Resilience in the Tropical Dry Forest under natural and anthropogenic alterations

by

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Abstract

The primary objectives of this thesis included contributing to: (i) the state of knowledge on the TDF physiological response to climatic variables; (ii) the understanding of forest resilience through assessing productivity response to temperature and precipitation; and (iii) assessing the influence of legislation on the resilience and extent of tropical forests. Here, I present research which evaluates the resilience of the TDF both over decadal time periods and on regional, country, and cross-continental scales. This resilience is tested under a variety of climatic conditions, as well as under different legislative scenarios, and is then projected into the future.

Chapter 2 provides a critical review of the current state of knowledge about the latitudinal variations in TDF expression, while also considering how the phenology, biomass, species diversity, and forest dynamics vary with precipitation, temperature, and natural disturbances. Finally, this study assesses the resilience of the TDF, using these ecosystem variations and projections of climatic change. Gaps in current research and information are outlined, and future paths to provide further insight into forest resilience are suggested.

Forest management and forest resilience under anthropogenic changes in Costa Rica are assessed in Chapter 3. In this Chapter I found that forest recovery began before the majority of the legislative policies were put into place, and there is no increase in the rates of recovery after these policies were implemented. The trends in forest decline and subsequent recovery more closely follow the economic trends, with the recovery beginning when the meat market crashed and continuing with the diversification of the economy. These trends suggest that the Payments for Ecosystem Services and Protected Areas programs are not assisting the resilience of the forest. This result is supported by the finding that there are only 13 of the Protected Areas, encompassing less than 10% of the protected forests, which would experience a moderate or high probability of deforestation if the legislation was revoked.

The future resilience of a regional scale TDF to climate change is assessed in Chapter 4. I found that the temperature is projected to warm between 2°C and 5°C and precipitation is projected on average to decrease below historic levels; however, it is mostly within the extremes of historical data. We also found that in the province, there is a quadratic relationship between biomass and Vapour Pressure Deficit (VPD), unlike the theoretical algorithms used by MODIS, which assume a linear relationship. This non-linear relationship means that above a certain point, increased wetness decreases the productivity in the Guanacaste forests. When these productivity trends are projected into the future, most forested areas are simulated to have stable or slight increases in productivity due to this quadratic function and a slight drying trend in climate.

Finally, in Chapter 5, the entire Meso and South American TDF is assessed for its water use efficiency, as well as for long-term changes that have already occurred. I found that TDFs across Meso and South America use water more efficiently in dry years compared to wet years. Overall, the productivity of the forests is correlated to the amount of precipitation, but changes in temperature have no impact on the productivity of the forests. The El Nino Southern Oscillation conditions can alter the productivity up to 30% at higher latitudes, but there is little variation near the equator. Overall, there are sites in Mexico which are greening and sites in Brazil which are losing productivity. There is no consistent correlative change in any climatic or geophysical variables. There are correlative changes with soil moisture, precipitation, and growing season duration at different sites.

Preface

This thesis is an original work by Kayla Dawne Stan. Chapter 2 was published in Forests as "Stan, K. & Sanchez-Azofeifa, A. Tropical Dry Forest Diversity, Climatic Response, and Resilience in a Changing Climate. *Forests* (2019) 10(5), and Chapter 3 was published in Regional Environmental Change as "Stan, K. & Sanchez-Azofeifa, A. Deforestation and secondary growth in Costa Rica along the path of development. *Reg Environ Change* (2019) 19: 587. https://doi.org/10.1007/s10113-018-1432-5." Additionally, Chapter 4 is under review with minor revisions at Regional Environmental Change and Chapter 5 are currently under review.

This dissertation was completed with the guidance of Dr. A. Sanchez-Azofeifa. The research and analysis conducted in Chapters 2 and 3 were my original work. Chapter 4 was developed and analyzed in collaboration with S. Calvo-Rodriguez, M. Castro, L. Dong, and J. Chen. I contributed to project formation, data collection, analysis, and writing of the final manuscript. S. Calvo-Rodiguez and M. Castro also contributed to data analysis and some data collection. J. Chen and L. Dong contributed to the data collection. Chapter 5 was a collaborative project working with C. Rankine, S. Duran, M. Hesketh, and C. Portillo-Quintero. I contributed to the project formation, data collection, data analysis and the manuscript writing. S. Duran and C. Portillo-Quintero contributed to data collection. M. Hesketh, C. Rankine contributed to data collection and the development of the data analysis methodology.

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CHAPTER 1- Introduction

1.1 Introduction

The resilience of biomes, especially those with high biodiversity, has become of increasing concern due to projections of increasing drought and extreme events under climatic change (Ponce-Campos et al., 2013; Gazol et al., 2018). Additionally, with more sophisticated and powerful computational systems, there has been a suite of complex Earth System Models (ESMs) developed which combine global atmosphere, hydrosphere, and biosphere feedbacks along with human management (Pongratz et al. 2018; Prinn 2013); however, the relationships between these systems (especially between the biosphere, atmosphere, and anthroposphere) are often poorly understood and are, therefore, not well represented within models (McDermid et al., 2017; Pongratz et al., 2018; Smith et al., 2016). ESMs are increasingly used to answer questions about biome change globally. Additionally, they are used to make decisions relating to policy implementation for the protection of these biomes and mitigation of climatic change, making the relationships and feedbacks between these systems crucial to understand (Bush & Lemmen, 2019; Prinn 2013). The resilience of ecosystems under threat of climatic and anthropogenic change is especially critical to study and more fully understand.

One such biome which has been understudied historically, and is often not even explicitly modelled, is the Tropical Dry Forest (TDF). TDFs are defined as forests with >50% deciduousness which grow in areas with a mean annual temperature >25^{o}C, precipitation between 700-2000 mm, and a dry season rainfall of <100 mm for at least three months (Sanchez-Azofeifa et al., 2005). They are present on five continents (North, Central and South America, Africa, Asia, and Australia) and cover a latitudinal gradient of more than 40° (Miles et al., 2006). Much of the remaining extent (between 50% - 75%) of this biome is found across Mesoamerica (Mexico and Central America) and South America, with hotspots in Mexico, Bolivia, and Brazil (Hesketh & Sanchez-Azofeifa, 2014; Portillo-Quintero & Sanchez-Azofeifa, 2010).

There is a high population density in areas within the TDF due to the climatic conditions, geographic extent, and high density of freshwater sources throughout these areas (Farjado et al. 2005; Portillo-Quintero & Sanchez-Azofeifa, 2010; Portillo-Quintero et al. 2015). This high population density results in TDFs experiencing the third highest deforestation rate globally (Hansen et al., 2010; Portillo-Quintero & Sanchez-Azofeifa, 2010; Coelho et al., 2016). In addition to this high level of alteration, much of the TDF in Meso and South America is not legally protected and is at risk of deforestation in favour of agricultural areas and urban development (Portillo-Quintero & Sanchez-Azofeifa, 2010). The one exception to this is Costa Rica, which experienced high deforestation rates before the meat market crash in the 1980s'. This crash prompted economic diversification. Governments throughout the 1990's implemented a series of conservation legislation which has turned Costa Rica into an example to follow for modern conservation policy and environmental protection programs (Bender 2012, Powell et al 2002, Sanchez-Azofeifa et al. 2003).

In addition to direct anthropogenic alteration, TDFs, like much of the globe, are at risk due to climatic change and there is high uncertainty of this biome's response to these changes (Navar-Chaidez 2011; Poorter et al. 2016; Haselhorst et al. 2017; Golicher et al. 2012; Magrin et al. 2014; Seiler et al. 2014). ESMs cannot agree on the climatic changes that will occur in the regions containing TDFs. They also vastly differ on the resilience of the biome with some models predicting severe decreases in biodiversity and biomass (Golicher et al. 2012; Magrin et al. 2014; Seiler et al. 2014) and others predicting resilience throughout the TDF due to rapid drought recovery (Golicher et al. 2012; Magrin et al. 2014; Seiler et al. 2014).

TDFs are not explicitly considered in ESMs despite their widespread presence around the globe. It is, therefore, imperative to use both in-situ and remote sensing historical data to develop relationships for assessing TDF resilience under varying climatic conditions and legislative measures. The literature currently does not have a holistic assessment of how TDFs will respond to climate change over a long-term period, nor has the physiological variation in these responses been documented across the latitudinal gradient of the TDFs. Given these gaps, there is a lack of knowledge about the current resilience of the TDFs biomes, and without understanding these relationships in the present, they cannot be accurately represented in future change models.

The overall objectives of this thesis are, therefore, to assess:

1) The current state of knowledge surrounding the spatial variation of the physiological response in the TDF to climatic variables and extreme events.

2) The productivity response to temperature and precipitation at a local and continental scale to determine the current state of forest resilience and project this resilience into the future using climatic models

3) The influence of legislation on the resilience and extent of the forests under both agro-dominated and conservation conscious systems.

These objectives will be explored using four stand-alone papers, all of which look at the resilience of the TDFs in a changing globe:

Chapter 2 - **Tropical Dry Forest diversity, climatic response, and resilience in a changing climate** (Stan and Sanchez-Azofeifa, 2019a) - This literature review looks at the body of knowledge surrounding the succession, structure, biomass, and phenology of the TDF across the Neotropics. Additionally, it considers the variation in these characteristics along a latitudinal gradient and the response of these components to variations in temperature, precipitation, and extreme climatic events. Finally, it considers the future projections of climatic variation and assesses the resilience of the TDF using historical responses. This chapter also presents gaps in the current research in TDFs, and suggests paths forward to more holistically characterize the current and future resilience of the TDFs. While there have been other recent reviews of the TDF (Becknell et al. 2012; Banda-R et al. 2016; Allen et al. 2017), each of these reviews focuses on a particular component of the TDF. Becknell et al. (2012) focus on aboveground biomass, especially considering precipitation variation across the continent. Banda-R et al. (2016) provide a comprehensive review and meta-analysis of floristic composition and biodiversity across Central and South America, and Allen et al. (2017) focus on the resilience of the forests through the lens of belowground biomass and rooting structure. These reviews have not considered or assessed the role of climate and climate change on the TDFs. As such, this paper provides a comprehensive review of the current state of TDF through the lens of resilience and the biome's physiological response to variations in climate.

Chapter 3 - **Deforestation and secondary growth in Costa Rica along the path of development** (Stan and Sanchez-Azofeifa, 2019b) - Like many of the countries where TDFs are found, Costa Rica has a history of deforestation and degradation; however, in more recent decades it has become a flagship country for environmental conservation legislation and a front runner for carbon stock trading and payments for ecosystem services programs. This complex history provides a useful case study for both assessing the impact of economic drivers, land cover change, and legislative measures on the destruction and resilience of tropical forests. Additionally, this type of history of forest change has not previously been compiled for Costa Rica. In this study, I use a series of historical forest maps from 1960 to 2013 to build a forest change history. This data is then combined with biophysical, climate, and legislative data to build a Bayesian statistical model to project forest changes into the future. Additionally, the impact of the Protected Areas conservation legislation is tested by assessing the threat to each area if it were no longer legally protected. This information can be transferred to other countries which are implementing conservation and payments for ecosystem services legislation to more effectively conserve forests that are in danger of deforestation.

Chapter 4 **- Climate change scenarios and projected impacts for the forest productivity in the Guanacaste province: lessons for tropical forest regions** – (Stan et al., under review).This chapter uses climate models to assess the historical variation of temperature and precipitation and project these variations into the future in the region with the most historical alteration to the forests, and home to Costa Rica's TDFs, Guanacaste. The productivity of the forests in Guanacaste's National Parks is compared against the Vapor Pressure Deficit (VPD), a measure of atmospheric moisture. The relationship built is used to project the productivity of the forests into the future, assessing their resilience to future climatic conditions. The relationship built between climate and forests in this region is crucial for a two reasons. First, it tests the MODIS algorithm assumptions, which uses a linear relationship between the VPD-scalar and the resulting productivity. This study directly tests whether this relationship holds in the TDFs of Guanacaste, and if it does not hold, it indicates that these MODIS products should not be directly translated into future projections based solely on these theoretical relationships. Second, this relationship between the Costa Rica TDFs can be tested against other Meso and South American TDFs to better understand the regional variation in water stress management systems. This comparison against other regions can then be used to directly assess where TDFs are more in danger of climate-induced degradation and where the forests are more resilient to variations in temperature and precipitation.

Chapter 5 **- Tropical Dry Forest Resilience and Water Use Efficiency: An analysis of productivity under climate change** (Stan et al., under review)**-** This final study culminates in an assessment of resilience in the TDFs across sites in Meso and South America using a cross continental analysis. While there is research into the local and regional response of TDFs to climatic variables, there has not been an analysis of the response of the whole Meso and South American TDF to climatic variables. Additionally, there has been no long-term analysis of TDF's response to a changing climate.

This study aims to fill this gap in the literature due to widespread concerns that droughts will increase in the future and this increase will put TDFs at risk because they are already water limited. This study compiles a series of published litterfall study sites in the TDF, as well as remote sensing spectral vegetation indexes and climate data. These data are used to assess the climatic variables which have impacted TDF productivity over the past 20 years. Additionally, the forest's productivity under El Nino Southern Oscillation (ENSO) conditions is tested to assess the biome's ability to be resilient to dry and wet conditions. ENSO periods are projected to increase in magnitude and frequency over the next century, making the historical changes to productivity important to assess. Overall, this study is designed to determine the current drought management potential of TDFs so that ESMs can be better programmed to reflect this resilience, thereby improving forest change projections.

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CHAPTER 2 - Tropical Dry Forest diversity, climatic response, and resilience in a changing climate

Abstract

Central and South America tropical dry forest (TDF) is a water-limited biome with a high number of endemic species and numerous ecosystem services which has experienced a boom in research in the last decade. Although the number of case studies across these seasonal, water-limited, tropical forests has increased, there has not been a comprehensive review to assess the physiological variability of this biome across the continent and assess how these forests respond to climatic variables. Additionally, understanding forest change and resilience under climatic variability, currently and in the future, is essential for assessing the future extent and health of forests in the future. Therefore, the objective of this paper is to provide a literature review on the variability of TDF diversity and structure across a latitudinal gradient and to assess how these components respond to differences in climatic variables across this geographic area. We first assess the current state of understanding of the structure, biomass, phenological cycles, and successional stages across the latitudinal gradient. We subsequently review the response of these five areas to differences in precipitation, temperature, and extreme weather events, such as droughts and hurricanes. We find that there is a range of adaptability to precipitation, with many areas exhibiting drought tolerance except under the most extreme circumstances, while being susceptible to damage from increased extreme precipitation events. Finally, we use this climatic response to provide a commentary on the projected resilience of TDFs under climatic changes, finding a likelihood of resilience under drying scenarios, although model projections do not agree on the magnitude or direction of precipitation change. This review of quantitative studies will provide more concrete details on the current diversity that encompasses the TDF, the natural climatic ranges under which this ecosystem can survive and thrive, and can help inform future forest management practices under climate change scenarios.

Keywords: Tropical Dry Forests; climate change; resilience; drought tolerance; forest structure; succession; biomass; water use efficiency

2.1 Introduction

Changes in climate are heavily impacting both natural and developed areas in Central and South America (Magrin et al. 2014; Thiede et al. 2016; Yamamoto et al. 2018). Over the past five decades, climatic phenomena have been responsible for 88 percent of disasters, globally (Pivetta et al. 2016). These climatic disasters include increases in hurricanes and tropical storms in areas that have previously not seen this scale of storm, as well as increases in droughts and flooding due to extreme El Niño and La Niña events (Bender et al. 2010; Cai et al. 2015; Magrin et al. 2014; Yamamoto et al. 2018). Climatic changes have impacted biomes around the globe, with recent increases in disturbance decreasing ecosystem recovery rates, and variations to precipitation and temperature which directly impacts forest phenology, flowering rates and times, photosynthesis, water use, and nutrient transport. The changes that occur in tropical dry forests (TDFs) is of particular interest as the countries in which they are located house high population densities and much of the forest is converted for agriculture and cattle (Miles et al. 2006; Wright 2005).

TDFs encompass 42% of the tropical forest regions and have focal points in Central and South America, Africa, Central Asia, India, and Australia (Buzzard et al. 2016; Miles et al. 2006; Quesada et al. 2009). Only 2% of the TDFs are intact and only 8% are legally protected (Buzzard et al. 2016; Wright 2005), but they contain high levels of biodiversity, with 12 distinct floristic groups in the Central and South American TDF and the number of unique tree species in stands ranging from 100 at high latitudes to over 1000 near the equator (Banda-R et al. 2016; Golicher et al. 2012; Powers et al. 2009). Additionally, between 50% and 75% of the remaining TDF is thought to be located in Central and South America, predominantly in Mexico, Bolivia, and Brazil (Figure 2.1; Hesketh and Sanchez-Azofeifa 2013; Portillo-Quintero and Sanchez-Azofeifa 2010). An area with a mean annual temperature >25 °C, precipitation between 700–2000 mm with a dry season of <100 mm for at least three months, which comprises >50% deciduous trees, defines the TDF ecosystem (Sanchez-Azofeifa et al. 2005a). Additionally, TDFs are water-limited and have high biodiversity typified by trees, lianas, shrubs, herbs, graminoids, and bromeliads (Kennard 2002).

TDFs have the third highest deforestation rate globally and are subject to high anthropogenic alteration (Coelho et al. 2016; Hansen et al. 2010; Portillo-Quintero and Sanchez-

Azofeifa 2010). Much of this deforestation is due to high population densities, which creates a predominantly fragmented landscape (Fajardo et al. 2005; Portillo-Quintero and Sanchez-Azofeifa 2010). The high population densities in TDFs are due to climate, geography, and a high number of neotropical freshwater sources (Portillo-Quintero et al. 2015); however, despite its regional and global importance, it remains severely under-studied relative to the humid forest (Sanchez-Azofeifa et al. 2005). Only 14% of tropical forest scientific papers, until 2005, focused on tropical dry forests, with a heavy emphasis on Costa Rica, Mexico, and Brazil (Calvo-Rodriguez et al. 2017; Portillo-Quintero and Sanchez-Azofeifa 2010; Sanchez-Azofeifa et al. 2005a). Since 2005, research into TDFs has been increasing but it still only comprises less than 25% of research into tropical forests annually (Figure 2.2).

Much of the TDFs in Central and South America remain unprotected, highly fragmented, and at risk of being cleared (Portillo-Quintero and Sanchez-Azofeifa 2010). In Brazil, for example, more than 90% is comprised of secondary forests, which have recovered after being cleared or burned for agriculture (Coelho et al. 2016; Garaglio et al. 2010). In contrast, Costa Rica is an exception where legislative, social, and economic changes have led to regeneration rates exceeding current deforestation rates (Robalino et al. 2017; Stan and Sancez-Azofeifa, 2019). Conservation strategies, aimed to protect TDFs in different countries have ranged from the implementation of payments for ecosystem services to the creation of conservation areas and community-based management systems (Robalino et al. 2017; Porter-Bolland et al. 2012). The degradation and anthropogenic protections detailed above do not take into account forest alteration under climatic change. With an uncertain future in temperature and precipitation regimes in a highly populated and fragmented ecosystem, it is essential to understand the relationship between the TDF ecosystem and climatic variables and how they respond under natural stresses.

Scientific reviews dealing with TDF biomass and resilience came out in 2012 (Becknell et al. 2012), 2016 (Banda-R et al. 2016), and 2017 (Allen et al. 2017). Becknell et al. (2012) focused on above-ground biomass of mature and secondary dry forests around the globe, with no discussion of the climatic impact on the structure, successional stages, and phenological cycles. While a discussion of correlations with precipitation was present, there was no consideration for extreme climatic events, or the effects of temperature, which ultimately impact the water available to ecosystems. Banda-R et al. (2016) extensively reviewed the diversity of Neotropical dry forests, with similarity analyses, and the categorization of TDF sites into 12 major floristic groups. Allen et al. (2017) wrote a predominantly qualitative review which focused on below-ground biomass and the impact of drought on TDF root systems. None of these reviews, however, discuss the effects of climate variability and climate change on TDFs (Allen et al. 2017; Banda-R et al. 2016; Becknell et al. 2012).

Here we review the tropical dry forest across Central and South America in terms of successional stages, forest structure, above-ground biomass, and phenology. Additionally, we discuss the response of these TDF features to changes in climate, including precipitation, temperature, and extreme events, and assess the potential resilience of TDFs using these parameters for projections of future climatic change.

2.2 Components of Tropical Dry Forests

2.2.1 Forest Dynamics

Forest dynamics describe how forests grow, change, and react to environmental pressures, with key components of tree mortality, growth, and recruitment (Grebner et al. 2013; Ma et al. 2016). Anthropogenic influences, especially agricultural activities, are the primary cause of tropical dry forest alteration. Land abandonment leads to the growth of secondary TDFs interspersed with primary old growth forests as documented in Costa Rica (Cao et al. 2017; Li et al. 2017). The methodology that is most appropriate to study and group successional stages is disputed, with long-term studies, palynology, chronosequences, and stand reconstruction all suggested as best practices (Johnson and Miyanishi 2008; Quesada et al. 2009). Chronosequences, or grouping stages into early, intermediate, and late-stage based mainly on time since abandonment, is one of the most common study methods but has also garnered criticism because it assumes a consistent history between different locations (Chazdon et al. 2007; Kalacska et al. 2005; Madeira et al. 2009; Quesada et al. 2009). Despite the criticism of chronosequence analysis of successional stages, the replication it provides and its ability to capture TDF heterogeneity make it the most feasible procedure for studying its rapidly changing dynamics (Quesada et al. 2009). The structure of the forests, both horizontally and vertically, also defines successional stages. In early-stage succession, there is a matrix of seedlings, herbs, grasses, and sparse woody vegetation (Kennard 2002; Portillo-Quintero and Sanchez-Azofeifa 2010). As succession progresses, there is a higher proportion of trees, shrubs, and bromeliads, the increased presence of lianas, and canopy coverage of 63%–80% (Kennard 2002; Martinez-Ramos et al. 2018). The intermediate stage typically has the highest net primary productivity and species richness, as well as the highest density of lianas (Derroire et al. 2016; Hernandez-Ramirez and Garcia-Mendez 2015; Kennard 2002). Late stage forests, however, are typically considered to have the highest species evenness (Figure 2.3; Coelho et al. 2016; Derroire et al. 2016; Quesada et al. 2009). Later successional stages also exhibit reduced regeneration capabilities as there is less sapling recruitment in stands >15 years old, resulting in slower recovery from events and slower species turnover (Hernandez-Ramirez and Garcia-Mendez 2015; Kennard 2002).

Recruitment rates are highest in early stage forests, although climate moderates these rates (Hernandez-Ramirez and Garcia-Mendez 2015; Kennard 2002; Martinez-Ramos et al. 2018). In Mexican sites, there is reduced recruitment and sapling development in wetter years thought to be due to reduced flowering and seed production in nearby stands compared to dry years (Martinez-Ramos et al. 2018; Singh and Kushwaha 2005; Wright and Calderon 2006). This trend is also replicated in shrubs, which is problematic for the recruitment of and subsequent biomass growth of pioneer species in newly abandoned pastures (Brienen et al. 2010; Lebrija-Trejos 2008; Martinez-Ramos et al. 2018).

The previous land use of secondary TDFs and individual site characteristics are impactful for the resulting species recruitment rate, diversity, and mortality (Derroire et al. 2016). Plots with a history of use as cultivated lands had a significantly lower species evenness and slower recruitment rates when compared to plots with a history of being used as unmanaged pasture land (Derroire et al. 2016). In Costa Rica, pasture sites had a much lower rate of species recruitment compared to low-intensity use plots, and site-specific conditions, such as proximity to seed sources were highly impactful for plot structure and diversity (Chazdon et al. 2007). Seed sources from proximal old growth forests also tend to drive the eventual species makeup of the secondary forest (Castillo-Nunez et al. 2011; Derroire et al. 2016). In all Costa Rican successional stages, the most abundant species are dispersed by either wind or by animals, particularly birds (Hilje et al. 2015; Powers et al. 2009). Additionally, many species are unique to a single successional stage, irrespective of latitude. In Brazil, only 13.5% of species were common across all successional stages, with 43.2% of species unique to only one successional stage (Coelho et al. 2016). A similar trend occurs in Costa Rican sites, 18% of species found in all forest plots, and 48% unique to a single site, with 19% represented by only by a single individual (Powers et al. 2009).

Overall, the literature characterizes the successional stages of tropical dry forests, across the entire latitudinal gradient, into early, intermediate, and late stages by age, with some research, also distinguishing primary forests as a separate class. As succession increases, each stage has a more complex composition and structure, although some factors such as primary productivity are highest in intermediate forests across the Neotropics. Finally, across all the Central and South American TDFs, recruitment rates, and regenerative capabilities decrease as successional stage increases.

2.2.2 Forest Structure

Forest structure is highly dependent on forest age and the level of disturbance in both primary and secondary forests. In general, the measurable structure in a forest can be broken up into stem density, basal area, number of canopy levels, and in the case of tropical dry forests, liana infestation (Hesketh and Sanchez-Azofeifa 2013).

Stem density in TDFs is highly variable across the continent and between plots. In Brazil, early stages have the lowest stem density and late-stage the highest, with small diameter trees most prevalent in the intermediate stages (Coelho et al. 2016; Madeira et al. 2009). In Bolivia, stem density is most variable in the late-stage (Kennard 2002), while these young forests have a greater abundance of small stems, as well as a low canopy cover (Kennard 2002), which allows for higher herb and grass abundance in early successional stages. North of the equator, in Mexico, the density of stems with the diameter at breast height (DBH) between 0.10–0.30 m varied by plot, but typically decreased with stand age. Furthermore, the density of stems >0.30 m increased asymptotically with stand age. Stem density is also impacted by the underlying geomorphology, with ridgelines and low slopes having a higher stem density in Mexican sites compared to regions with intermediate slopes (Jaramillo et al. 2003). In Venezuela, stem density is the lowest compared to all other biomes, except the plains, and the basal area is third smallest above only the plains (i.e., Llanos) and the mid-elevation Andean forest (Vilanova et al. 2018).

The basal area and DBH of successional stages also varies across the continent. As the successional stage increases, the basal area of plants increases in the Southern Hemisphere (Coelho et al. 2016; Kennard 2002). In the Northern Hemisphere, a local-level analysis found that the Yucatan has a smaller basal area compared to other TDF sites across Mesoamerica and that secondary forests never recovered a basal area comparable to the primary mature forests (Hernandez-Ramirez and Garcia-Mendez 2015). Slopes impact the basal area of tree stems with the total basal area increasing from 20.84 m^3/ha to 27.06 m^3/ha from the ridgeline to the lower slopes, respectively, in Chamela, Mexico (Jaramillo et al. 2003).

Liana infestations, more common in disturbed areas, also have a spatial structure component, and impact the resulting forest structure by negatively affecting the basal area and DBH in infested forests (Duran et al. 2015; Pena-Claros et al. 2012). Lianas in Bolivia can cover between 8%–15% of stands (Kennard 2002), although the density of vines correlates to the level of disturbance in a patch (Schnitzer and Bongers 2011). The higher abundance of TDF lianas compared to wet and moist forests is thought to be due to liana advantages in the dry season, including a faster green-up, slower senescence, the heightened solar radiation in arid forest zones, and the greater availability of this radiation throughout the year (Dewalt et al. 2010; Duran et al. 2015; Kalacska et al. 2008; Schnitzer 2005). Additionally, liana presence is highly correlated to elevation, with sharp declines in liana presence above 1000 masl (Duran et al. 2015; Van Der Heijden and Phillips 2008).

Overall, late-stage forests in Yucatan, Mexico have the smallest basal area, followed closely by Brazil and Venezuela, while both Chamela, Mexico, and Bolivia have the largest basal area (Coelho et al. 2016; Hernandez-Ramirez and Garcia-Mendez 2015; Jaramillo et al. 2003; Kennard 2002; Vilanova et al. 2018) [48,49]. Instead of a latitudinal gradient, studies appear to find that areas closer to the Pacific have a smaller overall basal area. Stem density did not show a consistent pattern across the continent, varying widely between successional stages and individual plots (Coelho et al. 2016; Jaramillo et al. 2003; Kennard 2002; Madeira et al. 2009; Vilanova et al. 2018). Liana infestations follow a different pattern entirely, more closely associated with disturbance, rainfall, and elevation.

2.2.3 Phenological Cycles

TDFs of the Neotropics have a mix of deciduous and evergreen species, with at least 50% of the species exhibiting a deciduous nature (Sanchez-Azofeifa et al. 2005a). The phenology of the TDF, seasonal cycles of the expression in TDFs, include periods of tree growth and dormancy, green-up and senescence, flowering, and fruiting (Reich and Borchert 1994). In

TDFs, these patterns are driven by seasonal patterns variations in precipitation with the wet season bringing green-up and growth and the dry season resulting in senescence and dormancy (Reich and Borchert 1994). This phenological cycle and its variation across latitudinal gradients have been identified as essential for proper classification of the dry forest and as a research priority; however, there is still a significant gap in the direct quantification of its phenological signature (Hesketh and Sanchez-Azofeifa 2013; Portillo-Quintero and Sanchez-Azofeifa 2010; Portillo-Quintero et al. 2015; Sanchez-Azofeifa et al. 2005a). Additionally, remote sensing of phenological components, such as green-up, is not accurate, with a 1–3 week discrepancy between satellite and in situ data for the start of green-up. Satellite data, instead, corresponds to the peak rate of change in the green-up (Rankine et al. 2017).

In the few studies that have analyzed this pattern, the level of deciduous species is thought to be related to the duration and severity of the dry season, variability in soil moisture, and micro-scale environmental conditions including rooting depth, temperature, and plant available water content (Elliot et al. 2006; Hulshof et al. 2013; Portillo-Quintero and Sanchez-Azofeifa 2010; Singh and Kushwaha 2005). Additionally, there are differences in phenological cycles across countries and successional stages. Leafing intensity for early successional stages during the dry season and at the beginning of the rainy season is highest away from the equator (Mexico and Brazil), while it is reduced in equatorial regions (Costa Rica) (Lopezaraiza-Mikel et al.2013). In Costa Rica, the total phenological cycle varies between 150–358 days, depending on the presence of late-season rains, which extends the forests' maturity period (Castro et al. 2018). Leafing intensity between successional stages is not significantly different; however, there are significant differences in the number of species that have 50%–100% of their leaves in the Brazilian and Costa Rican rainy seasons between stages (Lopezaraiza-Mikel et al. 2013). Under drier conditions, all stages experience earlier senescence; however, increased senescent individuals is gradual in the early stages but abruptly changes in intermediate and late stage forests (Pezzini et al. 2014).

2.2.4 Above-Ground Biomass (AGB)

AGB is a measure of all living plant mass that is located above the ground (Ravindrath and Ostwald 2008). Mass from stems, leaves, seeds, branches, and bark (Ravindrath and Ostwald 2008). These values are directly correlated to precipitation values and the number of dry season months (Becknell et al. 2012). On a continental scale, there is a latitudinal gradient both in the current aboveground biomass and the potential AGB. Mexico and Brazil are found to have the lowest biomass present, while the highest values are found in Costa Rica (Becknell et al. 2012). The potential for the recovery of AGB is vital in secondary TDFs, and the highest potential AGB resides in the central latitudes, with lower values away from the equator (Poorter et al. 2016). Tree growth and mortality drive biomass change between years (i.e., the potential for biomass). Tree mortality in early stage TDF is quite small; however, this rate increases to a level comparable to wet forests in late successional stages (Rozendaal et al. 2016). This low mortality among early TDF stages reduces species turnover and the rate of AGB accumulation in these forests (Rozendaal et al. 2016).

There is no consistent difference between the AGB in TDFs and nearby moist forests. Some studies find TDF sites with far less AGB than floodplain forests, but 3–4 times more when compared to pastures (Jaramillo et al. 2003; Navar-Chaidez 2010). In Mexico, ABG varied across latitudinal gradients and between successional stages but had only 25% of the biomass when compared against the values found in the same stages of wet forests (Rozendaal et al. 2016). There is a similar situation in Venezuela where TDFs exhibit the lowest biomass of all biomes (Vilanova et al. 2018); however, this is not consistently replicated by other studies which finds that TDFs have a much higher biomass compared to rainforests of a similar age (Achard et al. 2004; Brown 1997; Defries et al. 2002; de Jong et al. 2008; Houghton 1999; IPCC 2006). The types of plants that contribute the most to biomass also differ between wet and TDFs. In the TDF, the contribution of multi-stemmed individuals was higher than moist forests (45.8%–56% of the AGB) (Rozendaal et al. 2016).

In Mexico, the AGB is typically dependent on a few select species, although the exact composition is site dependent. Some sites have 80% of the AGB explained by two species from the Mimosa genus (Mimosa acantholoba var. and Mimosa tenuiflora), while others have eight species accounting for the same biomass (Rozendaal et al. 2016). The Chamela Biological Station (Jalisco, Mexico) has the most number of species accounting for AGB at 16–17 species (Rozendaal et al. 2016). On a micro level, these differences could be due to the factors impacting the forest growth and development, with the variability in AGB in Southern Mexico predicted by the distance to streams, solar irradiance, and altitude (Corona-Nunez et al. 2017) in some sites and elevation and slopes found as the most important in other plots (Jaramillo et al. 2003).

Despite micro-scale variations in above-ground biomass, which are driven by species composition and micro topographical features, there is an overall continental latitudinal trend in above-ground biomass. The above-ground biomass is, in general, highest in the equatorial regions, and reduces moving farther away from the equator (Achard et al. 2004; Brown 1997; Defries et al. 2002; de Jong et al. 2008; Houghton 1999; IPCC 2006; Rozendaal et al. 2016; Vilanova et al. 2018). Much of the current AGB and growth research uses traditional forest inventories; however, dendrochronological methodologies have recently been used to more accurately describe growth patterns at a fine temporal resolution in the boreal forests (Montoro-Girona et al. 2016a; Montoro-Girona et al. 2016b). These approaches could be transferred to TDF regions to explore their growth response and incorporate them into non-linear models (Montoro-Girona et al. 2016a; Montoro-Girona et al. 2016b).

2.2.5 Biodiversity

Much like the AGB, there are latitudinal trends in the species diversity found across TDFs, although micro-scale differences moderate this effect. Overall, species diversity is lower away from the equator, with plots in Mexico and Brazil typically having 90–100 flora species (Hernandez-Ramirez and Garcia-Mendez 2015; Rito et al. 2017), and equatorial latitudes having much higher diversity. In Costa Rica, plots had over 135 tree species alone and in Panamanian sites, it is estimated that there are over 1000 flora species (Golicher et al. 2012; Powers et al. 2009). Both near the equator and at higher latitudes there are typically more species that are only common to a single plot or successional stage in the TDFs. In Brazil, only 13.5% of species were common across all successional stages, with 43.2% of species unique to only one successional stage (Coelho et al. 2016). A similar trend occurs in Costa Rican sites, 18% of species found in all forest plots and 48% unique to a single site, with 19% represented by only by a single individual (Powers et al. 2009).

Species composition also differs by country. In Brazil, Fabaceae was the most speciose of the families (Coelho et al. 2016; Rito et al. 2017). The family accounted for 25% of the species in the early stage, 41.5% of the intermediate stage, and 21.4% of the late stage. The family with the highest number of individuals, however, was the Anacardiaceae family, accounting for 50% and 25% of individuals, respectively, for late and intermediate stage sites, respectively (Coelho et al. 2016). In Costa Rica, however, there was a wider range of abundant species depending on the location and successional stage of the plot. In general, *Quercus oleoides, Rehdera trinervis*, and *Cochlosperum vitifolium* were abundant in many of the plots (Powers et al. 2009). In all Costa Rican plots and successional stages, the most abundant species are dispersed by either wind or by animals (Powers et al. 2009). Other studies find that the majority of species in Costa Rican TDF sites have a monoecy breeding system (Hilje et al. 2015). Of the animals, in Santa Rosa National Park, birds were found to disperse the highest number of individuals and species, followed by other animals, such as bats; however, insects, were the most dominant pollinators in Santa Rosa National Park (Hilje et al. 2015). Very little is known about pollinators in other parts of the TDFs; however, given the commonalities between Santa Rosa and other TDF sites, it should be expected that other TDFs across the Americas exhibit similar characteristics.

The factors correlating with species richness also varied depending on site and location. Away from the equator, namely Mexico and Brazil, Bolivia, climatic variables, including precipitation/evapotranspiration, and irradiance have the most significant impact on species diversity and species turnover (Power et al. 2016; Saiter et al. 2015; Segura et al. 2002; Trejo and Dirzo 2002; Vargas-Rodriguez and Vazquez-Garcıa 2005). There is also an indication that the number of dry months negatively correlates with species diversity and turnover in these latitudes (Golicher et al. 2012). In the equatorial latitudes, soil and stand age dominate the local and regional scale species variation (Powers et al. 2009). Secondary forest sites also indicate that late-stage forests can recover tree and liana diversity comparable to primary mature forests (Hernandez-Ramirez and Garcia-Mendez 2015).

2.3 Tropical Dry Forest Response to Variations in Climate

Over the past century, there has been a rise in global temperature with a reduced range in daily temperature fluctuations (Easterling et al. 2000). Additionally, precipitation in the mid to high latitudes has increased and decreased in the equatorial areas (Easterling et al. 2000). These precipitation trends vary on a local and regional scale, however, based on geographic and topographic influences. Temperature and precipitation also vary by year, with large latitudinal variations based on the El Nino Southern Oscillation (ENSO) (Cai et al. 2015). There have also been increases in the number of extreme events that have occurred globally, including tropical storms, droughts, and fires (Easterling et al. 2000). Ecosystems differentially respond to these variations and changes based not only on the individual species but also based on the ecological networks and the relationship of the community to the surrounding abiotic environment (Walther 2010).

Of the climatic variables, the response to temperature and precipitation has been found to explain the majority of variation between different TDFs sites, with rainfall explaining the majority of the differentiation, followed by temperature (Mendivelso et al. 2014; Vilanova et al. 2018).

2.3.1 Temperature

While temperature has less impact on the variability in phenology, biomass, structure, and successional stages in TDFs compared to precipitation, it does provide a moderating effect (Reich and Borchert 1994; Alvarez-Davila et al. 2017). An example of this moderating effect is the limited range of optimal temperature for photosynthesis to occur in both tropical dry and tropical wet forests (29–32°C) (Slot and Winter 2017). The photosynthetic activity of the leaves in trees and lianas decreases if the temperature deviates from this range (Slot and Winter 2017).

Temperature is also critical for succession through the recruitment of new species and plant flowering (Haselhorst et al. 2017). The magnitude and timing of flowering and pollen production are directly related to temperature, with warmer temperatures increasing flower production (Haselhorst et al. 2017; Pau et al. 2013). The effect is stronger in wet forests but is still present in seasonally dry tropical forests, with consistent increases in both temperature and flower production since 2000 (Pau et al. 2013). Temperature and temperature related variables also accounted for 57% of the variation in succession (forest structure compared to the fallow age) in TDF sites in Mexico (Lebrija-Trejos et al. 2011).

2.3.2 Precipitation

Successional stage and flowering regimes are also affected by water availability with corresponding increases in precipitation and the magnitude of flowering and pollen production (Haselhorst et al. 2017). Flowering timing is also highly related to the onset of the rainy season in TDFs (Haselhorst et al. 2017). Successional stages have a mixed relationship with differences in precipitation. Early successional stages with limited water availability recruit more drought tolerant species but have limited regrowth and sprouting, leading to a slower recovery rate (Markesteijn et al. 2011; McLaren and McDonald 2003; Rozendaal et al. 2016). Proximity to old growth areas also moderates recovery rates, along with the seed dispersal mechanisms (mostly controlled by wind) and species recruitment derived from nearby neighbors (Derroire et al. 2016). Precipitation regimes or water availability do not significantly change the rate at which species diversity increases in areas, nor the species evenness between different sites (Derroire et al. 2016); however, sites in Brazil did find that the higher precipitation can offset the damages that anthropogenic alterations cause to species diversity (Rito et al. 2017). Additionally, evapotranspiration rates, combined with water deficits, drive tree species assemblages in the Mata Atlantica, TDFs, and Caatinga biomes in Brazil (Saiter et al. 2015). While species diversity may not be significantly related to precipitation, biomass and water availability are positively correlated. In Bolivia, for example, TDF gross primary productivity (GPP) anomalies have historically (from 1980–2009) been correlated to precipitation anomalies ($R^2 = 0.8$) and increases in the dry season by one day could decrease GPP by up to 1.2% (Seiler et al. 2014). On a global scale, there is a significant decrease in AGB when plots have a longer dry season, with an average reduction of 40 Mg/ha per additional month in the dry season, although this is highly variable by plot (Figure 2.4; Becknell et al. 2012).

Disturbed TDFs recover quickly, regaining their maximum biomass, species richness, and structural composition within 30–50 years, though their maximum biomass remains smaller than primary forests (Becknell et al. 2012; Derroire et al. 2016; Poorter et al. 2016; Powers et al. 2009); however, biomass differentiation can be seen earlier in wetter sites (Navar-Chaidez 2010). After twenty years of recovery, secondary forest sites that have a higher annual rainfall have higher biomass, although this saturates above 2500 mm/year or in tropical wet forests (Figure 5; Navar-Chaidez 2010; Poorter et al. 2016). The combination of stand age and mean annual precipitation in TDFs are significantly related to AGB with a logarithmic function (Becknell et al. 2012). As stands get older, their biomass increases and at 80 years of age, sites that receive <1000 mm per year average 100 Mg/ha, ones that have <1500 mm/year reach 150 Mg/ha, and ones that have between 1500–2000 mm/year can average ~225 Mg/ha of biomass (Becknell et al. 2012). Linearly related to annual biomass growth is the climatic water deficit (Poorter et al. 2016). Combined with rainfall seasonality and the increases in dry season length having a correlative 1.2%/day decrease in biomass, the water availability in secondary tropical forests accounts for 59% of the biomass variation after 20 years of recovery, making it one of the most critical variables (Poorter et al. 2016; Seiler et al. 2014). For mature forests, an increase in mean annual precipitation of 500 mm can increase the maximum biomass by 94 Mg/ha (Poorter et al. 2016).

2.3.3 Natural Disturbances

While not common, natural disturbances are of concern especially as we move into a future with an uncertain climate, where extreme events, such as El Niño Southern Oscillation, are expected to increase in frequency and intensity (Cai et al. 2015). Natural disturbances are expected to increase under climate change in terms of frequency and severity, with increases in fires, insect outbreaks, and wind storms already seen in the boreal forest (Navarro et al. 2018; Seidl et al. 2014). In the TDFs, tropical storms, fires, and droughts are of concern.

2.3.3.1. Tropical Storms

In the past decade there have been increases in tropical storms, including Hurricane Otto, the first hurricane to hit the Costa Rican coastline in 2016 (going through the heart of the largest patch of TDF in the country) and Hurricanes Jova (Category 2) and Patricia (Category 4), the first hurricanes to hit the TDF ecosystem on the Mexican Pacific Coast in 2011 and 2015, respectively (Gavito et al. 2018). These extreme increases in precipitation lead to saturation and super-saturation levels, which negatively impact tree development and water transport and can induce early dormancy (Kanniah et al. 2013; Xie et al. 2015). Additionally, hurricanes and extreme precipitation events affect the decomposition levels in forests, both during the event and in subsequent years. In the case of the Mexican TDF, a decrease in litterfall decomposition was observed the year following Hurricane Jova. A drop of ~30 mg/day for late-stage forests at Chamela. Further, a reversal of these trends occurred after Patricia (Gavito et al. 2018). The litterfall did return to normal after two years, however, indicating a level of resiliency in the forests. The vegetation on the coastal plains of Jalisco, Mexico also exhibited a significant decrease in the enhanced vegetation index (EVI) after both hurricanes (Tapa-Palacios et al. 2018). Other studies found that deciduous forests showed a higher resilience than semi-deciduous ones (Renton et al. 2018). With two hurricanes so close together, however, it was also noted that the ecosystem had a higher resistance to the first hurricane compared to the second one despite the high resiliency and rapid return to normality for the litterfall, nutrients, and decomposition rates (Gavito et al. 2018).

Old growth forests in Mexico experience higher severe damage (uprooted, broken trunk, bent trunk; 14%) compared to secondary forests, while secondary forests have a higher tree mortality (7%) in the post-Patricia aftermath (Jimenez-Rodriguez et al. 2018). A minor hurricane, such as Jova, halved the number of tree cavities that birds could use for nesting, while larger events had a more substantial effect, shifting the flower and fruit phenology in both deciduous and semi-deciduous areas (Renton et al. 2017). Fruit and flower abundance also significantly decreased in the year following Hurricane Jova compared to the one following Hurricane Patricia, and the decrease was more significant for the semi-deciduous forests. Higher fragmentation leads to increased vulnerability and leaves the remaining patches more susceptible to fires post-hurricane. When further extrapolating the damage to the vegetation community and the animals that live there, the hurricanes significantly decreased both bat and small mammal community diversity post-hurricane, but recovery of these populations occurred rapidly (Tapia-Palacios et al. 2018). If the frequency of such storms increases in areas that contain TDFs, as we have seen since 2010, there may come the point in time when the resilience of the forests is not substantial enough to mitigate the loss in resistance in both the fauna and flora (Holm et al. 2017).

Given the increases in the number of these storms impacting the TDFs, their projected rise in the future, and the current lack of information about their impact on TDF resilience in the short and long term, this line of research is increasingly relevant. Differentiating between the types of damage caused by wind, uprooted versus broken trunks or standing dead trees, and their impact on ecological functions should be a focus for research in coming years.

2.3.3.2. Fire

Extreme events are projected to increase on both ends of the spectrum, and fires are predicted to be of growing concern despite no evidence of species shifts compared to the early Holocene when fires were more prevalent (Gavito et al. 2018; Power et al. 2016). It is also important to note, however, that fires are not considered part of the natural Central and South America TDF matrix with few natural fires documented and a much higher prevalence of anthropogenically started fires (Middleton et al. 1997). Although fires are not considered to be part of the TDF ecosystem naturally, there is evidence to suggest that some species are becoming fire adapted. In the Nicaraguan TDF, there are three main fire adaptations that species exhibit:

resistance (low mortality), resprouting (vigorous sprouting post-fire), and recruitment (increased seeding post-fire) (Otterstrom et al. 2006). The resilience of TDFs to fire is poorly understood, however, and is a knowledge gap that requires more research. Paleoecological studies could be useful in assessing long-term interactions between natural disturbances, as has been done to assess insect outbreaks in the boreal forest (Montoro-Girona et al. 2018).

2.3.3.3. Drought

There is a positive correlation between recovery from drought globally, post-drought temperature, and precipitation. The humid tropics are typically considered to have the highest recovery time; however, the seasonality of rainfall helps the TDF recover quickly. The typical recovery times were <6 months, with some pockets of 7–12 months for the ecosystem to fully recover (Schwalm et al. 2017). Drought has also been significantly correlated to the reduction in fine-root and ectomycorrhizal-root biomass (Valdes et al. 2006). Consistent long-term droughts (6–30 years) have been shown to negatively affect growth, although the amount and duration required is predominantly species based (Alvarez-Davila et al. 2017). With shorter droughts mitigated using similar techniques that the forests use in the dry season and early brown down (Alvarez-Davila et al. 2017; Pau et al. 2010).

Younger successional stages have indications of stronger regulatory responses compared to late stages during drought (Bretfeld et al. 2018), with the highest evapotranspiration demand found in 80-year-old forests (Bretfeld et al. 2018), where leaf area index tends to be higher (Kalacska et al. 2005). Water use efficiency, the ability for an ecosystem to assimilate the same or more carbon (Keenan et al. 2013) is higher in areas such as Mexico and south-central Brazil, where TDFs and savannas are present, (4–9 g C hPa0.5/ kg H2O) compared to the tropical wet forests, such as the Amazon (0–3 g C hPa0.5/ kg H2O) (Konings and Gentine 2017). Under drought conditions, the water use efficiency of TDFs is expected to increase by as much as 38% compared to average years (Seiler et al. 2014).

2.4 Resilience under Climatic Change

The IPCC fourth report predicted by the end of the XXI century that there would be high rates of extinction, with savanna and drought tolerant vegetation replacing tropical forests. Increases in extreme events will exacerbate this transition. The fifth IPCC report goes further, predicting changes in rainfall, temperature, seasonality, reductions in biodiversity and loss of species even within protected areas (Mendivelso et al. 2014); however, global and regional climatic models cannot agree on the scope of climatic change within the TDF habitat. There is a clear consensus that temperatures in the TDFs will increase, but the magnitude of change ranges from 1.5 °C to 6 °C (Mendivelso et al. 2014; Taylor et al. 2013) and may be moderated by the successional stage, with late-stage forests removing up to 120 W/m2 of heat energy (Coe et al. 2017). Land surface temperature, which drives this forest-atmosphere energy exchange, has been studied at the Santa Rosa National Park Environmental Monitoring Super Site (Cao and Sanchez-Azofeifa 2017) and been found to be dependent on the successional stage, with the highest surface temperature found in early stage forests. Precipitation models do not have any prediction consistency with drops of 10%–15% in the Argentinian Chaco up to 50% in Costa Rica or increased precipitation up to 50% in the same regions (Alvarez-Davila et al. 2017; Chadwick et al. 2015; Huang et al. 2015; Salazar et al. 2016).

Based on the information above, Central and South America TDFs are resilient to the current climatic conditions and this resilience is likely to continue, even as the climate warms. The species in the TDF may be slightly altered to include more drought-adapted when they go through successional changes, and there will be a reduction in the biomass currently in mature forests if reduced rainfall occurs; however, these changes will be well within the range of current phenotypic variation, and the phenological cycles, structure, and successional paths will be maintained. Under extreme precipitation scenarios, TDFs are more resilient to drought, with the ability to within decadal-scale droughts, compared to increased precipitation (Alvarez-Davila et al. 2017; Esquivel-Hernández et al. 2017; Schwalm et al. 2017). These projections of resilience also do not take into account a large part of the TDF matrix, human alteration, which may increase pressure on the ecosystem to provide services and space for communities. These pressures could increase rates of deforestation and fragmentation, further exacerbating any apparent changes to climate, and also further increasing temperatures and thereby decreasing the water availability for remaining fragments. Forest management practices, including legislative protection, payments for ecosystem services, and community-based management systems may help reduce these anthropogenic pressures (Stan and Sanchez-Azofeifa et al. 2019).

2.5 Conclusions

Overall, we find that across the entire Neotropical dry forest literature, the forest structure has a longitudinal gradient with increasing basal area in the west. However, phenological cycles, biodiversity, and above-ground biomass all have latitudinal gradients with equatorial regions experiencing higher AGB and biodiversity, less deciduousness, and longer growing seasons. There are local-scale variations in the structure, species composition, liana density, and phenologic characteristics, which are modified by slope, elevation, level of disturbance, and rainfall. The phenological cycles across the continent and the impact of species composition on resilience are poorly understood, and require improved research for proper generalizations.

The TDFs require optimal temperatures for growth, rapid successional development, and consistent flowering times. Variations in precipitation do not impact forest ecological processes as much, with drier areas recruiting more drought tolerant species and flowering later to accommodate this lack of water. Droughts are required on a decadal time scale to damage the ecological functioning of TDF permanently. Floods and tropical storms, however, have greater impacts on the resilience of the TDF. Unfortunately, given the relatively recent occurrence of these disasters impacting TDFs, there is very little research into the full interactions between these disturbances and the ecosystem. This lack of research is important to understand for climate change scenarios, though there is no agreement between models on the direction or magnitude of changes in the Central and South American climates, even under consistent emission scenarios. Even if model projections, which suggest dry areas will become even more water limited are realized, the biomass response of forests indicates that it will be resilient under these conditions, with changes to more drought tolerant species assemblages and reductions in biomass.

Overall, increasing research needs to be presented on the impacts of tropical storms and flooding on TDFs. The impact of increasing soil saturation on TDF structure, biomass, phenology, and succession is also not well understood, however, and remains a large gap as we approach a time of climatic volatility. There are also gaps in long-term paleoecological studies related to the impact of non-linear forest growth on ecosystem structure and disturbance recovery. Best practices in forest management and legislation under climate change scenarios is also crucial for a holistic understanding of forest resilience, and different practices must be tested and assessed. The role that plant functional type plays in resilience and how it changes under climate change has not been studied and is essential for a comprehensive analysis of future TDF resilience. Finally, understanding of how effectively TDF plants use water is critical when projecting future precipitation changes.

Additionally, within the literature, there remains a severe bias in the location of studies, despite the increase in remote sensing papers about the TDF. Mexico, Costa Rica, and Brazil comprise the majority of the body of TDF literature in Central and South America, leading large gaps in TDF response information in the other 15 countries that house this ecosystem. Further, there is also a significant bias of research between continental and Caribbean dry forests and old and neotropical TDFs. Integrating in situ localized TDF response with regional, remote sensing, carbon flux systems, and modeling data is another crucial step to take within the research, as is incorporating structurally based information from light detection and ranging (LiDAR) and associated systems with spectrally based modeling infrastructure. Finally, direct resilience studies under climate change, with both in situ and remote sensing methodologies, will be an essential step for research to take to directly and concretely determine where these forests are resilient, and where they are not. Defining these locations can also assist in determining if there are intervention strategies that can be used to help preserve this biodiverse ecosystem.

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Figure 2.1:

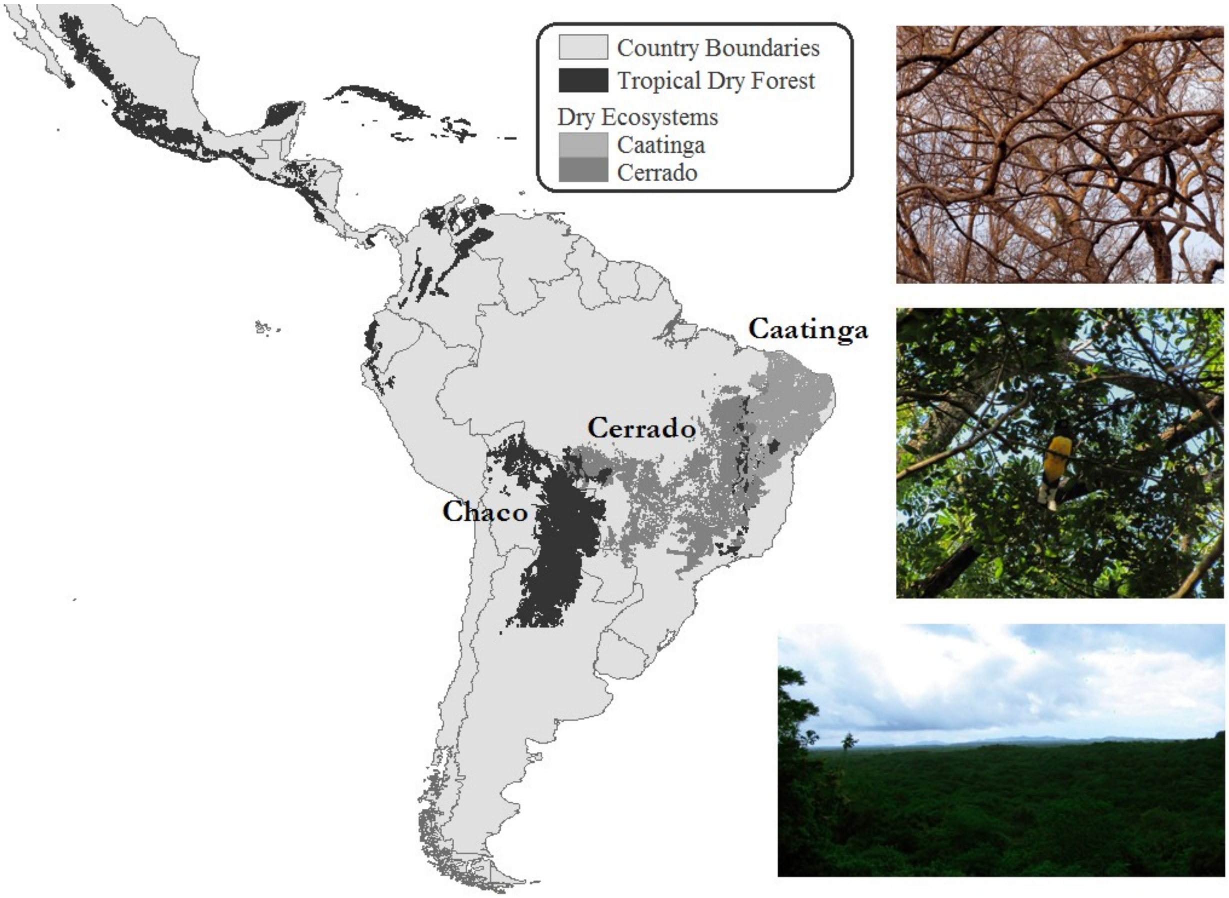

Country Boundaries
Tropical Dry Forest
Dry Ecosystems
Caatinga
Cerrado
Caatinga
Cerrado
Chaco

Figure 2.2:

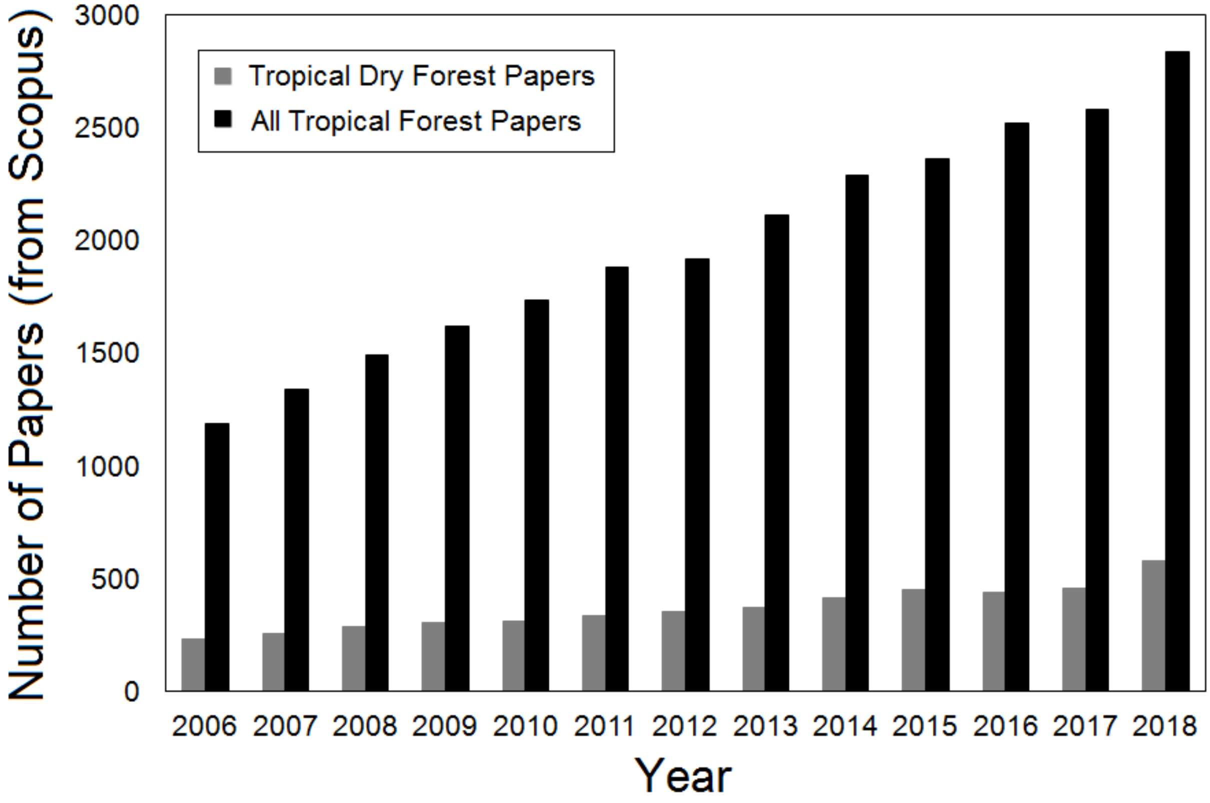


Figure 2.3:

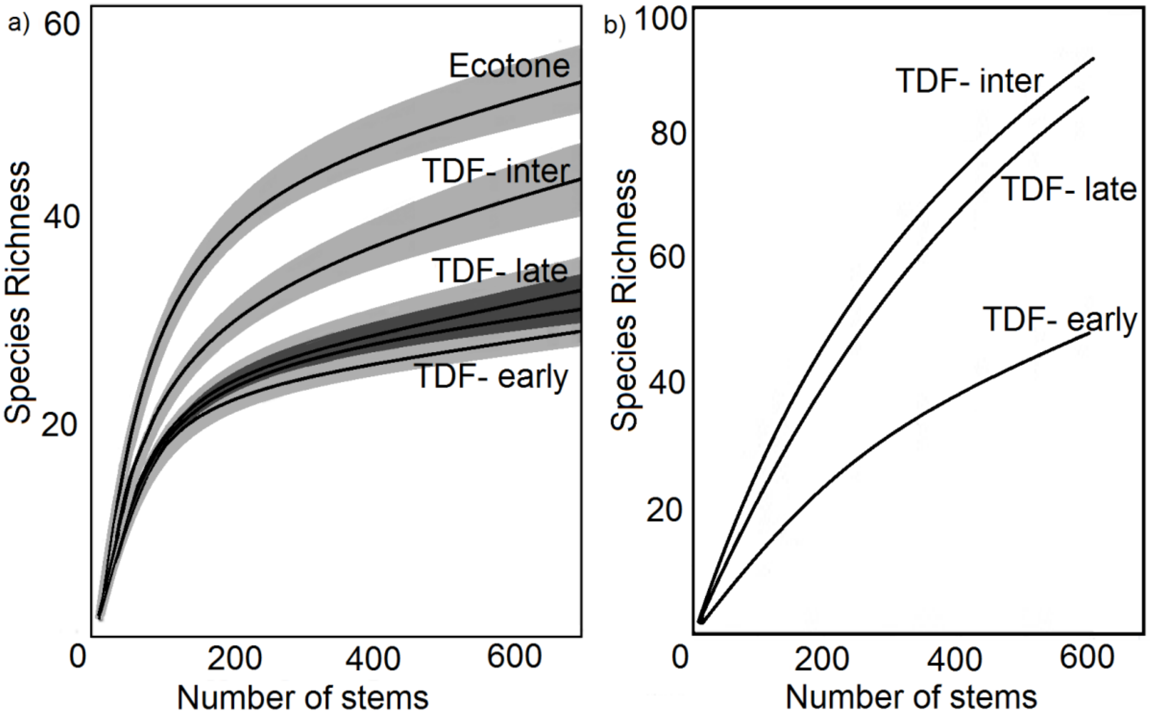


Figure 2.4:

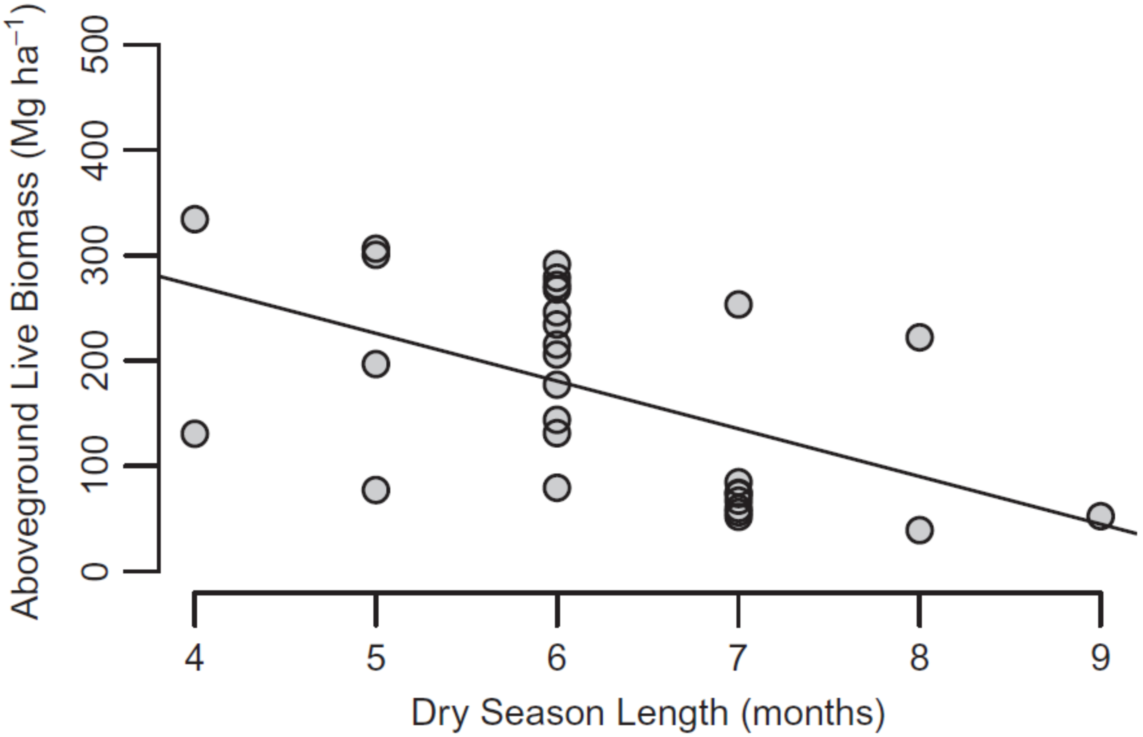
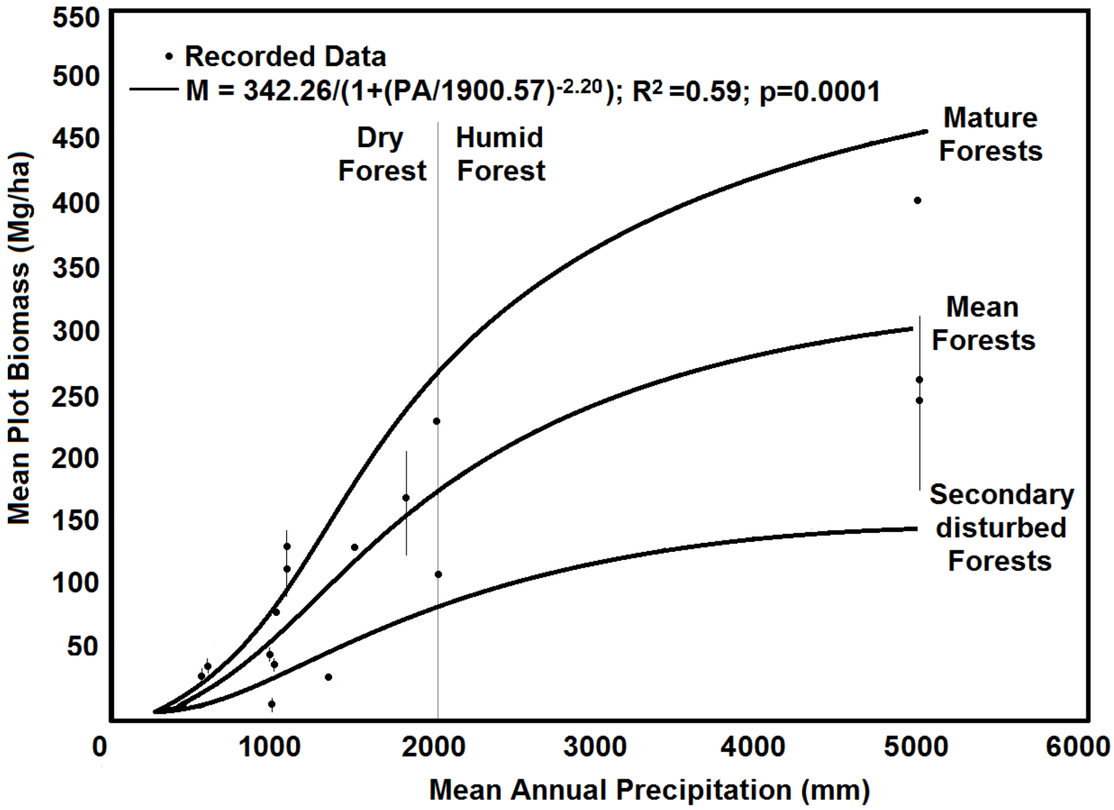


Figure 2.5:



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CHAPTER 3 - Deforestation and secondary growth in Costa Rica along the path of development

Abstract

Over the past 50 years, Costa Rica has experienced extensive landscape changes; however, the scale and rate of these changes has et to be documented in the literature. It is, therefore, important to understand the historical changes that have occurred and how the forests will change in the future, which provides the objective of this study. To determine the historical deforestation trends and link them to the different biogeophysical and socioeconomic variables, forest maps from 1960-2013 were used in the Dinamica Environment for Geoprocessing Objects (Dinamica EGO) to create deforestation models for Costa Rica. The base model was built and analyzed for changes in landscape metrics such as patch size between 1960 and 2013. After validation of the model's ability to replicate patterns, the landscape change was then projected to 2069. The historical model validated at 85% accuracy within 600m for both the 2005-2013 and 1997-2005 iterations. All national future projections exhibited an increase in forest area, including the most extreme deforestation scenarios.

Future projections are increasingly important given changes in the global socio-political structure, climatic change, and the ever-increasing globalization of capitalistic endeavours. The trajectory of the forest in Costa Rica can also serve as a way to track both these global pressures on the natural landscape, and as a proxy for how to manage deforestation in other similar political and geographic areas of the tropics.

Keywords: Land Cover Change, Environmental Modelling, Dinamica EGO, Deforestation Trends, Environmental Legislation

3.1 Introduction

In Costa Rica, the economic incentives for expanding the cattle industry began in the 1950s, with an increase in the international market price of meat driven by a majority of exports being directed towards the United States (McDade 1994). In the 1960s, pasture land expanded by 62%, with much of the growth located in Guanacaste (Mc Dade 1994). By 1972, Guanacaste was the centre of Costa Rican cattle ranching and was the site of over 40% of production in this industry (Ibraham et al., 2000), leading Costa Rica to have one of the highest deforestation rates globally (Sanchez-Azofeifa et al. 2001).

In the 1980s there was a collapse of the meat market, leading to farm abandonment, and increased government interest in conservation in the latter part of the decade (Bender 2012, Sanchez-Azofeifa et al. 2003). This resulted in over 25% of the country belonging to Protected Areas, with only restricted uses allowed, and incentives introduced to diversify the economy (Bender 2012; Powell et al 2002). The effectiveness of Protected Areas, however, continues to remain debated in the literature (Lopez-Carr and Burgdorfer 2013; Joppa and Pfaff 2010; Pfaff et al 2017; Robalino et al 2017). At a coarse scale, Protected Areas appear to increase the amount of forest that remains intact; however, at a fine scale, there is micro fragmentation and degradation that persists (Barber et al 2012). The effectiveness of both Protected Areas and local participation in forest management is largely considered site-specific. Regions directly adjacent to Protected Areas are also important to monitor for spillover effects and increased degradation (Andram et al 2008; Robalino et al 2017; Ferraro et al 2011).

Protected Area status does not correlate with soil, topography, remoteness, population growth, economic considerations, and infrastructure pressures for deforestation protection (Ellis and Porter-Bolland 2008, Porter-Bolland et al 2012), making it essential to consider the economic pressures on current forest extent in Costa Rica. Recent economic endeavours include ecotourism, technology manufacturing, and payments for ecosystem services markets, but much of the GDP still comes from cash crops and cattle (Jones and Spadafora 2017; Le Coq et al 2015). With projections of food shortages due to population growth, agricultural expansion may be required, leaving the future of the Costa Rica's non-protected forest in question (Mancosu et al 2015).

Technology and methodology advancements over the past decade have enhanced the quality and quantity of land cover change (LCC) research in tropical environments (Fischer and Lindenmayer 2007; Kuenzer et al 2014; Verburg et al. 2015). Cellular automata models use an algorithm to drive how different pixel changes migrate through multiple time steps, which makes the model highly applicable in time-series LCC analyses and project landscape changes into the future (Wolfram 1983; Mas et al 2014). One such platform, Dinamica Environment for Geoprocessing Objects (EGO), combined this statistical power with the information-dense geographic information systems field (Soares-Filho 2009). This created an open source platform that has been increasingly used for Amazonian deforestation, urban studies, and policy assessment due to its high adaptability, communicability, and ability link inter-scale information (Soares-Filho et al. 2014; Leite et al. 2012; Nunes et al. 2012; Stan et al 2015).

Despite these advances, there remain gaps in integrating biophysical, socio-economic, and legislative information in the LCC modelling field and with the variability of quality information in different study areas of Costa Rica, which provides motivation for this study. The objective of this paper is, therefore, to 1) study the areal extent and spatial pattern of the Costa Rican forests between 1960 and 2013 and 2) determine how those changes will progress into the future (2013-2069). These changes will be based on modifying the historical rates and include the development of the Protected Areas legislation. Patch metrics and fragmentation will be including as a measure of connectivity. Both provincial and national boundaries will be used to find differences in socio-political areas across the country. The deforestation models will be constructed using the Dinamica EGO platform and will include biophysical, socio-economic, and legislative variables as change driver inputs.

3.2 Study Area

This study was conducted in Costa Rica (Figure 3.1). The country's extent is estimated to be 51,100 km^2, with a population of 4.9 million people, and an estimated GDP of $57.4 billion as of 2016 (World Bank Development Data Group 2017). There are two coastlines and two mountain ranges spanning the centre of the country, the Cordillera Volcanica and the Cordillera de Talamanca (Stansifer et al. 2017), and the main forest types are montane forest, coastal mangroves, seasonally tropical dry forests, and an array of humid/rain forests, although these are not differentiated in this study (Holdridge 1967). Despite its small area, Costa Rica has one of the highest biodiversity index ratings globally due to its high number of species and endemic organisms (National Biodiversity Institute 2014; Global Environmental Facility 2007). This biodiversity is balanced by cleared rangeland and agriculture areas which support farming, ranching, growing urban areas, and a dense network of roads to connect the country (Zahawi et al 2015; Lopez 2003). The climate ranges from semi-arid to humid zones with a consistent temperature and a dry season ranging from 1 to 7 months (Enquist 2002).

3.3 Data

The Dinamica Environment for Geoprocessing Objects (Soares-Filho et al. 2009) requires at minimum two landscape maps. In this case, the historical landscape maps from 1960, 1979, 1986, 1997, 2005, 2010, and 2013, utilized in the historical analysis, were classified by Sanchez-Azofeifa (2015). The 1960 map was generated using aerial photographs from 1950 and 1965. The maps from 1979, 1986, 1997, 2005, and 2013 were all generated by Landsat images, while the 2010 map was generated using the SPOT satellite (Sanchez-Azofeifa 2015). The maps from 1997-2013 had 1500 control points, were independently validated in the field, and had errors of 5-10% (Sanchez-Azofeifa 2015). The original images were pre-processed for relative humidity and aerosols (Sanchez-Azofeifa 2015), classified into forest/non-forest regions (Sanchez-Azofeifa 2015), and resampled to 240 m for modelling. This resolution was chosen to balance the original 30 m image resolution with the biogeophysical datasets which ranged between ~ 120 m and county-based resolution. The interest of the Costa Rican government and researchers has been on collecting forest data which leads to this forest/non-forest classification, instead of including other land covers such as agriculture and silviculture as has been done in other LCC models (Rosa et al. 2014).

Biophysical maps including geology, topography, slopes, river and water routes, biological corridors, geomorphology, and watershed delineation were used as supplementary information for the predictive models and scenarios (Figure 3.2; Table 3.1). Legal boundaries of land, including Protected Areas, indigenous zones, and biological reserves were included (Table 3.1). One final class of variables also inputted into the models was anthropogenic information on population change, road development, and land usability assessments (Table 3.1).

3.4 Methods

Using Dinamica EGO, the amount and pattern of forest cover in 1960, 1979, 1986, 1997, 2005, and 2013 were assessed for the first study component. This long history of maps is important for understanding the entire picture of how the state of the current Costa Rican forest system has occurred and for consistency of analysis. The maps were analyzed for changes from forest to non-forest and non-forest to forest, by province and for the country. The images were assessed for both deforestation and regeneration to determine the overall trends and an inflection point of shifting trends. Additionally, patch numbers, sizes, and distances apart were calculated for forest and non-forest. Mean patch sizes and distances were assessed for the statistical difference between 1960, 2013, and the 2069 projections.

For the second component, using the historical changes from the past 2 decades (1997-2013) as a baseline, a Dinamica EGO model was built and validated. The 1997, 2005, and 2013 maps were chosen because of their consistency in classification techniques (from Landsat), validation against independent field measures, and the number of years between the calibration/validation (2005-2013) and transferability data (1997-2005). These features help to reduce non-systematic errors within the model and increase the model's ability to replicate both quantity and patterns of change in the projected forests. The biophysical and socioeconomic variables were used as auxiliary data to create a cube map for comparing areas of deforestation and regrowth. The level of each variable is compared to the changes or stability in an area and assigned a weight of evidence using a Bayesian statistical algorithm (Soares-Filho et al. 2009; Ferreira et al. 2012; Maeda et al. 2010). These variable weights are then used on the initial map to create a probability map of how likely it is that each individual cell changes to another cover type (Soares-Filho et al. 2009; Ferreira et al. 2012). The complex topography and competing driving variables in various portions of the country made it essential to run the model by province and subsequently consolidate the national results. It is also important to note that the intraprovincial drivers have more impact compared to interprovincial drivers on the forest change. The impact of elevation dynamics with micro-meteorology, soil, and human factors varies across the study, impacting ecozones differentially. This was evident by the model's ability to replicate the historical change forest at a provincial level and not when combined into a generalized national model.

Two functors, a series of algorithms that perform a particular operation (Expander and Patcher; Soares-Filho et al 2009), and the rate of change are utilized to project the landscape forward in time. The model's Expander and Patcher functions work complementarily (Soares-Filho et al 2009) with Expander contracting or expanding existing patches using the historic metrics and Patcher using the fragmentation metrics to create new patches of an appropriate size, isometry, and isolation (Berberoglu et al. 2016; Soares-Filho et al. 2009; Maeda et al. 2010). The fragmentation metrics are optimized using the historical data, to replicate the pattern of landscape development as the model is stepped into the future. The amount of land allocated to each functor is based on the rate of change and identification of the historical landscape changes in particular areas. For validation, Dinamica EGO compares the later time step map to the model simulation in an iterative manner, with a moving window size from 1 (the same pixel) to 13 pixels. The amount of deforestation is driven by the transition matrix, and the model validates the accuracy of the location of deforestation/regrowth. The model was validated at 85% within 2.5 pixels for the 2005-2013 time-step and performed consistently (also 85% accurate within 2.5 pixels) for the 1997-2005 time-step which was used to assess transferability between years. Moving into the future projections, it is essential that the time steps must be equivalent to those found in both the training and transferability data (i.e. 8 years).

The historical rates of change (1997-2013) were used to create a business-as-usual future scenario, and these rates were modified by province to increase deforestation by 1%, 2%, and 5%, and increase regrowth by 1%, 2%, and 5% (coded DF1, D2, DF5, RF1, RF2, and RF5, respectively). These rates provide an array of moderate and extreme scenarios and encompass the historical rates of change, even from the height of deforestation in the 1960s era (Sanchez-Azofeifa et al. 2007).

The changes in forest cover were assessed provincially and then aggregated to a national level, just as in the historical assessment. While transboundary impacts are important to consider, the historic model found that within province drivers outweigh the interprovincial effects.

To test the importance or relevance of Protected Areas, they were included and removed from a future BAU scenario model. The Protected Areas dataset is used in the models and to determine the effectiveness of this policy, and uses all Protected Areas designated by 2008, as the area set aside post 2000 is <3%. The probability of each area being deforested was then assessed in a severity index. If the majority of the park had an average probability of deforestation at >40% it was multiplied by the potentially affected area to determine the "Severity Index" or the potential impact if the area was not protected.

3.5 Results

3.5.1 Historical Model/Business As Usual

Between 1960 and 2013 there was a drop in the total amount of forest from just over 30,000 km^2 to nearly 26,000 km^2 with a high rate of deforestation from 1960 until 1986 (Figure 3.3 & 3.4). Subsequently, there was an apparent reversal of the trend with net regrowth up until 2013 (Figure 3.3 & 3.4); however, only half of the forest has been recovered. The Cartago, Guanacaste, and Puntarenas provincescontributed the most to Costa Rican deforestation (70%; Figure 3.4), with the 1960-1979 era contributing the most to the deforestation across all provinces with >40% in the southern provinces, and 30-40% in the north. Regrowth has been more consistent across the time periods, but Guanacaste has seen the highest proportion of overall regrowth (Figure 3.4). Overall 69% of the total deforestation occurred between 1960 and 1986, and 66% of the regrowth occurred in the post-1986 era (Figure 3.4).

T-tests were used to establish changes in the patch sizes and showed a significant decrease in the mean ($p= 0.02$). In 1960 the average patch size was approximately 33 km^2, while in 2013 it was <1 km^2, an ~100% drop (Table 3.2). There was an increase in the number of smaller non-forest patches, which drove a patch size decrease in the non-forest class, although it was not significant (mean 1960: 54.2 km^2; mean 2013: 3.4 km^2; $p= 0.15$). Patch distance was slightly different with significant decrease in distance between 1986 and 2013 for both forest (1960: 0.8 km; 2013: 0.5 km; $p < 0.0001$) and non-forest (1960: 1.0 km; 2013: 0.6 km; $p < 0.0001$). The greatest decrease in patch size occurred in 1960-1986, similarly to the highest deforestation rates (Figure 3.5). After 1986, the patch sizes stabilized (Figure 3.5).

3.5.2 Projections

The BAU scenario exhibited an expansion of forest to the 1960's extent by 2040, and stabilization in 2062 at 32,314 km^2. The most extreme deforestation scenario (DF5) stabilized in 2068 at 27,156 km^2, a 2,000 km^2 increase compared to present. The highest regrowth scenario, RF5, levelled in 2063 at 34,456 km^2 of forest. Mean patch size was not predicted to change significantly between 2013 and 2069 (Table 3.2) in any scenario, and there is a non-significant difference between the business as usual and larges regrowth scenario (BAU: 4.4 km^2; RF5: 16.0 km^2; $p = 0.19$). This also applies for the non-forest, where there is a non-significant decrease in patch size between the BAU and regrowth scenarios (BAU: 3.8 km^2; RF 5: 1.8 km^2; $p= 0.27$).

Changes in forest extent are not equally distributed between all seven provinces of Costa Rica, though all experienced net regrowth in the BAU scenario. Deforestation centered in the Puntarenas and Guanacaste provinces, while the north and patches adjacent to large tracts of current forest experience regrowth (Figure 3.6). In the most extreme deforestation scenario (DF5), the Puntarenas province experienced net deforestation, and Guanacaste had an approximately net zero change.

In the Protected Areas scenario, we found that there were 13 Protected Areas > 1 km^2 that an average probability of being deforested >40% for >50% of the park (Figure 3.7). When multiplied by the potentially impacted area within the park, Golfo Dulce and Santa Rosa National Park would have the most severe impact on the environment if they were no longer Protected Areas.

3.6 Discussion

Resistance is the forest's ability to persist through change, and resilience is the system's having the ability to recover to a state near its original (Duveneck and Scheller 2016). The future projections assess the Costa Rican forest's resistance and resiliency under both extreme and moderate projection scenarios. Even the highest deforestation rates only produce forest loss in Puntarenas, with a net-zero change in Guanacaste. Puntarenas and Guanacaste are, therefore, the provinces to monitor closely for symptoms of change and increasing deforestation and to implement pilot projects or community management techniques to avoid deforestation.

When looking at historical deforestation, especially from 1960 - 1986, economic factors drove forest loss, with ranching as the primary driver during this time (Castillo et al., 2014; De Sey et al 2015; Gasparri and de Waroux 2015). Within that time period, there were five economic phases that have been identified: (i) 1950-1963 - Shifting from an agriculturally-based to international trade economy (ii) 1963-1973 - expansion of internal regional agriculture trade markets (iii) 1974-1978 - Industrial development and increased imports (iv) 1978-1982 -

economic crisis (v) 1983-1989 post-crisis recovery (Sanchez-Azofeifa 2000). In the post-1989 era, Costa Rica has moved beyond this post-crisis recovery into the conservation-based, diversified economy. While reforestation efforts in the later 1970s were insufficient to reverse forest loss, carbon sequestration initiatives increased interest in environmental conservation (Sanchez-Azofeifa et al. 2001). Conservation areas initially reduced deforestation in localized areas, but over time this was insufficient to balance agricultural expansion (Sanchez-Azofeifa et al. 2003), a finding echoed here. Between the late 1980s and 1990s Costa Rica experienced a great degree of diversification as well as several new government driven reforestation policies (Sanchez-Azofeifa 2000). These changes on economic and conservation policies were also in tandem with the sale of their land by many rural farmers, who in turn migrated to the country's largest cities. With these changes in both migration, economic and environmental policies, new environmental education programs were created to support elementary and high school education with the goal of building a collective sustainable conscience in the country (Castillo et al. 2013). This fundamental shift in how the human-environment interaction is framed in Costa Rica indicates that the regeneration seen in most recent decades is supported by a strong foundation of environmental conscientiousness. This interplay of government, economic, and cultural shifts supports the continuation of this trend into the future.

The regeneration of forest patches is a promising result, but its non-significance means additional measures are imperative for increasing forest connectivity. Fragmentation damages the diversity and quality of remaining forests, with the edges experiencing extreme temperature and water conditions (Ribeiro et al. 2009; Magnago et al. 2015). Road density and topographic features may permanently restrict patch sizes growth and ultimately reduce the total secondary forest connectivity. Road construction is typically precipitated by economic drivers that exacerbate environmental damage and degradation, i.e. logging, mineral extraction, or farmland (Laurance et al. 2014), further reducing ecosystem functioning and services (Lewis et al. 2015). Tree mortality and invasive species can impact patch interior vapour pressure deficit, temperature, and soil moisture content (Laurance 2008).

Costa Rica is considered one of the leaders in the Americas on environmental policy, due to its innovative environmental management and sustainable development projects. The areas protected by legislation increased greatly between 1950 and 1990 as did the number of foreign visitors to these areas with the rise of the Costa Rican ecotourism industry (Robalino et al. 2017).

Even as early as the mid-1990s, Costa Rica had more conservation projects than its larger counterparts (Blum 2008). One of the central focuses of the initiatives was on education; however, there remains conflict about program effectiveness among educators, policymakers, and industry (Blum 2008).

Additionally, while the land tenure system in much of Central and South America are not well defined, and create increased complexity relating to the agriculture-forest interface, Costa Rica is unique in its definitions and subsequent restrictions relating to forest use. Costa Rica has very stringent and explicit land tenure considerations for both public and private lands which reduces the variability across the country, the former highly supported by a modernization of the national land registry where every parcel of land is registered, and information is publicly available. The 1995 7575 Forest Law redefined the forest use rights and set a precedent for sustainable management and conservation (Corbera et al. 2011). It restricted the access to public forests and the withdrawal of any forest resources. For private land, land ownership must be proved for 10 years before changes to reserve designation can be made, and finally, the indigenous rights are controlled by the Indigenous Integral Development Associations, restricting their access to commercial forest production (Corbera et al. 2011). This combination of factors results in a strict land tenure system where small landowners with no title and large commercial farms are not problems for deforestation dynamics like they would be in other countries which host the Tropical Dry Forest.

In this paper, we investigated the relevance or effectiveness of a command and control policy, Protected Areas, which designates areas are not used for agriculture or industry (Lambin et al. 2014). Only thirteen PAs, of the 25% of the country, have a high/medium probability of deforestation in the majority of the park. This is a relatively small portion of the country where deforestation is of concern without legal protection and is consistent with the 7-9% of the forests experiencing reduced deforestation after receiving the PA designation found in other studies (Andam et al 2008, Sanchez-Azofeifa et al. 2007). This low percentage is indicative of the fact that historically many of the Protected Areas were located in high slope and undesirable areas where there was little initial deforestation (Pfaff et al. 2009). This reinforces the need to mindfully consider at-risk locations and ecosystems which could benefit from protection instead of the current practice of choosing areas unsuitable for human use and thus having a low deforestation rate and impact (Andam et al 2008). The high-risk PAs found may be good places to invest money to enforce restrictions and work with the community to create a local management strategy (Porter-Bolland et al 2012). With a more targeted funding, a more holistic approach can be applied to hotspot areas to help balance the economic and environmental services pressures. In other areas, such as Brazil, it has been suggested that investing in the local economy and local businesses may be more sustainable than Protected Areas (Pfaff et al. 2014).

This targeted approach can extend into national management and monitoring programs. Forest inventories completed by SINAC have been a source of high-quality data but at high cost. While their pilot inventory in 2001 was conducted thoroughly by using a combination of aerial photography and in-situ study for the entire country, this style of inventory is costly to repeat on an annual basis (Kleinn et al. 2001). With the identification of deforestation hotspots, it is economical to conduct detailed remote sensing monitoring in these locations but wall-to-wall estimations of forest cover are redundant assuming that social and environmental conditions continue based on our current understanding of the environmental and societal drivers. By the 2060s when the regrowth and deforestation rates stabilize in our model, it may be possible to further reduce the inventory requirements. This would free up capital to be invested in programs, such as payments for ecosystem services, which could use the additional funding to increase buy-in from industry.

A more targeted approach to mapping would also be of benefit when looking at the data that is need to provide a more comprehensive modelling and land dynamics analysis approach. While this has historically not happened, the Costa Rican Central Bank, as part of its participation on the World Bank's Wealth Accounting and Valuation of Ecosystem Services (WAVES), is starting to generate more comprehensive land cover and land use map for 2017 and onwards. Wall-to-wall mapping and models in Costa Rica is also problematic because of the importance of intraprovincial drivers. Models, including the one utilized in this paper, have difficulty replicating patterns when it is run in a generalized national model. This is because of the presence of east-west and north-south variability on both bio-physical and socioeconomic factors driving land cover change; as such interactions associated with the estimation of forest cover change are not uniform across the entire country. Therefore, modelling the entire country at once leads to problematic results. By dividing this up by province or by hotspot, it largely controls for these differences in biosphere-hydrosphere-pedosphere-atmosphere-anthroposphere relationships.

When we look at other policies that have been implemented in Costa Rica, one of the most prevalent ones is the Reduction of Emission from Deforestation and Forest Degradation (REDD+) policy. REDD+ was designed to reduce emissions from deforestation and forest degradation by using positive incentives (Mbatu 2016). In Costa Rica, the first phase of REDD+ was implemented in 2008, and the Emission Reductions Payment Agreement phase was implemented for 2015-2020 (REDD CR 2018). There has been research that shows stakeholder buy-in is considered imperative for REDD+ to be effective; however many stakeholders are concerned about the transparency of the governing process (Cadman et al. 2017). It is interesting to note that the Costa Rican regeneration rates exceeded the deforestation rates long before the conceptualization of the REDD+ program and the implementation of the REDD+ program has not altered regeneration or deforestation rates, according to our study. As a result, it is unlikely that the REDD+ policy will have any additional impacts, positive or negative on the future forest in Costa Rica.

3.7 Conclusion

Costa Rica's deforestation history is divided up into two major sections, with the pre-1980 era heavily dominated by agriculture/cattle driven deforestation, and post-1980 exhibiting a period of regrowth. This forest regeneration is projected to continue nationally until it stabilizes with a balance of deforestation and regrowth in the 2060s. Assuming climate change does not play a role, the forest extent is currently sustainable or projected to expand. The Puntarenas and Guanacaste provinces are projected to have the highest deforestation. Protected Areas still have some relevance, with 9 of the regions experiencing more than a medium probability of deforestation without the legislation. These areas could provide an interesting case study to test how community style management and control style protection can work in concert moving forward.

Moving forward, a land classification which differentiates the types of land uses over the economic eras of Costa Rica and pasture lands for cattle from croplands, and allows for the explicit extraction of plantations through time, is needed. The dynamics of each land use on forest change is limited based on the available data, and to truly understand the system in Costa Rica, these explicit databases must be created for a more comprehensive understanding of the

Costa Rican land system and how it impacts the change in forest cover through different eras in history.

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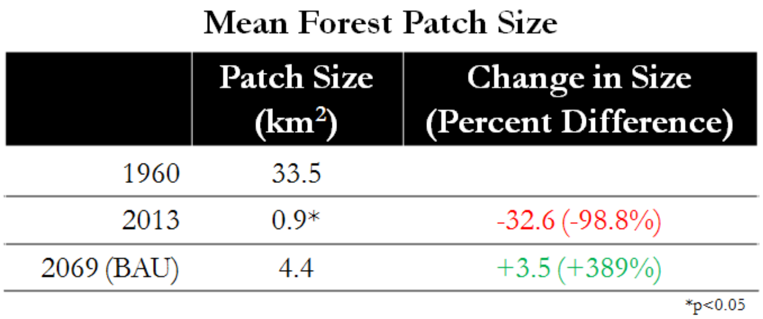
Table 3.1:

Map Name	Type/Resolution	Source	Year
Biogeophysical Variables			
Biologic Corridors	Shapefile / min area = 18 km^2	Programa Corredores Biológicos SINAC 2009	2008
Biotic Zones	Shapefile / min area = 2.5 km^2	Centro Científico Tropical (CCT) / Ministerio de Agricultura y Ganadería (MAG)	N/A
Digital Elevation Model	Raster / 11 m	Proyecto Atlas Digital de Costa Rica	N/A
Fire Risk	Shapefile / min area = 14 m^2	Part of Ana Irene Jimenezès work - Utilization of a Geographic Information System for the Determination of Risk Zones in order to Secure Forest Plantations	N/A
Geology	Shapefile / min area = 1643 m^2	José Alberto Fernández Solórzano	
Geomorphology	Shapefile / min area = 0.30 km^2	Unkown - Atlas of Costa Rica	
Rivers	Shapefile / line data	GEOTECNOLOGIAS S.A.	N/A
Slopes	Raster / 11 m	Derived from the DEM	N/A
Soils	Shapefile / min area = 1.5 km^2	MSc. Rafael Mata, Alban Rosales y Alexis Vásquez, DAngelo Sandoval	2008
Watersheds	Shapefile / min area = 1124 m^2	Ing. Vladimir Jiménez	2008
Socioeconomic Variables			
Distance to Roads	Raster / 240 m	Unkown - Atlas of Costa Rica	2008
Population Change	Shapefile / District level data	GEOTECNOLOGIAS S.A.	1997 - 2000
Protected Areas (including biological reserves)	Shapefile / min area = 23, 143 m^2	SINAC	2008
Usability	Shapefile / mean area = 40.8± 225 km^2	Unknown - Atlas of Costa Rica	2008

Table 3.2:



Mean Forest Patch Size

	Patch Size (km^2)	Change in Size (Percent Difference)
1960	33.5	
2013	0.9*	-32.6 (-98.8%)
2069 (BAU)	4.4	+3.5 (+389%)

*$p<0.05$

Figure 3.1:


NICARAGUA
Caribbean Sea
ALAJUELA
GUANACASTE
HEREDIA
COSTA RICA
CARTAGO
LIMON
SAN JOSE
Pacific Ocean
PUNTARENAS
PANAMA

Figure 3.2:

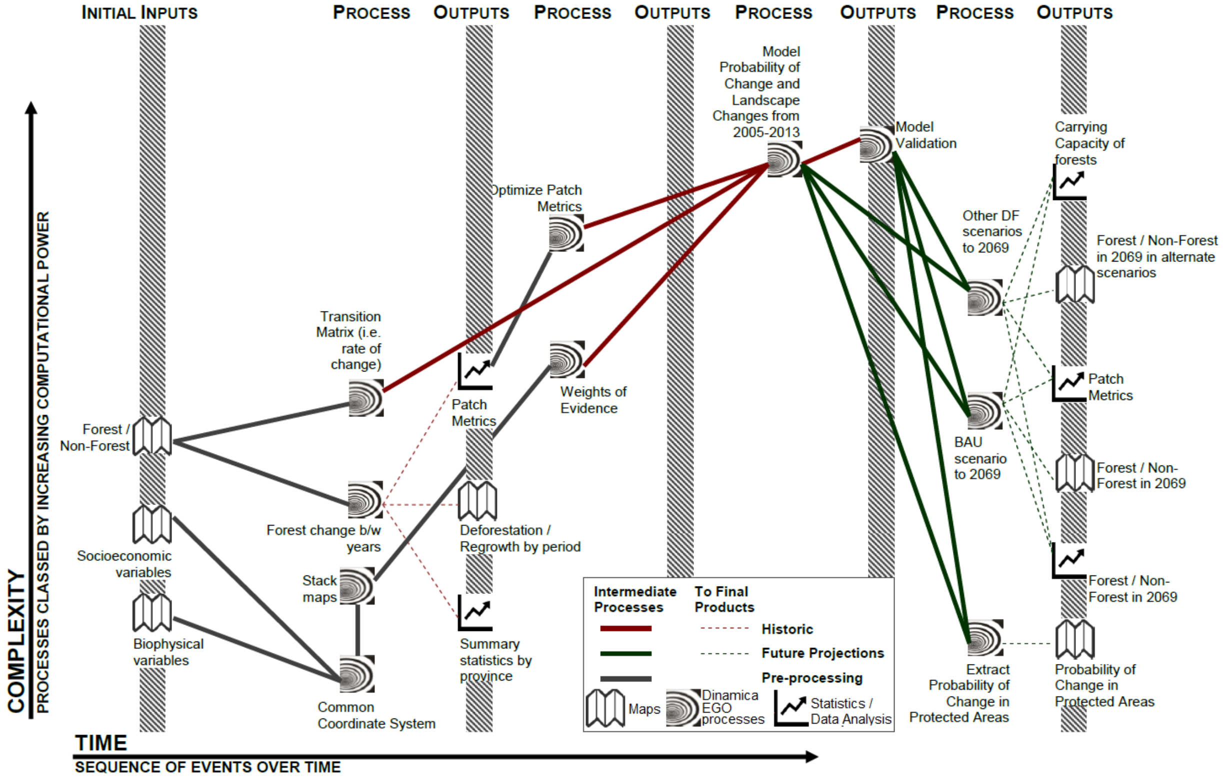


Figure 3.3:

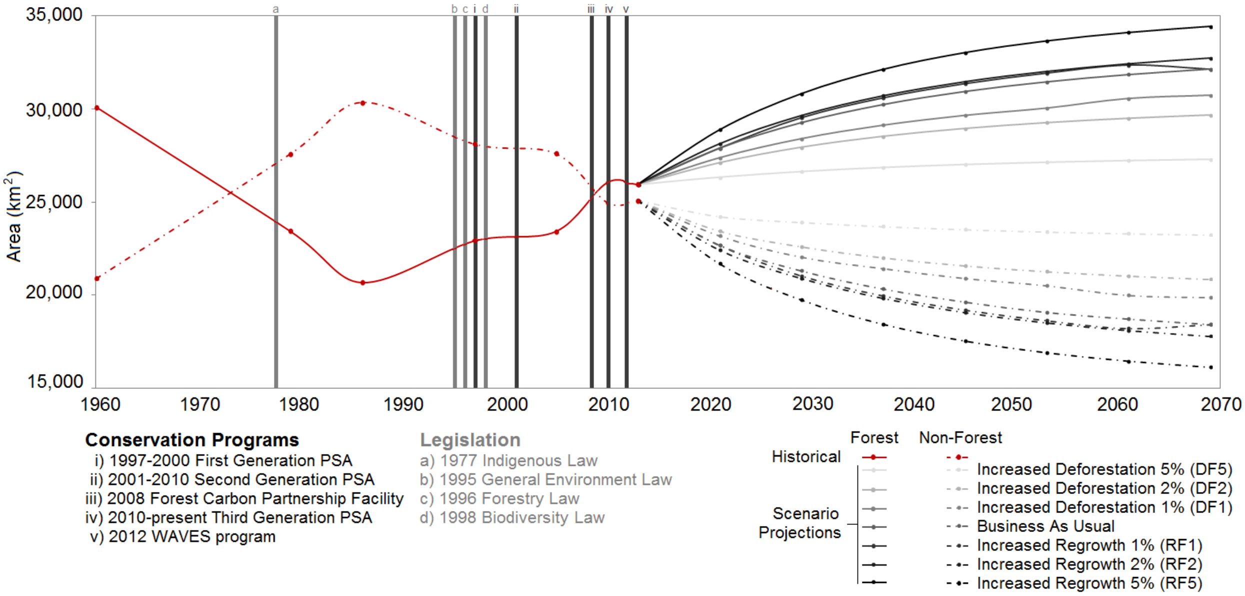


Figure 3.4:

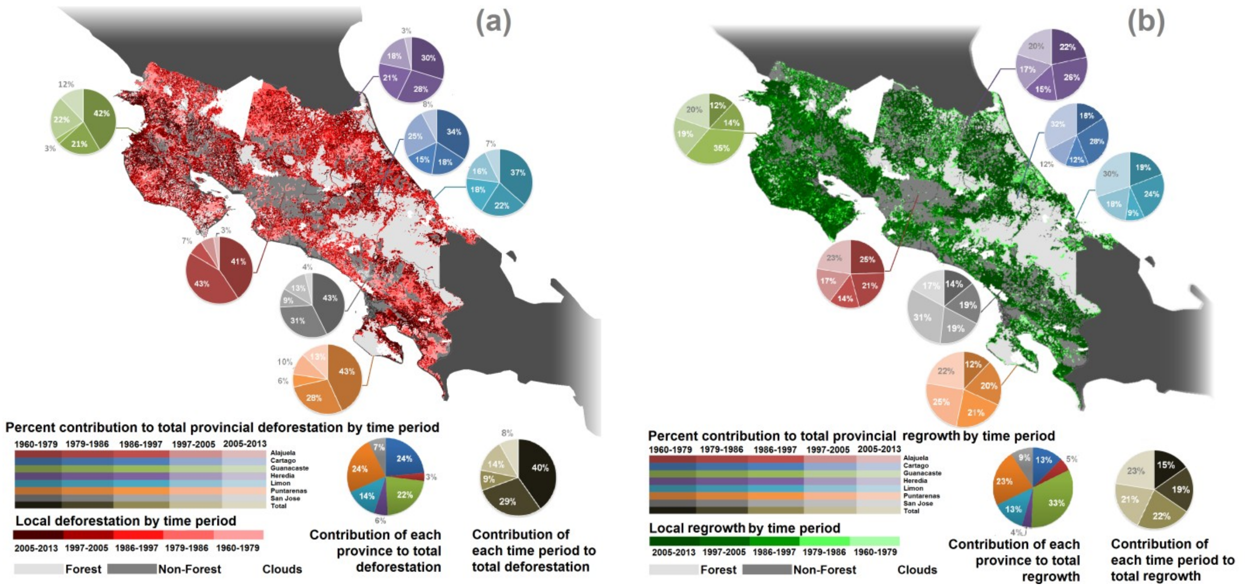


Figure 3.5:

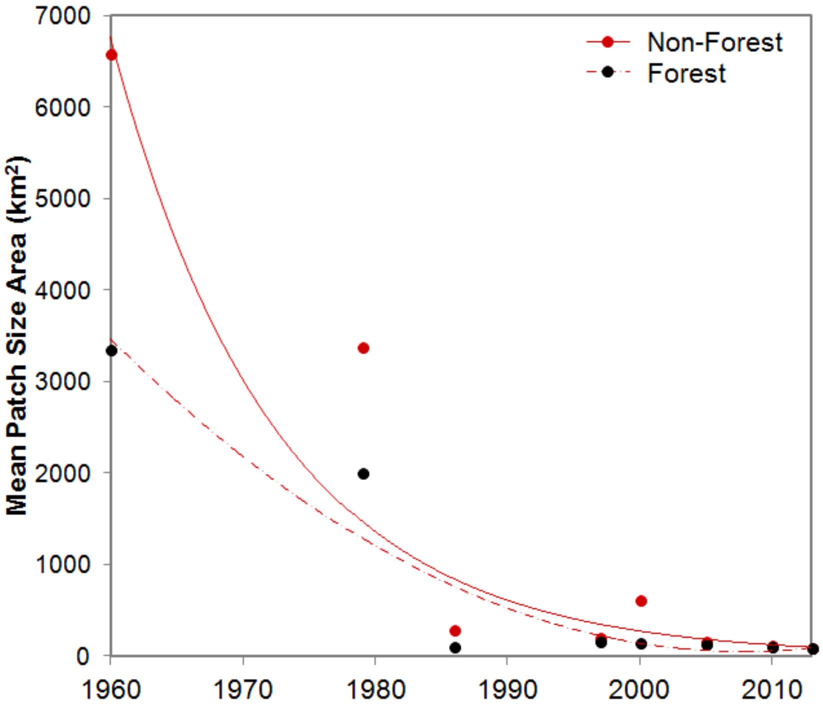


Figure 3.6:

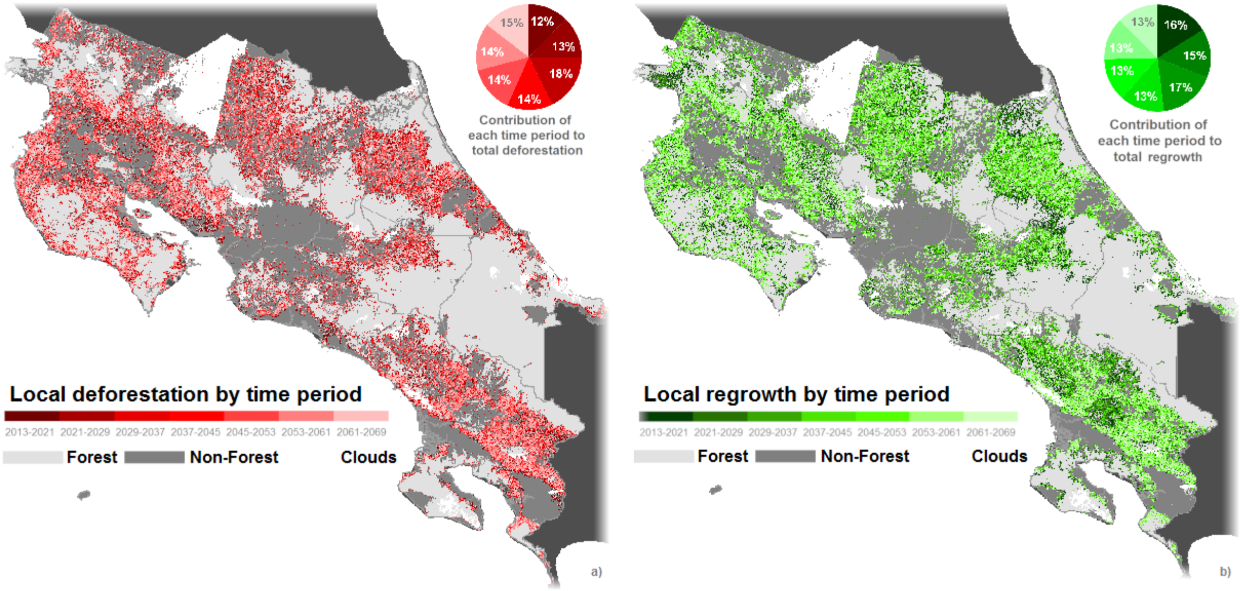
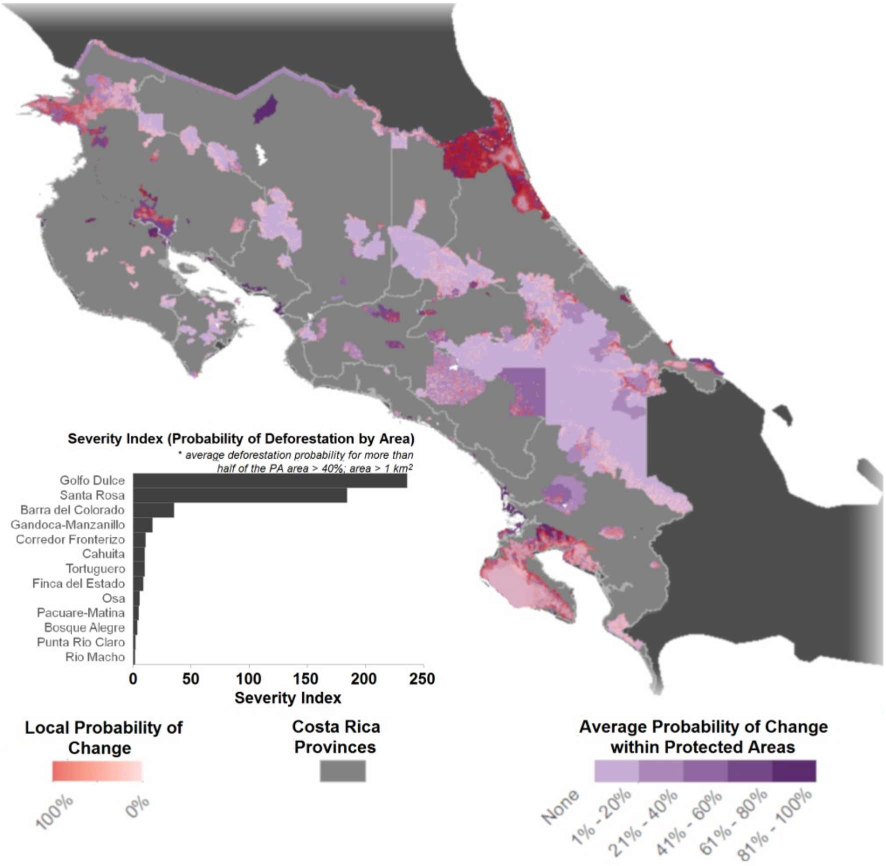


Figure 3.7:



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CHAPTER 4 - Climate change scenarios and projected impacts for the forest productivity in the Guanacaste province: lessons for tropical forest regions

Abstract

The Guanacaste Province of Costa Rica is home to highly diverse forests which are under threat of degradation due to ongoing climatic changes. There is concern that increasing temperatures and changes in precipitation will force these forests outside of their optimal growth ranges leading to degradation, measured using forest productivity. The objectives of this study are, therefore, to project and assess climatic changes in Guanacaste and the to build a relationship between these climatic changes and forest productivity with the goal of projecting productivity trends into the future. The ClimateSA model was used to project the RCP 4.5 and 8.5 scenarios from 2018 until 2080 and then assess these projections for the mean and extreme future conditions. Furthermore, the MODIS Gross Primary Productivity (GPP) algorithm was used to build a relationship between forest productivity and the Vapour Pressure Deficit scalar (VPD scalar) and project GPP alteration under future climatic scenarios both seasonally and annually. Results indicate that Guanacaste's mean annual precipitation will stay within the historic levels for both the RCP 4.5 and 8.5 scenarios. The monthly and annual temperatures increase in all projections. Results also indicate that the productivity-climate relationship follows a quadratic relationship between GPP and the VPD scalar. This quadratic relationship leads to areas with higher precipitation (high VPD scalar) experiencing an increase in GPP as they dry in the future. In drier areas (low VPD scalar), reduced precipitation will stabilize or decrease GPP.

Keywords:

Climate change, productivity, Guanacaste, tropical dry forest, climate-biosphere interactions

4.1 Introduction

Climate change, and its impact on ecosystems globally, has become of increasing scientific concern with a growing body of academic literature building relationships between the climate and biosphere and using these relationships to project ecosystem changes into the future of uncertain climatic change (Navar-Chaidez 2011; Poorter et al. 2016; Haselhorst et al. 2017; Golicher et al. 2012; Magrin et al. 2014; Seiler et al. 2014). On a regional scale, the Intergovernmental Panel on Climate Change (IPCC) climate models project, for Central America, dry season temperature increases of 1°C to 5°C by 2080, and 1.3°C up to 6°C in the wet season. Magrin et al. (2014) estimates that for Central America the overall precipitation in the wet season in 2080 will decrease by 30% or increase 5%, with a high level of spatial variability. Some of these same studies suggest more frequent and severe droughts, while other find potential evidence for increasing hurricane frequency in the same region (Cai et al. 2015; Stott et al. 2016). These climate and earth system models have such a high uncertainty because the feedbacks between the earth, ocean, and atmosphere cannot be fully realized in a model system (Gross et al. 2018). Additionally, the relationships that are incorporated into each model system often differ, as there have been many different foundational assumptions and equations developed which relate these land-climate functions (Bonan 2019).

There are positive relationships that have been built based on in-situ and remote sensing data between precipitation and biomass, recovery rate after disturbance, and pollen production (Navar-Chaidez 2011; Poorter et al. 2016; Haselhorst et al. 2017). Temperature has been likewise linked to flower production and species recruitment (Haselhorst et al. 2017; Pau et al. 2013). Increased frequency of extreme events, especially hurricanes, has been correlated with decreasing forest recovery and resiliency in the subsequent events (Gavito et al. 2018). When these land-climate models are projected into the future, however, often there are mixed results, with some models predicting severe decreases in biodiversity and biomass (Golicher et al. 2012; Magrin et al. 2014; Seiler et al. 2014); while other models indicate that tropical forests will mitigate their alteration through microclimatic modifications and quick drought recovery times (Golicher et al. 2012; Magrin et al. 2014; Seiler et al. 2014). These changes, both climatically and in the biosphere, are subject to regional scale variations and the response of the biomes present in each location.

Costa Rica is of particular interest for the relationship between climatic change and forest ecosystems as its policies have focused heavily on conservation (Sanchez-Azofeifa 2003; Stan and Sanchez-Azofeifa 2019a), resulting in Protected Area designations for over 25% of the country, thereby making climatic change an important driver of ecosystem resilience or degradation. The country's forests are economically important as 65% of incoming visitors report that ecotourism is their primary reasons for travelling to Costa Rica (ICT, 2017). While Costa Rica has been extensively studied concerning its sustainability, conservation strategies, and the biodiversity and structure of its forest (Castro et al. 2018; Sanchez-Azofeifa et al. 2007, 2009; Stan and Sanchez-Azofeifa 2018), projections of climatic change and their impact on forest productivity in the country is not as well understood.

As such, the main objectives of this study are: a) use a regional climate model to project a set of average and extreme climate scenarios for the Guanacaste Province in Costa Rica, using different atmospheric carbon projections. These scenarios are compared with the historical data, regarding both the time series and spatial distribution of the changes, b) to relate the historical climate data to Guanacaste's past Gross Primary Productivity, and c) to use the climate change projections to evaluate the future GPP of Guanacaste's forest. We hypothesized that regional droughts will increase with higher temperatures and reductions in precipitation. These increases in drought will lead to severe reductions in GPP across the entire region. We expect that this assessment will help inform conservation programs that are the cornerstones of the country’s environmental legislation and determine if degradation, defined here as a reduction in biodiversity and reduced ecosystem services supply, will increase in severity and extent as we move into warmer climatic regimes. Additionally, the relationship between climate projections and productivity can subsequently be expanded to other parts of Central and South America where similar ecosystems exist.

4.2 Study Area

The Guanacaste Province is located in the northwest portion of Costa Rica and is bordered by Nicaragua, and the Costa Rican Provinces of Puntarenas and Alajuela (Figure 4.1). With an area of 10,140 km^2, the landscape is dominated by farmlands and highly fragmented patches of forest, including tropical dry, moist/wet forest and rainforest (Stansifer et al. 2017;

Holdridge 1967). Liberia is the capital city and contains over a quarter of the province's 325,000 people (INEC, 2011).

The first National Park in Costa Rica was established in the Guanacaste Province in 1971 (Santa Rosa National Park), and today the province is home to 8 terrestrial National Parks, covering over 1300 km^2. According to Janzen (2000), biodiversity in Guanacaste represents approximately 2.4% of the world's terrestrial biodiversity and 60% of all biodiversity in Costa Rica.

The Guanacaste landscape is a mix of natural, secondary, and managed land. Much of the forest in Guanacaste was lost between 1950 and 1980 with the rise of ranching and land use intensification for cattle and agriculture (Augelli, 1989, Arroyo-Mora et al. 2005, Calvo-Alvarado et al. 2009). There has been a reversal of this trend in the post-1980 era, with the diversification of the Costa Rican economy. Although the Guanacaste Province continued to focus on extensive/intensive cattle ranching, with the average farm size double the national average (0.54 km^2 versus 0.26 km^2), Guanacaste also has the highest proportion of forest regeneration in the country (National Agricultural and Farming Census of Costa Rica, 2015). In the primary and secondary growth forests, there is a mixture of tropical dry, moist/wet forest and rainforest according to the Holdridge life-zones (Holdridge, 1967; Jadin et al. 2016). Within the National Parks of Guanacaste analysed in this study, there are 8 Holdridge life-zones (1967): premontane rain forest, premontane wet forest, lower montane rain forest, tropical wet–premontane transition, premontane moist–basal transition, tropical dry forest, tropical moist forest, and tropical dry–moist transition. Tropical dry forests can be found in the Guanacaste lowlands and are ecosystems adapted to dry climatic conditions and rainfall seasonality, ranging from 500-2500 mm per year and a minimum 3-month dry season (Sanchez-Azofeifa et al. 2005). Precipitation in moist and humid forest ranges from 2000-4000 mm per year and above 8000 mm per year for the rain and cloud forests found in the highlands of the Guanacaste mountain range. The province typically experiences a dry season from late November until May, followed by two rainy seasons abutting a month-long dry spell. The smaller rainy season is from May to July and the main one from August to November (Janzen and Hallwachs 2016). The status of the El Niño Southern Oscillation and the North Atlantic Oscillation climate systems can greatly affect the extent of the dry season and the intensity of the precipitation (Babcock et al. 2016).

4.3 Data and Methods:

4.3.1 Data sources

Historical data was derived from the 1901-2009 CRU-TS 3.1 dataset (Mitchell & Jones 2005), comprised of land-based climate stations and six monthly variables. Future projections were based on the IPCC AOGCMs CMIP5 models for both the RCP 4.5 and 8.5 carbon concentration scenarios. Model data was validated against ground data collected from seven climate stations across the province and against GPP data from eddy covariance towers (SI 4.1 & 4.2). The Gross Primary Productivity (GPP) products were collected from the MODIS MOD17A2H V006 product at a 500-meter pixel size resolution for the 8 terrestrial National Parks in Guanacaste and averaged within those areas. We selected these sites since they have document little or no land cover change (Stan and Sanchez-Azofeifa, 2018). Values were aggregated into monthly composites from years 2000 to 2015.

4.3.2 ClimateSA Model

The ClimateSA model, developed by Hamann et al. (Hamann et al. 2013) as part of a suite of regional climate models covering the Americas and Europe (Wang et al. 2016; Castellanos-Acuna et al. 2018), was used in this paper. The climate data generated by this model comparison package is available at http://tinyurl.com/ClimateSA, and is based on the methodology described by Hamann et al. (2013). ClimateSA is a model comparison package which compiles historical data from 1900-2013 and a suite of 16 CMIP5 accepted models projecting climate variables up to 2080. The model uses historical in-situ data, interpolated using eco-zones and digital elevation models, from sites across South America. The historical climate variables, from the 2005 CRU-TS3.1 dataset and updated with the 2013 CRU-TS 3.22 (Mitchell and Jones 2005), were downscaled to the region of interest using a temperature lapse algorithm known as the "Delta Method" (Mitchell and Jones 2005). The “Delta Method” is used in the ClimateSA model to integrate the historical and future scenario data, as well as to project monthly and annual variables averaged over a 30 year climate period to 2080 using a bilinear interpolation on an anomaly grid (Wang et al. 2012). The temperature lapse algorithm was interpolated by the Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly et al. 2008), which is especially useful in mountainous regions to create weather anomalies associated with rain shadows, or valley temperature inversions (Hamann et al. 2013).

Future climate projections used in this paper are part of the Coupled Model Intercomparison Project phase 5 (CMIP5) for the World Climate Research Project, and produce basic and derived variables including Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP), and the Climatic Moisture Deficit (CMD). These models are a derivative of the Atmosphere-Ocean General Circulation Model (AOGCM) suite and are applied using two of the IPCC Representative Concentration Pathways (RCP) 4.5 and 8.5. Future projections were limited to three time-steps, which followed the historical climatic periods of 30 years (Hamann et al. 2013): 2011-2041, 2041 - 2070, and 2071 - 2100, considered to be 2020, 2050, and 2080 respectively (Wang et al. 2012).

The ClimateSA suite is of particular use as it allows for the long term comparison of historical data, as well as future data, that has been downscaled to a resolution which is useful at regional scales. Guanacaste is a small province, with many models covering the entire area in few pixels, and not allowing for the discrimination of climatic differences between regions in the province. Additionally, ClimateSA provides a suite of variables which are essential for not only the understanding of how the climate will change in Guanacaste, but also for projecting the productvity of the forests into the future.

4.3.3 Data Analysis

The assessment of climate change and forest response involved a two-fold analysis. The first part of the analysis involved regression of ClimateSA data against field data with the objective of validating the model data. Double-mass curves (Gao et al. 2017) were used to compare stations internal consistency within the stations' data quality control. The model results were validated against the in-situ station measurements and subsequently, used to determine the spatial variation and net change of temperature and precipitation across the province.

For future scenario development, the Ensemble and most extreme models were run to project the smoothed average and most extreme climate change scenarios for Guanacaste. The Ensemble model is the statistical mean of the other 15 models (ACCESS 1-0, CanESM2, CCSM4, CESM1-CM5, CNRM-CM5, CSIRO-Mk3-6-0; GFDL-CM3; GISS-E2R, HadGEM2-ES, INM-CM4, IPSL-CM5-MR, MIROC5, MIROC-ESM, MPI-ESM-LR, MRI-CGCM3) and, as a result, averages the model anomalies and extremes within the scenario projections (Soares et al. 2012).

We assessed the changes in the Guanacaste climate between present to 2080 using the ClimateSA models for the 4.5 and 8.5 RCP scenarios (Riahi et al. 2007; Clarke et al. 2007). These scenarios were originally set out in the IPCC AR5 (2014). The RCP 4.5 scenario increases the minimum, mean, and maximum annual temperatures by 2.0°C by 2080 without significantly changing the precipitation. The Ensemble RCP 8.5 scenario increases the minimum, mean, and maximum temperatures by 3.7°C by 2080, again without significant changes to the precipitation. These scenarios were chosen as the RCP 4.5 scenario is the low emission scenario that is currently viewed as a target for emissions, and the RCP 8.5 scenario is the business as usual scenario.

The changes from the historical rates, projected by the model to 2020, 2050, and 2080, were calculated over the entire province. This change assessment applied to the annual and monthly temperature (Mean, Min, and Max), and the monthly precipitation. The Climatic Moisture Deficit (Equation 1) was calculated separately to compare to previous levels of moisture deficit on both a monthly and annual time-scale.

$$CMD = ETo - P \qquad Equation\,(1)$$

Where ETo is the reference atmospheric demand and P is precipitation. The reference atmospheric demand was calculated through the Penman-Monteith equation to determine the incoming solar radiation values (Allen et al. 1998, Wang et al. 2012).

Future scenarios of the monthly and annual temperature and precipitation were also extracted from the model for eight protected areas in the province. We extracted from the model future projections of maximum, minimum, average temperature and annual precipitation using a 500 m by 500 m grid covering all of the Guanacaste province. The former allows for the integration of Moderate-resolution Imaging Spectroradiometer (MODIS) satellite products and climate data in the second part of the analysis. The minimum, mean, and maximum annual temperatures and MAP were averaged for each protected area in Guanacaste.

The impact on forest productivity, defined as the capability of vegetation to uptake carbon during photosynthesis and store it as biomass in the ecosystem (Nightingale et al. 2004), was analyzed via the quantification of changes in Gross Primary Productivity (GPP) for the eight protected areas selected inside the province. The GPP monthly averages were compared against the VPD scalar used by the MODIS GPP algorithm (Running and Zhao, 2015). The relationship in the historical data was then used to project the changes in GPP moving into the future using the climatic variables from the ClimateSA model. The VPD scalar is used in the MODIS GPP algorithm (Running and Zhao, 2015), through the following formulas:

$$GPP = \varepsilon \times APAR \qquad \textit{Equation (2)}$$

$$\varepsilon = \varepsilon_{max} \times TMIN_{scalar} \times VPD_{scalar} \qquad \textit{Equation (3)}$$

$$APAR = IPAR \times FPAR \qquad \textit{Equation (4)}$$

where:

GPP = Gross Primary Productivity

ε = efficiency

ε_{max} = maximum efficiency

APAR = absorbed photosynthetically active radiation

$TMIN_{scalar}$ = scalar for minimum temperature

VPD_{scalar} = scalar for vapour pressure deficit

IPAR = incident photosynthetically active radiation

FPAR = fraction of photosynthetically active radiation

Over a long time frame, APAR is assumed to be constant in an inter-annual context for this tropical ecosystem (Goetz et al. 2000) and was therefore not modified in the GPP equation. For the efficiency coefficient (ε), the minimum temperature scalar requires a temperature fluctuation between -7°C and 9.94°C for the forest that is found in Guanacaste (Channan et al. 2014). Since the temperature in Costa Rica never comes close to this range, the efficiency and GPP range solely relies on the VPD scalar. The combination of these equations, therefore, results in:

$$GPP = \varepsilon_{max} \times VPD_{scalar} \qquad \textit{Equation (5)}$$

This proportionality between the VPD scalar and the MODIS GPP can, therefore, be tested for the Guanacaste region using regression statistics. The VPD scalar can be determined by the formula (Abtew and Melesse, 2013):

$$VPD\_scalar = e_s(1 - \frac{e_a}{100})$$ *Equation (6)*

where:

$$e_s = 0.611^{17.27 \times T_{ave}/(T_{ave}+237.3)}$$

$$e_a = 0.611^{17.27 \times T_{min}/(T_{ave}+237.3)}$$

These formulas are used to calculate the VPD scalar to develop the relationship between the scalar and the MODIS GPP products in the protected areas. It is then used to project the GPP moving into the future, derived from the temperature and VPD scalar (Equation 6). This calculation was done for both the RCP 4.5 and RCP 8.5 projections. These values were compared to historic GPP and its variability to determine if the productivity will change outside of the range of natural variability. The climate variables and the GPP were linearly regressed to determine if any of the variables have a significant correlative relationship ($p \leq 0.05$).

4.4 Results

4.4.1 Climate Variables

The climate variables were assessed both historically and with future projections after being validated against in-situ station data ($p<0.05$; slopes: 0.9-1.05; $R^2=0.6$). MAT historically averaged 25°C per year since the 1920s, although there is a trend of temperature increasing by 0.16 °C per decade since 1950 (Figure 4.2). Since 2000, the monthly average temperature ranged from 24°C to 28°C, with monthly temperature extremes ranging between a minimum in the mid-teens to maximums in the low thirties relatively consistently throughout the decade. When the temperature is projected forward into 2020, the average increases to just over 26°C for both the RCP 4.5 and RCP 8.5 Ensemble Scenarios. The range of mean temperatures projected in different models consistently varies by 2°C in 2020, 2050, and 2080, while the difference between the minimum and maximum temperature varies by 14.2°C (Table 4.1).

When the temperature is considered by seasons, there are significant differences in the wet and dry season maximum and minimum temperatures ($p<0.01$), but not in the average temperatures ($p>0.10$; SI 4.3). There are also significant differences between the historical minimum, average, and maximum seasonal temperatures, and those projected in each season of the RCP 8.5 scenario ($p<0{,}001$). The low emission scenario does not exhibit a significant difference from historical seasonal temperatures ($p>0.10$).

This is consistent with the monthly temporal distribution of the temperature data which remains relatively consistent. There is an increase in temperature to its peak in April, before dropping off in May and June, slightly increasing in July and August, and then returning to its decline, for the coldest month in January. The mean and maximum temperatures exhibit this slightly bimodal pattern, which is not found for minimum temperature. This pattern occurs in the monthly data since 2000 and is carried forward in the projections.

Overall, the temporal distribution of the temperature does not change, and we find a relatively consistent increase in temperature across all months in the projections. The average temperature is larger for the RCP 8.5 scenario, and the extreme scenarios indicate an average temperature distribution of ~3^{o}C with between 28.0^{o}C and 30.1^{o}C for the RCP 8.5 scenario (Table 1).

Historical precipitation is characterized by a wet season between May and November and a dry season for the rest of the year. This trend is projected to continue into 2080. October historically had the highest precipitation in a month, and there is typically a slight bimodal trend to the rainy season. Rain increases in May and June, before dipping in July and resurging in August through November. Mean annual precipitation ranged as low as 857 mm in dry years to as high as 2639 mm during wet years.

For the future projections, the monthly ranges fall well within the historical monthly values. The rainfall remains distributed with a slight bimodality, with the highest rainfall in October (Figure 4.3). For the projections, there is a slight decrease between 2020 (2180 mm) and 2050 (1948 mm), before an increase in 2080 (2396 mm) for the RCP 4.5 scenario, and there is a slight but consistent increase between 2020 and 2080 (2070 mm, 2184 mm, and 2433 mm, respectively, for 2020, 2050 and 2080) for the RCP 8.5 scenario. The precipitation in the extreme models has a high variability. The most concerning, however, is the RCP 8.5 scenarios in 2020 and the RCP 4.5 scenario in 2050 which exhibit the extreme model's precipitation below the historical average precipitation (2538 mm and 2518 mm, respectively compared to 2644 mm historically). Overall, the projected average precipitation is consistently below the historical average precipitation for both scenarios in all projection periods.

4.4.2 Derived Variables

Annually, there has been a climatic moisture deficit of between 200-600 mm since 2000; however, this deficit is projected to increase to between 700-800 mm in the RCP 4.5 and 8.5 scenarios (Figure 4.4). Spatially, the most impacted by the increased climatic moisture deficit are the mountain slopes and the northern coast. Historically, and in future projections, there is a slight bimodality in the moisture deficit which is consistent with the precipitation distribution throughout the year. The highest historical monthly deficit between 2000 and 2012 is just under 600 mm in a single month, in 2011. Additionally, the length of the moisture deficit ranges between five and seven months, depending on if there is any precipitation during the dry season. In moving forward, this trend continues with seven months of water deficiency for both scenarios over all the years.

The GPP VPD scalar relationship based on the historical MODIS and climatic variables is found to be quadratic and significant (Figure 4.5; $p \leq 0.05$). The relationship becomes:

$$GPP = -6.5325 \times VPD\_scalar^2 + 8.8933 \times VPD\_scalar - 1.2138 \quad \textit{Equation (7)}$$

With this GPP model, the majority of months have the modelled values fall well within one standard deviation of the MODIS average GPP; however, some protected areas separate from the model and the MODIS values. This decoupling happens at the inflection point of the GPP VPD scalar relationship, at VPD scalar values of approximately 0.67. The decoupling effect should be considered when interpreting the future model, with wetter sites experiencing slight increases in GPP as they dry, and drier sites experiencing a decrease in GPP. Many of the protected areas continue to have a GPP well within the historical range of variability (Figure 4.6). There are some extreme changes with GPP increases in Volcan Tenorio and decreases in GPP in Palo Verde and Barra Honda.

4.5 Discussion

4.5.1 Climate Variables

The temperature rise of 3.7°C in the RCP 8.5 projections is nearly double the RCP 4.5 scenario and contradicts other national studies projecting climatic change which indicate minimum temperature rises of between 4-6°C (Taylor et al. 2013). The rise is temperature can be found in both the dry and the wet season, but the wet season is project to have a larger increase in temperature in all scenarios. These increase in temperature of concern, especially for the health of the citizens that live in the province; however, there has been increasing research that suggests that policies, such as those implemented in Costa Rica can contribute to keeping the global temperatures within the 2.0^0C range set out as part of the national voluntary commitments from the 2015 UNFCCC Conference of the Parties in Paris (Pont and Meinshausen 2018).

The changes found in precipitation are minimal, with no significant changes between the historical and future projections in either the wet or dry season. The timing of precipitation also shows no indication of changing, with the dry season remaining between November/December to April. The average mean annual precipitation, although there is a slight drop in Guanacaste, is well within the historical variability that the province has previously experienced. One of the things not considered in the precipitation values, which may alter the precipitation regimes is the El Niño Southern Oscillation. Modelling changes in the ENSO cycle can be crucial for understanding the alteration to the precipitation regimes and should be considered in future studies (Hofhansl et al. 2014).

4.5.2 Derived Variables

The increased temperature and constant precipitation produce spatially variable GPP changes, largely based on the current precipitation regimes. The quadratic relationship developed between the GPP and the VPD scalar, and therefore also the precipitation, differs from the traditionally assumed positive linear correlation used by MODIS. (Figure 4.5). Instead, there is a clear break and reversal in trends on either side of the 0.67 VPD scalar. This trend reversal means that, unlike the theoretical approach, there is less productivity when areas are too wet, as well as when they are too dry, and there is an optimal level of water available to the plants resulting in higher productivity. This more complex relationship stabilizes the GPP moving into the future projection years. Areas with the highest precipitation amounts are projected to have an increase in GPP with higher VPD deficits, while the drying in already semi-arid zones may experience severe drops in GPP in some months.

This type of non-linear relationship, however, has been previously found in Central and South American forest ecosystems (Alvarez-Davila et al. 2017), sub-tropical forests in China (Liu et al. 2017; Tong et al. 2014; Chen et al. 2017), and in the Eurasian steppe and Tibetan

Plateau ecosystems (Cuicui et al. 2017). This non-linear relationship found in Costa Rica results in GPP decreases in the Barra Honda, Santa Rosa, Palo Verde, and Diria National Parks.

The GPP projections in this study contradict the 2-4% annual drop and the 80% projected decrease in GPP for these same scenarios; however, the GPP drops from the other studies were projected for agricultural land (Liang et al. 2017; Taranu 2016). Agricultural lands have reduced microclimate stability compared to more complex ecosystem structures like forests, resulting in the likely GPP drop in agriculture areas being higher than in forest regions. It should also be noted that this study does not consider the breakdown of GPP into Net Primary Productivity and respiration rates. The stabilization of the GPP found in this study, could be related to changes in one or both parts of these equations, and this should be further isolated in future research.

Other characteristics may also influence how this productivity change manifests within the protected areas in Guanacaste. Forests at younger successional stages are typically characterized by fast-growing plants with higher growth rates but also shorter life cycles (Lopezaraiza-Mikel et al. 2014). These characteristics indicate that these plants will be resource intensive, and therefore be subject to a higher sensitivity when there are climatic changes (Sanaphre-Villanueva et al. 2017). These findings are especially true in water-limited areas, such as the tropical dry forest areas of the Guanacaste region (Greenwood et al. 2017). One such pattern that may impact these regions that is largely understudied is the ENSO cycle, which is projected increase in severity and frequency (Cai et al. 2014). These cycles can impact primary productivity production in Costa Rican forests by up to 20%, with decreased precipitation primarily contributing to this productivity drop (Hofhansl et al. 2014). These forests, however, are well adapted to droughts, and are able to recover from short-term droughts quickly, with lasting impacts only being seen after droughts last more than 6 years (Stan and Sanchez-Azofeifa, 2019; Mendivelso et al. 2014).

Costa Rican dry forests have historically stayed green for longer times than dry forests in Mexico or Brazil (Lopezaraiza-Mikel et al. 2014), which are typically considered more water limited (Lopezaraiza-Mikel et al. 2014). However, it has been shown that increases in temperature and frequency and severity of droughts could alter the composition, structure, and biogeography of these tropical dry forests (Maza-Villalobos et al. 2013). Increases in tree mortality are associated with climate-induced physiological stress. Additionally, interactions with other climate-mediated processes, i.e. insect outbreaks and wildfire, have been reported and are on the rise in multiple ecosystems (Allen et al. 2010; Greenwood et al. 2017). These considerations are important especially in 2020 for the RCP 8.5 scenario and 2050 for the RCP 4.5 scenario because all model projections exhibit a decrease in precipitation below historical averages. This increase in drought could result in the induction of physiological stress beyond changing GPP during these periods, although future modelling would be needed to test this assumption.

The projected effects of climate change on productivity will likely have a limited impact on the supply of carbon sequestration potential, an ecosystem service directly linked to productivity. Given the results from the productivity projections in our study, rates of carbon uptake are unlikely to be substantially altered from their historical curves related to the forest successional stage (Diaz-Gustavo et al. 2015). Palo Verde and Barra Honda may experience a decrease in the rates of carbon assimilation due to the seasonal drops in productivity. The high sensitivity of carbon sequestration to projected warming scenarios has been significant in the less equatorial tropical dry forests of Yucatan (Mexico), where carbon uptake and biomass accumulation showed decreases with increasing air temperature and the number of rain days (Dai et al. 2015). Changes to the phenological cycle or growing season length are not, however, considered. Additionally, the productivity and carbon sequestration potential has also been found to be modified by local site characteristics, such as soil quality, slope, elevation, and species composition, none of which have been incorporated in this study (Hofhansl et al. 2014). To more fully articulate the future resilience of the forests, these aspects should all be considered, and incorporated into future projections.

The consequences of changing ecological landscapes at local and regional scales hinder the projection of global vegetation response to climate changes (Enquist 2002). However, our study quantifies for the first time by how much these forests in Guanacaste will be affected by projected climate change (i.e. increasing temperatures and precipitation regime alteration).

4.6 Conclusions

The National Parks of Guanacaste, which range over a number of life zones, indicate forest resilience under projected changes in climate for Costa Rica. Our results indicate that the primary productivity will follow one of three paths, seasonally decreasing, increasing, or maintaining current levels, in contradiction to our initial hypothesis. Moreover, the quadratic VPD - productivity relationship contradicts the typically used MODIS algorithm, although this relationship has been replicated in other semi-arid ecosystems. This is an important finding when projecting the regional vegetation response to climate change into the future. The current global ESM models average these relationships over many regions, and understanding the local and regional scale response to climate is essential for predicting the resilience of these biomes.

These results from Guanacaste can be tested across similar life-zones across Central and South America to see if the VPD scalar GPP relationship can be replicated. If this finding can be replicated, then it can be included into the new generation of climate models, for a more comprehensive and realistic prediction of future conditions. Additionally, these results can help assess if climatic models working on the sub-country scale give projections consistent with the Global and Regional Climatic Models used in the same areas. If these results are reproducible in similar life-zones in other locations, it may be possible to both use and project GPP changes in larger Central and South America. These projections can be instrumental in developing mitigation and adaptive strategies in forest management in coming decades.

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Table 4.1

Scenarios/Year	Ensemble Min	Ensemble Ave	Ensemble Max	Extreme Average (Low)	Extreme Average (High)
RCP 4.5					
2020	19.8^{o}C	26.4^{o}C	34.0^{o}C	25.5^{o}C	27.7^{o}C
2050	20.8^{o}C	27.1^{o}C	34.8^{o}C	26.2^{o}C	28.1^{o}C
2080	21.0^{o}C	27.5^{o}C	35.2^{o}C	26.8^{o}C	28.3^{o}C
RCP 8.5					
2020	19.9^{o}C	26.5^{o}C	34.2^{o}C	25.6^{o}C	27.0^{o}C
2050	21.2^{o}C	27.6^{o}C	35.3^{o}C	26.9^{o}C	28.3^{o}C
2080	22.6^{o}C	29.2^{o}C	36.8^{o}C	28.0^{o}C	30.1^{o}C

Figure 4.1:

Nicaragua
Costa Rica
Panama
La Cruz
Guanacaste
Santa Rosa
Rincon de la Vieja
Liberia
Volcan Tenorio
Bagaces
Tilaran
Filadelfia
Canas
Arenal
Palo Verde
Santa Cruz
Juntas
Barra Honda
Nicoya
Hojancha
Carmona
Guancaste
National Parks
Towns
Major Cities
Roads
Water
Non-Forest
Secondary Forest
Primary Forest
Plantations

Figure 4.2:

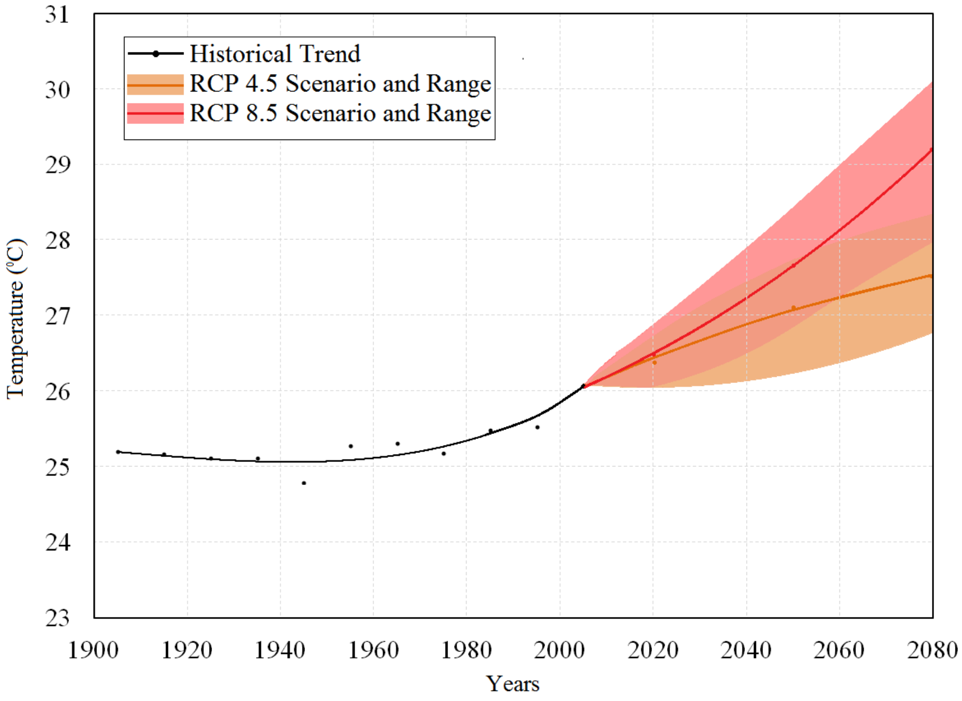
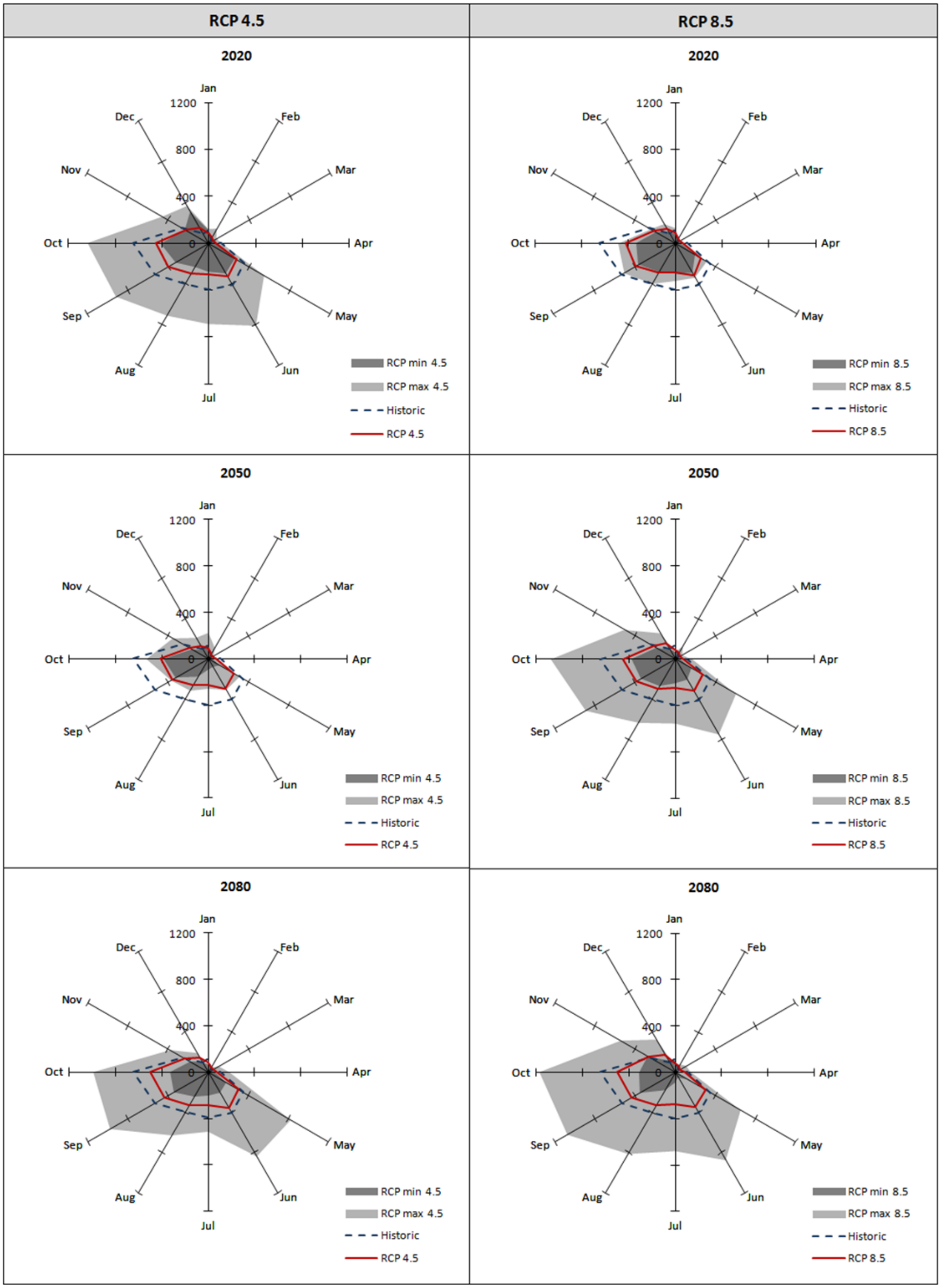

Historical Trend
RCP 4.5 Scenario and Range
RCP 8.5 Scenario and Range
Temperature (°C)
31
30
29
28
27
26
25
24
23
1900
1920
1940
1960
1980
2000
2020
2040
2060
2080
Years

Figure 4.3:



RCP 4.5
RCP 8.5
2020
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
1200
800
400
0
RCP min 4.5
RCP max 4.5
Historic
RCP 4.5
2020
RCP min 8.5
RCP max 8.5
Historic
RCP 8.5
2050
RCP min 4.5
RCP max 4.5
Historic
RCP 4.5
2050
RCP min 8.5
RCP max 8.5
Historic
RCP 8.5
2080
RCP min 4.5
RCP max 4.5
Historic
RCP 4.5
2080
RCP min 8.5
RCP max 8.5
Historic
RCP 8.5

Figure 4.4:

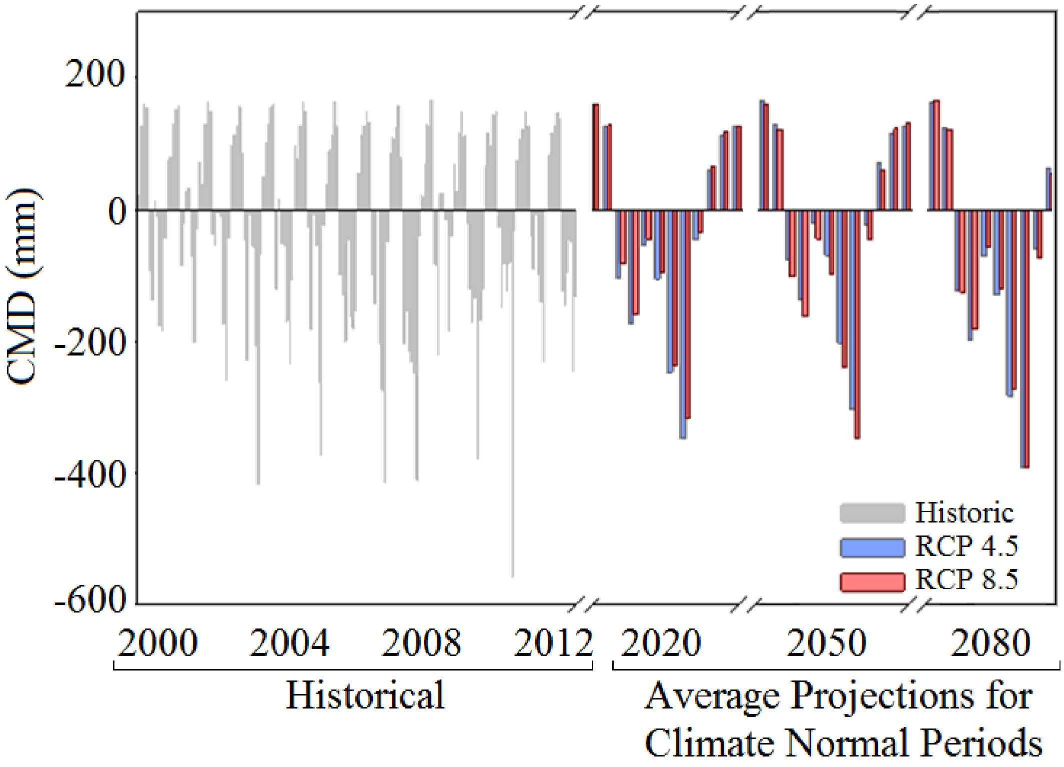


Figure 4.5:

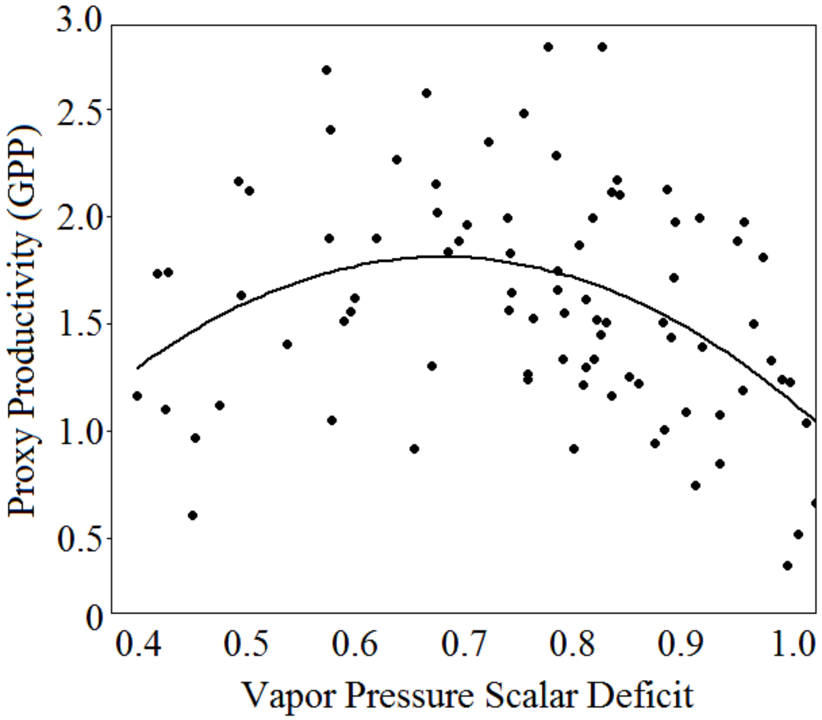
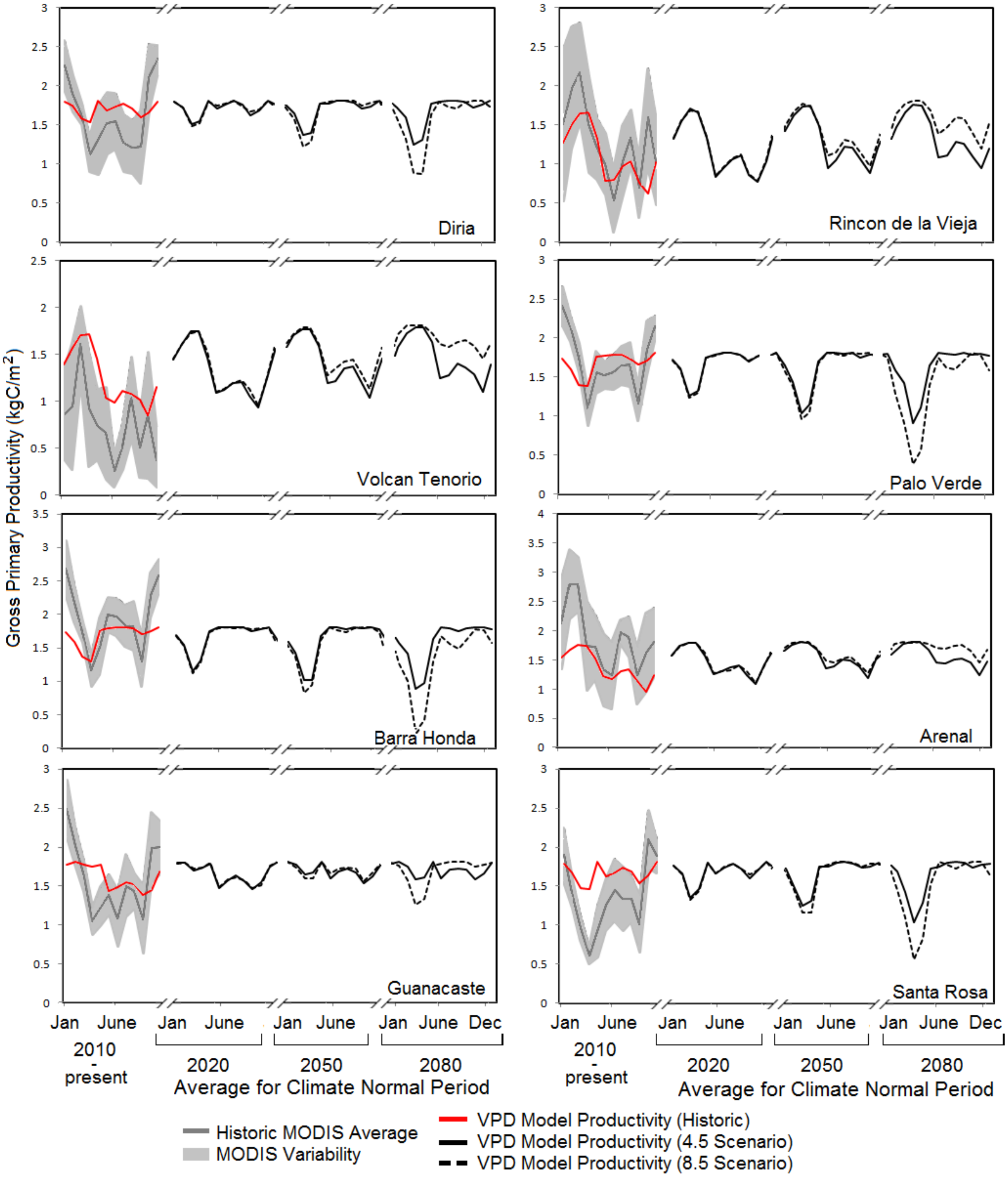


Figure 4.6:


Gross Primary Productivity (kgC/m^2)
Diria
Rincon de la Vieja
Volcan Tenorio
Palo Verde
Barra Honda
Arenal
Guanacaste
Santa Rosa
0
0.5
1
1.5
2
2.5
3
3.5
4
Jan
June
Dec
2010 - present
2020
2050
2080
Average for Climate Normal Period
Historic MODIS Average
MODIS Variability
VPD Model Productivity (Historic)
VPD Model Productivity (4.5 Scenario)
VPD Model Productivity (8.5 Scenario)

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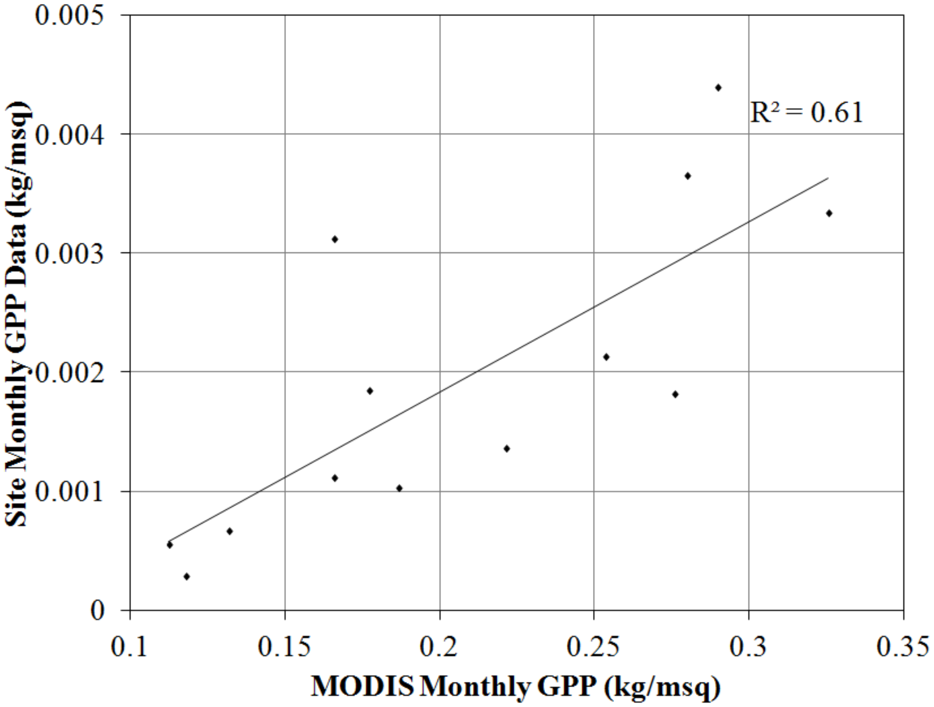
5.8 Supplementary Information

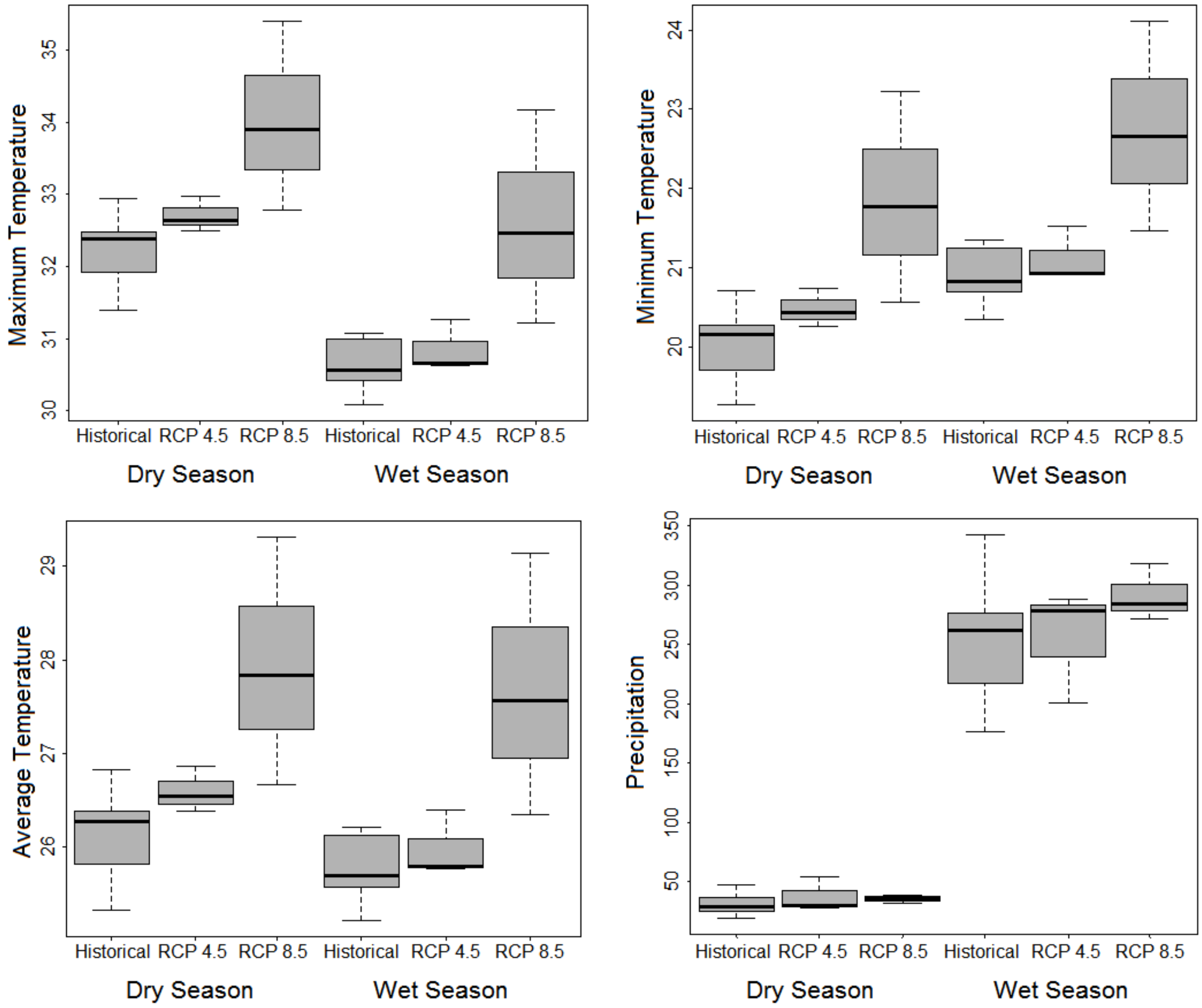
SI 1: Listing of data from in-situ stations used to validate the ClimateSA model data. Data includes station location, collection institute, type of data gathered at each sites and the collections date.

Name	Collection Institute	Type of Data Gathered	Collection Dates
Santa Elena, La Cruz	Instituto Meteorológico Nacional de Costa Rica	Precipitation/Mean, Min, Max Temperature	01/85 to 12/06
Palo Alto, Montezuma	Instituto Meteorológico Nacional de Costa Rica	Precipitation	01/90 to 12/15
Santa Rosa	Guanacaste Conservation Area/Site Monitoring (CEOS)	Precipitation	01/10 to present
La Guinea	Instituto Meteorológico Nacional de Costa Rica	Precipitation/Max, Min Temperature	01/05 to 12/15
Finca Brasilia del Oro	Instituto Meteorológico Nacional de Costa Rica	Precipitation	01/03 to 12/15
Liberia Airport West	Instituto Meteorológico Nacional de Costa Rica	Precipitation/Mean, Min, Max Temperature	11/98 to 12/15
HDA Mojica	Instituto Meteorológico Nacional de Costa Rica	Precipitation/Mean, Min, Max Temperature	05/99 to 12/15

SI 2: The correlation between MODIS GPP data and in situ eddy covariance GPP measurements. The monthly remote sensing data was compared against the station data.



SI 3: Seasonal differences between the historical and future projections of precipitation and mean, maximum, and minimum temperatures. Data is split into the wet and dry season and compared for differences.



CHAPTER 5 - Tropical Dry Forest Resilience and Water Use Efficiency: An analysis of productivity under climate change

Abstract

Tropical dry forests (TDFs) worldwide have an environment-sensitive phenological signal, which easily marks their response to the changing climatic conditions, especially precipitation and temperature. Using TDF phenological characteristics as a proxy, this study aims to evaluate the current continental response of TDFs to climate change across the Americas. Here we show that TDFs are resilient to water stress and droughts, increasing their rain use efficiency (RUE) in drier years, and recovering to average RUE in the year following the drought. Additionally, we find that productivity trends over the past 18 years are spatially clustered, with sites in the northern hemisphere experiencing increased productivity, while equatorial regions have no change, and the southern hemisphere exhibiting decreased productivity. Finally, we show that the El Nino Southern Oscillation can vary TDF productivity up to 30%, with greater variation at higher latitudes.

Keywords: Water Use Efficiency, Tropical Dry Forest, Resilience, iEVI, droughts, water stress, MODIS, ENSO

5.1 Introduction

Tropical Dry Forests (TDFs) support high densities of human populations given their climatic and geographic properties and have direct links to the health of many of the neotropical freshwater sources (Portillo-Quintero et al., 2014). Between 50%-75% of the remaining TDFs are located in Meso and South America (Hesketh & Sánchez-Azofeifa, 2013; Miles et al., 2006). These forests are severely under-studied relative to humid forests despite their significance (Calvo-Rodriguez et al., 2017; Sánchez-Azofeifa et al., 2005). Until 2005, only 14% of tropical forest papers assessed the TDF, with an important bias to Costa Rican and Mexican study sites (Portillo-Quintero & Sánchez-Azofeifa, 2010; Sánchez-Azofeifa et al., 2005), and in the most recent decade, only up to 25% of the papers focused on this ecosystem (Stan and Sanchez-Azofeifa 2019).

The productivity of a forest is inherently linked with biomass accrual and can be measured using leaf growth or woody mass (Reich, 2012; Skovsgaard and Vanclay, 2008). In both cases, this measure of biomass is linked to the ability of the forest to sequester carbon, a fundamental ecosystem service, as well as to the ecosystem resilience, thereby indicating forest health (Albrecht and Kandji, 2003; Spasojevic et al., 2016). Resilience, in this case, is defined as the ability of an ecosystem to recover to equal functionality after a disturbance or the amount of disturbance that can be withstood while the ecosystem maintains its ability to function (Spasojevic et al. 2016; Holling 1996). Given the uncertainty of the future climate regimes and projections of decreased rainfall, the resilience of the forests is uncertain, especially with regard to biodiversity, productivity, and carbon sequestration potential (Allen et al. 2017). Some research suggests that the Tropical Dry Forest will not have the capability to adapt to increased drought durations leading to reduced carbon sequestration potential (Allen et al. 2017); however, this has not been tested in long-term cross continental assessments.

With the severe threats already coming from anthropogenic sources from high deforestation rates and forest protection under 10% for most countries, this already strained ecosystem is located in an area that is projected to experience severe climatic changes (Portillo-Quintero & Sánchez-Azofeifa, 2010). While there have been studies correlating TDF development and growth to climatic variables, these have typically focused on local assessments and short time-frames (Ito & Inatomi, 2012; Navar-Chaidez, 2011; Saynes et al., 2005). There has not, however, been a holistic and cohesive analysis of the response of the whole Meso and South American TDFs to climatic variables, nor has there been a long-term analysis (since 2000) studying how these forests are responding to the ongoing changes in climate.

In this study we analyze the continental response of TDF productivity to site variables, including both climatic and biophysical characteristics. Additionally, we analyze the variability of productivity in response to water stress using a combination of *in situ* and remote sensing data, assess the forest productivity trends since 2000, and assess the impact that the El Niño Southern Oscillation (ENSO) cycles have on TDF productivity.

5.2 Methods

5.2.1 Literature Search and Site Selection

A literature search using the keywords TDF, tropical semi-deciduous forests, litterfall, annual net primary productivity (ANPP), biomass, and leaf litter was used to collect data regarding litterfall sites for this analysis. These sites were vetted against the Sanchez-Azofeifa et al. (2005) definition of Tropical Dry Forests, which includes restrictions on temperature, precipitation, elevation, and deciduousness, for site consistency. Only sites that included in-situ measures of biomass and litterfall and adhered to the above definition were included in the subsequent analysis. The sites were then and compared against both the TDF Forest map, as well as Google Earth images, to ensure there is continuous forest within a 1 km buffer of each point. Highly fragmented sites were moved to the nearest patch of continuous forests with a 1 km buffer; however, if there were no nearby sites with intact forests, the point was removed.

Of the original 50 TDF points collected from the literature survey, 32 sites remained for the analysis. The 32 sites span Mexico, Costa Rica, Venezuela, Brazil, Argentina, and Bolivia and are predominantly classified as late-stage forest, although there are three early stage sites and one intermediate stage site (SI 5.1; SI 5.2). The climate variables, including precipitation and temperature, elevation, litterfall amounts, successional stages, and forest type from each site were gathered from the original sites. These in situ data were used to develop relationships with remote sensing products to analyze productivity trends, and their relationship to site variables.

5.2.2 Remote Sensing Datasets

The remote sensing datasets used in this analysis included the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD13Q1 Enhanced Vegetation Index (EVI) and VI Quality Version 6 products for determining proxy productivity (Didan, 2015). The MODIS product was used because of the longevity, resolution, and fast return time of this satellite product. The EVI products were downloaded from February 2000 to February 2018 for each of the litterfall sites and integrated annually. This data was also assessed in TIMESAT for seasonality parameters, including the start, end, and length of season (Jönsson & Eklundh, 2004).

Relevant site parameters included climatic variables (precipitation, temperature, climatic moisture deficit (CMD), atmospheric heat moisture index (AHM), and evapotranspiration), as well as site specific variables (latitude, longitude, soil moisture, elevation). To ensure continuous data over the 18 year period that is covered by productivity, any variables that were not consistent over time, were collected from satellite or model products.

Precipitation was taken from the Tropical Rainfall Measuring Mission 3B43 product, given the product's longevity and the compiled satellite data's return time. Plots and years that could be were assessed against data that was collected *in situ* from each litterfall site. Despite the TRMM satellite decommissioning in 2015, the 3B43 product combines information from 8 earth observation sensors from a variety of different programs, so it continues to produce rainfall data.

Soil moisture for the litterfall sites came from the European Space Agency Climate Change Initiative (ESA-CCI) product. This daily soil moisture product is a compilation of multi-frequency radiometers including SMMR, SSM/I, TMI, AMSR-E, and Windsat, C-band scatterometers (ERS-1/2 scatterometer, METOP Advanced Scatterometer), and other microwave sensors including Soil Moisture and Ocean Salinity (SMOS) and SMAP and ran from 1978 to 2016.

There is no consistent measure of temperature, CMD, or AHM, from a remote sensing product for the entire 2000-2018 time period, therefore, these temperature data was from the ClimateSA model. The model has historical data derived from 1901-2009 CRU-TS 3.1, with updated data until 2013 by CRU-TS 3.22 until 2013.

To assess the impact of the ENSO periods on productivity, the data from 2000 was further subset into El Niño, neutral, and La Niña years as determined by the National Oceanic and Atmospheric Association (NOAA). The NOAA definition of ENSO is 15 consecutive months when the sea surface temperature (SST) in the equatorial Pacific Ocean is more than a ±0.5°C difference from the 40-year average SST.

5.2.3 Relationship between climate variables and productivity

To build the relationship between productivity and the climate variables, we first tested the reliability of the annually integrated Moderate Resolution Imaging Spectroradiometer Enhanced Vegetation Index measurements (iEVI) against the ground collection data. This *in situ* litterfall data was collected from the 6 of 32 sites across Meso and South America which have ground collection after 2000 (SI1). These six sites were used to determine the relationship between the annually integrated EVI (iEVI) and the ground measure of annual net primary productivity found at each site. This data was added to the global measure of this relationship, as originally developed by Ponce Campos et al. (2013). This relationship was used to determine the annual net primary productivity (ANPP) from the iEVI of all 32 sites for the subsequent analyses, because only using raw EVI data at various latitudes has been shown to have anisotropy issues (Breuning et al. 2015; Fensholt et al. 2010).

Once this relationship was established, the remaining years and sites were analyzed in TIMESAT. The iEVI at each site in every year was transformed through this aforementioned relationship to determine the measure of annual proxy productivity in each plot (Jönsson & Eklundh, 2004). This productivity data is used as the Annual Net Primary Productivity (ANPP) in all subsequent analyses. The EVI time series data is smoothed using the Savitsky-Golay method (Jönsson & Eklundh, 2004), and subsequently, the start, end, and length of the season are calculated based on 0.25 of the annual EVI amplitude.

The soil moisture, from the ESA-CCI, was averaged from the daily product into monthly products from 2000 to 2016. The TRMM precipitation data was compiled for the growing season, not for the calendar year. To calculate the evapotranspiration, a combination of the TRMM precipitation data and % forest cover was used in the Zhang et al. (2001) equation:

$$ET = \left(f \frac{1+2\frac{1410}{P}}{1+2\frac{1410}{P}+\frac{P}{1410}} + (1-f)\frac{1+0.5\frac{1100}{P}}{1+0.5\frac{1100}{P}+\frac{P}{1100}} \right) P \qquad (1)$$

where:

ET = evapotranspiration (mm)

f = percent forest cover within 1 km (%)

P = mean annual precipitation (mm)

To assess the relative importance of the site characteristics in explaining the variations in the ANPP at each plot, the ANPP, climate variables (precipitation, evapotranspiration, temperature, AHM, CMD) and site specific characteristics (elevation, latitude, longitude) over the most recent decade (2007-2017) were ordinated in a Principal Component Anaylsis. There were not enough sites with soil moisture data to include it in this analysis.

All factors, productivity and site variables, were tested for normality using the Shapiro-Wilks test. The sites' ANPP were then correlated against all of these variables, including the soil moisture, and the correlations were assessed for significance.

5.2.4 Rain Use Efficiency under wet and dry conditions

The relationship between ANPP and precipitation is the Rain Use Efficiency (RUE) (Huxman et al. 2004) and was calculated for the decadal average, as well as for the driest and wettest years. Decadal correlations calculated between proxy productivity and evapotranspiration are called Water Use Efficiency (WUE; Monson et al. 2010). Both the RUE and WUE are metrics assessing the productivity response of ecosystems to annual changes in available water (Bai et al. 2008).

Using the average, driest, and wettest years, the efficiency of the forest's use of water under differing conditions can be determined based on the slope of the relationship (Monson et al. 2010). The TDF sites were further subset into the severest droughts where precipitation >2 SD below the decadal average. The RUE for the droughts and the year following, when the rainfall returns to average, is also calculated. The sites that have a multi-year drought are also analyzed for changes in productivity, although there are insufficient sites for statistical analysis. The WUE was used also investigated in the wettest and driest years for comparison against other biomes, globally.

5.2.5 Productivity changes over the last two decades

The ANPP trends from each site were assessed over the past 18 years using a linear regression and tested for directionality and significance. Changes to the site specific variables were also assessed over this period using linear regressions and tested for significance. Both the productivity and site variables were assessed spatially for latitudinal patterns. Correlations between the direction and significance of productivity and the site characteristics were assessed.

5.2.6 El-Niño Southern Oscillation impact on productivity

The TDF sites were subset into El Niño, La Niña, and neutral years during the 2000-2018 period. El Ni Niño years were 2003, 2007, 2010, and 2015-2016. Neutral years were 2001-2002, 2004-2006, 2009, 2013-2014, and La Niña are found to be 2000, 2008, 2011-2012, and 2017-2018. The difference in the productivity of sites between ENSO cycles was tested by country t-tests for significance. It was done on a country basis rather than a site basis for sufficient number of samples to run the statistical tests with. Additionally, the difference between productivity in each phase of the ENSO cycle was compared against the 18 year ANPP average. The difference between years was interpolated across the remaining TDF in Meso and South America to assess the spatial patterns.

5.3 Results

5.3.1 Relationship between climate variables and productivity

The *in situ* and iEVI relationship of the Tropical Dry Forest follows the Ponce Campos regression closely, with the sites falling between the Mesic Grasslands and Forest classes (Figure 5.1). The precipitation data from the Tropical Rainfall Measuring Mission was also correlated against the *in situ* rainfall data and found to be both linear and significant ($p<0.05$).

A Principal Component Analysis and series of correlations were used to assess the relationship between the Tropical Dry Forest ANPP and site variables, both climatic and biophysical. In the Principal Component Analysis (PCA), points in Mexico, Bolivia, and Brazil cluster together, respectively, with Mexico clustering in higher productivity and MAP, Bolivia in the centre, and Brazil as the lowest productivity and highest moisture deficits. The first three components of the PCA explain 90% of the variance in the study sites. The first component is most highly correlated with the climatic moisture deficit (CMD), atmospheric heat moisture index (AHM), evapotranspiration, and longitude. The second component is most highly correlated to the temperature variables (MAT, MCMT, MWMT) and elevation, and the third component is most highly correlated with latitude. The precipitation variance is predominantly split between components 1 and 2 (Figure 5.2).

Significant correlations were observed between ANPP and precipitation ($p<0.001$; $R^2= 0.84$), evapotranspiration ($p<0.001$; $R^2 = 0.85$), elevation ($p=0.02$; $R^2=0.24$) and soil moisture ($p<0.001$; $R^2=0.95$). There is no correlation, however, between the ANPP and temperature-related metrics (mean annual temperature, mean coldest month temperature, mean warmest month temperature; $p>0.10$) or the length of the season ($p=0.32$).

5.3.2 Rain Use Efficiency under wet and dry conditions

In the TDF the average rain use efficiency (RUE) is 0.56 ($p<0.001$; R2 = 0.97), while the driest year of each site has a RUE of 0.78 ($p<0.01$; R2 = 0.91) and of 0.44 ($p<0.001$; R2 = 0.96) in the wettest year at each site (Figure 5.3). These values indicate the TDF sites can be equally or more productive in drier years. The Water Use Efficiency (WUE), a measure of ANPP under different evapotranspiration conditions, follows the same trend as the RUE, with the driest years having a WUE of 0.93 ($p<0.001$) and the wettest years having a lower WUE of 0.63($p<0.001$). The average water use efficiency for all sites was 0.72 ($p<0.001$).

The rain use efficiency in the year following the driest year recovers to the decadal average (0.56). In sites with severe droughts, >2 standard deviations lower than the decadal average rainfall, the RUE is higher than the driest year of all sites at 1.10 ($p<0.01$), and it does not recover back to normal despite average precipitation in the following year (RUE=0.623; $p<0.01$). The second year following the drought has a RUE which returns to average.

5.3.3 Productivity changes over the last two decades

When considering the resilience of the TDF under climatic changes, it is important to determine the direction, magnitude and spatial patterns of changes that are already occurring. For the long-term analysis, nine sites (4 in Brazil, 4 in Mexico, and 1 in Argentina) had significant changes in their productivity between 2000-2018 ($p<0.05$), seven (3 in Mexico, 1 in each of Venezuela, Costa Rica, Brazil, and Bolivia) had non-significant differences ($p>0.05$), and the remainder (across Mexico, Brazil, and Bolivia) exhibited no long-term change ($p>0.50$; Figure

5.4). Of the points that experienced significant changes, four (in Nayarit, Mexico; Jalisco, Mexico; Guerrero, Mexico) showed increasing ANPP, and five (in Piaui, Brazil; Bahia, Brazil; Argentinan Chaco) had a decrease in productivity.

Of the sites with increased ANPP in the long-term analysis, one site in Nayarit, Mexico had a corresponding increase in soil moisture ($p<0.05$) and the second site in the same region had an increased growing season between 2000-2018 ($p<0.05$; SI 5.1). Of the sites with decreased productivity, one of the Brazilian sites in Bahia State had a corresponding drop in both precipitation and soil moisture ($p<0.05$), while three other locations, two in Brazil and one in Argentina also saw a decline in soil moisture, without a significant change in precipitation (SI 5.3). The remainder of sites with significant differences in Jalisco, Mexico ($p=0.015$), Michoacan, Mexico ($p=0.015$), and Piaui, Brazil ($p=0.05$; 2 increased; 1 decreased ANPP) had no corresponding changes in any geo-climatic variables.

5.3.4 El-Niño Southern Oscillation impact on productivity

When the TDF sites were subset into their ENSO periods, the neutral years were found to be on average 7% ± 19% of the 18-year average productivity, with no particular latitudinal spreading of the trends. During ENSO years, Mexico has a significant increase in productivity compared to neutral years ($p=0.0003$) and La Niña years ($p=0.012$), with forests producing up to 30% ± 14% more productivity. In Brazil, there is a significant decrease in productivity in ENSO years compared to La Nina years, with up to 20% + 11% drop in productivity ($p=0.04$). Bolivia has the highest drop in productivity in ENSO years with up to a 30% ± 24% decrease in productivity, and a significant decrease compared to both neutral ($p=0.004$) and La Niña years ($p=0.0029$) (Figure 5.5). Argentinean sites have a significant increase in productivity compared to La Niña years ($p=0.03$; Figure 5.5). TDF sites closest to the equator experienced very little change in the productivity regardless of the ENSO subsetting. These patterns of productivity follow the precipitation teleconnections found during ENSO (Chiodi & Harrison, 2015).

5.4 Discussion

Rain Use Efficiency (RUE) is a measure of the amount of ANPP a site produces based on the mean annual precipitation. Higher RUE physiologically means that the ecosystem can produce the same or more leaves (assimilate more carbon) with less water (Keenan et al., 2013). It also provides a measure of resilience, as this is a drought mitigation strategy which is stressful for the plants to maintain. Biomes with a quick recovery to average efficiency in post-drought years indicate a level of ecosystem resiliency to reductions in the water supply (Huang et al., 2017). Our results, therefore, indicate a measure of resilience to drought conditions in Meso and South American TDF. The quick recovery time following droughts is replicated in other equatorial regions and globally in TDFs, while forests at higher latitudes recover slower (Tng et al., 2018; Yu et al., 2017). These areas of increased WUE in times of drought include the Amazon, Central Africa, Indonesia, and southern India (Yu et al., 2017), while the Australian TDFs have been found to have multiple drought adaptive strategies in its species to ensure resistance to drought conditions, and quick recovery in post-drought periods (Tng et al., 2018).

The TDFs also fit into the global context as one of the most water use efficient ecosystems. On average, the WUE is higher at 0.72 than biomes in Australia and the United States (Ponce-Campos et al. 2013). In dry years, however, Australian grasslands and forests have a higher WUE at 1.01 compared to the Meso and South American TDFs at 0.93 (Ponce-Campos et al. 2013), perhaps due to the adaptive drought strategies found in the forests (Tng et al., 2018).

The long-term trends indicate that there have been more significant changes to the productivity as the sites move away from the equator (Chen et al., 2017). Two-thirds of the sites that exhibit a change in productivity have a corresponding change in at least one of the correlated variables. Of the relevant variables, changes in soil moisture had an impact on the highest number of sites, making this a key parameter to monitor in the TDFs.

Changes in the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation system can impact the length of the dry season as well as the pattern and intensity of precipitation events (Babcock et al. 2016). ENSO years can bring extreme drought to Central America, especially in water-limited regions (Coelho and Goddard, 2009), as was seen in the 2015 Super El-Nino event which caused mass crop loss across Costa Rica, Guatemala, Honduras, and Nicaragua. These extreme events, are also projected to increase in frequency and severity, making it important to understand the biosphere response (Cai et al. 2015; Stott et al. 2016). Additionally, as a natural cyclical variation in precipitation, events can be useful for understanding the phenological response to large variations in precipitation and the post-event recovery time of these forests.

One essential aspect of resilience not considered in this study is the combined impact of species variation across the Tropical Dry Forest. As a biome that covers a 40° latitudinal gradient, there is substantial species variation across the biome, with lower species diversity found away from the equator (Hernández-Ramírez & García-Méndez, 2015; Rito et al., 2017). Additionally, flora cluster according to their geographic location with Mexican species differing from Central and South American (found in Costa Rica, Nicaragua, Venezuela and Columbia), and South American species groups (Central Brazil and Misiones for our sites) (Banda-R et al., 2016). While there has been research into the successional recovery of species richness after disturbance based on precipitation and dry season length, there has been no research the direct impact of species composition on water use efficiency across the biome (Derroire et al., 2016; Golicher et al., 2012; Power et al., 2016; Saiter et al., 2015). Consideration of this interplay between species richness, species composition, and water regimes is essential for understanding the true resilience of the TDF in Meso and South America under changing climatic conditions.

5.5 Conclusions

Overall, the water use efficiency found for the wettest and driest years indicates that the forest is resilient under dry and wet conditions. When there are severe droughts, we observed that TDFs require two years to repair the damage, and the efficiency is higher in the year following the drought, indicating a higher level of stress with severe droughts. Long-term trends show a North-South distribution of changes in productivity, with increased productivity in the north, little change in the equatorial latitudes, and decreased productivity in the south. These changes correlate to alterations in soil moisture, precipitation, and length of the growing season.

Acknowledgements

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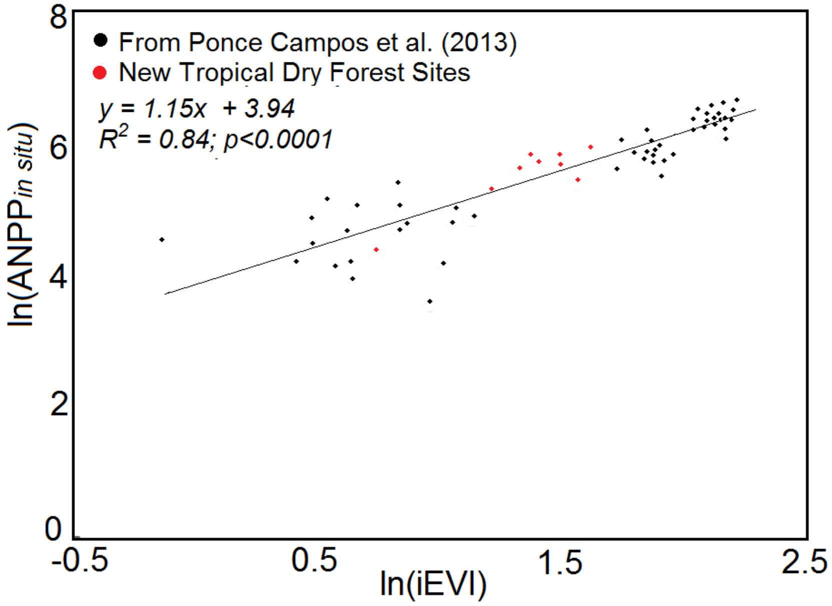
Figure 5.1:



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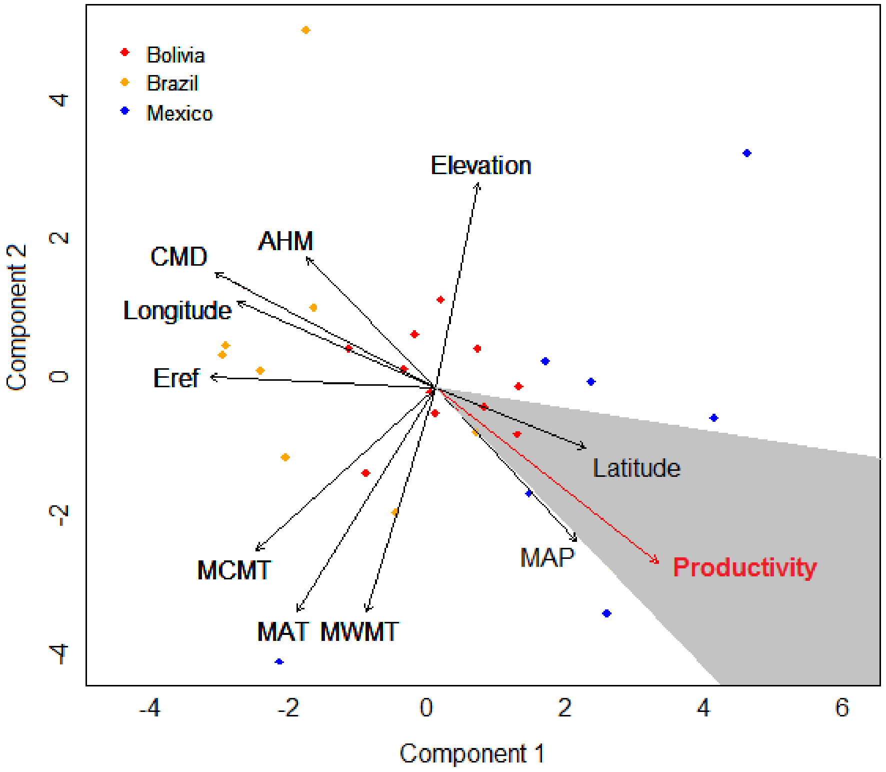

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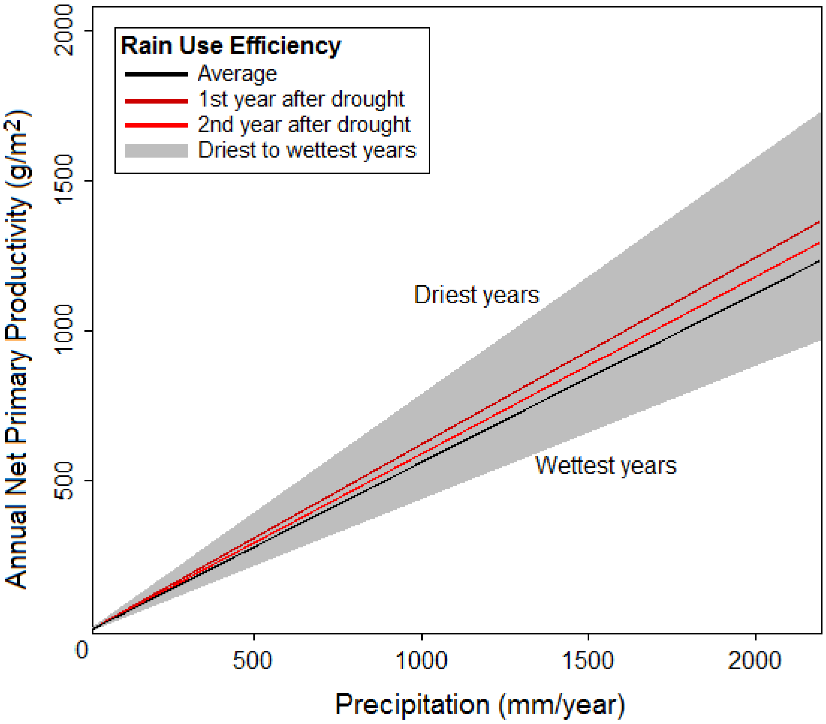


Figure 5.4

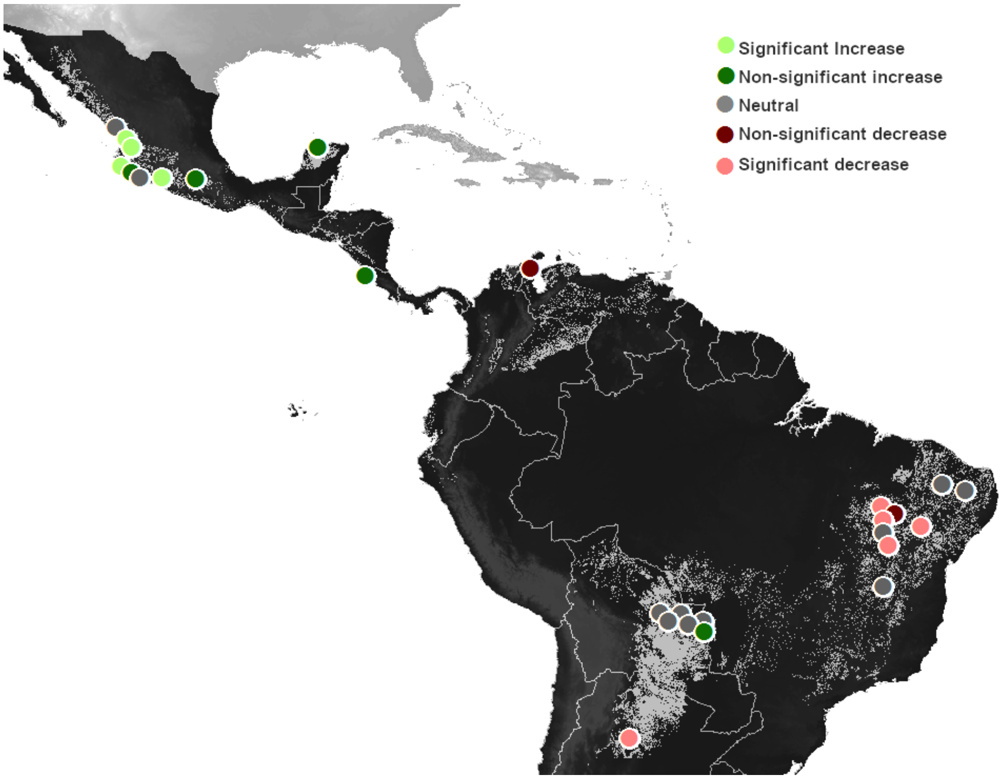
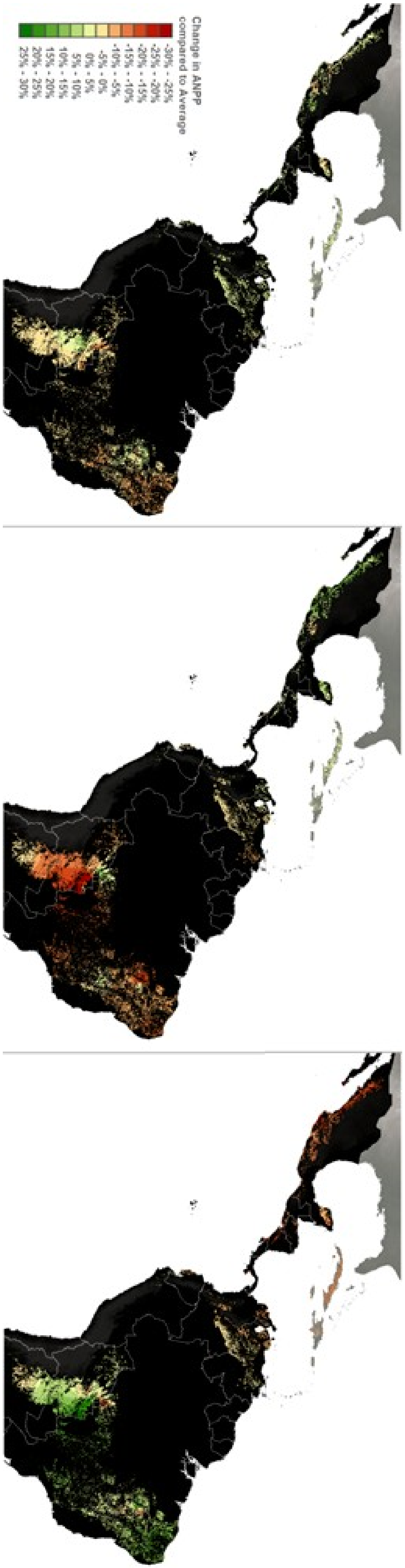


Figure 5.5


Change in ANPP compared to Average
-30% - -25%
-25% - -20%
-20% - -15%
-15% - -10%
-10% - -5%
-5% - 0%
0% - 5%
5% - 10%
10% - 15%
15% - 20%
20% - 25%
25% - 30%

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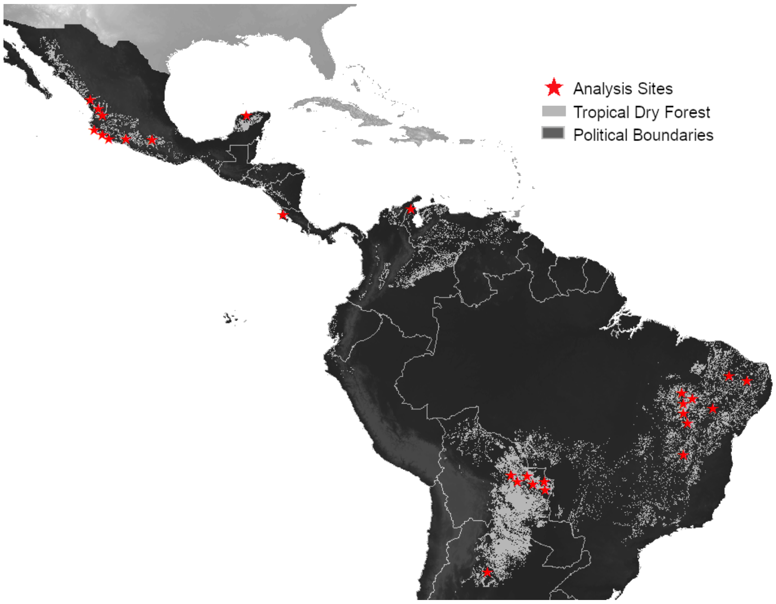
5.7 Supplementary Information:

SI 5.1: The Tropical Dry Forest sites, their successional stages, and the original study that conducted in-situ data analysis at these sites.

Country	Forest Stages	References
Argentina	Late	Carnevale & Lewis 2001; Gasparri & Menendez 2004
Bolivia	Late	Kennard 2002; Justiniano & Fredericksen 2000
Brazil	Early	Field data (Mata Seca)
	Intermediate	Field data (Mata Seca); Schessl et al. 2009
	Late	Field data (Mata Seca); Castro 1996; Lopes et al. 2009; Souto 2006; Schessl et al. 2008; Silva et al. 2007; Marimon-Junior & Haridasan 2005; Selva et al. 2007
Colombia	Late	Veneklass 1991
Costa Rica	Early	Kalascka et al. 2005
	Intermediate	Kalascka et al. 2005
	Late	Kalascka et al. 2005
Mexico	Early	Lawrence 2005
	Late	Martinez-Yrizar & Sarukhan 1990; Campo & Vazquez-Yanes 2004; Lawrence 2005; Lawrence & Foster 2002; Whigham et al. 1990; Saynes et al. 2005; Martinez-Yrizar et al. 1996; Gonzalez 1989
Puerto Rico	Late	Erickson et al. 2002
Venezuela	Late	Cuevas & Medina 1986; Medina & Zewler 1972; Clark et al. 2001



SI 5.2: The litterfall sites in the Tropical Dry Forest analyzed for productivity changes over the past 18 years and for the phenological response to changes in climatic variables including precipitation, evapotranspiration, temperature, and El Nino/La Nina years.

SI 5.3: The long-term trends in climatic and physical parameters and the corresponding changes in productivity, including the number and direction of change for the sites.

Long-Term Alterations in other parameters	**Total sites with a significant change ($p<0.05$)**	**Correlative with ANPP changes (Number of points / Change ANPP: Change variable)**
Precipitation	3 total	1 / Decrease: Decrease
Length of Growing Season	1	1 / Increase: Increase
Temperature	N/A	
Soil Moisture	10	1/ Increase: Increase 4/ Decrease: Decrease
Succession	NA	Increase : Late Stage Forest Decrease: 2 Intermediate Stage Forests Remainder Late Stage Forest

SI References:

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CHAPTER 6 - Conclusions

Changes in the climate are projected to have impacts across the globe, with some biomes shrinking, others expanding, and novel ecosystems projected to rise (Morse et al. 2014; Salazar et al. 2007). Increases in temperature, uncertain precipitation regimes, and increasing frequency of natural disturbances will impact the future resilience of ecosystems (Magrin et al. 2014; Cai et al. 2015). Additionally, anthropogenic changes further modify ecosystem's adaptability (Elmqvist et al. 2003). As such, it is essential to understand the current relationships between ecosystem resilience, climate variability, and anthropogenic alterations of the landscape. With the development of these relationships, we can more effectively and accurately project the future of our environment, the ultimate goal of Earth Systems Models (ESM) (Heavens et al. 2013).

Climatic adaptability is more heavily studied in northern ecosystems, such as in the Boreal Forests, as changes to the climate are more prevalent at northern latitudes (Pithan and Mauritsen, 2014). Changes in tropical rainforests (i.e. the Amazon) are also well studied because they contain high carbon storage potential and biodiversity while also experiencing significant anthropogenic alteration (Portillo-Quintero and Sanchez-Azofeifa, 2010; Hansen et al. 2010; Coelho et al. 2016). The Tropical Dry Forests (TDFs), however, have not been as well studied in terms of resilience and are, therefore, not thought to be resilient under climatic changes due to projections of this semi-arid biome becoming drier in the future (Allen et al. 2017). The TDFs, however, have a much more complicated relationship with both anthropogenic influences and climatic variables than has been previously thought. It is, therefore, essential to assess these relationships so that the future of this ecosystem can be better understood, projected more accurately within climatic models, and protected more effectively.

Tropical Dry Forests account for over to 40% of the tropical forest worldwide, and have been home to large populations over the past thousands of years (Portillo-Quintero et al. 2015; Portillo-Quintero and Sanchez-Azofeifa 2010). This close relationship with humans means and the quantity of ecosystems services the TDF provides these populations in the form of water provisions, soil erosion and flood protection, food, and carbon sequestration potential, make it essential to understand its ongoing resilience and any degradation potential these forests will encounter (Portillo-Quintero et al. 2014). The relationship between the forest resilience and both climatic and anthropogenic variables has formed the basis of this thesis.

6.1 Synthesis of significant contributions

The primary objectives of this thesis included contributing to: (i) the state of knowledge on the TDF physiological response to climatic variables; (ii) the understanding of forest resilience through assessing productivity response to temperature and precipitation; and (iii) assessing the influence of legislation on the resilience and extent of tropical forests. In the preceding chapters of this thesis, I present research which evaluates the resilience of the TDF both over decadal time periods and on regional, country, and cross-continental scales. This resilience is tested under a variety of climatic conditions, as well as under different legislative scenarios, and is then projected into the future.

The second chapter of this thesis provides a critical review of the state of knowledge surrounding the latitudinal variations in TDF expression, while also considering how the phenology, biomass, species diversity, and forest dynamics vary with precipitation, temperature, and natural disturbances. This review provided a much needed update on the state of knowledge of TDF research and encompassed a more comprehensive assessment than any recent review since 2010. This style of review is important for future work as it outlined a number of areas which, despite the increased research into the tropical dry forest remain poorly understood. These remaining gaps can be used to parameterize both the locations and the methodologies which would best serve to fill these gaps. The research in the tropical dry forest is heavily skewed to a few countries with Mexico, Costa Rica, and Brazil having the most research, followed by Panama, Bolivia and Argentina. There is little to no research, and therefore understanding, of the equatorial TDFs outside of Costa Rica and Panama, with large gaps across the Caribbean Islands, Colombia, Nicaragua, Guatemala, Honduras, El Salvador, and Venezuela. These are important areas to study as they have little or no legal protection and unique species composition, soils, topographies, and climatic regimes which result in potentially different resilience strategies (Banda-R et al. 2016; Portillo and Sanchez-Azofeifa 2010). This can also be extrapolated to other areas of the world (i.e. Africa, Central Indochina, and Australia) which have relatively less and comparatively newer research into dry ecosystems. Understanding the current state of knowledge can be useful to replicate methodologies which have proved effective in the Meso and South American TDFs, but also so that the relevant gaps which have been understudied can be filled in a more streamlined manner.

Additionally, there is a relatively large amount understood about the variation in aboveground biomass (AGB) variations across the TDF, but relatively little understood about forest structure, phenological cycling and the impact of successional stages and species composition on these variables. Particular branches of study include research into novel disasters which historically were not seen, but in recent years have occurred (i.e. forest fires, hurricanes). This new branch of study could then be used as a proxy for projecting the impact of increased prevalence of these extreme events, and also the impact they will have if the patterns shift and new areas become impacted by these events. An example of this would be to use Nicaraguan TDF response to the more frequent hurricanes it has experienced over the past hundred years to predict the response of Costa Rican TDFs if they become subject to tropical storms. The types of predictive analysis would likely need to be kept within relatively consistent species assemblages, and in relatively similar types of sites. This makes information such as soil type and moisture, species assemblages, and forest structure, via LiDAR scanning areas which should be focused on in the next decade of research.

Chapter 3 of this thesis looked at understanding the relative importance of anthropogenic changes to TDF resilience, with a particular focus on the conservation legislation and legal protections for areas. Costa Rica was chosen for this because it is often held up as one of the most conservation conscious countries in the region, and it implemented a string of conservation legislation before many other countries, making it an interesting case study. Additionally, with a long history of conservation legislation, it is one of the few countries in the world which can be used to test before and after legislation was implemented with a longer timescale. By understanding what has occurred in this country, frameworks and decision making recommendations can be made both to more effectively manage the Costa Rican forests but also to begin effectively protecting forests in other areas while not inhibiting their economic growth and development.

In the case of Costa Rica, it was found that the legislation had no impact on the regeneration of forests, with a regeneration rate averaging 0.39% per year before any conservation legislation was passed and 0.34% per year after the legislation was enacted. Additionally, less than 10% of the forests which are protected are at risk of being deforested. This combination of information indicates that legislation in Costa Rica has limited if any impact on the deforestation in Costa Rica, and instead economic diversification and education have contributed to the regeneration of the forests. This assessment has been replicated at a local scale in Costa Rica, but also in Mexico and Brazil, with the spillover effects due to changes in migration and road development outside of parks (Robalino et al. 2017; Pfaff et al. 2014). Instead properly valuated and incentivized economic solutions, such as Payments for Ecosystem Services, ecotourism development, or trading in carbon markets may instead provide more impactful management and conservation strategies (Robalino et al. 2017; Pfaff et al. 2014). By studying not only the successes in recovering forests, and the new policies designed to promote this continued growth (i.e. 60% of the land area recovered to forests by 2030; decarbonisation plan), but also the problems which are associated with these programs (i.e. identifying stakeholders, evaluating ecosystem services values, incorporating carbon markets, etc.) can provide a framework for implementing effective conservation programs more efficiently (Le Coq et al. 2017).

It should be noted, however, that a major caveat to this ability to transfer frameworks is the unique development of Costa Rica as a country. The country itself is very small, only ranging 51,100 km^2, with a population of 5 million people. Additionally, Costa Rica disbanded its army in the 1940s and rerouted that money into public services, most importantly in this case, education. Additionally. there were a number of governments over the past 50 years which have focused on conservation education, which has changed the culture of the country to be more favorable to conservation efforts and having an increased awareness and understanding of the importance that the environment plays in terms of both the economy and the quality of life of the people in the country. This social mindset cannot be replicated in other countries over the course of a few years or even a decade, but requires a constant and consistent push over the course of a generation.

One other caveat to the research in this chapter was that, given our current climatic system and the changes that are predicted to occur, the anthropogenic system does not work in isolation, and though there may continue to be extensive forests, this does not mean that the forests are healthy or that they will not be degraded. An assessment and projection of this degradation is essential. The degradation of the forests is important to assess especially in terms of carbon sequestration potential and its ability to provide ecosystem services. The relationship between plants and carbon is of particular interest, because there has been the idea that increased atmospheric carbon would in turn lead to increased water use efficiency, thereby increasing the resilience of ecosystems to drought over time (Adams et al. 2019). The rate of the forests acclimation to changes in carbon is largely understudied, and the forests may not increase their resilience fast enough to match the changes to both carbon and the climate (Adams et al. 2019) This caveat and gap in research provided the basis for Chapters 4 and 5. Both chapters assess the resilience of the TDF, with Chapter 4 focusing on the Guanacaste Province of Costa Rica and Chapter 5 assessing the water use efficiency of the TDF across Meso and South America.

The main finding of Chapter 4 was that in the province, there is a quadratic relationship between biomass and Vapor Pressure Deficit (VPD), unlike the theoretical algorithms used by MODIS, which assume a linear relationship. The MODIS relationship is a largely generalized function designed to work on all natural ecosystems around the globe. Additionally, the MODIS relationship does not explicitly account for TDF systems, despite the large extent it covers, instead having the forest largely aggregated into deciduous broadleaf forests and mixed forests, as the globe is divided into 10 natural vegetation land cover types (Running and Zhao 2010). This general MODIS model breaks down at local and regional scales, with similar quadratic functions found in other Meso and South American systems, as well as in China, Tibet, and Eurasia (Alvarez-Davila et al. 2017; Liu et al. 2017; Tong et al. 2014; Chen et al. 2017; Cuicui et al. 2017).

When these productivity trends are projected into the future, most forested areas in Guanacaste are simulated to have future productivity within its historical range. If these trends were instead projected using the global linear assumption, as is done in many ESMs (Fox et al. 2018), would lead to a 26% drop in the overall GPP. Productivity projections in ESMs can be improved using regionally developed relationships, such as the one developed here, or in more recent model systems, by assimilating more data to artificially adjust the trends in an area (Fox et al. 2018). This secondary methodology is useful if the regional relationships have not been well articulated, but often still perpetuate a lag in the response of the model system compared to observation data (Fox et al. 2018). Developing local and regional scale relationships though also has some caveats, the first is that much like the global relationship, life zones should be separated in future research, to develop a more consistent view of the individual life zone resilience.

Additionally, the VPD scalar, while relevant, only explains approximately 30% of the variability in the forest productivity in Guanacaste; therefore, additional regional scale relationships can be built to better parameterize the specific limitations of growth at each site (Gonzalez-M et al. 2018). Additionally, comparisons between MODIS productivity and other productivity metrics (i.e. eddy covariance, ANPP CASA model, FAPAR) can be used to characterize the uncertainty of the growth at individual sites (Chen et al. 2014; Cao et al. 2016; Castillo et al. 2018; Wang et al. 2014). Despite these caveats, this chapter has begun the process of creating regional relationships using globally recognized algorithms, and can be used to build other relationships and compare against other TDF ecosystems.

When TDF resilience was scaled up to Meso and South America, long term changes over the past 20 years, as well, as the continental relationships between climate and productivity were assessed. In particular, TDFs were assessed for WUE to determine the response of sites to changes in available water content, as well, as the changes due to El Niño Southern Oscillation conditions. It was found that TDFs use water more efficiently in dry years compared to wet years and recover from droughts within 1-2 years. This change in water use efficiency is replicated in other global studies which indicate that sites with higher water content have a lower WUE, although they caution that MAP is not the sole predictor of WUE, especially in the tropics (Adams et al. 2019). These results indicate a level of resilience to changes in moisture conditions. This resilience to reductions in moisture is also confirmed by local scale eddy covariance sites in Costa Rica which had reductions in GPP in drought years and recovery in the year following the drought (Castro et al. 2018). The El Niño Southern Oscillation conditions can alter the productivity up to 30% ± 20% at higher latitudes, but there is little variation near the equator. This is important to look at in conjunction with the long term trends which have been found in terms of productivity. There is a clustering of sites which have had increasing productivity over the past 20 years and a clustering of sites which have decreasing productivity. With a longer dataset, there may be the ability to correlate this clustering with the ENSO events, and this could be looked into in future research. Additionally, the variations by site should be considered, because despite large scale clustering of increasing and decreasing productivity, not all sites in each area have significant changes, indicating there may also be local scale moderators which have not been accounted for in the research. Testing different local site variables might be of use to differentiate this moderator.

The results from Chapters 4 and 5 agree with each other as well, although the specific mechanisms study are different. Both chapters find that the sites in the Guanacaste province have had non-significant changes over the past decade, and the site will be resilient to changes in the future, one based on the VPD relationship, and the other based on the WUE adaptability of the forests. One thing to note is that there is no apparent tipping point in the WUE, while there appears to be one in the VPD, potentially due to the different metrics assessed or potentially due to differences in regional versus global scale response. More research into regional compared to global scale response, particularly moderated by local scale processes is needed and is important in future studies of resilience.

Other research is concerned that forests are researching the limits of their Water Use Efficiency, and it is possible that if there is drying, the forests will not be able to adapt fast enough to maintain rates of carbon uptake (Adams et al. 2019). This is problematic especially since there is evidence that the slowing in carbon uptake in the tropics has already begun (Brienen et al. 2015; Feeley et al. 2007; Adams et al. 2019). These assessments, however, do not differentiate between wet and dry tropical forests, which may have different reactions to these drying conditions. Further research is needed particularly into where the this threshold or tipping point is for TDFs. This can be found by looking at multi-year droughts. Though there are few areas where this type of drought has occurred in Meso and South America, it is possible that there have been multi-year droughts in the Australian, African, and Central Indochina TDFs. These areas could be used as a proxy to assess if there are water limitation thresholds, and then test this against any location that has this type of exposure potential in South America. These tipping points are crucial to determine, as they will dictate when the forests begin to degrade and are no longer able to support the ecosystem services that are required by the surrounding populations.

This style of continental scale research can also be used as a starting point for multi-continent research to compare the response of the better understood South American Tropical Dry Forests to the African and Asian TDFs. While the results may not be useful as a proxy, as there are different species assemblages and the relative effect of anthropogenic alteration compared to climate influences may not be equivalent across all continents, the methodology can serve as a starting point for creating similar studies which can then be compared. This will further lead to a better understanding of this ecosystem and its resilience across the globe.

6.2 Challenges and Future Directions

Despite the completion of these studies, there remain gaps which should be filled by future research, including incorporating forest resilience in training ESMs with biosphere feedbacks, carbon storage assessments, and predicting the future extent and composition of the TDF. To properly assess these characteristics, there are additional questions and courses of study that can be pursued, including:

- How do species composition and richness impact the resilience of TDF sites?
- How does non-linear forest growth impact the resilience of TDFs?
- How does the severity and frequency of nature disturbance impact regeneration and recovery of TDFs?
- What impact do multi-year droughts have on the recovery of the TDFs and the water use efficiency of these forests?

These questions have not been answered, and they will provide further insights into the resilience of the TDFs. Additionally, one area which would be of particular interested is the ongoing provisioning of ecosystem services and if there are any tipping points to their ability to provide these services to nearby populations. Work such as that conducted by Agarwala et al. (2016) which looks at changes to species assemblages based on different intensities of human use may be of particular use to build on. Also differentiating TDFs across soils, climatic zones, and human use gradients as done by Gonzalez-M et al. (2018) before determining tipping points and resilience may provide a better understanding of the interactions between the forest and its local site characteristics. Beyond further research in African and Asian TDFs, filling in the gaps in the Meso and South American TDFs would be useful, with particular focus on the Caribbean islands, Columbia, Venezuela. This would provide better data for meta-analysis that are not so spatially auto-correlated to sites in Mexico, Costa Rica, and Brazil.

Finally, one further key both to improving the earth system models, but also to further understand the resilience is to integrate of multiple sources of data. In particular, integrating local and regional scale information is important for being able to scale data more accurately. Once there is better understanding and scalability between local and regional sites, they can then be used to produce predictions and parameterize the uncertainty in the models. Additionally, integrating new types of data, including LiDAR, SIF, new hyperspectral systems, and eddy covariance flux towers, can provide different new paths for understanding relationships and build correlations which have previously not been able to be seen with previous data types. These data can then be incorporated into the increasingly powerful ESMs, allowing for more sophisticated biosphere-atmosphere feedbacks and more comprehensive predictions about the potential alterations to TDF ecosystems. These can be tested between Meso/South American, African, Indian, and Australian TDFs to highlight different climate adaptation strategies that have evolved on these continents.

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