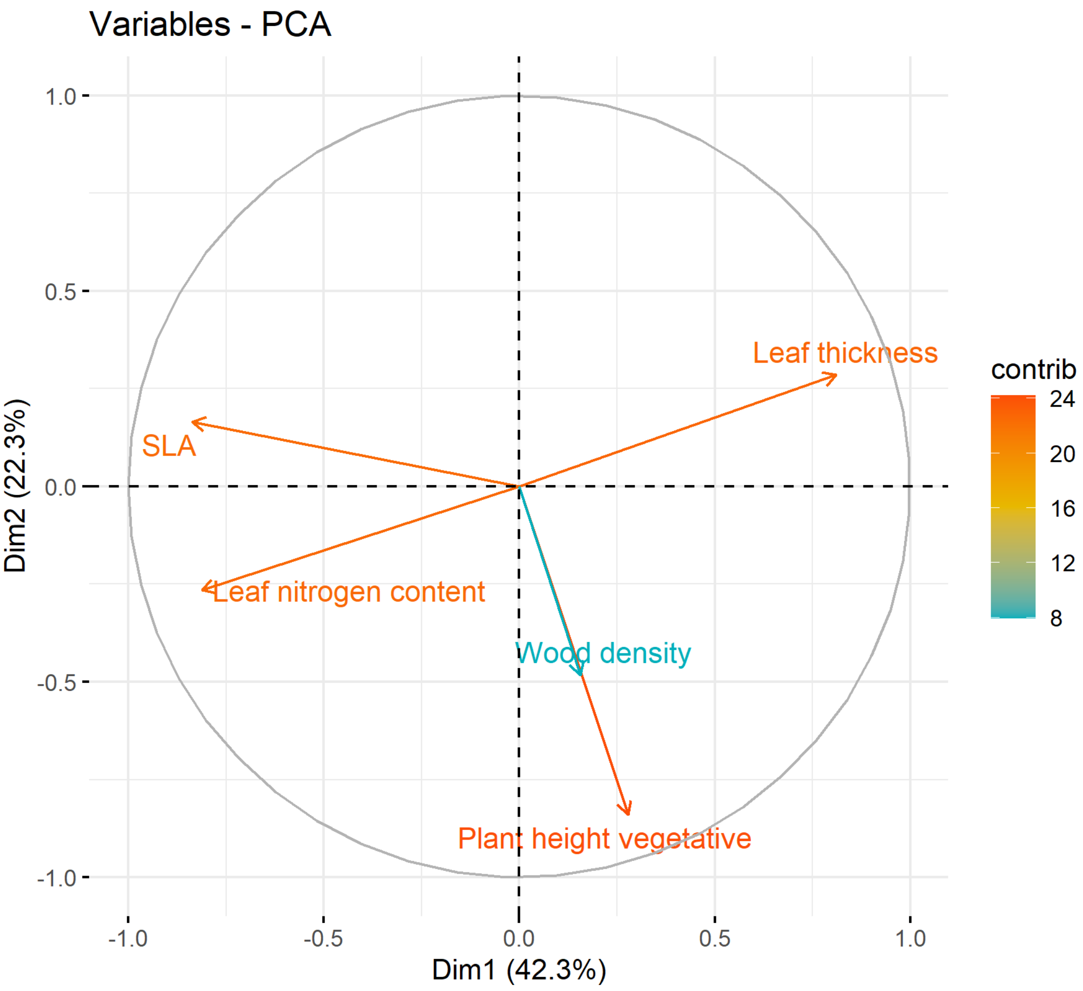

Figure. S25 Variables PCA, showing positively correlated variables pointing to the same side of the plot, and negatively correlated variables pointing to opposite sides of the graph. These considers the functional traits: SLA, Leaf nitrogen content, Leaf thickness, Plant height vegetative, and Wood density. Traits' contributions are shown by arrow's length and color as shown on the legend, going from a lesser contribution (towards blue), to a stronger contribution (towards red).

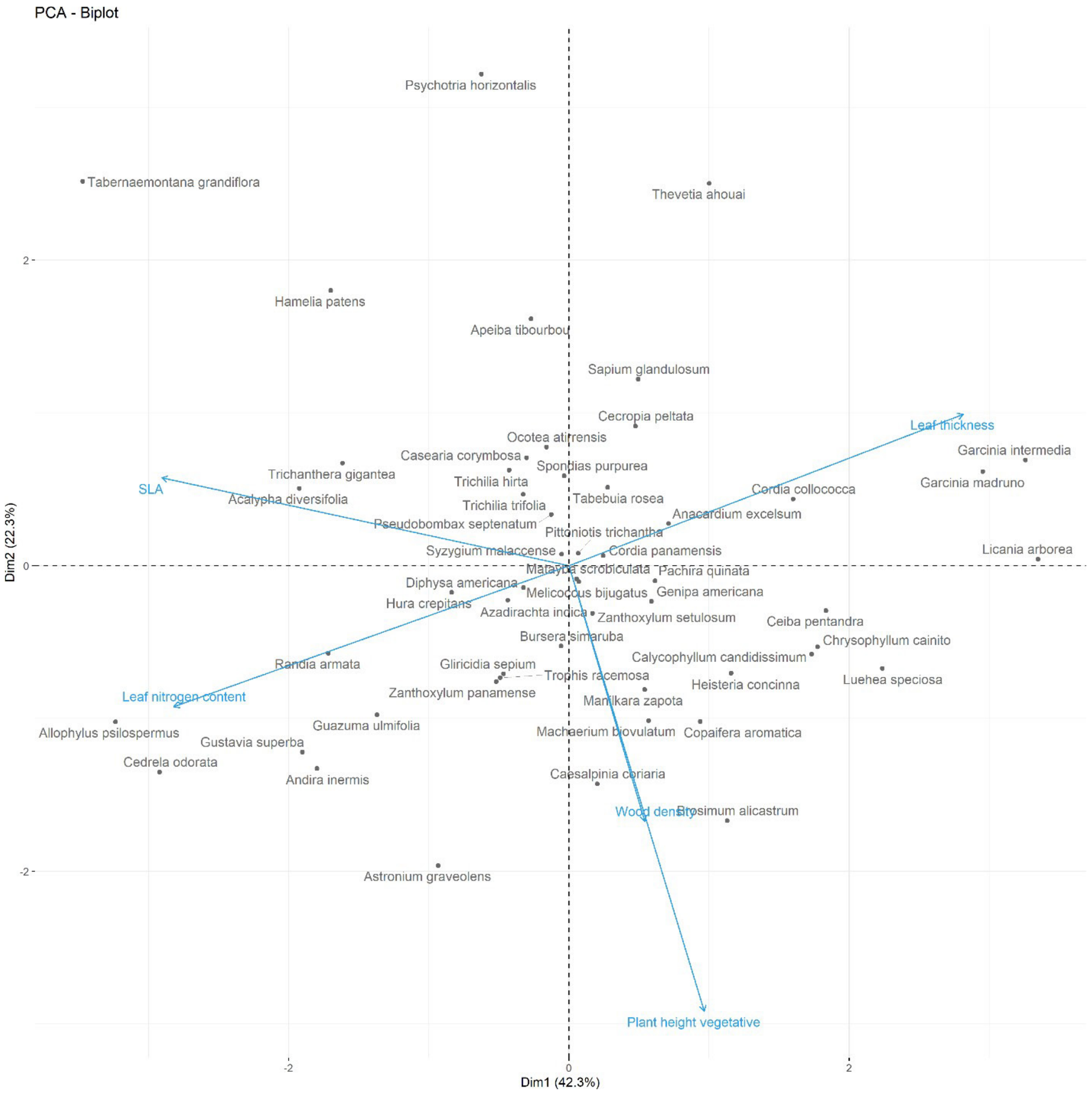

Figure. S26 PCA biplot of recorded species (in grey) and functional traits (in blue and with arrows). Values of the functional traits have been log-transformed prior to the PCA, to correct outliers' effect. All values considered are numeric values, considering SLA, leaf thickness, leaf nitrogen content, wood density, and plant vegetative height. There are no binary values.

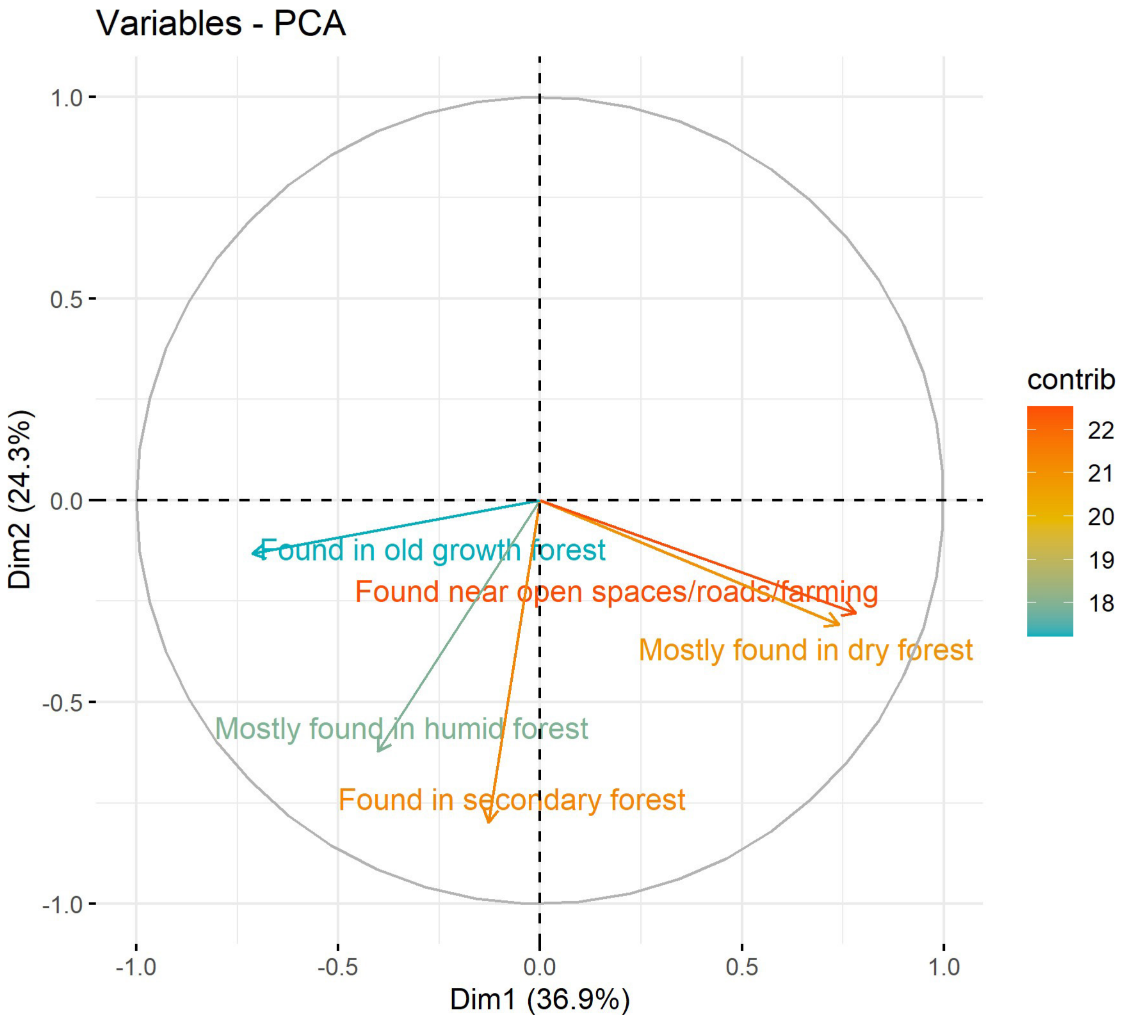

Figure. S27 Variables PCA, showing positively correlated variables pointing to the same side of the plot, and negatively correlated variables pointing to opposite sides of the graph. These considers: Species mostly found in dry forest, Species mostly found in humid forest, Species found near open spaces/roads/farming, Species found in secondary forest, and Species found in old growth forest. Traits' contributions are shown by arrow's length and color as shown on the legend, going from a lesser contribution (towards blue), to a stronger contribution (towards red).

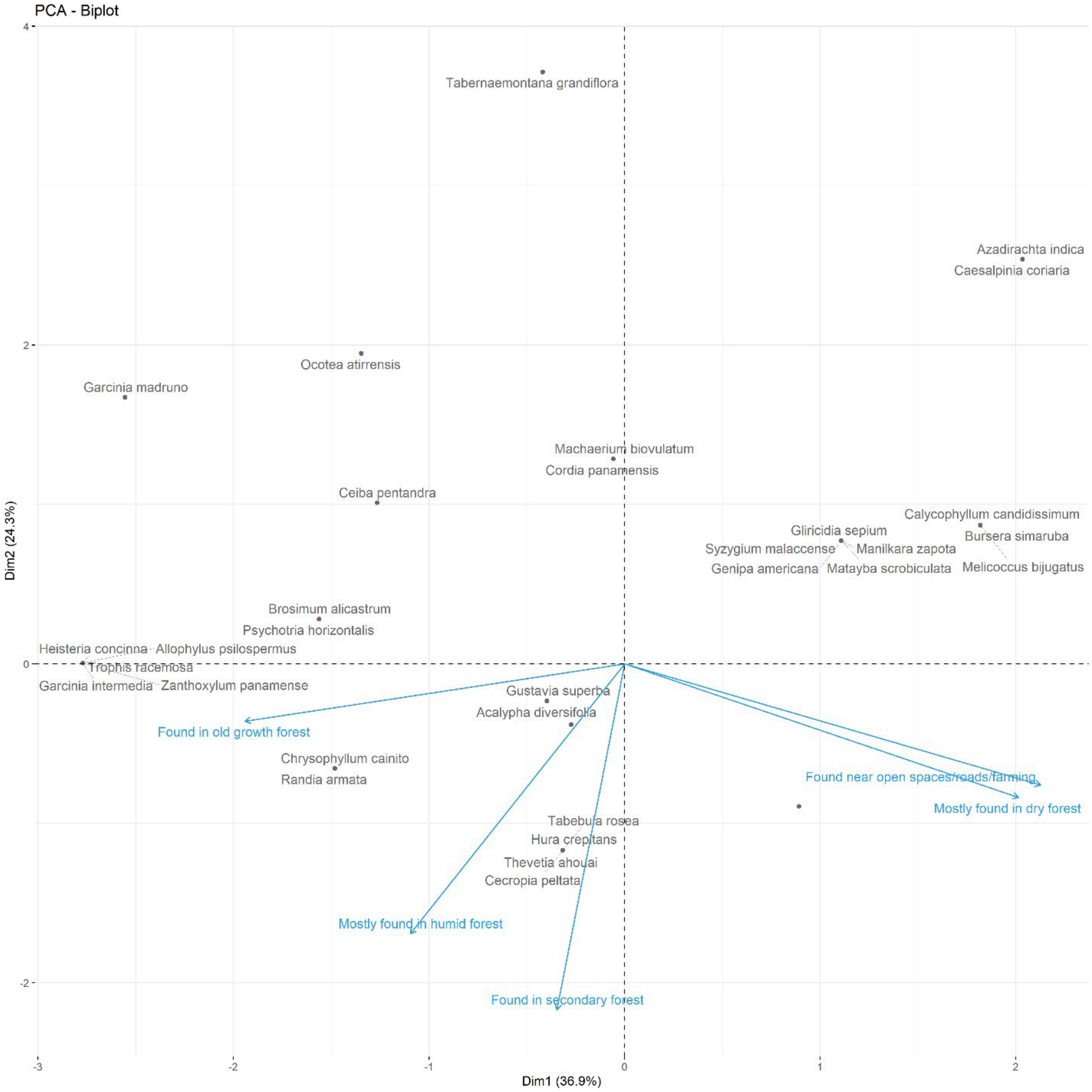

Figure. S30 PCA biplot of recorded species (in grey) and functional traits as binary data (in blue and with arrows). Values of the functional traits have been centered and scaled prior to the PCA, to correct outliers' effect. All values considered are numeric values, considering Pubescence, Deciduousness, Dispersal mode wind, Dispersal mode animals, and Dispersal by fruit opening.

(g) PCA of CWM values of functional trait per site and stratum, and land use practices

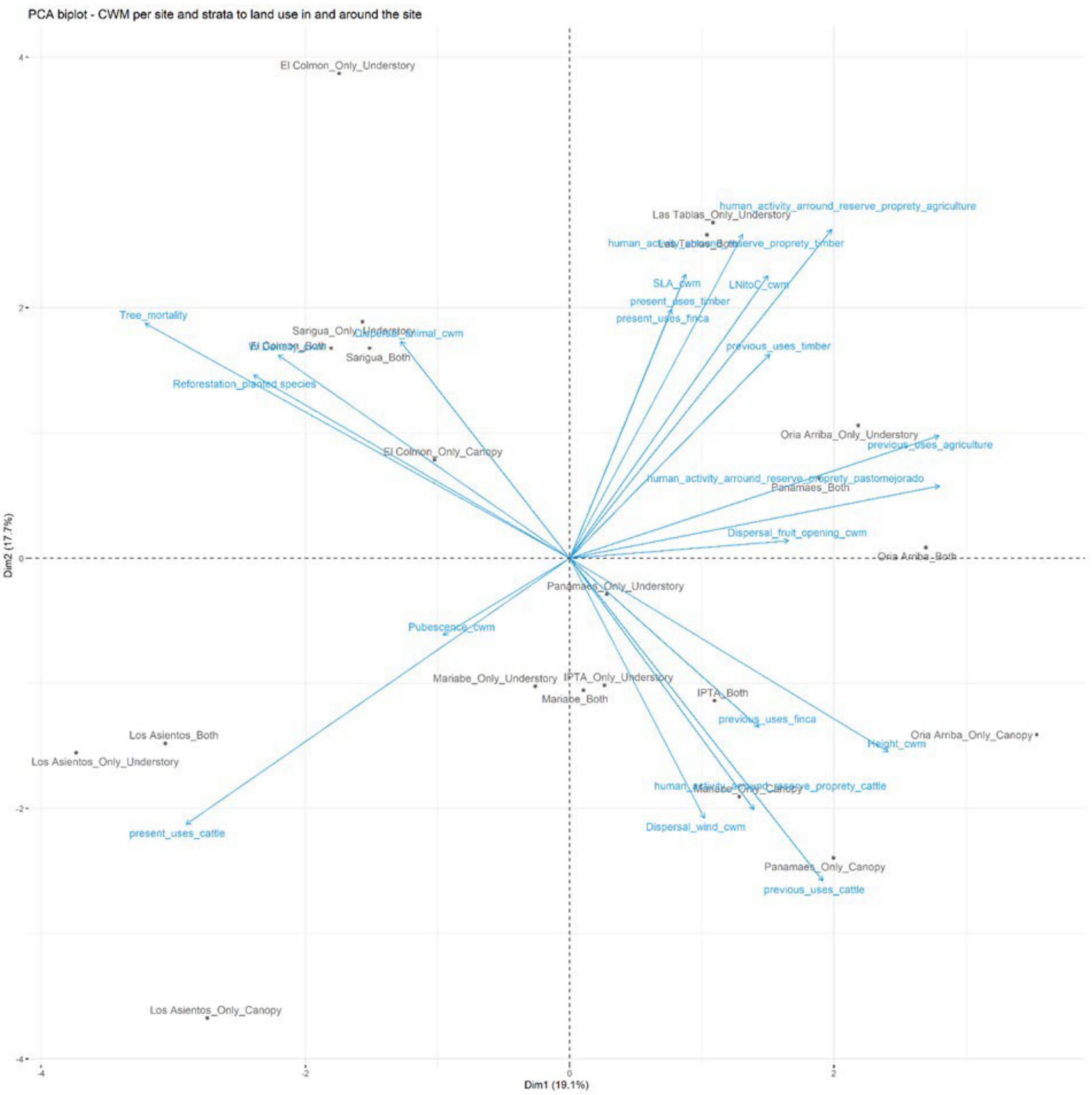

Figure. S31 PCA biplot of land use practices used at each site, considering each stratum per site and the CWM values of functional traits and dispersal mechanisms (in blue and with arrows). The 8 sites (El Colmón, IPTA, Las Tablas, Los Asientos, Mariabé, Oria Arriba, Panamaes, and Sarigua).