Title

Landscape Patterns of Diversity, Wood Density, and Protected Areas in Forests of Costa Rica

Author

Robinson, Chelsea

Publication Date

2018

UNIVERSITY OF CALIFORNIA

Los Angeles

Landscape Patterns of Diversity, Wood Density, and Protected Areas in Forests of Costa Rica

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Geography

by

Chelsea Marie Robinson

2018

ABSTRACT OF THE DISSERTATION

Landscape Patterns of Diversity, Wood Density, and Protected Areas in Forests of Costa Rica

by

Chelsea Marie Robinson
Doctor of Philosophy in Geography
University of California, Los Angeles, 2018
Professor Thomas Welch Gillespie, Chair

Costa Rica harbors high levels of biodiversity and endemism. While Costa Rica does tend to have good conservation policies in place, understanding the patterns of plant diversity and biomass can allow for better management priorities. Current technologies utilizing spaceborne or airborne remotely sensed imagery could be very useful to study terrestrial processes and allow for better monitoring of patterns of forests, both spatially and temporally.

Improvements in relating forest structure in highly complex and diverse forest environments to plant diversity are critical to the science goals of the UN-REDD+ program as well as for tropical forest research in general. The scope of the proposed dissertation will cover six chapters across distinct but interrelated topics concerning the forest of Costa Rica, which seeks to improve the existing methodologies and compare results to other datasets. Ideally, this research will be applicable to other tropical environments with both field-collected tree inventory data and appropriate remote sensing products. After the introductory chapters, I focus in on the

National Park of Braulio Carrillo for Chapters 3 and 4, then scale up to the entirety of the country of Costa Rica to look at sixteen years of forest change. The first chapter introduces the importance of understanding tropical forest diversity, biomass, and carbon dynamics, as well as some specific to the country of Costa Rica. The second chapter outlines the specific study area covered in Chapters 3 and 4 within Costa Rica's Braulio Carrillo National Park (BCNP), which protects a large elevational gradient from 55 to 2814 m above sea level, and the adjacent La Selva Biological Station (LSBS). In addition, this study area chapter also discusses the country of Costa Rica in general, specifically in terms of forest policies and protection. Chapter 4 analyzes wood density from 29 stand-dominant collected along the BCNP elevational gradient. The patterns of species wood density and aboveground biomass from field measured (tree cores) and database wood density values were assessed to examine how wood density and biomass are affected by changing elevations, both intraspecifically and at the stand-level. Chapter 5 scales the remote sensing analysis up to entirety of the country of Costa Rica. In this chapter, I assess the spatial patterns driving deforestation and afforestation across Costa Rica and protected areas. Forest loss and gains within the country for the years of 2000-2016 at 30 m spatial resolution were calculated, and we tested whether protected areas (PAs) indeed had less forest loss than non-protected areas. Chapter 6 concludes the dissertation with the general state of the forest in Costa Rica based on the research from the preceding chapters and suggests possibilities for future research utilizing new remote sensing and GIS technologies.

The scope of this Ph.D. dissertation spans a range of topics from field ecological questions to extrapolation mapping and quantitative ecology. The topics covered are temporally relevant and will directly address important goals outlined in UN-REDD+ scientific plans. Developing an understanding of diversity and successional stages both within and outside of protected areas may give us some insight on how to best manage tropical montane systems and may aid in developing conservation priorities, particularly in the face of climate change.

The dissertation of Chelsea Marie Robinson is approved.

Yongkang Xue

Gregory Stewart Okin

Philip W. Rundel

Sasan S. Saatchi

Thomas Welch Gillespie, Committee Chair

University of California, Los Angeles

2018

DEDICATION

I dedicate this dissertation to my family- to whom I owe my interest and curiosity in the natural world. As a child, we would explore tide pools or hike with various Audubon field guides. From then on, I knew I wanted to study the environment, and though my interest wavered between marine and terrestrial systems, I eventually ended up loving the terrestrial world of plants. I owe tons of gratitude to my mother, who basically raised me on her own. My doctoral committee chair, Tom Gillespie, was an enthusiastic educator during my B.A. years at UCLA and further piqued my interest in plants and forests and drew me away from the marine systems I had begun to work in. I owe much of my interest and research to the guidance of Tom over the last 12 years. Thanks to Sassan Saatchi, the UCLA Department of Geography, the UCLA Latin American Institute, and the UCLA Institute of the Environment and Sustainability for the support and funding over the years.

I would also like to dedicate this dissertation to my friends, both academic and non-academic, for supporting my strange “career” and listening to me drone on about how cool different plants are while on hikes with me, and still agreeing to come time and time again.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACRONYMS USED

AGB - Aboveground Biomass
BCNP - Braulio Carrillo National Park
CR - Costa Rica
DBH – Diameter at Breast Height
DEM - Digital Elevation Model
EAGB - Estimated Aboveground Biomass
FCPF - Forest Carbon Partnership Facility
FONAFIFO - National Forest Financing Fund (1996 Forestry Law)
IUCN - International Union for the Conservation of Nature
LSBS - La Selva Biological Station
LVIS - NASA’s Land, Vegetation, and Ice Sensor (lidar)
MODIS - Moderate Resolution Imaging Spectrometer
NDVI - Normalized Difference Vegetation Index
PA(s) - Protected Area(s)
PPSA - Costa Rica’s Payment for Ecosystem Services Programme
TEAM Network - Tropical Ecology Assessment & Monitoring Network
UAVSAR - Unmanned Aerial Vehicle Synthetic Aperture
UN -REDD+ - United Nations Reducing Emissions from Deforestation and Degradation
WD - Wood Density

ACKNOWLEDGEMENTS

Funding for much of the field work was provided by grants of Sassan Saatchi, the UCLA Geography Department, the UCLA Institute of the Environment and Sustainability, and the UCLA Latin American Institute. Much of the initial forest inventory data was provided by the TEAM Network, a collaboration between Conservation International, the Missouri Botanical Garden, the Smithsonian Institution, and the Wildlife Conservation Society, a joint NASA-Organization for Tropical Studies (OTS) project, and partially funded by these institutions, the Gordon and Betty Moore Foundation, and other donors. Forest inventory plots research at La Selva was also supported by the NSF LTREB program, most recently by NSF 1357177 to D.B. Clark (PI, Co-PIs D.A. Clark and J.R. Kellner).

I thank the staff of the La Selva Biological Station for logistic support and the National Park Service and the National Ministry of the Environment for permission to conduct this research. Thanks to David Clark, Johanna Hurtado Astaiza and the key contributions of the TEAM and NASA parabiologists, including Marcos Molina, Gilbert Hurtado, Juan Gabriel Huertas Reyes, and Wagner Corella, who conducted field surveys under challenging conditions, and aided with my own collections. I thank the staff of the La Selva Biological Station for logistic support and the National Park Service and the National Ministry of the Environment for permission to conduct this research. Many thanks to the UCLA Geography Department for their continued support over so many years, particularly the hard work of Kasi McMurray.

Chapter 3 has been published in MDPI's *Remote Sensing* special issue: "*Remote Sensing of Tropical Forest Diversity*," so I would also like to thank the editors and reviewers of the manuscript.

VITA

2009	B.A. Geography/ Environmental Studies Conservation Biology Minor Departmental Highest Honors University of California, Los Angeles
2012	M.A. Geography University of California, Los Angeles
2011-2018	Teaching Assistant/ Associate/ Fellow Department of Geography University of California, Los Angeles
2016	Advanced to Ph.D. Candidacy University of California, Los Angeles

PUBLICATIONS

Robinson, Chelsea, Sassan Saatchi, Maxim Neumann, and Thomas Gillespie. 2013. "Impacts of spatial variability on aboveground biomass estimation from L-band radar in a temperate forest." *Remote Sensing* 5 (3):1001-1023.

Meyer, Victoria, Sassan S Saatchi, Jerome Chave, James W Dalling, Stephanie A Bohlman, Geoffrey A Fricker, Chelsea Robinson, Maxim Neumann, and Stephen P Hubbell. 2013. "Detecting tropical forest biomass dynamics from repeated airborne lidar measurements." *Biogeosciences* 10 (8):5421-5438.

Gillespie, Thomas W, Geoffrey A Fricker, Chelsea Robinson, and Duccio Rocchini. 2015. "Biodiversity of the world: a study from space." In *Remote Sensing Handbook*, 485-498. Taylor and Francis.

Robinson, Chelsea, Sassan Saatchi, David Clark, Johanna Hurtado Astaiza, Anna Hubel, and Thomas Gillespie. 2018. "Topography and Three-Dimensional Structure Can Estimate Tree Diversity along a Tropical Elevational Gradient in Costa Rica." *Remote Sensing* 10 (4):629.

Chapter 1. Introduction

1.1 Background

Forests cover roughly 31% of the world's land surface, and are estimated to store 48% of the world's terrestrial carbon, although these are conservative estimates (Dixon et al. 1994, Fagan and DeFries 2009, FAO 2010, Groombridge, Jenkins, and Jenkins 2002). In the first decade of this century, 2000-2010, the global net forest loss was about 5.2 million hectares per year (Fagan and DeFries 2009, FAO 2010). Forests are important members of the carbon cycle, as they help to sequester carbon from the atmosphere through photosynthesis and the removal of forests as a result of land cover conversion releases carbon to the atmosphere. Forest loss is estimated to account for roughly 12-20% of global greenhouse gas emissions, mainly through deforestation and degradation of tropical forests (Saatchi, Harris, et al. 2011, Sandbrook et al. 2010, Van der Werf et al. 2009). Each year the world has less forested area, and the forests that remain are of lower quality. For example, the replacement of natural old-growth forests with a monoculture of an exotic species greatly reduces biodiversity (Groombridge, Jenkins, and Jenkins 2002). The storage of carbon in terrestrial systems is a large portion of the global carbon budget that is hard to quantify but very important (Fagan and DeFries 2009, Solomon 2007). Developing accurate estimates of global forest extent and growth is imperative in order to assess the amount of biomass and carbon stored in the forests of Earth and long-term global health. This deforestation is uneven around the world, and standardized methodology is necessary to monitor exactly how the forests are changing, both regionally and globally. In addition, the study of biomass and carbon sequestration has become increasingly important in the current era of projected climate change scenarios. However, there are still widespread uncertainties in measurements of forests that have limited efforts to obtain this seemingly simple dataset (Fagan and DeFries 2009, Grainger 2008, Houghton 2003, Yackulic et al. 2011). Current technologies utilizing spaceborne or airborne remotely sensed imagery could be very useful to study terrestrial processes and allow for better monitoring of forest stocks.

There has been extensive research on latitudinal patterns of biodiversity, but better understanding of drivers of biodiversity can be achieved through increasing attention to patterns of elevational gradients (e.g. mountainous regions). Montane environments provide ideal cases to study drivers of plant diversity due to variation in abiotic factors. Understanding the principal drivers that result in patterns of tree diversity with elevation changes can aid in conservation plans for both flora and fauna because the heterogeneity of vegetation types affects how other organisms are distributed in space.

This dissertation examines aspects of forests that can be assessed and monitored using remote sensing, including tree diversity, carbon storage, fire occurrence, and human population as well as the effect of protected areas on forest extent across the county of Costa Rica. In this dissertation, field survey data on forests and wood density were related to airborne and spaceborne imagery over Costa Rica. In order to fully discuss the results, we need to discuss the background for assessing diversity, wood density, biomass, and remote sensing.

1.1.1 Diversity

Biodiversity is the number, variety, and variability of organisms within an area, while biogeography is the study of the distribution of life - how organisms are positioned in space across the globe (Kreft and Jetz 2007, MacArthur 1965, MacDonald 2003, Magurran and McGill 2011). Both biodiversity and biogeography of all taxa are results of abiotic and physical characteristics on earth. Vegetation distributions are driven largely by abiotic factors that limit species to distinct ranges at which they can survive. The diversity of fauna is inherently dependent on the diversity and distribution of vegetation, as areas with greater habitat complexity can support more niches for fauna (MacDonald 2003, Willig, Kaufman, and Stevens 2003). These areas of greater habitat complexity and more niche availability may also contain more faunal diversity and these areas can be identified as priority areas for conservation efforts (Aynekulu et al. 2012).

The two main types of diversity that are often discussed are alpha and beta diversity. Alpha diversity is a simple definition of the richness in species numbers, essentially the total numbers of species of a certain taxa within a set unit area (Whittaker 1972). Alpha diversity may refer to the simple count of different species (or genera, or family) within an area, or it may be calculated as an index, which takes into account the evenness, or relative species' abundances within each site. Beta diversity is a metric that is used to define the difference or similarity in species composition between two sites. If the assemblages are similar then the sites have low beta diversity, but if the two sites have few species in common, then they would be said to have high beta diversity. There are various ways to report both of these diversity parameters. Alpha diversity indices include species richness, the Shannon-Weaver Index, Fisher's alpha, among others. Beta diversity can also be calculated by different methods. The simplest version of beta diversity is simply the shared taxa between two sites, usually species. There are also several indices that can be calculated for beta diversity, including the Jaccard and Sorensen indices. All of these beta diversity indices represent how similar or different two sites are. If the sites share very few species in common, then they are said to have high beta diversity. If the sites are very similar in species composition, then there are

There are two primary local factors that can be used to predict tree diversity: stem density and area. In general, sites with higher numbers of individuals per unit area, e.g. higher stem density, tend to have more species (Bhattarai and Vetaas 2006, Carpenter 2005, Condit et al. 1996, Gentry 1988, Giriraj, Murthy, and Ramesh 2008, Givnish 1999, Gotelli and Colwell 2001, Lieberman et al. 1996b, Lomolino 2001, Unger, Homeier, and Leuschner 2013). There are latitudinal differences in forest structure, as tropical forests at low latitudes tend to be much denser than temperate forests, which is important because areas with higher numbers of individuals per the same unit area may have more species (Bhattarai and Vetaas 2006, Carpenter 2005, Gentry 1988, Givnish 1999, Lieberman et al. 1996b, Lomolino 2001).

The relationship between area and diversity is one of the most fundamental laws in ecology and is formally recognized as the Species-Area relationship (Condit et al. 1996, Giriraj, Murthy, and Ramesh 2008, Hutchinson 1953, Levin 1992, Rahbek 2005, Rosenzweig 1992, Whittaker 1972, Wiens 1989, Willig, Kaufman, and Stevens 2003) The Species-Area relationship predicts that as the sampling area gets larger, there will be more species present up until some threshold. Due to simple geometry, the Species-Area relationship can be applied to both latitudinal and elevational patterns of biodiversity.

Diversity along elevational gradients was initially believed to decline linearly from the warmer lowlands to the cooler highlands, analogous to patterns exhibited by increasing latitude (MacArthur 1972, Nogues-Bravo et al. 2008, Rahbek 1995, Rohde 1992). However, recent studies that examine the full extent of elevational gradients show a clear humped pattern, characterized by a mid-elevation diversity peak (Acharya, Chettri, and Vijayan 2011, Aynekulu et al. 2012, Bhattarai and Vetaas 2006, Carpenter 2005, Feeley et al. 2013, Nogues-Bravo et al. 2008, Vazquez and Givnish 1998, Wolf and Alejandro 2003). In both cases, the highest part of the elevational gradient is species poor compared to lower areas, but the overall reported pattern in the intermediate elevation region varies. Recent research has both confirmed these varied relationships and has provided conflicting results, without fully resolving the underlying drivers for higher diversity. However, it seems like when the full elevational extent is sampled systematically, the unimodal form with a mid-elevation peak of diversity seems to be the most prevalent pattern in the literature. Extensive literature on biodiversity patterns across geographical gradients has attributed the drivers for these diversity patterns to climate, area, availability of unique niches, range size, and as a simple consequence of a bounded gradient. These biological and theoretical hypotheses of the drivers of biodiversity can be tested on montane forests at the landscape scale. Montane and premontane forests are important areas for biodiversity and ecosystem services across various continents, and are thought to represent greater than 10% of tropical forest cover globally (Churchill et al. 1995, Doumenge et al. 1995, La Torre-Cuadros, Herrando-Perez, and Young 2007, Stadtmüller 1987). Due to adiabatic cooling rates, there are calculable effects on temperature with elevation change, resulting in predictable abiotic changes. This allows for montane forests to act as in-situ laboratories for the testing of climate-change scenarios particularly systematic analysis of species turnover and patterns in species richness. Utilizing tree survey data along the BCNP montane gradient, I will determine if this montane forest has either a monotonic decrease or a unimodal mid-elevation peak of species diversity.

1.1.2 Wood Density

Wood density is a central variable in carbon calculations, and it correlates well with many morphological, mechanical, physiological, and ecological properties (Chave et al. 2006b). Wood specific gravity is also a convenient indicator of life history strategy in trees and one with direct importance for ecosystem studies, as quicker growing pioneer species have less dense wood as compared to slower-growing heartier later successional species (Chave et al. 2006b).

These varying life histories have an impact on how energy and carbon is allocated for the growth of the plant, either for quick growth and reproduction, or slower growing and better able to withstand environmental hazards (Chave et al. 2006b, Niklas 1992, Tilman 1988, Wright et al. 2003). High disturbance rates and high turnover rates are expected to favor faster-growing species, which are often the pioneer, early successional species (Connell 1978, Huston 1979, Muller-Landau 2004). The distribution of tree life history strategies in general and of wood specific gravities in particular within a tropical tree community is theoretically expected to vary among sites depending on disturbance regime, climate, and soil fertility.

The term “wood density” is derived from measurements of wood specific gravity, which is measured as oven-dry mass divided by fresh green volume, a unit-less quotient but in parallel SI units is often reported as wood density, with g/cm^3 (Brown 1997, Lawton 1984, Muller-Landau 2004, Reyes et al. 1992, Turner 2001). These characteristics can be measured using calipers or a water displacement method**.** Wood density is highly correlated with the density of carbon per unit volume and is thus useful as a proxy to estimate ecosystem carbon storage (Brown 1997, Fearnside 1997, Muller-Landau 2004, Nelson et al. 1999). As mentioned previously in this section, wood density is positively associated with successional stage of the plant, like the fast growing pioneer species with low wood density, which have low construction costs (Chave et al. 2006b, Favrichon 1994, Suzuki 1999). This is in contrast to plants with higher wood density, which tend to be slow-growing, long-lived, climax species. Higher wood density is thought to allow for a heartier individual and increased chance of survival against physical damage. At the stand level, wood density can vary depending on disturbance history due to the differences among life history, as discussed above. High disturbance rates and high turnover rates are expected to favor faster-growing species (Connell 1978, Huston 1979, Muller-Landau

2004). In the literature, mean wood density often differs inversely with soil fertility but independently of rainfall, seasonality, and temperature, as various patterns have been seen across different species and different sites.

Wood density is an important parameter for estimating aboveground biomass (AGB) and thus can be used as a proxy for the ecosystem service of carbon sequestration. Estimates of aboveground biomass are important in order to measure carbon storage at local, regional, and global scales. Using previously developed allometric equations, AGB can be estimated relatively simply at the individual tree level then summed to the hectare level with in-situ field data. However, utilizing these allometric equations places a lot of importance on the wood density, see below equation from Chave *et al*., 2005. Because of this, the more accurate we have the wood density values the more accurate the initial calculation of plot biomass and the scaling up will be for the region that is extrapolated from the plots.

Chave (2005) equations for wet forest stands, depending on availability of tree height.

With height: $AGB_{est} = \exp(-2.557 + 0.940 \times ln(\rho D^2 H))$ $\boldsymbol{OR}$ $0.0776 \times (\rho D^2 H)^{0.940}$
Without height: $AGB_{est} = \rho \times \exp(-1.239 + 1.980 \ln(D) + 0.207(\ln(D))^2 - 0.0281(\ln(D))^3)$

AGB_{est}= Aboveground Biomass Estimate
ρ = Wood Density
D = Tree Diameter at Breast Height (DBH)
H = Tree Height

From this equation, it is clear that WD, ρ, has a large impact on the calculation of EAGB for a single individual, and these discrepancies can result in overestimation or underestimation of AGB for the individual, and exacerbated when scaled up to the plot level and higher. Because of this, having good quality wood density data on different species or on the same species under different conditions. My project will seek to compare these patterns found in Braulio Carrillo to database values. My collaborators at the Tropical Ecology Assessment and Monitoring network (TEAM), a global network, have set up the survey plots along the elevational gradient within the BCNP that I have used in my project (http://www.teamnetwork.org/ 2015). For their carbon calculations, they utilize a single wood density value across all species of 0.60 g/cm^3. My collection of wood density along the gradient will help to see effect of elevation on carbon sequestration capabilities, both intraspecific and interspecific, to make estimates of AGB more accurate.

1.1.2 Biomass

Currently, forest volume, biomass, and total carbon storage can only be conservatively estimated and the accuracy varies widely depending on the methodology (Fagan and DeFries 2009, Saatchi, Marlier, et al. 2011). In order to truly measure aboveground biomass (AGB), all trees within a region would need to be cut and weighed, then dried and reweighed. To alleviate the destructive sampling necessary, allometric equations have been developed, relating tree diameter at breast height (DBH), tree height, and wood density to an estimated AGB. Using previously developed allometric equations, AGB can be estimated relatively simply at the hectare level with in-situ field data. However, utilizing these allometric equations places a lot of importance on the wood density, as described in the above section *Wood Density*. Developing accurate estimates of global forest extent and growth is imperative in order to assess the amount of biomass and carbon stored in the forests of Earth and long-term global health. In addition, the study of biomass and carbon sequestration has become increasingly important in the current era of projected climate change scenarios, as the storage of carbon in terrestrial systems is a large portion of the global carbon (Fagan and DeFries 2009, Kuper 2013, Solomon 2007). However, there are still widespread uncertainties in measurements of forests that have limited efforts to obtain this seemingly simple dataset (Fagan and DeFries 2009, Grainger 2008, Houghton 2003). Forests are changing unevenly worldwide, and standardized methodology is necessary to monitor exactly how the forests are changing, both regionally and globally. Current technologies utilizing spaceborne or airborne remotely sensed imagery could be very useful to study terrestrial processes and allow for better monitoring of forest stocks.

Utilizing remotely sensed imagery, the estimated AGB values within these plots can be extrapolated to larger areas, quickly developing larger-scale maps than feasible through solely ground collection alone. Typically, active remote sensors equipped with radar and lidar technology have the most sensitivity to biomass changes by collecting data on the surface roughness and landscape heterogeneity, both horizontally and vertically. A significant constraint in identifying forests with different conditions is the capacity to map them from space (Achard et al. 2007, Achard et al. 2008, Asner et al. 2012b). Current technologies utilizing remotely sensed satellite imagery could be very useful to study terrestrial processes and allow for better monitoring of forest stocks.

1.1.3 Remote Sensing

Remote sensing allows for the study of objects without direct contact, typically through the use of satellite imagery. Because of this, it can allow for broad mapping of forest extent, diversity, and ecological processes at a large scale more quickly than possible solely through assessment on the ground. Ground measurements are expensive, laborious, and time consuming as well as typically very limited spatially. Field collections have to be spatially limited due to time constraints and labor input, and remote areas may be difficult to access and sample; using imagery can allow for easier analysis of these areas without additional disturbance. Because of this, remote sensing is a practical necessity to measure and monitor forests globally. Monitoring forest biomass over regional and global scales is imperative with increasing concerns about climate change, as more attention needs to be focused on accurately estimations of carbon fluxes.

One project that requires robust estimates of forest carbon stocks in various countries is the United Nations Reducing Emissions from Deforestation and Degradation (UN-REDD). The UN-REDD Program is an initiative to combat climate change, by assigning a monetary value to a country's carbon stocks. The scientific goals of the UN-REDD program specifically ask for refinements in the remote sensing methodologies to estimate forest biomass over regional and global scales. In recent years, the international community has recognized the loss of diversity as a key threat to the sustainability of tropical ecosystems by impacting their ecological functions and services. This recognition contributed to the international negotiations of UN-REDD by adding biodiversity (REDD+) as an important component of mitigating climate change (Kuper 2013). A significant constraint in identifying forests with different conditions is the capacity to map them from space (Achard et al. 2007, Giacomo et al. 2008, Asner et al. 2012a). This dissertation will utilize airborne and spaceborne passive and active sensors to effectively monitor aspects about the forests Costa Rica important to conservations, policy-makers, and ecologists. The development of methods utilizing this type of technology allows for the mapping of ecological features that were previously only feasible through ground collection.

1.2 Rationale for these types of studies

Within the large-scale patterns of biogeography along latitudinal stretches, smaller regional-scale topographical changes along mountainous regions may cause high levels of species heterogeneity and turnover of species assemblages. Montane forest is an ideal environment on which to study drivers of patterns of diversity as well as potential consequences from climate change on vegetation. Montane forests have captivated researchers for centuries, perhaps most notably Naturalist Alexander von Humboldt, who was one of the first to document montane biogeography. Prior to his work, vegetation studies mainly focused on the individual plant - chiefly taxonomic classification of organisms based on Carl Linnaeus' method (Nicolson 1996). Humboldt progressively looked at vegetation at a larger ecological scale: how the character, morphology, and distribution of flora relied on underlying environmental parameters. Through the study of plant assemblages and the way in which climatic and topographical factors influenced these assemblages, he became a pioneer of biogeography (Livingstone 1993, MacDonald 2003). He noted shifts in plant assemblages and how species change with increasing elevation, particularly along Ecuador's Mount Chimborazo. While von Humboldt noted altitudinal patterns in vegetation classes within elevation bands along montane gradients, the mere count of different species in each elevation band is also an interesting topic, and von Humboldt's groundbreaking work undoubtedly paved the way for future biogeographers to study plant distribution. Since his work in the early 1800s, there have been a number of montane biodiversity studies attempting to determine the factors that drive high plant diversity. Reported driving factors include climate, area, availability of unique niches, and range size, among others. The abiotic variables of climate, namely temperature and precipitation are some of the simplest to examine, since they can often be predicted relatively easily over the landscape. Temperature of air parcels changes due to the adiabatic rate of cooling, which is variable in conjunction with the level of moisture in the air, but is easy to calculate and predictably decreases with increasing elevation.

The reliable temperature - elevation relationship and repeated surveys of the land may be able to note shifts in species composition over the same area. Studies have found that some species are shifting upwards in elevation, presumably to stay within the same temperature range (Bertrand et al. 2011, Borchert 1998, Brodie, Post, and Laurance 2012, Feeley et al. 2013, Lenoir et al. 2010). This upwards shift of certain species could be analogous to the changes in temperature induced by climate change, which could result in species shifting up to cooler regions, either to higher latitudes or higher elevations. Although plant species are unable to alter their ideal temperature range as rapidly as their environment is changing, they are able to shift their range as a population, as certain individuals perish in the increasingly harsh environment perish and some individuals flourish in the new climate. While one would assume an upward plant population shift to cooler regions, it has also been suggested there might be a downslope shift of species, as competition is less at the lower boundary of a species range (Lenoir et al. 2010). There are unknowns regarding how vegetation might be affected by climate change, but acquiring more time-series data of vegetation surveys may allow for insight into various possible future scenarios. Some studies have looked at past pattern shifts, but few have looked at present day shifts (Feeley and Silman 2010, Feeley et al. 2011, Feeley et al. 2013). This is surprising that more research has not yet been done, since roughly two-thirds of Earth’s flora are tropical plant, and tropical genera are expected to be particularly sensitive to a changing climate due to typically low climatic variability and increased niche specialization (Deutsch et al. 2008, Feeley and Silman 2010, Ghalambor et al. 2006, Janzen 1967, McCain and Grytnes 2001, McCain 2009).

In addition to making predictions for climate change scenarios, the understanding of spatial patterns of flora diversity and carbon storage can also allow for more precise plans for targeted areas of priority for conservation areas within biodiversity hotspots (Aynekulu et al. 2012). Overall, the techniques of remote sensing can allow for standard and repeatable measurements over an area. The coupling of various remote sensing imagery and ground data can allow for the emergence of spatial patterns of diversity and carbon sequestration, which have implications for monitoring and management of health of ecosystems.

This dissertation addresses the question: How can field-based methods, remote sensing, and geographic information systems (GIS), improve monitoring and conservation efforts in Costa Rica? To answer this question, we assessed a single elevational gradient with high resolution airborne imagery coupled with ground surveys and sampling and scaled up to the country using spaceborne satellite imagery systems. First the airborne lidar data was related to field based surveys on forest species composition and structure. Secondly, a field-based study on wood density was performed to evaluate errors in wood density databases and subsequent carbon sequestration. Finally, GIS and remote sensing layers were used to assess the changes over the entirety of the country of Costa Rica from 2000-2016. The methodology and findings from this dissertation will provide a framework for monitoring and measuring aspects about forests all over the world.

1.3 Structure of the Dissertation

The scope of the proposed dissertation will cover six chapters across distinct but interrelated topics along a montane gradient of elevation change, which seeks to improve the existing methodologies and compare results to other datasets. Ideally, this research will be applicable to other tropical environments with both field-collected tree inventory data and appropriate remote sensing products. The first chapter introduces the importance of understanding tropical forest diversity, biomass, and carbon dynamics, as well as specificity to the country of Costa Rica. The second chapter outlines the specific study area covered in

Chapters 3 and 4 within Costa Rica's Braulio Carrillo National Park, which protects a large elevational gradient, and the adjacent La Selva Biological Station. In addition, the study area chapter also discusses the country of Costa Rica in general, specifically in terms of forest policies and protection.

Chapter 3 proposes the use of airborne lidar to map tree diversity along an elevational gradient in Braulio Carrillo National Park, Costa Rica. This chapter will map tree canopy height over Braulio Carrillo National Park and La Selva Biological Station and estimate tree diversity utilizing lidar technologies. Chapter 4 focuses on wood density changes along the same elevational gradient, and how this affects biomass and carbon sequestration estimations. In this chapter, I look at intraspecific changes in wood density with changes in elevation, as well as examine changes in stand-level mean wood density along the same elevation gradient. This research utilizes tree cores sample I collected over a period from 2013-2016 from 574 individual trees from 29 unique species, at different elevation sites. Chapter 5 scales up to the country of Costa Rica, looking at general forest loss and conversion within and outside of protected areas at the 30 m scale. I analyzed this forest loss in conjunction with multiple remote sensing layers, including Normalized Difference Vegetation Index (NDVI), fire data, and human population. Chapter 6 concludes the dissertation with the general state of the forest in Costa Rica based on the research from the preceding chapters and suggests possibilities for future research utilizing new remote sensing and GIS technologies.

Chapter 3 utilized field inventory data coupled with large footprint (20 m) airborne lidar data over plots over the BCNP elevational gradient in order to quantify variations in topography and three-dimensional structure across plots and landscapes. A mid-elevation bulge in multiple diversity indices was observed within the plots and landscape, which supports much of the literature, as discussed above. Species richness and diversity were negatively correlated with elevation, while the two tallest relative height metrics (rh100, rh75) derived from lidar were both significantly positively correlated with species richness and diversity. The best lidar-derived topographical and three-dimensional forest structural models showed a strong relationship with the Shannon diversity index ($r^2 = 0.941$, $p < 0.01$), with ten predictors; conversely, the best species richness model was weaker ($r^2 = 0.599$, $p < 0.01$), with two predictors.

Chapter 4 found that wood density databases tended to have inflated values of wood density. The patterns of species wood density and aboveground biomass from field measured (tree cores) and database wood density values were assessed to examine how wood density and biomass are affected by changing elevations. At the species-level, individual tree species did not exhibit significant changes in wood density along elevational gradients. At the stand-level, we found wood density did not show a linear pattern with increasing elevations, but instead was highest at both the lowest and highest elevations with a decline at mid-elevations. We found that TEAM database values (0.60 g/cm^3) were significantly higher than field measured wood density for 58% of the species sampled, and that and estimates from the Global Wood Density Database had significantly higher wood density for 50% of the same species. If we expand to just within 1 standard deviation from the mean, TEAM values were significantly different then 80% of the species, and 69% of the Global Wood Density Database. Separating the individuals by diameter class and selecting 10% of each of the classes resulted in the best method ($r^2 = 0.98$) for reasonably capturing stand-level wood density. Our results suggest that there are decreases in wood density at mid-elevations and that we are currently overestimating carbon storage in montane forests in the tropics. We also suggest a method to collect estimates of wood density for plots and carbon storage in other tropical forests.

Chapter 5 scaled up to the country of Costa Rica, looking at general forest loss and conversion within and outside of protected areas at the 30 m scale. I analyzed this forest loss in conjunction with multiple remote sensing layers, including a Landsat-based dataset on forest coverage, Normalized Difference Vegetation Index (NDVI), fire data, and human population. In addition, I compared IUCN categories of protected areas to the country as a whole and by different provinces. This project had four different main findings.

Firstly, we found that deforestation has been occurring over the entirety of the country of Costa Rica since 2000. There has been some gain across the country, but very limited when you compare the gain and loss as percentages of the total land area. For protected areas, there has also been predominantly loss over the time period, but less so than in non-protected regions. Secondly, NDVI increased slightly over the time period of 2000-2016 for the entirety of the country and within the protected areas when averaged together (0.573 to 0.5995). When the PA change was analyzed individually using a paired t-test found a significant decrease of -0.0226, with a t-value of -6.7415 ($p < 0.001$). At the province level, it was determined the provinces decreased insignificantly by -0.0029. On average, some provinces increased in NDVI while other decreased. The third research objective noted that population was centered in a few major cities, specifically San Jose. The two provinces that were the most populous were San Jose and Alajuela, and they also increased the most during this time period. The country as a whole increased in population during this time, and all provinces showed an increase in population. For humans living within protected areas, they were mostly found in IUCN category VI, which signify “Protected Areas with sustainable use of natural resources,” which allows for the conservation of habitats, along with associated cultural values and traditional natural resource management systems,” so it is unsurprising that these are the protected areas with most human presence. In general, the PAs seem to have experienced a loss of human population during these years, though it was found to be insignificant. The final research question of this chapter looked at the pattern of fire across the country of Costa Rica. Fires during the 2000-2016 period were mainly in the lowland coastal areas, and focused on the drier western portion of the country. The incidence of fire was found to be negatively correlated with the forest area lost annually (r^2 = 0.25) there was less forest area lost in years with higher fire frequency. This correlation does not imply causation and instead shows that the forest loss is more likely due to forest conversion than fires. This chapter provided a good overview of the status of the Costa Rican forest from 2000-2016.

Chapter 6 concludes the dissertation with the general state of the forest in Costa Rica based on the research from the preceding chapters and suggests possibilities for future research utilizing new remote sensing and GIS technologies.

The scope of this Ph.D. dissertation spans a range of topics from field ecological questions to extrapolation mapping and quantitative ecology. The topics covered are temporally relevant and will directly address important goals outlined in UN-REDD+ scientific plans. Developing an understanding of diversity and successional stages both within and outside of protected areas may give us some insight on how to best manage tropical montane systems and may aid in developing conservation priorities, particularly in the face of climate change.

1.4 References

Achard, F., R. DeFries, H. Eva, M. Hansen, P. Mayaux, and H. J. Stibig. 2007. "Pan-tropical monitoring of deforestation." *Environmental Research Letters* 2 (4):045022.

Achard, Frédéric, Giacomo Grassi, Martin Herold, Maurizio Teobaldelli, and Danilo Mollicone. 2008. "Use of satellite remote sensing in LULUCF sector." Background paper at the IPCC Expert Meeting.

Acharya, Bhoj Kumar, Basundhara Chettri, and Lalitha Vijayan. 2011. "Distribution pattern of trees along an elevation gradient of Eastern Himalaya, India." *Acta Oecologica-International Journal of Ecology* 37 (4):329-336. doi: 10.1016/j.actao.2011.03.005.

Asner, Gregory, Joseph Mascaro, Helene Muller-Landau, Ghislain Vieilledent, Romuald Vaudry, Maminiaina Rasamoelina, Jefferson Hall, and Michiel van Breugel. 2012a. "A universal airborne LiDAR approach for tropical forest carbon mapping." *Oecologia* 168 (4):1147-1160. doi: 10.1007/s00442-011-2165-z.

Asner, Gregory P, Joseph Mascaro, Helene C Muller-Landau, Ghislain Vieilledent, Romuald Vaudry, Maminiaina Rasamoelina, Jefferson S Hall, and Michiel van Breugel. 2012b. "A universal airborne LiDAR approach for tropical forest carbon mapping." *Oecologia* 168 (4):1147-1160.

Aynekulu, Ermias, Raf Aerts, Pieter Moonen, Manfred Denich, Kindeya Gebrehiwot, Tor-Gunnar Vagen, Wolde Mekuria, and Hans Juergen Boehmer. 2012. "Altitudinal variation and conservation priorities of vegetation along the Great Rift Valley escarpment, northern Ethiopia." *Biodiversity and Conservation* 21 (10):2691-2707. doi: 10.1007/s10531-012-0328-9.

Bertrand, Romain, Jonathan Lenoir, Christian Piedallu, Gabriela Riofrio-Dillon, Patrice de Ruffray, Claude Vidal, Jean-Claude Pierrat, and Jean-Claude Gegout. 2011. "Changes in plant community composition lag behind climate warming in lowland forests." *Nature* 479 (7374):517-520. doi: 10.1038/nature10548.

Bhattarai, Khem Raj, and Ole R. Vetaas. 2006. "Can Rapoport's rule explain tree species richness along the Himalayan elevation gradient, Nepal?" *Diversity and Distributions* 12 (4):373-378. doi: 10.1111/j.1366-9516.2006.00244.x.

Borchert, R. 1998. "Responses of tropical trees to rainfall seasonality and its long-term changes." *Climatic Change* 39 (2-3):381-393. doi: 10.1023/a:1005383020063.

Brodie, Jedediah, Eric Post, and William F. Laurance. 2012. "Climate change and tropical biodiversity: a new focus." *Trends in Ecology & Evolution* 27 (3):145-150. doi: 10.1016/j.tree.2011.09.008.

Brown, Sandra. 1997. *Estimating biomass and biomass change of tropical forests: a primer*. Vol. 134: Food & Agriculture Org.

Carpenter, C. 2005. "The environmental control of plant species density on a Himalayan elevation gradient." *Journal of Biogeography* 32 (6):999-1018. doi: 10.1111/j.1365-2699.2005.01249.x.

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Folster, F. Fromard, N. Higuchi, T. Kira, J. P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riera, and T. Yamakura. 2005. "Tree allometry and improved estimation of carbon stocks and balance in tropical forests." *Oecologia* 145 (1). doi: 10.1007/s00442-005-0100-x.

Chave, Jérôme;, Helene C; Muller-Landau, Timothy R; Baker, Tomás A; Easdale, Hans; ter Steege, and Campbell Webb. 2006b. "Regional and phylogenetic variation of wood density across 2456 neotropical tree species." *Ecological applications* 16 (6):2356-2367.

Churchill, SP, H Balslev, E Forero, and et al. 1995. "Biodiversity and conservation of neotropical Montane Forests - Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium, The New York Botanical Garden, 21-26 June 1993 - Introduction." *Biodiversity and Conservation of Neotropical Montane Forests*:R11-R14.

Condit, R., S. P. Hubbell, J. V. Lafrankie, R. Sukumar, N. Manokaran, R. B. Foster, and P. S. Ashton. 1996. "Species-area and species-individual relationships for tropical trees: A comparison of three 50-ha plots." *Journal of Ecology* 84 (4). doi: 10.2307/2261477.

Connell, Joseph H. 1978. "Diversity in tropical rain forests and coral reefs." *Science* 199 (4335):1302-1310.

Deutsch, Curtis A, Joshua J Tewksbury, Raymond B Huey, Kimberly S Sheldon, Cameron K Ghalambor, David C Haak, and Paul R Martin. 2008. "Impacts of climate warming on terrestrial ectotherms across latitude." *Proceedings of the National Academy of Sciences* 105 (18):6668-6672.

Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski. 1994. "CARBON POOLS AND FLUX OF GLOBAL FOREST ECOSYSTEMS." *Science* 263 (5144):185-190. doi: 10.1126/science.263.5144.185.

Doumenge, C., D. Gilmour, M. R. Perez, and J. Blockhus. 1995. "TROPICAL MONTANE CLOUD FORESTS - CONSERVATION STATUS AND MANAGEMENT ISSUES." *Tropical Montane Cloud Forests* 110:24-37.

Fagan, Matthew, and Ruth S DeFries. 2009. *Measurement and Monitoring of the World's Forests: A Review and Summary of Remote Sensing Technical Capability, 2009-2015*: Resources for the Future.

FAO. 2010. "Global Forest Resource Assessment, Main report." *FAO Forestry Paper* 163:340.

Favrichon, Vincent. 1994. "Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise."

Fearnside, Philip M. 1997. "Wood density for estimating forest biomass in Brazilian Amazonia." *Forest ecology and management* 90 (1):59-87.

Feeley, Kenneth J, Miles R Silman, Mark B Bush, William Farfan, Karina Garcia Cabrera, Yadvinder Malhi, Patrick Meir, Norma Salinas Revilla, Mireya Natividad Raurau Quisiyupanqui, and Sassan Saatchi. 2011. "Upslope migration of Andean trees." *Journal of Biogeography* 38 (4):783-791.

Feeley, Kenneth J., Johanna Hurtado, Sassan Saatchi, Miles R. Silman, and David B. Clark. 2013. "Compositional shifts in Costa Rican forests due to climate-driven species migrations." *Global Change Biology* 19 (11):3472-3480. doi: 10.1111/gcb.12300.

Feeley, Kenneth J., and Miles R. Silman. 2010. "Biotic attrition from tropical forests correcting for truncated temperature niches." *Global Change Biology* 16 (6):1830-1836. doi: 10.1111/j.1365-2486.2009.02085.x.

Gentry, A. H. 1988. "CHANGES IN PLANT COMMUNITY DIVERSITY AND FLORISTIC COMPOSITION ON ENVIRONMENTAL AND GEOGRAPHICAL GRADIENTS." *Annals of the Missouri Botanical Garden* 75 (1):1-34. doi: 10.2307/2399464.

Ghalambor, Cameron K, Raymond B Huey, Paul R Martin, Joshua J Tewksbury, and George Wang. 2006. "Are mountain passes higher in the tropics? Janzen's hypothesis revisited." *Integrative and Comparative Biology* 46 (1):5-17.

Giacomo, Grassi, Monni Suvi, Federici Sandro, Achard Frederic, and Mollicone Danilo. 2008. "Applying the conservativeness principle to REDD to deal with the uncertainties of the estimates." *Environmental Research Letters* 3 (3):035005.

Giriraj, A., M. S. R. Murthy, and B. R. Ramesh. 2008. "VEGETATION COMPOSITION, STRUCTURE AND PATTERNS OF DIVERSITY: A CASE STUDY FROM THE TROPICAL WET EVERGREEN FORESTS OF THE WESTERN GHATS, INDIA." *Edinburgh Journal of Botany* 65 (3):447-468. doi: 10.1017/s0960428608004952.

Givnish, T. J. 1999. "On the causes of gradients in tropical tree diversity." *Journal of Ecology* 87 (2):193-210. doi: 10.1046/j.1365-2745.1999.00333.x.

Gotelli, N. J., and R. K. Colwell. 2001. "Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness." *Ecology Letters* 4 (4):379-391. doi: 10.1046/j.1461-0248.2001.00230.x.

Grainger, Alan. 2008. "Difficulties in tracking the long-term global trend in tropical forest area." *Proceedings of the National Academy of Sciences* 105 (2):818-823.

Groombridge, Brian, Martin D Jenkins, and Martin Jenkins. 2002. *World atlas of biodiversity: earth's living resources in the 21st century*: Univ of California Press.

Houghton, R. A. 2003. "Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850-2000." *Tellus Series B-Chemical and Physical Meteorology* 55 (2). doi: 10.1034/j.1600-0889.2003.01450.x.

http://www.teamnetwork.org/. 2015. "Tropical Ecology Assessment & Monitoring Network: Early Warning System for Nature." http://www.teamnetwork.org.

Huston, Michael. 1979. "A general hypothesis of species diversity." *American naturalist*:81-101.

Hutchinson, G Evelyn. 1953. "The concept of pattern in ecology." *Proceedings of the Academy of Natural Sciences of Philadelphia* 105:1-12.

Janzen, Daniel H. 1967. "Why mountain passes are higher in the tropics." *The American Naturalist* 101 (919):233-249.

Kreft, Holger, and Walter Jetz. 2007. "Global patterns and determinants of vascular plant diversity." *Proceedings of the National Academy of Sciences of the United States of America* 104 (14):5925-5930. doi: 10.1073/pnas.0608361104.

Kuper, Joe. 2013. "REDD in Costa Rica." Global Canopy Programme Consultant. http://theredddesk.org/countries/costa-rica.

La Torre-Cuadros, Mdla, S. Herrando-Perez, and K. R. Young. 2007. "Diversity and structural patterns for tropical montane and premontane forests of central Peru, with an assessment of the use of higher-taxon surrogacy." *Biodiversity and Conservation* 16 (10):2965-2988. doi: 10.1007/s10531-007-9155-9.

Lawton, Robert O. 1984. "Ecological constraints on wood density in a tropical montane rain forest." *American Journal of Botany*:261-267.

Lenoir, Jonathan, Jean-Claude Gegout, Antoine Guisan, Pascal Vittoz, Thomas Wohlgemuth, Niklaus E. Zimmermann, Stefan Dullinger, Harald Pauli, Wolfgang Willner, and Jens-Christian Svenning. 2010. "Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate." *Ecography* 33 (2):295-303. doi: 10.1111/j.1600-0587.2010.06279.x.

Levin, Simon A. 1992. "The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture." *Ecology* 73 (6):1943-1967.

Lieberman, Diana, Milton Lieberman, Rodolfo Peralta, and Gary S Hartshorn. 1996b. "Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica." *Journal of Ecology*:137-152.

Livingstone, David N. 1993. *The Geographical Tradition*: Wiley-Blackwell.

Lomolino, M. V. 2001. "Elevation gradients of species-density: historical and prospective views." *Global Ecology and Biogeography* 10 (1):3-13. doi: 10.1046/j.1466-822x.2001.00229.x.

MacArthur, Robert H. 1965. "Patterns of species diversity." *Biological reviews* 40 (4):510-533.

MacArthur, Robert H. 1972. *Geographical ecology; patterns in the distribution of species*. New York: Harper & Row.

MacDonald, Glen M. 2003. *Biogeography: Space, Time and Life*: John Wiley & Sons Inc.

Magurran, Anne E., and Brian J. McGill. 2011. *Biological Diversity: frontiers in measurement and assessment*: Oxford University Press.

McCain, Christy M. 2009. "Vertebrate range sizes indicate that mountains may be 'higher'in the tropics." *Ecology letters* 12 (6):550-560.

McCain, Christy M, and John-Arvid Grytnes. 2001. "Elevational gradients in species richness." *e LS*.

Muller-Landau, Helene C. 2004. "Interspecific and Inter-site Variation in Wood Specific Gravity of Tropical Trees1." *Biotropica* 36 (1):20-32.

Nelson, Bruce W, Rita Mesquita, Jorge LG Pereira, Silas Garcia Aquino De Souza, Getulio Teixeira Batista, and Luciana Bovino Couto. 1999. "Allometric regressions for improved estimate of secondary forest biomass in the central Amazon." *Forest ecology and management* 117 (1-3):149-167.

Nicolson, M. 1996. "Humboldtian plant geography after Humboldt: The link to ecology." *British Journal for the History of Science* 29 (102):289-310.

Niklas, Karl J. 1992. *Plant biomechanics: an engineering approach to plant form and function*: University of Chicago press.

Nogues-Bravo, D., M. B. Araujo, T. Romdal, and C. Rahbek. 2008. "Scale effects and human impact on the elevational species richness gradients." *Nature* 453 (7192):216-U8. doi: 10.1038/nature06812.

Rahbek, C. 1995. "THE ELEVATIONAL GRADIENT OF SPECIES RICHNESS - A UNIFORM PATTERN." *Ecography* 18 (2):200-205. doi: 10.1111/j.1600-0587.1995.tb00341.x.

Rahbek, C. 2005. "The role of spatial scale and the perception of large-scale species-richness patterns." *Ecology Letters* 8 (2):224-239. doi: 10.1111/j.1461-0248.2004.00701.x.

Reyes, Gisel, Sandra Brown, Jonathan Chapman, and Ariel E Lugo. 1992. "Wood densities of tropical tree species." *Gen. Tech. Rep. SO-88. New Orleans, LA: US Dept of Agriculture, Forest Service, Southern Forest Experiment Station. 15 p.* 88.

Rohde, K. 1992. "LATITUDINAL GRADIENTS IN SPECIES-DIVERSITY - THE SEARCH FOR THE PRIMARY CAUSE." *Oikos* 65 (3):514-527. doi: 10.2307/3545569.

Rosenzweig, M. L. 1992. "SPECIES-DIVERSITY GRADIENTS - WE KNOW MORE AND LESS THAN WE THOUGHT." *Journal of Mammalogy* 73 (4):715-730. doi: 10.2307/1382191.

Saatchi, Sassan, Miriam Marlier, Robin L. Chazdon, David B. Clark, and Ann E. Russell. 2011. "Impact of spatial variability of tropical forest structure on radar estimation of aboveground biomass." *Remote Sensing of Environment* 115 (11). doi: 10.1016/j.rse.2010.07.015.

Saatchi, Sassan S., Nancy L. Harris, Sandra Brown, Michael Lefsky, Edward T. A. Mitchard, William Salas, Brian R. Zutta, Wolfgang Buermann, Simon L. Lewis, Stephen Hagen, Silvia Petrova, Lee White, Miles Silman, and Alexandra Morel. 2011. "Benchmark map of forest carbon stocks in tropical regions across three continents." *Proceedings of the National Academy of Sciences* 108 (24):9899-9904. doi: 10.1073/pnas.1019576108.

Sandbrook, C., F. Nelson, W. M. Adams, and A. Agrawal. 2010. "Carbon, forests and the REDD paradox." *Oryx* 44 (3):330-334. doi: 10.1017/s0030605310000475.

Solomon, Susan. 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*. Vol. 4: Cambridge University Press.

Stadtmüller, Thomas. 1987. *Cloud forests in the humid tropics: a bibliographic review*: The United Nations University.

Suzuki, Eizi. 1999. "Diversity in specific gravity and water content of wood among Bornean tropical rainforest trees." *Ecological Research* 14 (3):211-224.

Tilman, David. 1988. *Plant strategies and the dynamics and structure of plant communities*: Princeton University Press.

Turner, Ian Mark. 2001. *The ecology of trees in the tropical rain forest*: Cambridge University Press.

Unger, Malte, Juergen Homeier, and Christoph Leuschner. 2013. "Relationships among leaf area index, below-canopy light availability and tree diversity along a transect from tropical lowland to montane forests in NE Ecuador." *Tropical Ecology* 54 (1):33-45.

Van der Werf, Guido R, Douglas C Morton, Ruth S DeFries, Jos GJ Olivier, Prasad S Kasibhatla, Robert B Jackson, G James Collatz, and James T Randerson. 2009. "CO 2 emissions from forest loss." *Nature geoscience* 2 (11):737.

Vazquez, J. A., and T. J. Givnish. 1998. "Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan." *Journal of Ecology* 86 (6):999-1020.

Whittaker, R. H. 1972. "EVOLUTION AND MEASUREMENT OF SPECIES DIVERSITY." *Taxon* 21 (2-3). doi: 10.2307/1218190.

Wiens, J. A. 1989. "SPATIAL SCALING IN ECOLOGY." *Functional Ecology* 3 (4):385-397. doi: 10.2307/2389612.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. "Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis." *Annual Review of Ecology Evolution and Systematics* 34:273-309. doi: 10.1146/annurev.ecolsys.34.012103.144032.

Wolf, J. H. D., and F. Alejandro. 2003. "Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico." *Journal of Biogeography* 30 (11):1689-1707. doi: 10.1046/j.1365-2699.2003.00902.x.

Wright, S Joseph, Helene C Muller-Landau, Richard Condit, and Stephen P Hubbell. 2003. "Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees." *Ecology* 84 (12):3174-3185.

Yackulic, Charles B, Matthew Fagan, Meha Jain, Amir Jina, Yili Lim, Miriam Marlier, Robert Muscarella, Patricia Adame, Ruth DeFries, and Maria Uriarte. 2011. "Biophysical and socioeconomic factors associated with forest transitions at multiple spatial and temporal scales." *Ecology and Society* 16 (3):15.

Chapter 2: Study Site- Costa Rica's Braulio Carrillo National Park and La Selva Biological Station

2.1 Study Site

The field component of this project was conducted in the northern central portion of Costa Rica, in Braulio Carrillo National Park (BCNP) and La Selva Biological Station (LSBS). Costa Rica's location in Central America, with the ocean on two borders, and to Nicaragua and Panama, has highly varied topography and geography, which has allowed for the evolution of high levels of biodiversity: while Costa Rica encompasses only 0.03% of the terrestrial world, it contains 4.8% of all described species (GOC 2009, Kuper 2013). BCNP is located on the volcanic Cordillera Central mountain range in the Heredia Province between the capitol of San José and Puerto Limón on the Caribbean side of the country. LSBS is connected contiguously to the extent of the BCNP at the northern end, in Puerto Viejo de Sarapiquí. The park extends from ~26 m above sea level up to ~2900m at the highest peak, in just 20 km (http://www.teamnetwork.org/). It is the only such remaining intact transect in Central America, and traverses several different ecoregions, from lowland tropical rainforest to cloud forests at high elevations, each with their own plant assemblages. The BCNP is said to contain more than 6,000 species of plants, representing 50% of the total plant species in the country of Costa Rica (http://www.teamnetwork.org/ 2015). This diverse plant life is able to support high levels of faunal diversity. Unlike the Costa Rican parks more frequently travelled by tourists, like as Poás Volcano National Park and Manuel Antonio National Park, BCNP is relatively unmaintained and untravelled, and consists of roughly 90% primary forest. In addition, the BCNP also protects areas important for the Sarapiquí watershed (http://www.teamnetwork.org/ 2015).

The elevation gradient within the BCNP is a Tropical Ecology Assessment and Monitoring Network (TEAM) site, meaning that there are standardized protocols for surveying and monitoring the vegetation and fauna within the park. The TEAM project is based at LSBS and aided by the Organization for Tropical Studies (OTS). In addition, the proximity to LSBS attracts many researchers from all ecological fields to the elevational gradient, from botanists to entomologists.

2.2 Costa Rican Policy

Costa Rica’s location in Central America, with the ocean on two borders, and to Nicaragua and Panama, has highly varied topography and geography which has allowed for the evolution of high levels of biodiversity: while Costa Rica encompasses only 0.03% of the terrestrial world it contains 4.8% of all described species (GOC 2009, Kuper 2013). Costa Rica as a whole is very proactive in terms of natural resource management and conservation of biodiversity. Costa Rica’s most well-known policy Payment for Ecosystem Services Programme (PPSA), that began in 1997, is widely considered to be the most successful for its kind (GEF 2005, Kuper 2013, SINAC 2009). Under the PPSA, Costa Rica pays private owners of forest to conserve forest or allow it to regenerate in return for the ecosystem services they produce. These ecosystems services include emissions mitigation, water resource protection, provision of scenic beauty, and protection of biodiversity. Until the 1980s, policies and incentives in Costa Rica favored deforestation, particularly for cattle rearing. Costa Rica saw a precipitous fall in forest cover, from 63% in 1960 to 21% in 1987 (GOC 2011). Though Costa Rica had begun to regain forest before the implementation of the PPSA, the policy was been instrumental in helping Costa Rica rebound to 2.67million ha or 52.4% forest cover in 2010 (51% according to the Food and Agriculture Organization of the United Nations (FAO) (FAO 2010, FONAFIFO 2012)/

The increase in forest cover is slowing, however, and the Government of Costa Rica estimates that under a business as usual scenario, the effects of PPSA would level off at 55%

forest cover (GOC 2011). To continue increasing forest cover, Costa Rica plans to extend PPSA by another 342,000 ha as the backbone of its REDD+ Programme (GOC 2013). In February 2013, Costa Rica submitted an Emissions Reduction Project Idea Note (ER-PIN) to the Forest Carbon Partnership Facility's (FCPF) Carbon Fund, which was approved in Paris in June 2013 (FCPF-CF 2013, GOC 2013). All the carbon elements of Costa Rica's REDD+ activities are included in the ER-PIN, which aims to mitigate emissions through avoided deforestation and increased carbon sequestration by 29.5m tC or approximately 108m tCO2e between 2010 and 2020. The current February 2013 version of the ER-PIN mistakenly states uses tCO2 instead of tC thereby understating emissions reductions by a factor of 3.67 (FONAFIFO 2012, Kuper 2013). Though private carbon projects are permitted, since REDD+ incentives will be offered under the existing national PPSA, there are no stand-alone early REDD+ initiatives aiming to sell emissions reductions from avoided deforestation in the voluntary market. Costa Rica officially became part of the REDD+ program in 2014.

2.3 Implications of this study

Improvements in relating forest structure in highly complex and diverse forest environments to plant diversity are critical to the science goals of the UN-REDD+ program as well as for tropical forest research in general. The scope of the proposed dissertation will cover six chapters across distinct but interrelated topics concerning the forest of Costa Rica, which seeks to improve the existing methodologies and compare results to other datasets. Ideally, this research will be applicable to other tropical environments with both field-collected tree inventory data and appropriate remote sensing products.

Costa Rica harbors high levels of biodiversity and endemism. While Costa Rica does tend to have good conservation policies in place, understanding the patterns of plant diversity and biomass can allow for better management priorities. Current technologies utilizing spaceborne or airborne remotely sensed imagery could be very useful to study terrestrial processes and allow for better monitoring of patterns of forests, both spatially and temporally.

The scope of this Ph.D. dissertation spans a range of topics from field ecological questions to extrapolation mapping and quantitative ecology. The topics covered are temporally relevant and will directly address important goals outlined in UN-REDD+ scientific plans. Developing an understanding of diversity and successional stages both within and outside of protected areas may give us some insight on how to best manage tropical montane systems and may aid in developing conservation priorities, particularly in the face of climate change.

2.4 References

FAO. 2010. "Global Forest Resource Assessment, Main report." *FAO Forestry Paper* 163:340.

FCPF-CF, FOREST CARBON PARTNERSHIP FUND – CARBON FUND. 2013. "Chair's Summary Online." Seventh Meeting (CF7). Paris, France.

FONAFIFO, CONAFOR. 2012. "Ministry of Environment." *Lessons Learned for REDD+ from PES and Conservation Incentive Programs. Examples from Costa Rica, Mexico, and Ecuador*.

GEF, GLOBAL ENVIRONMENTAL FACILITY. 2005. Project Executive Summary: Mainstreaming Market-Based Instruments for Environmental Management.

GOC, Government of Costa Rica. 2009. IV Informe de País sobre el Convenio de la Diversidad Biológica. San José, Costa Rica.

GOC, Government of Costa Rica. 2011. "Propuesta para la Preparación de Readiness R-PP. Submitted to FCPF April 2011."

GOC, Government of Costa Rica. 2013. "Emissions Reduction Program Idea Note (ER-PIN). ."

http://www.teamnetwork.org/. 2015. "Tropical Ecology Assessment & Monitoring Network: Early Warning System for Nature." http://www.teamnetwork.org.

Kuper, Joe. 2013. "REDD in Costa Rica." Global Canopy Programme Consultant. http://theredddesk.org/countries/costa-rica.

SINAC, Sistema Nacional de Áreas de Conservación. 2009. IV Informe de País al Convenio sobre la Diversidad Biológica. In *Mimeografiado*. San Jose, Costa Rics: GEF-PNUD.

Chapter 3. Topography and Three-Dimensional Structure Can Estimate Tree Diversity along a Tropical Elevational Gradient in Costa Rica

Abstract: This research seeks to understand how tree species richness and diversity relates to field data (1-ha plots) on forest structure (stems, basal area) and lidar derived data on topography and three-dimensional forest structure along an elevational gradient in Braulio Carrillo National Park, Costa Rica. In 2016 we calculated tree species richness and diversity indices for twenty 1-ha plots located along a gradient ranging from 56 to 2814 m in elevation. Field inventory data were combined with large footprint (20 m) airborne lidar data over plots in 2005, in order to quantify variations in topography and three-dimensional structure across plots and landscapes. A distinct pattern revealing an increase in species' richness and the Shannon diversity index was observed in correlation with increasing elevation, up to about 600 m; beyond that, at higher elevations, a decrease was observed. Stem density and basal area both peaked at the 2800 m site, with a mini-peak at 600 m, and were both negatively associated with species richness and diversity. Species richness and diversity were negatively correlated with elevation, while the two tallest relative height metrics (rh100, rh75) derived from lidar were both significantly positively correlated with species richness and diversity. The best lidar-derived topographical and three-dimensional forest structural models showed a strong relationship with the Shannon diversity index ($r^2 = 0.941$, $P < 0.01$), with ten predictors; conversely, the best species richness model was weaker ($r^2 = 0.599$, $P < 0.01$), with two predictors. We realize that our high r^2 has to be interpreted with caution due to possible overfitting, since we had so few ground plots in which to develop the relationship with the numerous topographical and structural explanatory variables. However, this is still an interesting analysis, even with the issue of overfitting. To reduce issues with overfitting we used ridge regression, which acted as a regularization method, shrinking coefficients in order to decrease their variability and multicollinearity. This study is unique

because it uses paired 1-ha plot and airborne lidar data over a tropical elevation gradient, and suggests potential for mapping species richness and diversity across elevational gradients in tropical montane ecosystems using topography and relative height metrics from spaceborne lidar with greater spatial coverage (e.g., GEDI).

3.1 Introduction

Tropical forests are experiencing high rates of deforestation and degradation; this has had in a strongly adverse impact on biodiversity and ecosystem services (Chapin et al. 2000, Jantz et al. 2015, Olivares et al. 2015). In recent years, the international community has recognized the loss of diversity—and the associated impact upon ecological functions and services—as a key threat to the sustainability of tropical ecosystems (Jantz et al. 2015). Quantifying patterns and understanding the processes that maintain species diversity across tropical landscapes are considered among the ten most challenging problems that require spatial data from combined ground and remote observations to resolve (Rose et al. 2015). Tropical montane forests are of particular interest because of their high diversity, the complexity of their landscapes, the intensity of degradation from anthropogenic forces, and their vulnerability to changing climate.

Patterns of diversity along elevational gradients in tropical montane forests have been the subject of many studies (Guo et al. 2013, Lieberman et al. 1996a, Whittaker and Niering 1975, Whittaker, Willis, and Field 2001). Diversity along elevational gradients was initially believed to decline linearly from the warmer lowlands to the cooler highlands, analogous to patterns exhibited by increasing latitude (Guo et al. 2013, MacArthur 1972, Nogues-Bravo et al. 2008, Rahbek 1995, Rohde 1992). However, recent tropical montane studies that examine the full extent of elevational gradients show a pattern characterized by a mid-elevation diversity peak of trees, epiphytes, and mammals (Acharya, Chettri, and Vijayan 2011, Aynekulu et al. 2012, Bhattarai and Vetaas 2006, Cardelus, Colwell, and Watkins 2006, Carpenter 2005, Gentry 1988, Feeley et al. 2013, Guo et al. 2013, McCain 2004, Nogues-Bravo et al. 2008, Vazquez and Givnish 1998, Whittaker and Niering 1975, Wolf and Alejandro 2003). Species diversity is hypothesized to be greatest midway up the gradient, at an ecotone type environment, with species intermingling from both lower and higher elevations (Cardelus, Colwell, and Watkins 2006, Homeier et al. 2010, Kuper et al. 2004, Lieberman et al. 1996a). However, the structure of the forest may also be a key mechanism for diversity patterns, and may also explain why there are more species at mid-elevations. In particular, field data suggests that stem density and biomass may be associated with diversity along elevation gradients, and new technologies such as lidar are available to examine the micro-topography and three-dimensional structure of tropical forests (Blair and Hofton 1999, Hofton et al. 2002, Lefsky et al. 2002).

Several aspects of forest structure data, including stem density, basal area, and aboveground biomass, are generally collected in the field and may be associated with tree diversity (Clark and Clark 2000, Girardin et al. 2014). In general, sites with higher numbers of individuals per unit area, e.g., higher stem density, tend to have more species (Bhattarai and Vetaas 2006, Carpenter 2005, Condit et al. 1996, Gentry 1988, Giriraj, Murthy, and Ramesh 2008, Givnish 1999, Gotelli and Colwell 2001, Lieberman et al. 1996a, Unger, Homeier, and Leuschner 2013). A similar pattern has also been noted for basal area and biomass of forests, with the high diversity in areas with the highest basal area (Bhuyan, Khan, and Tripathi 2003, Clark and Clark 2000, Liang et al. 2007). However, there have been a number of studies in lowland rainforests that have reported only weak relationships between diversity and basal area/biomass, as just a few large trees may contain much of the biomass (Slik et al. 2013, Wolf et al. 2012).

Canopy and understory structural variations and topographical metrics have been associated with patterns of diversity in tropical lowlands, and can be quantified through the use of lidar remote sensing (Fricker et al. 2015, Wolf et al. 2012). Lidar can provide waveforms of the returned energy from relatively small to large footprints, over large areas. Prior research has found that lidar waveform data closely matched field-collected vertical canopy profiles in the lowland forest (Drake, Dubayah, Knox, et al. 2002, Tang et al. 2012). If there is a reasonable relationship between the lidar-derived topography, and three-dimensional structure of a forest stand and plot data are representative of the landscape, it should be feasible to predict tree diversity across an entire area covered by a lidar swath. Utilizing lidar technology over larger areas may be assessed more quickly than ground-collected data alone, and may help to pinpoint critical areas for conservation priorities (Drake, Dubayah, Clark, et al. 2002, Dubayah and Drake 2000, Dubayah et al. 2010).

There are a number of theoretical and empirical reasons why lidar metrics on topography and three-dimensional structure should be associated with patterns of diversity. The topographic variables of elevation, slope, and aspect have been reported to show varying levels of predictive power for diversity; these can easily be quantified with lidar (Clark and Clark 2000, Homeier et al. 2010, Pires and Prance 1985). In particular, steep slopes generally result in areas with less soil development, lower levels of soil nutrients, and less water retention, and hence, less diversity than in valleys or on mild slopes (Austin, Pausas, and Nicholls 1996, Clark and Clark 2000, Homeier et al. 2010, Pires and Prance 1985, Wolf et al. 2012). In addition, it has also been hypothesized that aspect, or the orientation of a site, may be associated with diversity with areas with less direct sun light. Such areas may maintain higher water holding potential, and thus support greater species richness (Burnett et al. 1998, Wolf et al. 2012). Studies in tropical forests have clearly shown that the development of high and structurally complex canopies results in greater species richness (Macarthur and Klopfer 1961, Wolf et al. 2012). In particular, the mean and standard deviation of tree or canopy height have been associated with high levels of diversity in tropical forests, with taller trees and more heterogeneity in the canopy permitting a wider niche for other tree species to persist (Bergen et al. 2009, Fricker et al. 2015, Goetz et al. 2007). Recent studies have also shown that upper canopy variability is correlated with increased species richness among trees (>1 cm dbh), possibly due to partitioning of light resources (Wolf et al. 2012). In particular, metrics on canopy height and heterogeneity have been able to predict 25% of the variation of species richness for trees $\geq$ 10 cm dbh in lowland rainforests (Fricker et al. 2015).

This research seeks to assess how tree species richness and diversity changes along a Neotropical elevational gradient within Braulio Carrillo National Park in Costa Rica. This research has three primary research objectives. First, we test if species richness and diversity and the mid-elevation peak is associated with forest structure metrics (stems, basal area) collected in 1-ha plots in the field. Second, we test whether topographical and forest structural metrics derived from lidar were associated with tree species richness and diversity within 1-ha plots. Third, we examined if lidar-derived topographical and three-dimensional structural metrics within plots are representative of the overall landscape of Braulio Carrillo National Park.

3.2 Materials and Methods

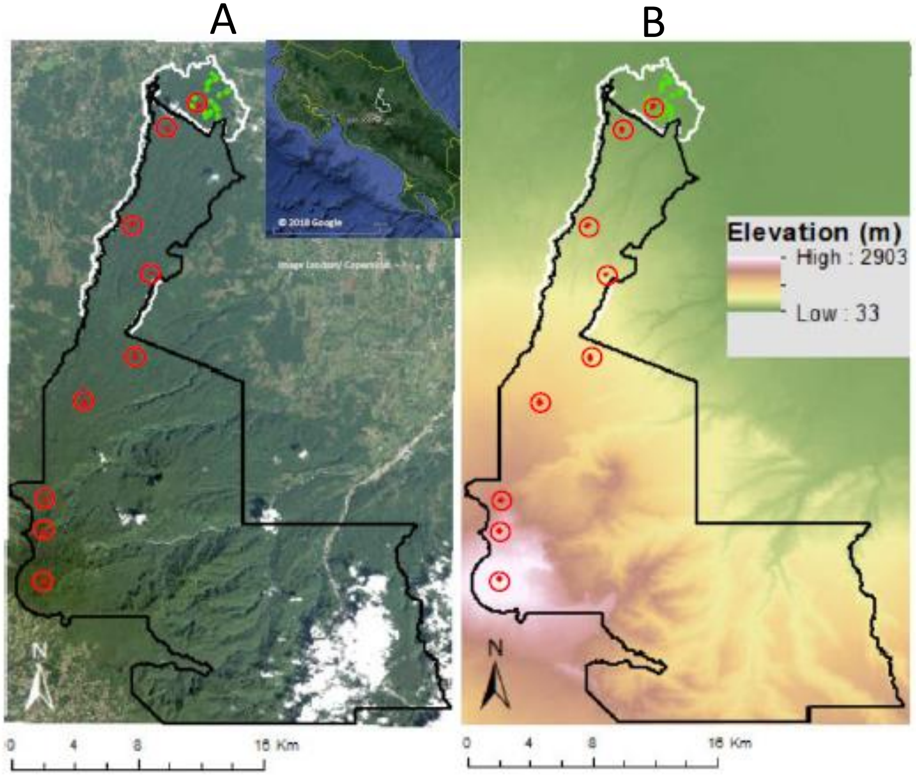
3.2.1 Study Area

This research was conducted along a unique tropical forest elevational gradient in Costa Rica, with 1-ha plots spanning from within the La Selva Biological Station at 56 m above sea level (m.a.s.l) up to 2814 m.a.s.l. in Braulio Carrillo National Park (BCNP). This elevational gradient, protected by a National Park, is quite unique for Central America, spanning several ecoregions, from lowlands to high elevation cloud forest, and providing the conditions for high species turnover and diversity (Clark, Hurtado, and Saatchi 2015). The lowland forest in this region has an average annual rainfall of ~4000 mm, with ~9000 mm at mid-elevations and ~3000 mm at the peak (Feeley et al. 2013, Holdridge 1966, Lieberman et al. 1996a). The average temperature is 26 °C in the lowlands; temperatures decrease with increased elevation, down to ~10 °C at the peak (Clark and Clark 2000). Soil types vary over the region, but all are influenced by the past activity of the Barva Volcano; parent materials of basaltic and andesitic lavas from the Plio-Pleistocene age are common along the gradient, with more agglomerate tuff-like soil at high elevations (Grieve, Proctor, and Cousins 1990). Due to volcanic activity, the soils are younger and have endured less weathering near the peak of the Barva Volcano (Grieve, Proctor, and Cousins 1990, Lieberman et al. 1996a). Besides the uniqueness of the protected area extending over multiple life zones, this area is also special because it offers paired field and airborne lidar data over a tropical elevation gradient, which few other places in the world offer (Drake, Dubayah, Knox, et al. 2002, Holdridge 1966). We use the term ‘landscape’ when we refer to the area within Braulio Carrillo National Park, which is a mountainous area surrounded by lowlands covered in agricultural land. Here, we are only concerned with the landscape of the mountainous and forested protected area of Braulio Carrillo National Park and La Selva Biological Station, covered by the lidar dataset.

3.2.2 Field Data

Vegetation surveys were conducted along the gradient within BCNP for 20 1-ha plots ranging from 56 m.a.s.l. to 2814 m.a.s.l. (Figure 1). Tree diameter at breast height (DBH, 1.3 m) was measured using a fabric diameter tape +/−1 mm resolution for all trees ≥10 cm DBH. Species were determined in field and identified using herbarium vouchers. Nine of the 1-ha plots were from a collaborative effort of Conservational International's TEAM Project (http://www.teamnetwork.org/ 2015), and 11 1-ha plots at <120 m.a.s.l. at the La Selva Biological Station, as part of the Carbono project (Clark and Clark 2000). For both datasets, the survey data from 2011 was used to assess patterns of tree species' richness, diversity and structural characteristics (stem density and basal area) along this elevational gradient. The data used in this study is currently available online, at http://www.teamnetwork.org/.

Figure 1. Map of Braulio Carrillo National Park using Landsat 8 data collected 26 January 2017, with 20 1-ha plot locations/Braulio Carrillo National Park (black outline) and La Selva Biological Station (white outline). Inset shows location of BCNP in the country of Costa Rica. Plots used in analysis are in Red (TEAM) and Green (Carbono), red circles are around TEAM elevation transect plots. B is a Digital Elevation Model (DEM) from the Shuttle Radar Topography Mission (SRTM).



3.2.3 Lidar Remote Sensing

Lidar data were used to assess topographic variation (elevation, slope, and aspect), as well as three-dimensional forest structure metrics (canopy height and understory variation) across the majority of BCNP and within the 1-ha plots (Table 1). We used NASA's Land, Vegetation, and Ice (LVIS) sensor, a medium altitude airborne laser altimeter system, operating up to 10 km above ground, with a varying footprint, but usually flown in a medium resolution with circular footprints of 10–30 m in diameter. LVIS was flown over BCNP in 2005 between March 22nd–30th on the DOE King Air B-200 platform (Blair, Hofton, and Rabine 2006, Dubayah et al. 2010, NASA). Within each footprint, lidar measures distance from the instrument to the surfaces below, resulting in several signal returns, effectively capturing canopy height with the first returns and a digital elevation model (DEM) with the last. The waveform outputs can help to derive canopy heights, vertical relative height metrics (rh metrics), and topographic features, relative to the WGS-84 ellipsoid (Dubayah et al. 2010). The DEM from the last return of the LVIS signal was used to calculate elevation, slope in degrees, and aspect which was converted to cos(aspect). For three-dimensional structure, the LVIS waveform was segmented into quartiles of energy, also known as relative height metrics (rh100, rh75, rh50, and rh25), to quantify three-dimensional forest structure (Blair, Hofton, and Rabine 2006). These relative height metrics allow for the assessment of forest structure from the upper canopy (rh100), the canopy (rh75) the sub-canopy (rh50) and the understory (rh25) at the 1-ha plot level. Past research has found that these four metrics provide enough information from the waveform to study forest structure (Blair and Hofton 1999, Dubayah et al. 2010, Fricker et al. 2015, Hofton et al. 2002).

While there is a temporal discrepancy between the LVIS data collection and more recent field collections, we did compare 2005 field data to the 2016 data for a few plots that were available, and these displayed similar values of diversity across all life forms; we are assuming the natural growth and treefall occurrence over the interim years. In addition, from multiple visits to the sites, we do not believe that the structure or levels of species richness have changed significantly between the time periods.

3.2.4 Data Analysis

Species richness and the Shannon diversity index were calculated for each plot (R Core Team , Whittaker, Willis, and Field 2001). Species richness was defined as the number of tree species $\geq$10 cm dbh per ha, while the Shannon diversity index is a metric of diversity that also includes information on evenness or the proportion of individuals of each species, so it also takes into account the community structure as a whole (S1) (Hurlbert 1971, Whittaker 1972). The mean and standard deviation of topographic metrics (elevation, slope, aspect) and three-dimensional structure metrics (rh25, rh50, rh75, rh100) were calculated at the plot level. Pearson correlations and regression analyses in R were used to determine the relationship between species richness and diversity and field data on forest structure (stem density and basal area from plots), and lidar-derived metrics (topographical metrics and forest three-dimensional structure within the plots).

In order to extrapolate the plot-level data to the landscape, we fit linear models that predict species richness and diversity from field- and lidar-derived topographical and three-dimensional forest structure metrics. For each response variable, we used the leaps package in R to optimize the multiple linear regression model by fitting an exhaustive set of models—including all combinations of predictor variables—and choosing the model that minimized the

Bayesian Information Content (BIC) (Lumley 2017, R Core Team). In addition to using BIC as a measure of performance on each fitted model, cross-validation was also performed to optimize the number of predictors included in the multiple linear regression, by estimating the testing Mean Squared Error (MSE) of optimal models with each number of predictors. Because many predictors were included in the multiple linear regressions compared to the number of observations in the data, our model was very flexible. We constrained this flexibility in order to reduce overfitting by using ridge regression.

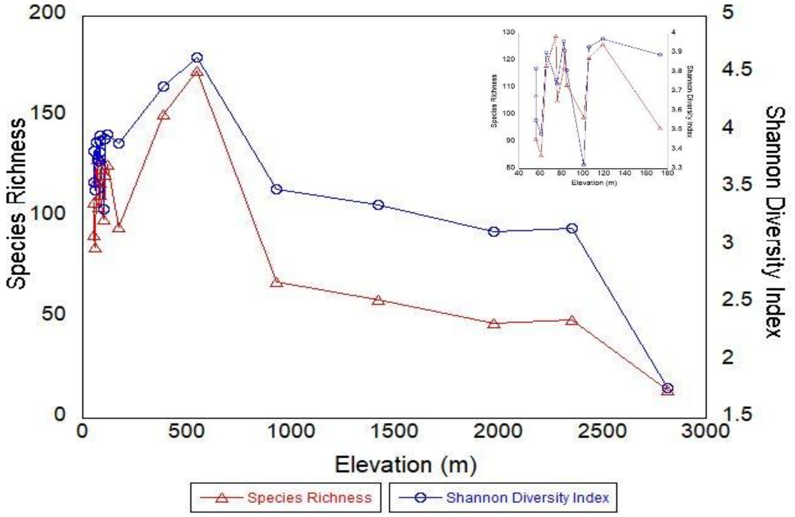
Ridge regression acted as a regularization method, shrinking coefficients in order to decrease their variability and multicollinearity. The linear regression and ridge regression models were compared using 5-fold cross-validation to estimate the testing MSE, in order to judge the extrapolation quality of our field data derived model (Dijkstra 2014, Giraud 2015). We compared the mean and standard deviation of topography and three-dimensional structure metric from the field plots with the landscape based on lidar derived metrics. We calculated canopy heights across 100 m bins of elevation, which we refer to as landscape data. Plot data was paired with lidar data, and a Shapiro-Wilk normality test showed that the differences between them were approximately normally distributed. Paired t-tests were performed between plot and landscape data to identify if topography (slope and aspect) and three-dimensional forest structure (rh100, rh75, rh50, rh25) from the plots were significantly different from landscape data.

3.3 Results

3.3.1 Species Richness, Diversity, and Forest Structure from Plots

There were 403 identified tree species ≥10 cm dbh in the 20 1-ha plots, representing 87 different families. Tree species richness and diversity changed in a non-linear fashion along the montane gradient (Figure 2); species richness (178 sp.) and Shannon diversity (4.64) both peaked at the plot located at 552 m elevation, VB3 (Table 1).

Figure 2. Species richness and Shannon Diversity Index along an elevation gradient in Costa Rica. The inset shows the variations of diversity across lowland sites where more plots were available for this study. Similar variability may exist in higher elevations but no additional replicates of plots were available to verify.



From the lowest elevation sites, species richness and diversity steadily increased up to 552 m, then declined, with an exceptionally large decline after the 2355 m plot. This 2355 m plot had a species richness of 49 and a Shannon diversity index of 3.2, and the highest elevation site (2813 m) had a species richness of 13 and a Shannon index of 1.77 (Table 1, Figure 2).

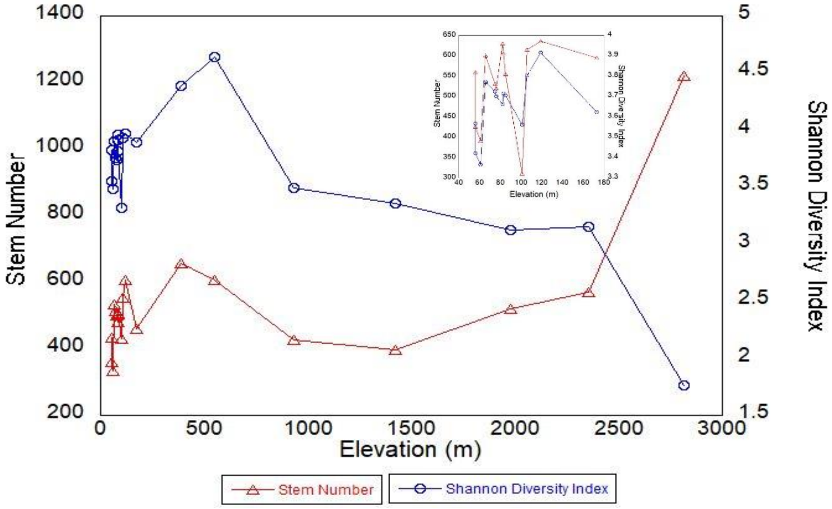
Stem density increased from 360 stems per hectare at the 56 m plot to 657 stems at 386 m; it then decreased to 606 stems at 552 m, and 397 stems at 1425 m, and exceptionally increased to 1221 stems at the 2814 m plot (Table 1). At lower elevations, basal area had a pattern similar to stem density, with a peak at the 106 m plot (28 m^2) and 552 m (27.5 m^2); it then decreased before a slight increase at 1425 m. The two highest plots, 2355 m and 2814 m, had the highest basal area along the elevational gradients (35.8 m^2 and 66.2 m^2 respectively).

Table 1. Data from 20 1-ha plots along an elevational gradient in Costa Rica. The relative height metrics (rh), slope, and aspect (cosine) were derived from lidar.

Plot	**Elevation (m)**	**Species Richness**	**Shannon Diversity Index**	**Stem Number (#)**	**Basal Area (m^2)**	**rh25 (m)**	**rh50 (m)**	**rh75 (m)**	**rh100 (m)**	**Slope (%)**	**Aspect (°)**
A3	56	107	3.82	433	26.7	11.8	21.3	27.1	35.7	6.9	204.2
A6	56	91	3.55	360	24.1	13	20.6	27.3	38.3	6.3	213.2
A1	61	85	3.48	332	27.9	14.5	22.8	28.9	38.8	6.4	187.6
L4	66	118	3.90	535	22.5	12	19	24.7	33.6	9	152.7
L5	75	129	3.76	512	22.0	14.3	23.6	28.7	38.3	15.9	282.9
P4	76	105	3.74	500	25.1	9.9	20.1	28.3	38.8	10.8	221
L3	82	117	3.96	481	27.0	10.2	17	22.6	31.5	10.5	154.3
P6	83	124	3.91	507	23.8	13.7	21.8	28.4	39.3	18.8	181.4
P3	85	111	3.81	502	25.5	12.7	21	26.4	34.3	14.3	190.8
VB1	101	99	3.32	430	22.9	12	20.9	27.3	37	6.9	183
L6	106	121	3.93	552	28.0	14.1	21.4	26.2	34.5	10.2	106.9
L2	119	126	3.97	607	23.6	13	21.1	27.3	38.1	19.9	215
VB2	173	95	3.89	461	25.2	9.9	17.4	22.6	31.5	7.6	184.5
VB4	386	151	4.39	657	27.1	11.2	21	28.4	39.2	20.6	165.4
VB3	552	173	4.64	606	27.5	11.6	18.5	23.7	32.2	10.8	42.2
VB7	933	68	3.49	426	20.4	5	12.9	20.4	29.7	14.2	164.2
VB8	1425	59	3.36	397	24	5.2	11.3	16.5	22.8	12.8	229.5
VB5	1976	47	3.12	521	26.9	4.1	9.8	14.2	20.1	9.5	135.7
VB10	2355	49	3.15	569	35.8	5.3	11.6	16.4	25	25.9	81.6
VB6	2814	14	1.76	1221	66.2	6.9	11.4	14.2	19.3	9.7	126.4

Species richness was not significantly correlated with stem density and basal area; however, Shannon diversity was significantly negatively correlated with stem density (Figure 3) and basal area (Table 2). The results of Pearson correlation tests between each of these response variables of species richness and diversity with stem density were $r = -0.272$, $p < 0.25$ and $r = -0.517$, $p < 0.02$, respectively. The results of Pearson correlation tests between each of these response variables and basal area were $r = -0.550$ $p < 0.002$ and $r = -0.739$, $p < 0.001$, respectively (Table 2).

Figure 3. Stem density and Shannon Diversity Index from field data along the elevation gradient. The inset shows the variations of the diversity and stem numbers across lowland sites where more plots were available for this study. Similar variability may exist in higher elevations but no additional replicates of plots were available to verify.



3.3.2 Lidar Metrics and Species Richness and Diversity

Topographic and three-dimensional structure were correlated with metrics of species richness and the Shannon diversity index (Table 2). Lidar metrics on topographic variables were more closely correlated with Shannon diversity than species richness. For the topographic variables, elevation was significantly correlated with species richness and diversity. For height metrics, species richness was correlated with the top two canopy height metrics, rh100 and rh75, and the standard deviation of the understory, while diversity was correlated with all four canopy height metrics and the standard deviation of the canopy layers. The lidar metrics derived from the quartiles of the lidar waveform were found to have a relatively linear relationship with tree species richness and diversity, particularly for lower rh metrics (Figure 4A & B). The multivariate regressions focused on the use of topographic and three-dimensional structure to predict species richness and the Shannon diversity index. Using best subset selection, the species richness model with optimal BIC included two predictors, rh100 and rh25 SD, and the model with the second-lowest BIC included three predictors, adding aspect to the model (Table 3). These models had r^2 values of 0.494 and 0.557, respectively. Applying this method to the multivariate regression predicting the Shannon diversity index selected an optimal model, with 10 predictors (Table 4, Figure 4).

Figure 4. Multiple diversity metrics within plots versus lidar-derived relative height metrics (A) Species richness: r^2 for rh100, rh75, rh50, and rh25: 0.55 0.56, 0.55, 0.50 respectively; (B) Shannon diversity index: r^2 for rh100, rh75, rh50, and rh25: 0.41, 0.40, 0.34, 0.26 respectively.

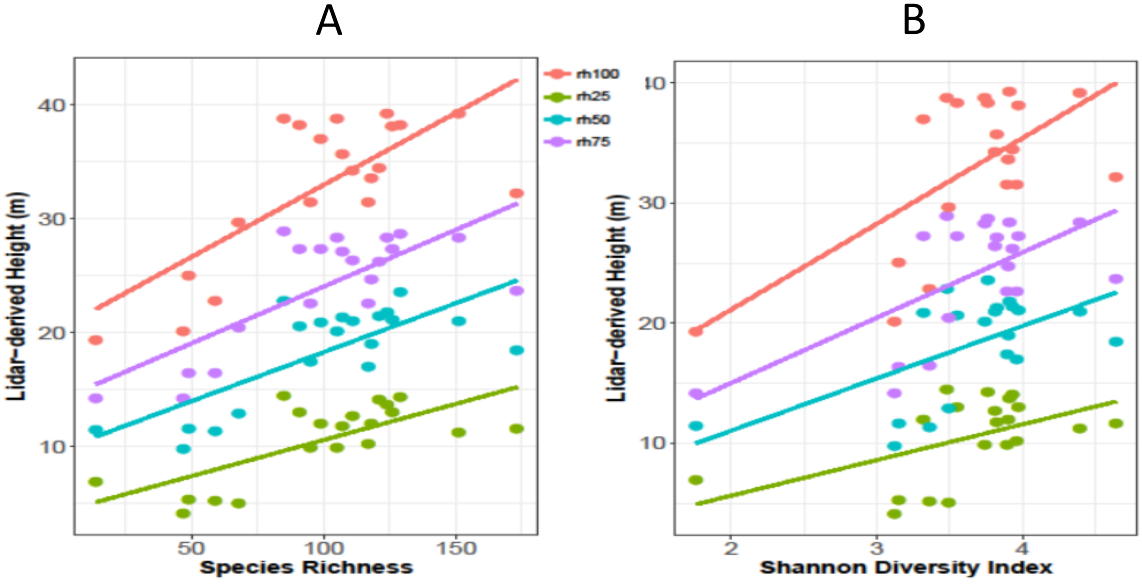


Table 2. Pearson correlation between two metrics of diversity (species richness and Shannon index) and field and lidar-derived data. * = $P < 0.05$, ** = $P < 0.01$.

	Species Richness	Shannon Diversity
Field data		
Stems	−0.272	−0.517 *
Basal Area	−0.550*	−0.739 **
Topography		
Elevation	−0.771 **	−0.743 **
Slope	0.098	0.131
Aspect	−0.027	−0.332
3-D structure		
rh100	0.741 **	0.644 **
rh75	0.751 **	0.630 **
rh50	0.745 **	0.581 **
rh25	0.707 **	0.510 *
rh100 sd	0.304	0.287
rh75 sd	0.313	0.267
rh50 sd	0.0389	0.063
rh25 sd	−0.228	−0.288

Table 3. Best subsets of lidar-derived predictors to model species richness along with the r^2 value and BIC of each model. The model with the optimal number of predictors for each response variable is bolded. Elevation = Elev., rh = relative height, SD = standard deviation.

Predictors	Selected Predictors in Model	r^2	BIC
1	Elev.	0.589	0.71
2	rh100 + rh25.SD	0.584	−4.637
3	**Aspect + rh100 + rh25.SD**	**0.599**	**−4.341**
4	Aspect + rh25 + rh50 + rh25.SD	0.579	−3.56
5	Aspect + Aspect.SD + rh25 + rh50 + rh25.SD	0.654	−3.269
6	Aspect + Aspect.SD + rh25 + rh50 + rh25.SD + rh100.SD	0.689	−2.429
7	Aspect + Slope.SD + Aspect.SD + rh25 + rh50 + rh25.SD + rh100.SD	0.711	−0.865
8	Elev. + Aspect + Slope.SD + Aspect.SD + rh25 + rh50 + rh25.SD + rh100.SD	0.721	1.363
9	Elev. + Aspect + Aspect.SD + rh25 + rh50 + rh75 + rh100 + rh25.SD + rh50.SD	0.745	2.574
10	Aspect + Slope.SD + Aspect.SD + rh25 + rh50 + rh75 + rh100 + Elev.SD + rh25.SD + rh50.SD	0.79	1.698

Table 4. Best subsets of lidar-derived predictors to model Shannon diversity index along with the R-squared value and BIC of each model. The model with the optimal number of predictors for each response variable is bolded. Elevation = Elev., rh = relative height, SD = standard deviation.

Predictors	Selected Predictors in Model	r^2	BIC
1	Elev.	0.547	−5.958
2	Elev. + rh25.SD	0.541	−10.202
3	Elev. + Slope + Aspect	0.737	−11.921
4	Elev. + Slope + Aspect + rh25	0.787	−15.231
5	Elev. + Slope + Aspect + Aspect.SD + rh25	0.824	−16.82
6	Elev. + Slope + Aspect + Aspect.SD + rh25 + rh25.SD	0.838	−15.455
7	Elev. + Slope + Aspect + Aspect.SD + rh25 + Elev.SD + rh75.SD	0.872	−17.257
8	Elev. + Slope + Aspect + Aspect.SD + rh25 + rh50 + Elev.SD + rh75.SD	0.878	−15.145
9	Elev. + Slope + Aspect + Aspect.SD + rh25 + rh50 + rh75 + Elev.SD + rh75.SD	0.914	−19.152
10	**Elev. + Aspect + Slope.SD + Aspect.SD + rh25 + rh50 + rh75 + rh100 + rh25.SD + rh50.SD**	**0.941**	**−23.79**

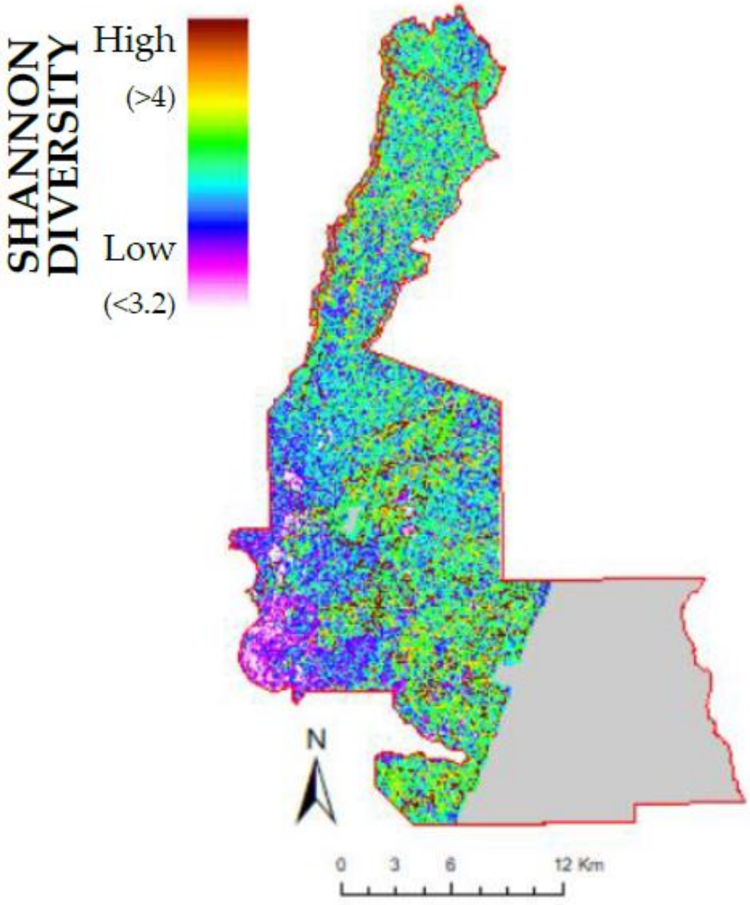
Regularization was performed on models for species richness and Shannon diversity index. We used a shrinkage parameter lambda, that minimizes the residual sum of squares, plus an L2 constraint, meaning that the shrinkage parameter lambda is the coefficient of an added term that is the sum of the squared coefficients. This constraint encourages the beta coefficient estimates to become smaller than they would be using ordinary least squares regression. Using L2 constraint, ridge regression optimized the shrinkage parameter lambda and yielded sets of coefficients (S2) with 14 degrees of freedom. This was done using the package glmnet; the value of our optimized lambda was 0.04037017 (Friedman, Hastie, and Tibshirani 2010). Comparison of multiple linear regression subset selection and regularization methods was performed using 5-fold cross validation to estimate the mean squared error on testing data. Cross validation on multiple linear regression subset selection models for species richness and Shannon diversity yielded average validation set mean squared errors of 572.2 and 0.02 respectively, while cross validation on models using ridge regression yielded higher mean squared errors of 2628.8 and 0.39 (Table 5). Overall, the reduced multiple linear regression models formed using best subset selection (10 predictors for diversity, 2 predictors for species richness) performed the best (Figure 5).

Table 5. Five-fold coefficient of variation (CV) estimates of Mean Square Error (MSE) for Multiple Linear Regression (MLR) subset selection and ridge regression models.

Model Method	**Shannon Diversity Model**	**Species Richness Model**
Best Subsets Multiple Linear Regression	0.018	572.172
Ridge Regression	0.387	2628.755

This map of Shannon Diversity Index over the Braulio Carrillo National Park area exemplifies the extrapolation capabilities, when using combined ground and airborne data (Figure 5). We see that the highest elevation areas (South West corner of BCNP, bottom left of map) tend to have the lowest species diversity. We obviously do not see a visible mid-elevation bulge of diversity in the raster image, but there are more pixels that are mid- to high-diversity in the center of BCNP, and in the mid-elevation region depicted in the digital elevation model of Figure 1b. There are some homogenous clumps of pixels in the middle of BCNP, which are likely artifacts caused by sharp changes in elevation, which can cause errors with lidar collection (Fricker et al. 2015). The southeast portion of BCNP was not covered by the lidar sensor, so we masked it out of the extrapolation.

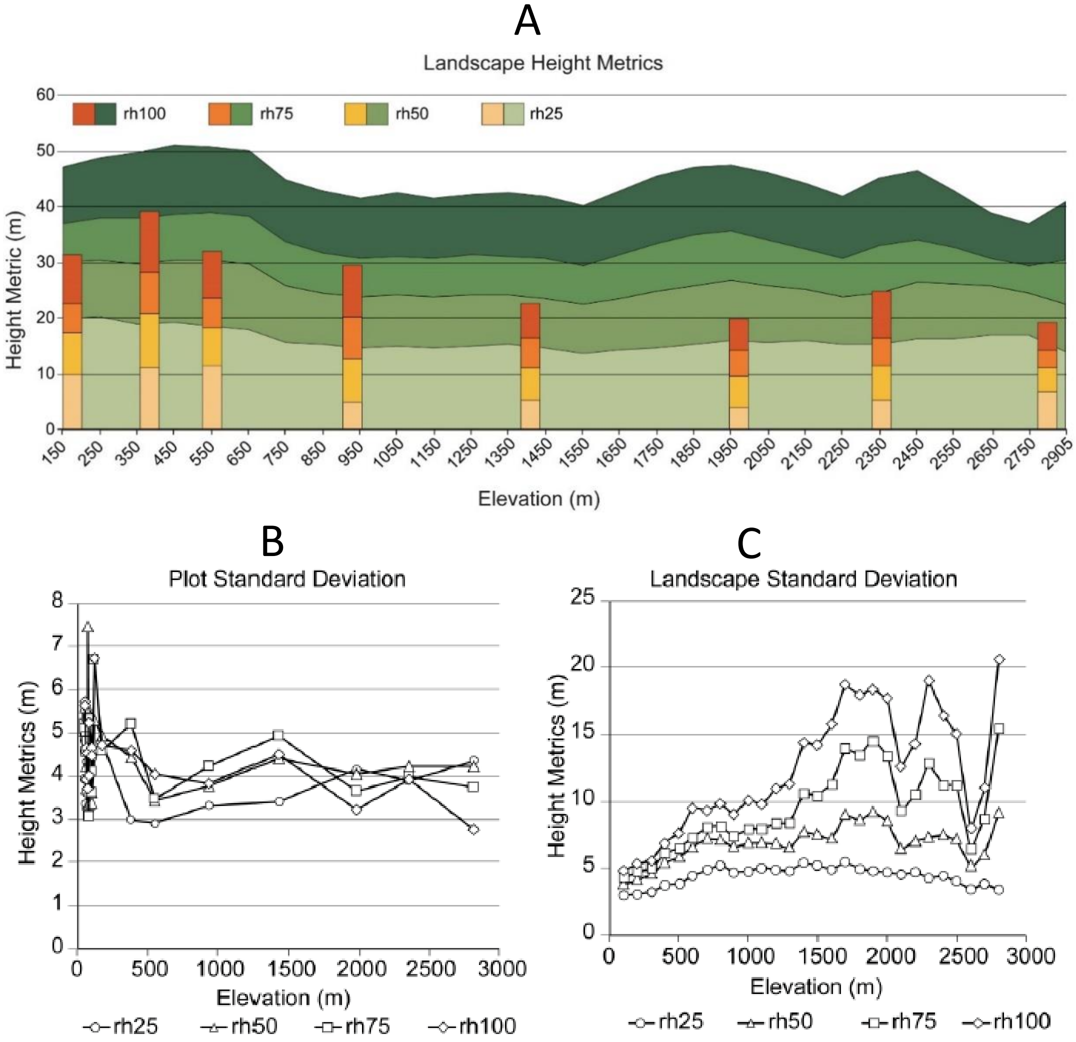
Figure 5. Map of predicted Shannon Diversity.



3.3.3 Plot and Landscape Data

Plot level lidar data on topography and three-dimensional structure were compared to landscape-level data in 100 m bins, in order to see if the lidar-derived topographic and height data from the plots was representative of the landscape as a whole. Slope and aspect from the plots were not significantly different than the landscape (*p* = 0.161, *p* = 0.818 respectively).

Figure 6. Plot-level and landscape-level mean lidar-derived relative height (rh) metrics across the elevational gradient (A). Red/orange shades are at the plot-level, green shades are the landscape patterns. Standard deviations of lidar-derived relative height (rh) metrics across the elevational gradients (B) Plot-level; (C) and landscape-level mean.



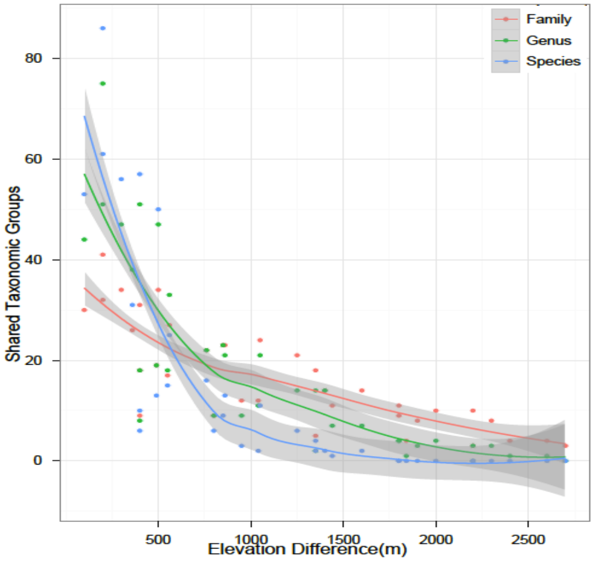
The mean canopy heights were correlated for the plots and landscapes ($p < 0.05$) (Figure 6A); however, the canopy heights were significantly taller across the landscape than plots ($p < 0.01$). There was a significant difference in standard deviation of plot and lidar derived landscape data ($p < 0.01$). The standard deviation from plots were relatively similar across the elevational gradient (generally within 2 m), while the standard deviation at the landscape scale showed wide variation in rh100 and rh75 and a clear increase in standard deviation with elevation (Figure 6B & C), with exceptions of the two highest elevation sites 2355 and 2814 m.

3.4 Discussion

3.4.1 Species Richness and Diversity

Overall, patterns of species richness and diversity decreased with elevation, with a peak at 552 m of the total 2906 m of elevation of the mountaintop. This peak in diversity had an overlap of species from both the higher and lower elevation plots, and had the highest number of shared species with the other sites, as determined through a test of beta diversity (Figure 7).

Figure 7. Simple beta diversity metric of shared species between sites based on elevation difference between the two sites. Jaccard and Sorensen indices showed same pattern, as did geographic distance instead of elevation difference.



This seemingly skewed bulge may also have to do with the geometry of a mountain or mountain range, as higher elevations cover less area as they come to a peak, compared with larger geographic areas at mid-elevations. According to the species-area relationship, larger geographic areas should support a greater variety of species (Whittaker, Willis, and Field 2001). As elevation increases in simple montane environments, the total area within zones of elevation decreases in accordance with basic geometry, which would support the idea that higher elevations would have fewer species. However, the ruggedness of terrain can influence the surface area in certain bands of elevation, making the area effectively larger (Whittaker, Willis, and Field 2001).

The mid-elevation bulge of tree diversity has been observed across continents and biomes in the Himalayas (Acharya, Chettri, and Vijayan 2011, Bhattarai and Vetaas 2006, Carpenter 2005), Costa Rica (Feeley et al. 2013), Mexico (Vazquez and Givnish 1998, Wolf and Alejandro 2003), Peru (Muenchow et al. 2013), and Ethiopia (Aynekulu et al. 2012). Although a monotonic linear decrease of diversity has been reported for many studies, it appears that many of these studies often do not sample the entire gradient, instead presenting a truncated form of the mid-gradient bulge pattern (Nogues-Bravo et al. 2008). These results suggest that if the entire elevational extent is not sampled, the overall patterns may not be correctly identified, and an incorrect assumption might be made regarding linear decreases in plant diversity with elevation change; this may cause the display of a mid-elevation bulge, as we found on our mountain gradient.

3.4.2 Forest Structure from Field Measurements

Patterns in species richness and diversity were not associated with increased stem density and basal area. When comparing the number of stems and basal area directly to the Shannon diversity index, we found that the three highest elevation plots (1976, 1355, and 2814 m) had a distinctly different pattern than the other sites. While most sites had a positive relationship between diversity and higher numbers of stems/larger basal area, the three high elevation plots displayed the opposite pattern. They were relatively species poor, but had higher stem density, particularly at the 2814 m site, where there were twice as many stems within 1-ha. Thus, stem number and basal area from plot data alone may not be used to predict tree species diversity at different elevations. This can be due to a variety of factors, including that our plot locations may not be representative of the gradient as a whole. Without replicates, we cannot know whether certain factors are solely due to the aspect of the plot locations.

3.4.3 Topography and Three Dimensional Structure from Lidar

Lidar metrics on topography and three-dimensional structure were associated with both species richness and diversity. We expected that high elevation, steep slopes, and slopes that receive the most solar radiation would have low species richness and diversity, while high forest canopies with high canopy heterogeneity would have greater species richness and diversity. The topographic metrics of elevation were the most important in this study. Although mean and standard deviation of slope and aspect was not correlated with species richness or diversity, these topography metrics improved diversity models, and combined, could explain more of the variance than the three-dimensional structure metrics. High forest canopies and understories had the highest species richness and diversity, while high canopy heterogeneity—as measured by the standard deviation—have greater diversity. This suggests that high canopies with greater variation allow for more species to persist, resulting in higher diversity.

3.4.4 Plots vs. Landscape

We found that forest canopy height structure displayed a non-linear relationship along the gradient, with various peaks of canopy height. At the landscape scale, when we calculated canopy height across the same elevation as plots in 100 m bins, we found two peaks of canopy height—the highest around 500 m and a secondary peak at 1900 m, with maximum heights of 52 and 45 m respectively. The height metrics extracted from just within the field plots resulted in similar patterns across mean height metrics as those of the landscape scale, although landscape values were generally taller than plots. This can have implications when we use the relationship developed from the plots to the landscape. At the plot level, we found the standard deviation of the height metrics was highest at the lower elevation sites; however, the landscape scale clearly had higher standard deviations of the height metrics increasing with elevation. This high variation in the forest canopy, and difference between the landscape and plot level analysis, could be due to higher disturbance in highlands versus lowlands, which could also affect the diversity and observed shifts in composition (Feeley et al. 2013). These results differ slightly from findings on the same gradient from a study published in 1996, with ground-measured height displaying peaks of height at 300 m and 1750 m elevation, with heights of 47 m and 31 m respectively (Lieberman et al. 1996a). This is also different from what has been found in the Andes, where tree height and biomass decrease with elevation (Girardin et al. 2014). However, tree height does not always simply decrease with elevation in the Neotropics. In terms of plot locations, they were placed for field surveys, and the lidar was collected years later. If the lidar was collected before setting up the plots, the sampling could have changed, and we may have obtained slightly different results. With the lidar data, we would have had better knowledge of the topography and structural variations, and preferentially chosen certain slopes or elevations based on features seen in that data. We recommend that non-linear models be tested in the future (e.g., below and above 552 m), along with other biodiversity metrics—such as butterfly and bird diversity—that are available for some of the plots in this study.

3.4.5 Modeling Diversity and Species Richness

Lidar metrics of topography and three-dimensional structure can be used to predict tree diversity and species richness to a lesser extent along elevational gradients, in areas without ground data. There have been a number of studies that have examined tree species richness and diversity from plots, and spectral sensors and indices (e.g., NDVI), over tropical forests; however, these have only been able to explain between 30% and 40% of the variation in tropical tree species richness (Cayuela et al. 2006, Feeley, Gillespie, and Terborgh 2005, Pau, Gillespie, and Wolkovich 2012). Active remote sensing, such as airborne radar and small footprint lidar, have been able to explain between 25% to 44% of the variation in tree species richness (10 cm dbh) within tropical forests (Gillespie et al. 2009, Fricker et al. 2015, Wolf et al. 2012). Our results from large footprint lidar can explain 94% of the variation in tree diversity, and 49% of the variation in tree species richness. This suggests that large footprint lidar can be used to quantify tree diversity and species richness in regions with 1-ha plots, and may be able to estimate diversity and species richness along elevational gradients of forests in the tropics. For diversity, a number of topography and height metrics best explain tree diversity patterns, and these should be tested in other regions. However, since we tested a number of variables (n = 20) that have been associated with tree diversity from the literature (and observed that there was not a linear relationship with diversity), fewer variables and non-linear models should also be tested in the future. We realize that many variables, with so few plots, can cause an issue with overfitting. It is difficult to avoid overfitting in our situation, because the data collection is limited to small sample sizes, coupled with the presence of a lot of noise in real life. However, this is still an interesting analysis, even with the issue of overfitting. For species richness, the overall canopy height (rh100) and the heterogeneity in the understory (standard deviation of rh25) may be the two best metrics associated with tree species richness at 1-ha for tree 10 cm dbh. Tree species richness may be the best variable to test in the future using air and spaceborne lidar data, since the two metrics are easy to calculate, extrapolate, and because they explain nearly half of the tree species richness. We would expect to find canopy height and understory structure to be correlated with diversity for other tropical forests along elevational gradients. Indeed, Guo et al. (2013) identified peaks of diversity in the tropics, and these peaks may be directly related to canopy height and topographic complexity.

3.4.6 Future Research

Active remote sensing systems like lidar sensors are becoming increasingly popular, making new forest analyses possible. Lidar has the ability to collect tree height and other aspects of forest structure and topography that are important for accurate measurements and monitoring of forest inventory information (Chambers et al. 2007, Lefsky et al. 2002, Simonson, Allen, and Coomes 2012, Fernandez-Ordonez, Leblon, and Soria-Ruiz 2009). LVIS lidar has been collected along elevational gradients for a number of forests across the United States; however, the coverage over tropical forests remains limited to Costa Rica (Land, Vegetation, And Ice Sensor (LVIS) (Blair, Hofton, and Rabine 2006)). Globally comparative canopy height data (e.g., relative height) are available from the Geoscience Laser Altimeter System (GLAS) sensor, and have been found to correlate with results from LVIS (Saatchi, Harris, et al. 2011, Sun et al. 2008). Thus, it should be possible to compare topography and three-dimensional structure data from GLAS tracks to tropical field plots, in order to test results from our research, and possibly map diversity and species richness. NASA's Global Ecosystem Dynamics Investigation Lidar (GEDI) will provide a global dataset in the future on canopy structure, similar to GLAS and LVIS, but with a footprints of 25 m. This dataset may be used to maps patterns of vegetation structure using relative height metrics and diversity across elevational gradients in the tropics, and at larger scales than the LVIS airborne lidar used in this study.

3.5 Conclusions

We examined tree species richness and diversity from field data (20 1-ha plots) on forest structure (stems, basal area) and large footprint lidar derived data on topography and three-dimensional forest structure along an elevational gradient in Brauilo Carrillo, Costa Rica. This study is special because airborne lidar data, with paired field collections, is rare over tropical elevation gradients. Slope and aspect from the plots seemed to be representative of the surrounding landscape of the national park; however, the canopy height was significantly taller across the landscape, and there were differences in standard deviation of lidar derived plot and landscape data. Species richness and the Shannon diversity index showed a distinct pattern of increasing up to about 600 m elevation, and then decreasing at higher elevations. Stem density and basal area were negatively associated with species richness and diversity, with both peaking at about 2800 m. Elevation was negatively correlated with species richness and diversity, while the two tallest relative height metrics (rh100, rh75) derived from lidar were both significantly positively correlated with species richness and diversity. The best lidar-derived topographical and three-dimensional forest structural models showed a strong relationship with the Shannon diversity index ($r^2 = 0.941$, $P < 0.01$), with ten predictors, while the best species richness model was weaker ($r^2 = 0.599$, $P < 0.01$), with two predictors (rh100, standard deviation of rh25). The resultant map of Shannon Diversity modeled using supplementary equation S2 shows the lowest diversity at the highest elevations in the southwest of BCNP, with higher pixel values of diversity in mid-elevation areas. This suggests a potential for mapping species richness and diversity across elevational gradients in tropical montane ecosystems using spaceborne lidar.

3.6 Supplementary Materials:

Supplementary Equation S1: The equation used to calculate the Shannon Diversity Index is as follows (Hurlbert 1971, Whittaker 1972):

$$H' = -\sum_{i=0}^{S} p_i ln\, p_i \qquad \text{(S1)}$$

where;
H’ = Calculated Shannon diversity index
p_i = proportion of individuals belonging to the *i*th species ($\frac{Ni}{N}$).
S = numbers of species encountered
$\sum$ = sum from species 1 to species S

Supplementary Equation S2: The equation used to create Figure 5 of Shannon Diversity was as follows, with an r^2 of 0.76:

$$\text{eH}' = 5.789 - 0.0010E + 0.0453S - 0.0046A - 0.134rh25 + 0.124rh50 - 0.0389rh75 \text{ -}0379rh100, \qquad \text{(S2)}$$

where:
eH’ = Estimated Shannon diversity index
E = Elevation
S = Slope
A = Aspect

rh25: relative height of 25% of the canopy density
rh50: relative height of 50% of the canopy density
rh75: relative height of 75% of the canopy density
rh100: Mean canopy height within the footprint

This equation was used in ENVI’s band math to calculate the new layer of Shannon diversity.

3.7. References

Acharya, Bhoj Kumar, Basundhara Chettri, and Lalitha Vijayan. 2011. "Distribution pattern of trees along an elevation gradient of Eastern Himalaya, India." *Acta Oecologica-International Journal of Ecology* 37 (4):329-336. doi: 10.1016/j.actao.2011.03.005.

Austin, M. P., J. G. Pausas, and A. O. Nicholls. 1996. "Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia." *Australian Journal of Ecology* 21 (2):154-164. doi: 10.1111/j.1442-9993.1996.tb00596.x.

Aynekulu, Ermias, Raf Aerts, Pieter Moonen, Manfred Denich, Kindeya Gebrehiwot, Tor-Gunnar Vagen, Wolde Mekuria, and Hans Juergen Boehmer. 2012. "Altitudinal variation and conservation priorities of vegetation along the Great Rift Valley escarpment, northern Ethiopia." *Biodiversity and Conservation* 21 (10):2691-2707. doi: 10.1007/s10531-012-0328-9.

Bergen, K. M., S. J. Goetz, R. O. Dubayah, G. M. Henebry, C. T. Hunsaker, M. L. Imhoff, R. F. Nelson, G. G. Parker, and V. C. Radeloff. 2009. "Remote sensing of vegetation 3-D structure for biodiversity and habitat: Review and implications for lidar and radar spaceborne missions." *Journal of Geophysical Research-Biogeosciences* 114:13. doi: 10.1029/2008jg000883.

Bhattarai, Khem Raj, and Ole R. Vetaas. 2006. "Can Rapoport's rule explain tree species richness along the Himalayan elevation gradient, Nepal?" *Diversity and Distributions* 12 (4):373-378. doi: 10.1111/j.1366-9516.2006.00244.x.

Bhuyan, Putul, ML Khan, and RS Tripathi. 2003. "Tree diversity and population structure in undisturbed and human-impacted stands of tropical wet evergreen forest in Arunachal Pradesh, Eastern Himalayas, India." *Biodiversity & Conservation* 12 (8):1753-1773.

Blair, J. B., and M. A. Hofton. 1999. "Modeling laser altimeter return waveforms over complex vegetation using high-resolution elevation data." *Geophysical Research Letters* 26 (16):2509-2512. doi: 10.1029/1999gl010484.

Blair, J. Bryan, Michelle Hofton, and David Lloyd Rabine. 2006. Processing of NASA LVIS elevation and canopy (LGE, LCE and LGW) data products, version 1.01. edited by Code 694 NASA Goddard Space Flight Center.

Burnett, Michael R, Peter V August, James H Brown, and Keith T Killingbeck. 1998. "The Influence of Geomorphological Heterogeneity on Biodiversity I. A Patch-Scale Perspective." *Conservation Biology* 12 (2):363-370.

Cardelus, C. L., R. K. Colwell, and J. E. Watkins. 2006. "Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak." *Journal of Ecology* 94 (1):144-156. doi: 10.1111/j.1365-2745.2005.01052.x.

Carpenter, C. 2005. "The environmental control of plant species density on a Himalayan elevation gradient." *Journal of Biogeography* 32 (6):999-1018. doi: 10.1111/j.1365-2699.2005.01249.x.

Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. "Consequences of changing biodiversity." *Nature* 405 (6783):234-242. doi: 10.1038/35012241.

Clark, David B, and Deborah A Clark. 2000. "Landscape-scale variation in forest structure and biomass in a tropical rain forest." *Forest ecology and management* 137 (1):185-198.

Clark, David B., Johanna Hurtado, and Sassan S. Saatchi. 2015. "Tropical rain forest structure, tree growth and dynamics along a 2700-m elevational transect in Costa Rica." *PloS one* 10 (4):e0122905.

Condit, R., S. P. Hubbell, J. V. Lafrankie, R. Sukumar, N. Manokaran, R. B. Foster, and P. S. Ashton. 1996. "Species-area and species-individual relationships for tropical trees: A comparison of three 50-ha plots." *Journal of Ecology* 84 (4). doi: 10.2307/2261477.

Dijkstra, T. K. 2014. "Ridge regression and its degrees of freedom." *Quality & Quantity* 48 (6):3185-3193. doi: 10.1007/s11135-013-9949-7.

Drake, Jason B., Ralph O Dubayah, Robert G. Knox, David B. Clark, and J.B. Blair. 2002. "Sensitivity of large-footprint lidar to canopy structure and biomass in a neotropical rainforest." *Remote Sensing of Environment* 81 (CHECK).

Drake, Jason B., Ralph O. Dubayah, David B. Clark, Robert G. Knox, J. Bryan Blair, Michelle A. Hofton, Robin L. Chazdon, John F. Weishampel, and Steve Prince. 2002. "Estimation of tropical forest structural characteristics using large-footprint lidar." *Remote Sensing of Environment* 79 (2):305-319.

Dubayah, R. O., and J. B. Drake. 2000. "Lidar remote sensing for forestry." *Journal of Forestry* 98 (6):44-46.

Dubayah, R. O., S. L. Sheldon, D. B. Clark, M. A. Hofton, J. B. Blair, G. C. Hurtt, and R. L. Chazdon. 2010. "Estimation of tropical forest height and biomass dynamics using lidar remote sensing at La Selva, Costa Rica." *Journal of Geophysical Research: Biogeosciences* 115 (G2).

Feeley, Kenneth J., Johanna Hurtado, Sassan Saatchi, Miles R. Silman, and David B. Clark. 2013. "Compositional shifts in Costa Rican forests due to climate-driven species migrations." *Global Change Biology* 19 (11):3472-3480. doi: 10.1111/gcb.12300.

Fricker, G. A., J. A. Wolf, S. S. Saatchi, and T. W. Gillespie. 2015. "Predicting spatial variations of tree species richness in tropical forests from high-resolution remote sensing." *Ecological Applications* 25 (7):1776-1789. doi: 10.1890/14-1593.1.

Gentry, A. H. 1988. "CHANGES IN PLANT COMMUNITY DIVERSITY AND FLORISTIC COMPOSITION ON ENVIRONMENTAL AND GEOGRAPHICAL GRADIENTS." *Annals of the Missouri Botanical Garden* 75 (1):1-34. doi: 10.2307/2399464.

Girardin, Cecile A. J., William Farfan-Rios, Karina Garcia, Keneth J. Feeley, Peter M. Jorgensen, Alejandro Araujo Murakami, Leslie Cayola Perez, Renate Seidel, Narel Paniagua, Alfredo F. Fuentes Claros, Carla Maldonado, Miles Silman, Norma Salinas, Carlos Reynel, David A. Neill, Martha Serrano, Carlos J. Caballero, Maria de los Angeles La Torre Cuadros, Maria J. Macia, Timothy J. Killeen, and Yadvinder Malhi. 2014. "Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects." *Plant Ecology & Diversity* 7 (1-2):161-171. doi: 10.1080/17550874.2013.820806.

Giraud, Christophe. 2015. *Introduction to High-Dimensional Statistics*. Boca Raton, Florida: Chapman & Hall/CRC.

Giriraj, A., M. S. R. Murthy, and B. R. Ramesh. 2008. "VEGETATION COMPOSITION, STRUCTURE AND PATTERNS OF DIVERSITY: A CASE STUDY FROM THE TROPICAL WET EVERGREEN FORESTS OF THE WESTERN GHATS, INDIA." *Edinburgh Journal of Botany* 65 (3):447-468. doi: 10.1017/s0960428608004952.

Givnish, T. J. 1999. "On the causes of gradients in tropical tree diversity." *Journal of Ecology* 87 (2):193-210. doi: 10.1046/j.1365-2745.1999.00333.x.

Goetz, Scott, Daniel Steinberg, Ralph Dubayah, and Bryan Blair. 2007. "Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA." *Remote Sensing of Environment* 108 (3):254-263. doi: 10.1016/j.rse.2006.11.016.

Gotelli, N. J., and R. K. Colwell. 2001. "Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness." *Ecology Letters* 4 (4):379-391. doi: 10.1046/j.1461-0248.2001.00230.x.

Grieve, I. C., J. Proctor, and S. A. Cousins. 1990. "SOIL VARIATION WITH ALTITUDE ON VOLCAN BARVA, COSTA-RICA." *Catena* 17 (6):525-534. doi: 10.1016/0341-8162(90)90027-b.

Guo, Qinfeng, Douglas A Kelt, Zhongyu Sun, Hongxiao Liu, Liangjun Hu, Hai Ren, and Jun Wen. 2013. "Global variation in elevational diversity patterns." *Scientific reports* 3:3007.

Hofton, M. A., L. E. Rocchio, J. B. Blair, and R. Dubayah. 2002. "Validation of Vegetation Canopy Lidar sub-canopy topography measurements for a dense tropical forest." *Journal of Geodynamics* 34 (3-4):491-502. doi: 10.1016/s0264-3707(02)00046-7.

Holdridge, LR. 1966. "The life zone system." *Adansonia* 6 (2):199-203.

Homeier, Juergen, Siegmar- W. Breckle, Sven Guenter, Ruetger T. Rollenbeck, and Christoph Leuschner. 2010. "Tree Diversity, Forest Structure and Productivity along Altitudinal and

Topographical Gradients in a Species-Rich Ecuadorian Montane Rain Forest." *Biotropica* 42 (2):140-148. doi: 10.1111/j.1744-7429.2009.00547.x.

http://www.teamnetwork.org/. 2015. "Tropical Ecology Assessment & Monitoring Network: Early Warning System for Nature." http://www.teamnetwork.org.

Hurlbert, Stuart H. 1971. "The Nonconcept of Species Diversity: A Critique and Alternative Parameters." *Ecology* 52 (4):577-586. doi: 10.2307/1934145.

Jantz, Samuel M., Brian Barker, Thomas M. Brooks, Louise P. Chini, Qiongyu Huang, Rachel M. Moore, Jacob Noel, and George C. Hurtt. 2015. "Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation." *Conservation Biology* 29 (4):1122-1131. doi: 10.1111/cobi.12549.

Kuper, W., H. Kreft, J. Nieder, N. Koster, and W. Barthlott. 2004. "Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests." *Journal of Biogeography* 31 (9):1477-1487. doi: 10.1111/j.1365-2699.2004.01093.x.

Lefsky, Michael A., Warren B. Cohen, Geoffrey G. Parker, and David J. Harding. 2002. "Lidar remote sensing for ecosystem studies: Lidar, an emerging remote sensing technology that directly measures the three-dimensional distribution of plant canopies, can accurately estimate vegetation structural attributes and should be of particular interest to forest, landscape, and global ecologists." *BioScience* 52 (1):19-30.

Liang, Jingjing, Joseph Buongiorno, Robert A Monserud, Eric L Kruger, and Mo Zhou. 2007. "Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality." *Forest Ecology and Management* 243 (1):116-127.

Lieberman, D., M. Lieberman, R. Peralta, and G. S. Hartshorn. 1996a. "Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica." *Journal of Ecology* 84 (2):137-152. doi: 10.2307/2261350.

Lumley, Thomas. 2017. "R package: leaps. Regression Subset Selection. Thomas Lumley based on Fortran code by Alan Miller."

Macarthur, R., and P. H. Klopfer. 1961. "POPULATION EFFECTS OF NATURAL SELECTION." *American Naturalist* 95 (885):195-&. doi: 10.1086/282175.

MacArthur, Robert H. 1972. *Geographical ecology; patterns in the distribution of species*. New York: Harper & Row.

McCain, C. M. 2004. "The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica." *Journal of Biogeography* 31 (1):19-31.

NASA. "Land, Vegetation, and Ice Sensor." Goddard Space National Aeronautics and Space Administration http://lvis.gsfc.nasa.gov.

Nogues-Bravo, D., M. B. Araujo, T. Romdal, and C. Rahbek. 2008. "Scale effects and human impact on the elevational species richness gradients." *Nature* 453 (7192):216-U8. doi: 10.1038/nature06812.

Olivares, Ingrid, Jens-Christian Svenning, Peter M. van Bodegom, and Henrik Balslev. 2015. "Effects of Warming and Drought on the Vegetation and Plant Diversity in the Amazon Basin." *Botanical Review* 81 (1):42-69. doi: 10.1007/s12229-014-9149-8.

Pires, Joao Murca, and Ghillean T Prance. 1985. *The vegetation types of the Brazilian Amazon*. New York, USA: Pergamon Press.

R Core Team. "R: A Language and Environment for Statistical Computing." In. Vienna, Austria. https://www.R-project.org.

Rahbek, C. 1995. "THE ELEVATIONAL GRADIENT OF SPECIES RICHNESS - A UNIFORM PATTERN." *Ecography* 18 (2):200-205. doi: 10.1111/j.1600-0587.1995.tb00341.x.

Rohde, K. 1992. "LATITUDINAL GRADIENTS IN SPECIES-DIVERSITY - THE SEARCH FOR THE PRIMARY CAUSE." *Oikos* 65 (3):514-527. doi: 10.2307/3545569.

Rose, R. A., D. Byler, J. R. Eastman, E. Fleishman, G. Geller, S. Goetz, L. Guild, H. Hamilton, M. Hansen, R. Headley, J. Hewson, N. Horning, B. A. Kaplin, N. Laporte, A. Leidner, P. Leinagruber, J. Morisette, J. Musinsky, L. Pintea, A. Prados, V. C. Radeloff, M. Rowen, S. Saatchi, S. Schil, K. Tabor, W. Turner, A. Vodacek, J. Vogelnaann, M. Wegmann, and D. Wilkie. 2015. "Ten ways remote sensing can contribute to conservation." *Conservation Biology* 29 (2):350-359. doi: 10.1111/cobi.12397.

Slik, J. W. F., G. Paoli, K. McGuire, I. Amaral, J. Barroso, M. Bastian, L. Blanc, F. Bongers, P. Boundja, C. Clark, M. Collins, G. Dauby, Y. Ding, J. L. Doucet, E. Eler, L. Ferreira, O. Forshed, G. Fredriksson, J. F. Gillet, D. Harris, M. Leal, Y. Laumonier, Y. Malhi, A. Mansor, E. Martin, K. Miyamoto, A. Araujo-Murakami, H. Nagamasu, R. Nilus, E. Nurtjahya, A. Oliveira, O. Onrizal, A. Parada-Gutierrez, A. Permana, L. Poorter, J. Poulsen, H. Ramirez-Angulo, J. Reitsma, F. Rovero, A. Rozak, D. Sheil, J. Silva-Espejo, M. Silveira, W. Spironelo, H. ter Steege, T. Stevart, G. E. Navarro-Aguilar, T. Sunderland, E. Suzuki, J. W. Tang, I. Theilade, G. van der Heijden, J. van Valkenburg, T. Van Do, E. Vilanova, V. Vos, S. Wich, H. Woll, T. Yoneda, R. G. Zang, M. G. Zhang, and N. Zweifel. 2013. "Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics." *Global Ecology and Biogeography* 22 (12):1261-1271. doi: 10.1111/geb.12092.

Tang, Hao, Ralph Dubayah, Anu Swatantran, Michelle Hofton, Sage Sheldon, David B. Clark, and Bryan Blair. 2012. "Retrieval of vertical LAI profiles over tropical rain forests using waveform lidar at La Selva, Costa Rica." *Remote Sensing of Environment* 124:242-250.

Unger, Malte, Juergen Homeier, and Christoph Leuschner. 2013. "Relationships among leaf area index, below-canopy light availability and tree diversity along a transect from tropical lowland to montane forests in NE Ecuador." *Tropical Ecology* 54 (1):33-45.

Vazquez, J. A., and T. J. Givnish. 1998. "Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan." *Journal of Ecology* 86 (6):999-1020.

Whittaker, R. H. 1972. "EVOLUTION AND MEASUREMENT OF SPECIES DIVERSITY." *Taxon* 21 (2-3). doi: 10.2307/1218190.

Whittaker, R. J., K. J. Willis, and R. Field. 2001. "Scale and species richness: towards a general, hierarchical theory of species diversity." *Journal of Biogeography* 28 (4). doi: 10.1046/j.1365-2699.2001.00563.x.

Whittaker, Robert H, and William A Niering. 1975. "Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient." *Ecology* 56 (4):771-790.

Wolf, J. H. D., and F. Alejandro. 2003. "Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico." *Journal of Biogeography* 30 (11):1689-1707. doi: 10.1046/j.1365-2699.2003.00902.x.

Wolf, Jeffrey A, Geoffrey A Fricker, Victoria Meyer, Stephen P Hubbell, Thomas W Gillespie, and Sassan S Saatchi. 2012. "Plant species richness is associated with canopy height and topography in a neotropical forest." *Remote Sensing* 4 (12):4010-4021.

CHAPTER 4: Wood Density along an Elevational Gradient in a Neotropical Forest in Costa Rica

Abstract

Wood density is an important parameter when calculating aboveground biomass of trees, which directly relates to the carbon storage of forests. Accurate wood density at the species and plot-level can provided estimates of carbon storage at regional scales and have important implications for calculating the carbon budget. This research examines tree species and plot-level wood density and aboveground biomass measures along an elevation gradient in Braulio Carrillo National Park in Costa Rica. Tree cores were taken from 29 stand-dominant species over a series of nine 1-ha plots along an elevational gradient from 55 to 2814 m. The patterns of species wood density and aboveground biomass from field measured (tree cores) and database wood density values were assessed to examine how wood density and biomass are affected by changing elevations. At the species-level, individual tree species did not exhibit significant changes in wood density along elevational gradients. At the stand-level, we found wood density did not show a linear pattern with increasing elevations, but instead was highest at both the lowest and highest elevations with a decline at mid-elevations. We found that TEAM database values (0.60 g/cm^3) were significantly higher than field measured wood density for 58% of the species sampled, and that and estimates from the Global Wood Density Database had significantly higher wood density for 50% of the same species. If we expand to just within 1 standard deviation from the mean, TEAM values were significantly different then 80% of the species, and 69% of the Global Wood Density Database. Separating the individuals by diameter class and selecting 10% of each of the classes resulted in the best method (r^2 = 0.98) for reasonably capturing stand-level wood density. Our results suggest that there are decreases in wood density

at mid-elevations and that we are currently overestimating carbon storage in montane forests in the tropics. We also suggest a method to collect estimates of wood density for plots and carbon.

4.1 Introduction

Wood density is an important variable for understanding carbon cycle processes and life history strategies for different tree species. Many past studies have investigated wood density (WD) and the subsequent biomass estimations and stressed the importance of developing databases for wood density values across species and forest types (Chave et al. 2006a, Fearnside 1997, Larjavaara and Muller-Landau 2012, Muller-Landau 2004, Nogueira, Fearnside, and Nelson 2008, Zanne et al. 2009). By understanding the underlying variations in wood density, it is feasible to be able to more accurately estimate biomass at larger scales, which is a large source of uncertainty in climate change models.

Wood density is also an important parameter for estimating aboveground biomass (AGB) and thus can be used as a proxy for the ecosystem service of carbon sequestration. There is little known about the changes in wood density for individual species along elevational gradients in the tropics. Wood density correlates well with many morphological, mechanical, physiological, and ecological properties (Chave et al. 2006a). Wood specific gravity is also a convenient indicator of life history strategy in trees and one with direct importance for ecosystem studies, as quicker growing pioneer species tend to have less dense wood as compared to slower-growing heartier later successional species (Chave et al. 2006a, Niklas 1992, Tilman 1988, Wright et al. 2003). Growth rates tend to be inversely related to the wood density, that is, species with on average lower wood density are putting in less cost to their growth and can grow quickly, whereas denser individuals are investing more into their tissues and tend to be more slow growing. In addition, the trunk with denser wood will also be stronger and thus have an increased chance of survival against physical damage (Muller-Landau 2004). Within tropical tree communities, the distribution of tree life history strategies in general and of wood specific gravities in particular is theoretically expected to vary among sites, particularly along an elevational gradient.

Some studies on aboveground biomass in the tropics suggest that biomass is highest at mid-elevations (Lieberman et al. 1996b). However, linear decreases in aboveground biomass have also been reported with the highest biomass in the lowlands (Moser, Hertel, and Leuschner 2007), or the inverse with high biomass in the highlands (Whittaker and Niering 1975). Wood density may mirror biomass estimates along elevational gradients. In particular, high winds, disturbance regimes, and high turnover at mid-elevations, may select for individuals and species with higher wood densities. High disturbance rates and high turnover rates are expected to favor faster-growing species, which are often the pioneer, early successional species (Connell 1978, Huston 1979, Muller-Landau 2004). However, across these studies, each uses different measurements and calculation of wood specific gravity, or exclude some trees in the stand due to lack of wood density data, and there is a need for a standardized approach.

Currently, biomass and total carbon storage can only be conservatively estimated and the accuracy varies widely depending on the methodology (Fagan and DeFries 2009, Saatchi, Harris, et al. 2011). In order to truly measure aboveground biomass (AGB), all trees within a region would need to be cut and weighed, then dried and reweighed. To alleviate the destructive sampling necessary, allometric equations have been developed, relating tree diameter at breast height (DBH), tree height, and wood density to an Estimated AGB (EAGB). Using previously developed allometric equations, EAGB can be estimated relatively simply at the hectare level with in-situ field data. However, utilizing these allometric equations such as Chave et al. (2014) places a lot of importance on the wood density (Chave et al. 2014), (Supplementary Eq. S1). The more accurate the wood density values, the more accurate the initial calculation of plot biomass. From this equation, it is clear that D (tree diameter) and ρ (wood density, WD) have a large impact on the calculation of EAGB for a single individual, and using a non-accurate values for WD could result in overestimation or underestimation of AGB for the individual, which can be exacerbated when scaled up to the plot level and higher. Thus having high quality wood density data on different species or on the same species under different conditions is imperative for increasing the accuracy of estimates.

This study has four primary questions regarding wood density and aboveground biomass along a tropical forest gradient in Costa Rica. First, does the wood density of dominant trees species measured from tree cores vary across an elevational gradient? Second, do these tree core values match database values for the same species? Third, how does stand-level mean wood density change as elevation increases? We hypothesized that trees would have denser wood at high elevations to be able to withstand high winds, however, we would expect lower wood density at mid-elevations due to higher rates of disturbance. Fourth, how many individuals need to be randomly sampled before we can accurately estimate the stand-level mean of wood density? We would expect to be able to accurately estimate the stand-level average of WD using random sampling techniques when stratifying sampling methods by diameter class. This would increase efficiency in the field to collect this important dataset.

4.2 Methods

4.2.1 Study Area

This research was conducted along a tropical forest elevational gradient in Costa Rica, spanning from 1-ha lowland plots located within the La Selva Biological Station at 55 meters above sea level (masl) up to 2814 masl in Braulio Carrillo National Park (BCNP) (Figure 1). The lowland forest in this region has an average annual rainfall of ~4000 mm, with ~9000 mm at mid-elevations and ~3000 mm at the peak (Feeley et al. 2013, Holdridge 1966, Lieberman et al. 1996b). The average temperature is 26°C in the lowlands and decreases up the elevation to ~10°C at the peak (Clark and Clark 2000). Soil type varies over the region but all are influenced by the volcanic activity of Barva Volcano at the peak of BCNP, with parent materials of basaltic and andesitic lavas from the Plio-Pleistocene age, with more agglomerate tuff-like soil at high elevations (Grieve, Proctor, and Cousins 1990) . Due to the volcanic activity, the soils are younger and have endured less weathering near the peak of Barva Volcano (Grieve, Proctor, and Cousins 1990, Lieberman et al. 1996b).

4.2.2 Field data and laboratory measurements

Annual vegetation surveys were conducted along the gradient within BCNP from nine 1-ha plots ranging from 55 masl to 2814 masl from a collaborative effort of Conservational International’s TEAM Project (http://www.teamnetwork.org/site/volcan-barva) and NASA’s Jet Propulsion Laboratory (Figure 1B). Individual tree diameters were measured using a fabric diameter tape +/- 1 mm resolution, and species were determined in field and compared to herbarium vouchers. Each individual was identified to species and tree diameter at breast height (DBH) was measured for all trees $\geq$ 10 cm DBH for nine 1-ha plots. Based on this species inventory data for the plots, dominant species were selected for each site, as well as were found in multiple of the plots to see how they changed intraspecifically with elevation change. From these 29 dominant species individuals were scouted and identified in the field adjacent to TEAM’s 1-ha plots. Core samples were taken outside of the permanent plots in case the cores affected the tree’s subsequent growth rate. The selected individuals were cored using an increment borer, and brought to the laboratory for measurements in drinking straws. We attempted to sample between 6-10 individuals for each species, across a range of DBH and from about six to twelve species per elevation zone, determined by the locations of the existing TEAM plot (See Supplementary Material Table S1 and S2). We also used species lists from the Carbono project based in the lowlands of La Selva, and designed to be stratified across soil types and micro-topographic gradients (Clark and Clark 2000). This resulted in overall sampling of 524 individual trees across 29 species, at nine different elevation sites, if we counted all of the lowland sites < 100 m together.

Green volume of the tree cores was measured using both the geometric caliper method and the water displacement method to compare following the methods in Chave et al. (2005) (Chave et al. 2005). The samples were oven-dried for ~72 hours until a constant weight was reached, then they were reweighed for dry mass values. These green volume and dry mass measurements were used to calculate wood density for inner/outer wood, then averaged for the individual, and then averaged for each sampled species at each site (Table 1). Database wood density values were assigned for all of the individuals from the compiled Global Wood Density Database (Chave et al. 2006a, Zanne et al. 2009). These measured wood density values of dominant species were combined with database values for the remainder of the species present within the 1 ha plots to develop a stand level average. For the 8,312 total individuals in each field plot, 3,641 individuals’ species were contained within the database. Individuals who did not have their species in the database were assigned the average for their genus (*n* = 4,163). If that was unavailable, then they were assigned their family average (*n* = 508). We also attempted to use the United Nations Food and Agriculture Organization (FAO) database of wood density values, but found that very few of our measured species were in the database (8 of the 29 species). In this manner, each individual in the dataset had a database wood density value associated with it. From field-collected data on species, averages were calculated for each species at each plot and compared to the same species at different elevation plots, as well as these database values. We also examined at the elevational trend of the species and stand-level average of WD using regression analyses and an ANOVA tests run in R.

4.2.3 Stand-level averages

We determined a species average WD at each elevation plot to compare with database values for the same species from the tree cores taken in the field and measure in the laboratory. Stand-level averages of wood density were determined using a combination of field collected WD and database values for non-collected species. The 20 m x 20 m subplots were bootstrapped to determine 95% confidence intervals at the 1-ha scale. These were then compared to elevation to note the pattern of changing WD along the montane gradient. This was conducted on all individuals of all life forms, as well as trees palms, and tree ferns varied from plot to plot (Figure 15). We also compared this data with WD solely from databases, as well as compared to the TEAM network's oft-used value of 0.60 g/cm, which is used in the EAGB calculations for every individual regardless of species (http://www.teamnetwork.org/ 2015).

4.2.4 Intraspecific test

Across the elevation gradient sites, we were limited in search time for individuals from the desired species outside of the plots. Because of this, tree cores were taken from the first individuals we encountered and identified as one of our dominant species, and not systematically over a range of DBH sizes. In December 2016, a smaller field study was conducted to systematically sample from a single species, *Pentaclethra macroloba*, or Pracaxi. This species is a canopy tree from the *Fabaceae* family that is very abundant surrounding La Selva Biological Station. It was selected because of its relative abundance in proximity to the laboratory which would allow for systematic sampling across DBH classes. We also had some data on *Pentaclethra macroloba* at two of our previous sites up to 400 m, so we knew it was an important part of the lowland ecosystem. During this side assessment, 69 new individuals were sampled, from the DBH ranges of 10-20 cm, 20-30 cm, 30-40 cm, 50-70 cm, and >70 cm. These cores were measured in the lab in the same manner as the larger study detailed above, following the protocol of Chave *et al.* (2005).

4.2.5 Testing sampling methods

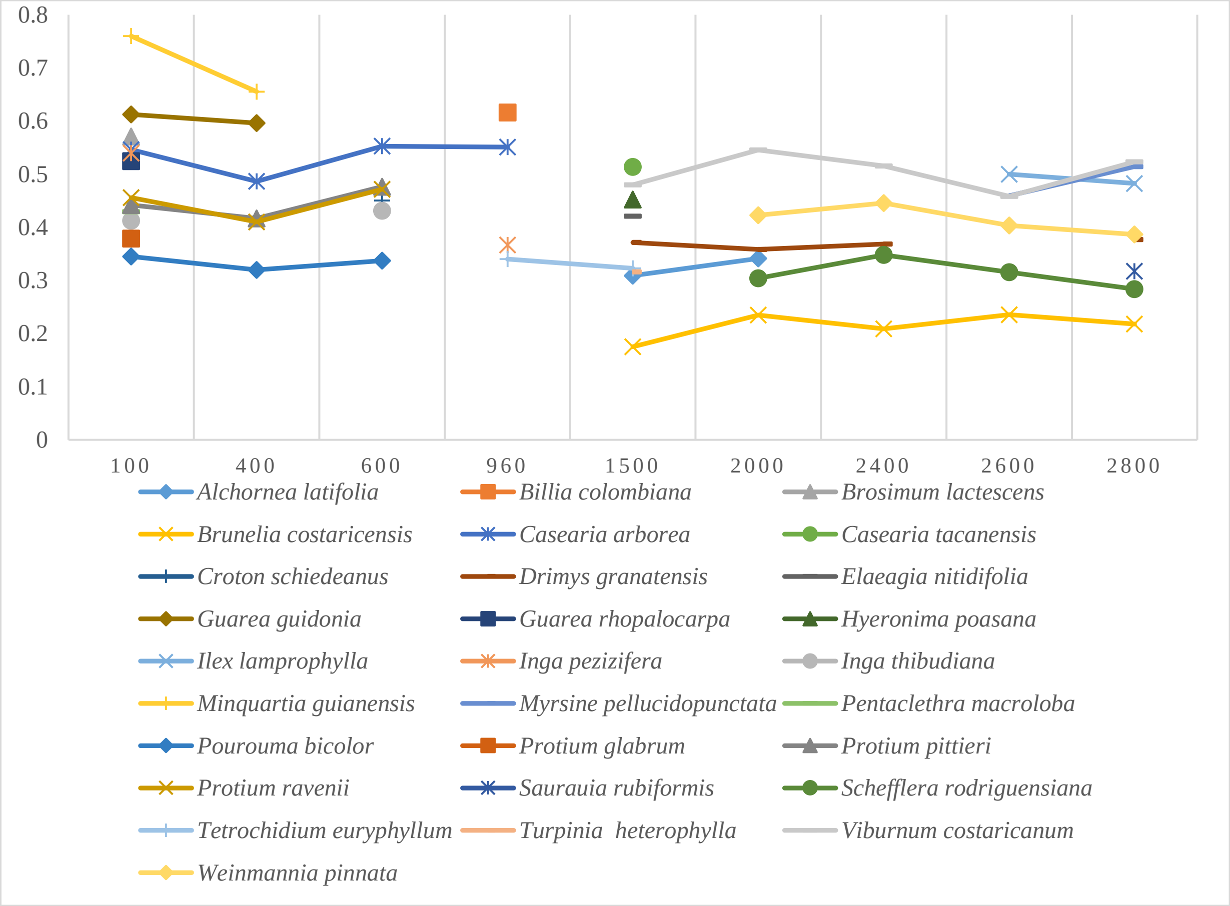
The identification of specific species within a diverse tropical forest can be time consuming, and finding enough individuals of each desired species at each elevational increment can be difficult. To alleviate some of the necessary search time, we tested to see if randomly selecting individuals could capture and reasonably estimate the stan d-level average of WD on our full datasets, utilizing both our own samples of wood density and the database values for species that did not get cored in this study. We tested three methods on the dataset to test the estimation potential from randomly sampling, as follows- increasing in specificity: 10% of the population, 10% of each DBH class averaged and applied to themselves, and 10% of each DBH class averaged and applied to the whole plot. These methods assume that we already know the number of stems and DBH for the individuals in the plot, so we should have a good vegetation surveys in place already. First, we randomly selected 10% of all of the individuals in the plot, using R, and calculated the WD average for that proportion and then applied that average to the remainder of the individuals at that site. The second level of sampling testing separated species by DBH class (10-20 cm, 20-30 cm, 30-40 cm, 50-70 cm, and >70 cm), and randomly selecting 10% of the individuals for each class. The average of each class determined by this sampling was then averaged and then applied on the plot as a whole and to the remainder of the individuals. The third method similarly randomly sampled 10% of each DBH class, but then the average for each class was applied to just the individuals of the same DBH class. These three methods resulted in three assigned WD values for each individual, which was then used within the Chave allometric equation for wet forest to calculate an estimated aboveground biomass (EAGB) (Chave 2005). The resulting EAGB values were then compared to the EAGB calculated from original measured/database values without sampling. From these three sampling methods compared to the full dataset, we hoped to find a way to limit the time spent on taxonomic specificity when collecting tree cores for stand-level WD assessments in the future.

4.3 Results

4.3.1 Changes in wood density based on field measurements

There was a non-linear pattern in WD with increasing elevation for each species cored (Figure 8), with some species slightly increasing in WD, while others had decreased WD with increased elevation. Trees at lower elevations tended to have higher wood density than trees at higher elevations (Supplementary Tables S1 and S2). However, all species were found to have non-statistically significant amounts of change of WD with increased elevation.

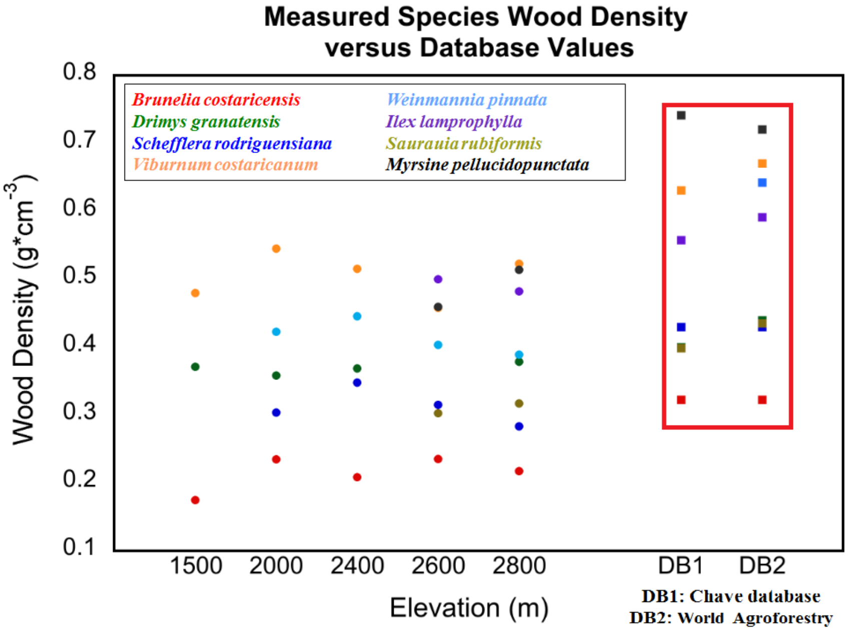
Figure 8. Measured species wood density (g/cm^3) at nine sites across an elevational gradient.



4.3.2 Comparison of species wood densities to database values

A comparison of field collected values for species tended to be lower than Global Wood Density Database values for the same species (Figure 9, (http://www.teamnetwork.org/ 2015, Zanne et al. 2009)). The value of 0.60 g/cm^3, previously used by TEAM, seems to be quite high based on both database values and species composition and field-measured WD from this study. Only one site had a plot-level average close to 0.60 g/cm^3, and this plot at the highest elevation has very unique species composition and structural characteristics in that it is a cloud forest (Figure 9). We found that the Global Wood Density Database had wood densities more than two standard deviations away for 50% of the selected species (Table 6, Table 7). If we expand to more than 1 standard deviation from the mean, 69% of the selected species were significantly different than the Global Wood Density Database (Table 7). Using a paired t-test, my measured wood density values across all species were significantly less than their database values, by an average of -0.105 g/m^3 (p-value < 0.0001).

Figure 9. Selected highland species with database values outlined in red box.



4.3.3 Wood density relationship with elevation

There was a significant difference in the plot-average WD values for just the species cored in the field and averaged across the plot, determined using an ANOVA test. For solely the species cored, there was a non-linear pattern in WD with increasing elevation (Figure 10). This varied widely from the database values for the species cored. Utilizing all of the individuals within the plot, including those species not field-measured for our study, also yielded similar results (Figure 11). Wood density averaged at the stand level did not show a linear pattern, but instead showed a trough at mid- to high-elevations with higher wood densities at both lower and higher elevations (Figure 11). There was high variation within the lowland (<100m) plot stand average wood densities.

Table 6. Analysis of mean and standard deviation (SD) of wood density from tree corers compared to Global Wood Density Database (GWDDB). Green means the database (DB) value falls within 1 SD of our values, yellow the DB falls between 1 and 2 SD, red the DB is more than 2 SDs from our measured mean for the species.

Scientific name	**Mean wood density**	**SD wood density**	**GWDDB**
Alchornea latifolia	0.32522	0.09785	🟥 **0.42667**
Billia colombiana	0.61617	0.05167	🟨 **0.69**
Brosimum lactescens	0.57115	0.02917	🟥 **0.656**
Brunelia costaricensis	0.21824	0.04587	🟥 **0.3225**
Casearia arborea	0.53404	0.12501	🟩 **0.574**
Casearia tacanensis	0.51394	0.00956	🟥 **0.62724**
Croton schiedeanus	0.45019	0.10714	🟩 0.515
Drimys granatensis	0.36807	0.03058	🟥 **0.4**
Elaeagia nitidifolia	0.42104	0.04215	
Guarea Guidonia	0.59383	0.05851	🟩 **0.565**
Guarea rhopalocarpa	0.52467	0.02602	🟨 **0.56038**
Hyeronima poasana	0.4521	0.05214	🟥 **0.63798**
Ilex lamprophylla	0.49179	0.10427	🟩 **0.558**
Inga pezizifera	0.41583	0.12015	🟨 **0.65334**
Inga thibudiana	0.41622	0.17635	🟩 **0.57975**
Minquartia guianensis	0.7076	0.09955	🟩 **0.78671**
Myrsine pellucidopunctata	0.48536	0.04513	🟥 **0.74182**
Pentaclethera macroloba	0.41043	0.0579	🟥 **0.603**
Pourouma bicolor	0.33503	0.11104	🟩 **0.35322**
Protium glabrum	0.37855		
Protium pittieri	0.43882	0.05636	🟩 **0.47476**
Protium ravenii	0.44093	0.1031	🟨 **0.576**
Saurauia rubiformis	0.31705	0.0233	🟥 **0.39854**
Schefflera rodriguensiana	0.31258	0.04974	🟥 **0.43**
Tetrochidium euryphyllum	0.33375	0.03346	🟥 **0.4543**
Turpinia heterophylla	0.31638	0.01435	🟥 **0.39408**
Viburnum costaricanum	0.5096	0.1028	🟨 **0.63112**
Weinmannia pinnata	0.41426	0.04372	🟥 **0.63381**

Table 7. The percentages of each species that are found to be significant for each level of significance, and for both types of wood density database values.

	<1 SD	1>SD>2	> 2 SDs	> 1 SD
GWDDB	0.308	0.192	0.5	0.692

Figure 10. Wood density values across an elevational gradient for measured species, 0.6 baseline, and database values for cored species only.

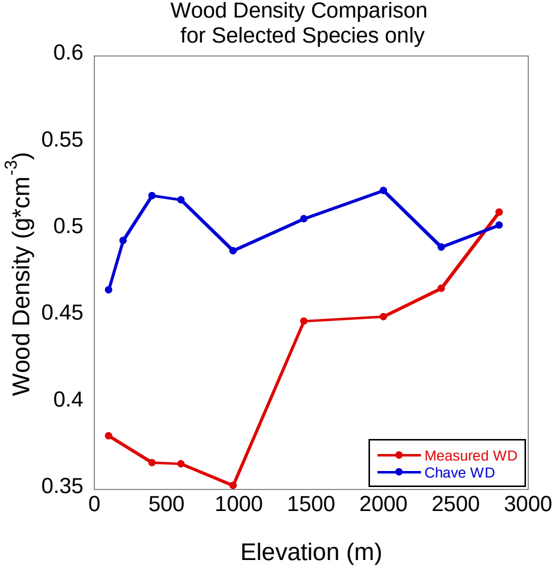
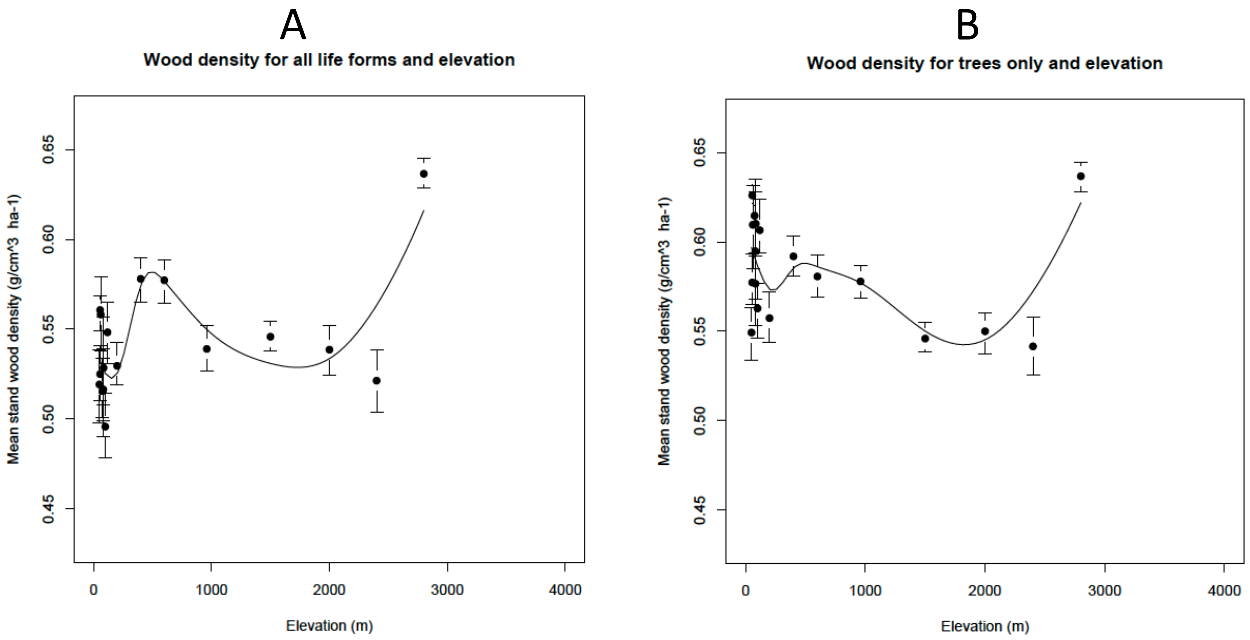


Figure 11. Pattern of wood density from both measured species and database values along the elevational gradient for (A) all life forms and (B) trees only. The bars were the 95% confidence intervals when assessing bootstrapping subplot averages. Figure 15 shows the distribution of the different life forms.



4.3.4 Intraspecific test

For the intraspecific test looking at just *Pentaclethra macroloba* below 100 m, 69 individuals were sampled from the DBH ranges of 10-20 cm, 20-30 cm, 30-40 cm, 50-70 cm, and >70 cm. The numbers were skewed over the DBH classes, with more individuals of the smaller DBH classes sampled (Figure 12A). However, this pattern holds when compared to the counts of all individuals across all 20 1-ha sites of which we had survey data (Figure 12B). For all 1-ha sites, there simply are more individuals of the smaller DBH classes, while the larger the tree diameter is, the fewer in number they are.

Wood density values for *Pentaclethra macroloba* was highest for the individuals within the smallest and largest DBH classes (Figure 13). After the first DBH class segment, the overall WD is lower, but then steadily increases as the DBH increases as the tree ages. In all cases, on average the outside half of the tree core was found to be denser than the inner part of the same tree core, although we are mostly concerned with the core’s overall average WD for scaling up purposes. The error bars on the figure are highest for the smallest DBH class, but this was likely tied to the larger quantity of individuals sampled for that DBH class (Figure 12A).

Figure 12. A) Number of *Pentaclethra macroloba* individuals sampled below 100m elevation during December 2016, based on five DBH classes: 10-20 cm, 20-30 cm, 30-40 cm, 50-70 cm, and >70 cm. B) The number of individuals across all 20 1-ha plots, showing similar distribution of tree sizes.

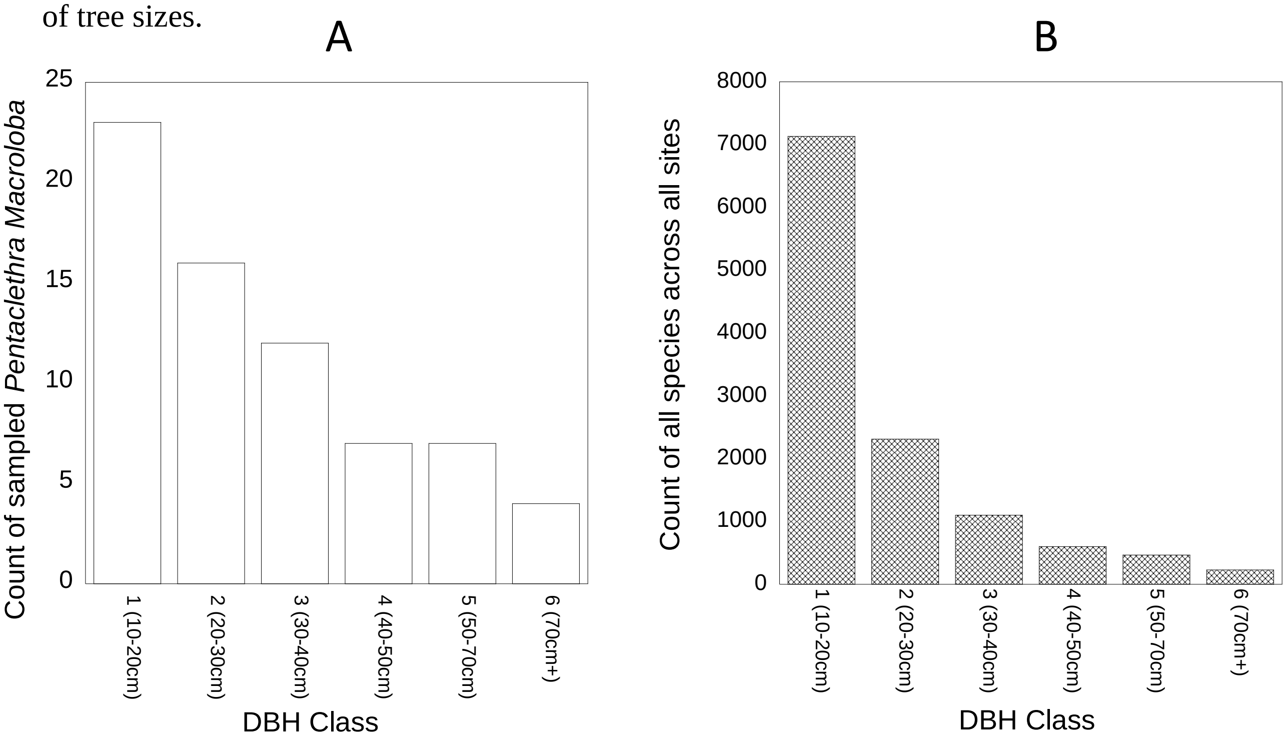
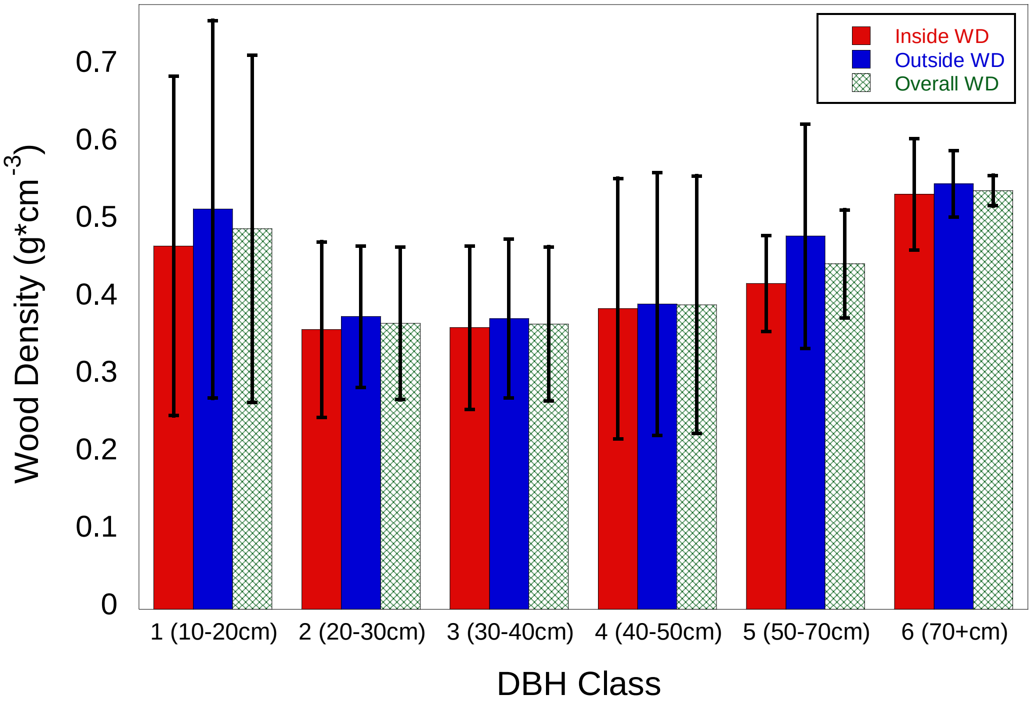


Figure 13. Pattern of wood density for *Pentaclethra macroloba* individuals, separated by inside and outside WD, and across the five DBH classes: 10-20 cm, 20-30 cm, 30-40 cm, 50-70 cm, and >70 cm.



4.3.5 Sampling methods

The sampling tests were run to determine if we could limit the time spent on taxonomic specificity when collecting tree cores for stand-level WD assessments in the future. Based on the three different sampling methods, the simplest method of randomly selecting 10% from all of the individuals can reasonably estimate wood density at the stand level across all of our sites with an r^2 of 0.88 (Figure 14).

However, when we separated the trees in the plot into DBH size classes and randomly sampled 10% of each of those groups and applied the average either to the entire plot or to each DBH class and then average up to the stand level, it resulted in an r^2 of 0.98 when compared with the "true" stand wood density of the site. Depending on the inventory data available, 10% of any of the individuals can reasonably provide a good estimate of WD at the stand level, but using DBH to select a more varied range of individuals will increase the possibility of estimating WD, while limiting the necessity to identify specific individuals of certain species in a highly diverse tropical forest.

Figure 14. Sampling test for how many individuals are needed to be sampled to acquire an accurate stand-level average wood density for precise above ground biomass estimates.

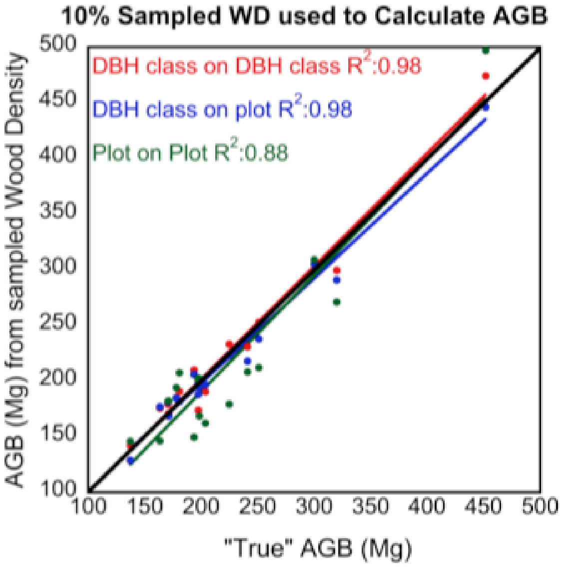
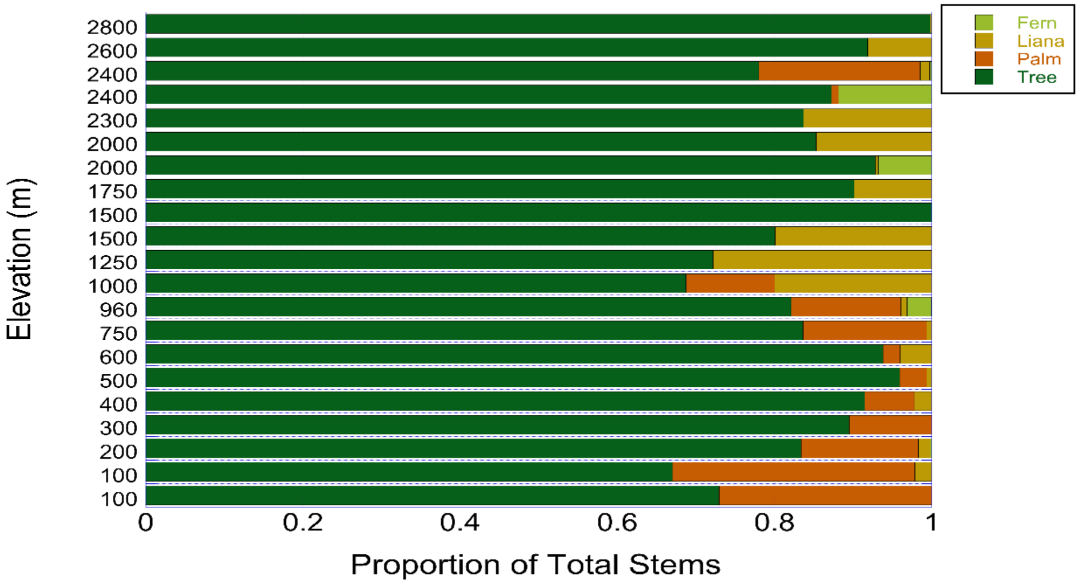


Figure 15. Life forms across elevations.



4.4 Discussion

Based on our analysis of tree wood density, the database values for wood density are often higher than measured in the field. This causes issues when estimating aboveground biomass (AGB) because the equation relies heavily on wood density as a parameter. These higher WD values can inflate and thus overestimate AGB, which gets exacerbated moving from the individual, to the stand, to the country, and even global levels. Accurate estimates of AGB are especially important in this current era of climate change where monitoring of terrestrial carbon sinks and sources is vital. While there can be large differences inter-specifically in wood density, a tropical forest is expected to have a heterogeneous mix of high and low density species, and a stand-average WD value may be the best way to assess patterns at a larger scale. The lowland Carbono plots <100 masl, specifically, seem to display high variation. These lowland plots were designed to be stratified across soil types and micro-topographic gradients, which has the potential to affect the wood densities due to drainage and soil wetness. However, our plots along the elevation gradient do not have replicates so we cannot test these factors. Assuming our single vegetation survey plots are representative of the surrounding forest at that elevation, we found a mid-elevation trough of lower wood densities, with higher wood density at both lower and higher elevations.

Since WD is tied to the life history strategy of the species and individual circumstances, perhaps it can tell us something about the dynamics of the site. More disturbed sites will be more likely to have secondary forest species and pioneer individuals that need to grow quickly and invest less into dense sturdy wood. Lower elevations may be subject to more anthropological influence and disturbance, while high elevations may be more affected by increased wind velocity as air passes over the mountaintop. Perhaps the mid-elevation trough of lower wood densities is a result of orographic wind, steep slopes, and landslides which end up favoring the growth of less dense, rapidly growing species, whereas the highest elevation, more of a plateau, is less susceptible to landslides and the species composition includes more naturally dense species and individuals to withstand the high wind speeds. The WD value utilized by TEAM, 0.60 g/cm^3, was only exhibited at the highest elevation site, at 2800 masl. Because of this, we believe that this value may not be representative values for all sites, resulting in overestimation of aboveground biomass and carbon storage. This high elevation site was very unique structurally and very species-poor compared to all other plots.

The more tailored stratified sampling for the intraspecific test of wood density looked at the 69 individuals of *Pentaclethra macroloba* that were sampled below 100m, from the DBH ranges of 10-20 cm, 20-30 cm, 30-40 cm, 50-70 cm, and >70 cm. The wood density results showed that for *Pentaclethra macroloba* wood density is highest for the individuals within the smallest and largest DBH classes (Figure 13). After the first DBH class segment, the overall WD is lower, but then steadily increases as the DBH increases as the tree ages. In all cases, on average the outside half of the tree core was found to be denser than the inner part of the same tree core, although we are mostly concerned with the core's overall average WD for scaling up purposes. This pattern of differing wood densities throughout the lifespan of a tree may be tied to the life history of this canopy species. Initially as the tree enters the smallest DBH class we measured, the higher wood density may help the individual establish in the highly competitive understory. As the tree grows, it then needs to reach the canopy quickly to get out of the light-limited understory. To do so, the tree grows more vertically instead of getting denser and stronger wood. As it continues to grow, it can get invest more in growing girthier and stronger more dense wood, as it has already reached the canopy level and the crown is in sunlight. The results from this intraspecific study were very interesting, and it would be a good motivation to sample other species in a similar manner to see if the pattern is the same for other canopy species. In addition, these trees within the smaller DBH classes are more abundant in this forest type, and the larger tree sizes are rarer.

Based on our sampling tests, it seems as if the goal for large-scale biomass estimations requires just the overall idea of what is happening on the landscape versus intraspecific variation, random sampling of individuals in a stratified manner based on diameter can provide a good idea of stand-average wood density. Depending on the inventory data available, 10% of any of the individuals can reasonably provide a good estimate of WD at the stand level, but using DBH to select a more varied range of individuals will increase the possibility of estimating WD, while limiting the necessity to identify specific individuals of certain species in a highly diverse tropical forest. Since a diverse tropical forest theoretically should contain a variety of wood densities and life history strategies, the overall species composition is likely a main driver behind the stand averages. Future studies could utilize this method of sampling by diameter class to aid in determining patterns of stand WD, helpful when attempting to monitor aboveground biomass and dynamics of carbon sequestration on a landscape.

While WD data at the stand-level did not show a linear pattern with elevation, the data does show a similar pattern to a study by collaborators over a Peruvian gradient, albeit with slightly different extents in the lowlands and highlands due to a taller mountaintop at 3500 masl compared to our 2800 masl. For the center of the elevation gradients, there is a pattern for both the Costa Rican and Peruvian datasets of a mid-elevation trough of wood densities, with higher wood densities at lower and higher elevations. The plots with the highest wood density, around 600m in elevation, also tended to have the highest levels of tree diversity (Robinson et al. 2018).

4.4.1 Uncertainties

Even if it were possible to measure wood density of all individuals so we have a good idea of the average, there are other potential uncertainties. Possible error concerns the error in measurement if measurements are not standardized, both in the field and the laboratory. For example, wood density may vary with the height on the tree that is cored. Traditionally, these tree cores for WD purposes have been taken at the height of where Diameter at Breast Height (DBH) is measured (~1.37 m). However, this height is rarely measured in the field, and while accuracy is attempted, there could easily be ± several centimeters of error. If the core is taken from low down on the trunk versus higher towards the canopy, there could be different and erroneous values measured for that individual.

Besides the field collections, variations in the laboratory measurements of the tree cores can also cause some uncertainty. The geometric caliper method and the water displacement method, when both completed, provided similar results, but the caliper method assumes a perfect cylinder of the tree core, which is often a mistaken assumption, as the cores may get divots or grooves. The water displacement method is great for both regular and irregularly shaped samples (Muller-Landau 2004). These differences when measuring green volume affect the final calculation of wood density. Various studies may have done one method over the other, and it is important to note the possible differences this may have introduced. Another variation from within lab measurements could be the temperature at which the tree cores are dried, standard is 105°C, but some studies report using 50-70°C instead of standard 105°C (Muller-Landau 2004).

Even with the measurements standardized and individuals all accurately identified and tabulated at the species level, there are still errors that can occur. The variations of sampled individuals' WD within different species can be seen in Supplementary Figure S1 A-C. S1A combines all samples and looks at the count of individuals sampled versus the coefficient of variation (CV) for each species. S1B shows the CV for individuals separated out by the elevational site they were sampled from, and S1C shows the count of individuals of each species sampled from each elevation site. Plot location and abiotic driving factors such as topographical variations, precipitation regime, soil fertility, and other ecological processes can all affect the growth of an individual and it is difficult to account for all of these variations.

4.4.2 Implications

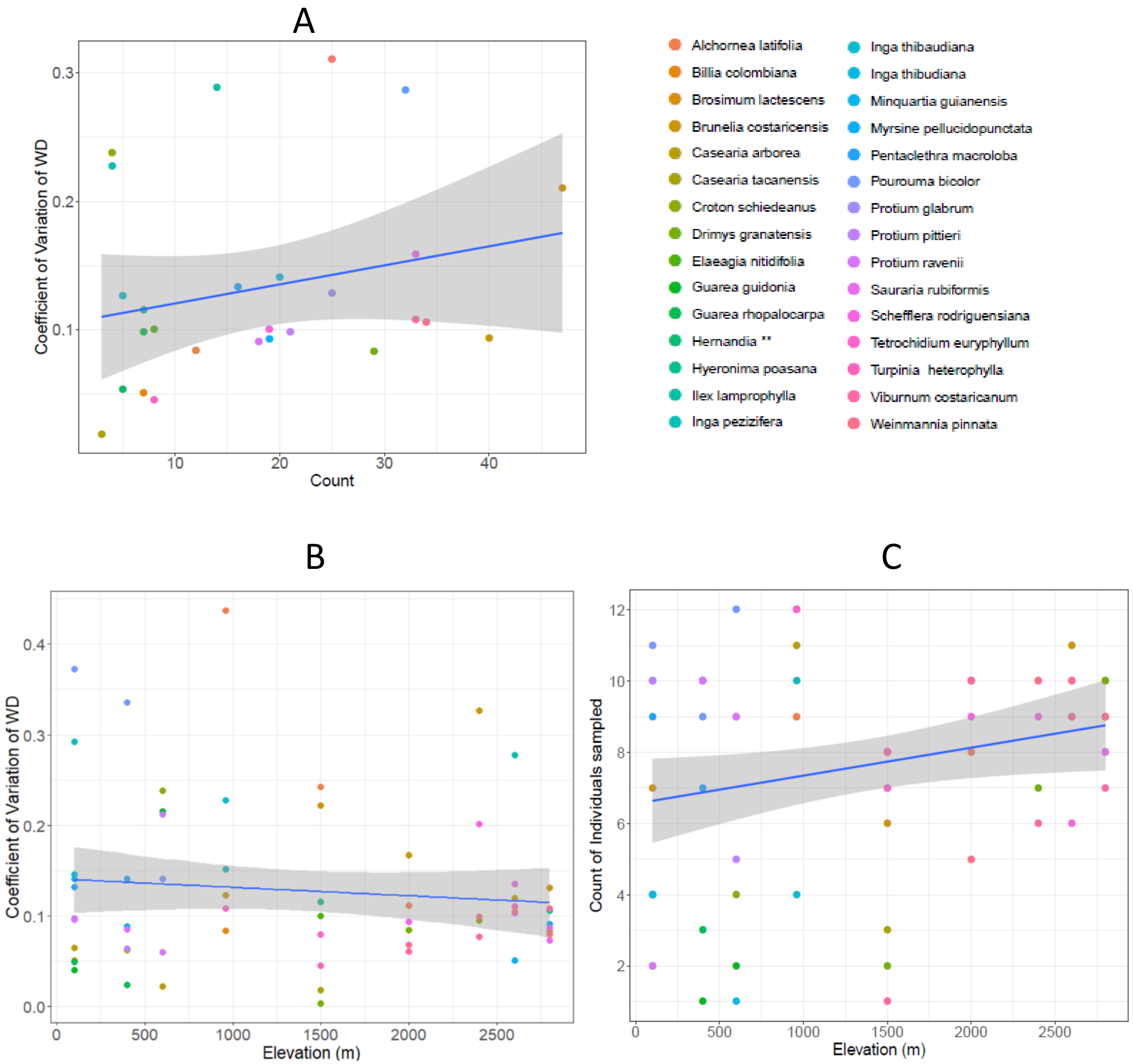
Developing accurate estimates of global forest extent and growth is imperative in order to assess the amount of biomass and carbon stored in the forests of Earth and long-term global health in the current era of projected climate change scenarios, due to the large portion of carbon stored in terrestrial systems carbon (Fagan and DeFries 2009, Solomon 2007, Trumbore, Brando, and Hartmann 2015). However, there are still widespread uncertainties in measurements of forests that have limited efforts to obtain this seemingly simple dataset (Fagan and DeFries 2009, Grainger 2008, Houghton 2003). Forests are changing unevenly worldwide, and standardized methodology is necessary to monitor exactly how the forests are changing, both regionally and globally.

4.5 Conclusions

Field measurements of wood density are imperative to accurately get an idea of stand-average wood density for biomass estimations since database values can vary significantly from database values, taken over different sites. However, it seems as though a randomly selected sampling of tree cores of individuals across diameter classes is sufficient to produce similar AGB results rather than carefully choosing and identifying certain species to sample, whose intraspecific variation may complicate the overall pattern in the stand when an average may be a better parameter. Sampled tree cores in this study were found to be significantly lower than database values for the same species, and quite lower than the 0.60 g/cm^3 used in TEAM calculations for this field site. Future work will analyze the effect of tree size on the wood density across several of the species cored for this project more in depth.

4.6 Supplementary Materials

Supplementary Figure S1: Variations in wood density measurements. A is the coefficient of variation of WD for each species combined from the different elevational plots. B is the coefficient of variation of WD for each species at each elevational site. C shows the count of measured individuals of each species across elevations.



SUPPLEMENTARY EQUATIONS

Supplementary Equations S3 & S4: Chave *et al.* (2014) allometric equations for wet forest stands, depending on availability of tree height.

$EAGB = 0.0673*(\rho D^2 H)^{0.976}$ when Height is available, or (S3)

$EAGB = exp = [-1.803-0.976E+0.976\ln(\rho) + 2.673 \ln(D) - 0.0299[\ln(D)]2]$ (S4)

EAGB = Estimated Aboveground Biomass
ρ = Wood Density
D = Tree Diameter at Breast Height (DBH)
H = Tree Height

4.7 References

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Folster, F. Fromard, N. Higuchi, T. Kira, J. P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riera, and T. Yamakura. 2005. "Tree allometry and improved estimation of carbon stocks and balance in tropical forests." *Oecologia* 145 (1). doi: 10.1007/s00442-005-0100-x.

Chave, J., H. C. Muller-Landau, T. R. Baker, T. A. Easdale, H. ter Steege, and C. O. Webb. 2006a. "Regional and phylogenetic variation of wood density across 2456 Neotropical tree species." *Ecol Appl* 16 (6):2356-67.

Chave, Jerome, Maxime Réjou-Méchain, Alberto Búrquez, Emmanuel Chidumayo, Matthew S Colgan, Welington BC Delitti, Alvaro Duque, Tron Eid, Philip M Fearnside, and Rosa C Goodman. 2014. "Improved allometric models to estimate the aboveground biomass of tropical trees." *Global change biology* 20 (10):3177-3190.

Clark, David B, and Deborah A Clark. 2000. "Landscape-scale variation in forest structure and biomass in a tropical rain forest." *Forest ecology and management* 137 (1):185-198.

Connell, Joseph H. 1978. "Diversity in tropical rain forests and coral reefs." *Science* 199 (4335):1302-1310.

Fagan, Matthew, and Ruth S DeFries. 2009. *Measurement and Monitoring of the World's Forests: A Review and Summary of Remote Sensing Technical Capability, 2009-2015*: Resources for the Future.

Fearnside, Philip M. 1997. "Wood density for estimating forest biomass in Brazilian Amazonia." *Forest ecology and management* 90 (1):59-87.

Feeley, Kenneth J., Johanna Hurtado, Sassan Saatchi, Miles R. Silman, and David B. Clark. 2013. "Compositional shifts in Costa Rican forests due to climate-driven species migrations." *Global Change Biology* 19 (11):3472-3480. doi: 10.1111/gcb.12300.

Grainger, Alan. 2008. "Difficulties in tracking the long-term global trend in tropical forest area." *Proceedings of the National Academy of Sciences* 105 (2):818-823.

Grieve, I. C., J. Proctor, and S. A. Cousins. 1990. "SOIL VARIATION WITH ALTITUDE ON VOLCAN BARVA, COSTA-RICA." *Catena* 17 (6):525-534. doi: 10.1016/0341-8162(90)90027-b.

Holdridge, LR. 1966. "The life zone system." *Adansonia* 6 (2):199-203.

Houghton, R. A. 2003. "Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850-2000." *Tellus Series B-Chemical and Physical Meteorology* 55 (2). doi: 10.1034/j.1600-0889.2003.01450.x.

http://www.teamnetwork.org/. 2015. "Tropical Ecology Assessment & Monitoring Network: Early Warning System for Nature." http://www.teamnetwork.org.

Huston, Michael. 1979. "A general hypothesis of species diversity." *American naturalist*:81-101.

Larjavaara, Markku, and Helene C Muller-Landau. 2012. "Temperature explains global variation in biomass among humid old-growth forests." *Global Ecology and Biogeography* 21 (10):998-1006.

Lieberman, Diana, Milton Lieberman, Rodolfo Peralta, and Gary S Hartshorn. 1996b. "Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica." *Journal of Ecology*:137-152.

Moser, Gerald, Dietrich Hertel, and Christoph Leuschner. 2007. "Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in Ecuador and a pan-tropical meta-analysis." *Ecosystems* 10 (6):924-935.

Muller-Landau, Helene C. 2004. "Interspecific and Inter-site Variation in Wood Specific Gravity of Tropical Trees1." *Biotropica* 36 (1):20-32.

Niklas, Karl J. 1992. *Plant biomechanics: an engineering approach to plant form and function*: University of Chicago press.

Nogueira, Euler Melo, Philip Martin Fearnside, and Bruce Walker Nelson. 2008. "Normalization of wood density in biomass estimates of Amazon forests." *Forest Ecology and Management* 256 (5):990-996.

Robinson, Chelsea, Sassan Saatchi, David Clark, Johanna Hurtado Astaiza, Anna Hubel, and Thomas Gillespie. 2018. "Topography and Three-Dimensional Structure Can Estimate Tree Diversity along a Tropical Elevational Gradient in Costa Rica." *Remote Sensing* 10 (4):629.

Saatchi, Sassan S., Nancy L. Harris, Sandra Brown, Michael Lefsky, Edward T. A. Mitchard, William Salas, Brian R. Zutta, Wolfgang Buermann, Simon L. Lewis, Stephen Hagen, Silvia Petrova, Lee White, Miles Silman, and Alexandra Morel. 2011. "Benchmark map of forest carbon stocks in tropical regions across three continents." *Proceedings of the National Academy of Sciences* 108 (24):9899-9904. doi: 10.1073/pnas.1019576108.

Solomon, Susan. 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*. Vol. 4: Cambridge University Press.

Tilman, David. 1988. *Plant strategies and the dynamics and structure of plant communities*: Princeton University Press.

Trumbore, S, P Brando, and Henrik Hartmann. 2015. "Forest health and global change." *Science* 349 (6250):814-818.

Whittaker, Robert H, and William A Niering. 1975. "Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient." *Ecology* 56 (4):771-790.

Wright, S Joseph, Helene C Muller-Landau, Richard Condit, and Stephen P Hubbell. 2003. "Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees." *Ecology* 84 (12):3174-3185.

Zanne, Amy E, G Lopez-Gonzalez, David A Coomes, Jugo Ilic, Steven Jansen, Simon L Lewis, Regis B Miller, Nathan G Swenson, Michael C Wiemann, and Jerome Chave. 2009. "Global wood density database."

Chapter 5. **Costa Rican Forest Patterns and Trends: Forest loss, landscape heterogeneity and fires in the 21st century using remote sensing (2000 to 2016)**

Abstract

Tropical forest degradation and loss are a primary driving force in the loss of global diversity and terrestrial carbon sequestration. In this chapter, I assess the spatial patterns driving deforestation and afforestation across Costa Rica and protected areas. Forest loss and gains within the country for the years of 2000-2016 at 30 m spatial resolution were calculated, and we tested whether protected areas (PAs) indeed had less forest loss than non-protected areas. This dissertation chapter had four main research objectives. First, we examined forest cover change in Costa Rica from 2000 to 2016 to determine if there were patterns within provinces and across protected areas. Second, we identified changes in NDVI in protected areas from 2000 to 2016. Third, we identified patterns in population within the country and across protected areas with differing levels of protection. Fourth, we looked at patterns in fire frequency and extent within and outside protected areas. Firstly, we found that deforestation has been occurring over the entirety of the country of Costa Rica since 2000. There has been some gain across the country, but very limited when compared to the loss. For protected areas, there has also been predominantly loss over the time period. Our second research question examined NDVI changes. In general, NDVI increased slightly over the time period of 2000-2016 for the entirety of the country and within the protected areas when averaged together (0.573 to 0.5995). When the PA change was analyzed individually using a paired t-test found a significant decrease of -0.0226, with a t-value of -6.7415 ($p < 0.001$). At the province level, it was determined the provinces decreased insignificantly by -0.0029. On average, some provinces increased in NDVI while others decreased. The third research objective noted that population was centered in a few major cities, specifically San Jose. The two provinces that were the most populous were San Jose and Alajuela, and they also

increased the most during this time period. The country as a whole increased in population during this time, and all provinces showed an increase in population. For humans living within protected areas, they were mostly found in IUCN category VI during 2016. In general, the PAs seem to have experienced a loss of human population during these years, though it was found to be insignificant. The final research question looked at the pattern of fire across the country of Costa Rica. Fires during the 2000-2016 period were mainly in the lowland coastal areas, and focused on the drier western portion of the country. The incidence of fire was found to be negatively correlated with the forest area lost annually ($r^2 = 0.25$) there was less forest area lost in years with higher fire frequency. This correlation does not imply causation and instead shows that the forest loss is more likely due to forest conversion than fires. This dissertation chapter examined the effect of protected versus non-protected status on forest loss and land conversion. Developing an understanding of diversity and successional stages both within and outside of protected areas may give us some insight on how to best manage tropical montane systems and may aid in developing conservation priorities, particularly in the face of climate change.

5.1 Introduction

Forests cover roughly 31% of the world's land surface, and are estimated to store 48% of the world's terrestrial carbon, although these are conservative estimates (Dixon et al. 1994, Fagan and DeFries 2009, FAO 2010, Groombridge, Jenkins, and Jenkins 2002). In the first decade of this century, 2000-2010, the global net forest loss was about 5.2 million hectares per year (Fagan and DeFries 2009, FAO 2010). Forest loss is estimated to account for roughly 12-20% of global greenhouse gas emissions, mainly through deforestation and degradation of tropical forests (Saatchi, Harris, et al. 2011, Sandbrook et al. 2010, Van der Werf et al. 2009). Developing accurate estimates of global forest extent and growth is imperative in order to assess the amount of biomass and carbon stored in the forests of Earth and long-term global health. Deforestation is uneven around the world, and standardized methodology is necessary to monitor exactly how the forests are changing, both regionally and globally. Each year the world has less forested area, and the forests that remain are of lower quality. For example, the replacement of natural old-growth forests with a monoculture of an exotic species greatly reduces biodiversity and may affect other ecosystem services (Groombridge, Jenkins, and Jenkins 2002, Jantz et al. 2015, Kuper 2013). Current technologies utilizing spaceborne or airborne remotely sensed imagery could be very useful to study terrestrial processes at large scales, which will allow for better monitoring of forest stocks and limit the need for extensive and costly measurements in the field (Fagan and DeFries 2009, Grainger 2008, Houghton 2003). Protecting areas by designating them as national parks, national forests, or biological reserves has been shown to be the simplest and most common approach to conserving the remaining forests (Pfaff et al. 2007, Pfaff et al. 2009, Sanchez-Azofeifa et al. 2007, Sanchez-Azofeifa et al. 2003).

One project that requires robust estimates of forest carbon stocks in various countries is the United Nations Reducing Emissions from Deforestation and Degradation (UN-REDD). The UN-REDD Program is an initiative to combat climate change, by assigning a monetary value to a country’s carbon stocks. The scientific goals of the UN-REDD program specifically ask for refinements in the remote sensing methodologies to estimate forest biomass over regional and global scales. In recent years, the international community has recognized the loss of diversity as a key threat to the sustainability of tropical ecosystems by affecting their ecological functions and services (Jantz et al. 2015, Kuper 2013). This recognition contributed to the international negotiations on the reduction of emissions from deforestation and degradation by adding biodiversity (REDD+) as an important component of mitigating climate change, and offering tradeable credits and financial incentives for reducing emissions (Edenhofer et al. 2011, Pfaff et al. 2007, Sanchez-Azofeifa et al. 2003, Sanchez-Azofeifa et al. 2007, Solomon 2007). A significant constraint in identifying forests with different conditions is the capacity to map them from space (Achard et al. 2007, Asner et al. 2012a, Giacomo et al. 2008). Quantifying the patterns and understanding the processes that maintain species diversity across tropical landscapes are considered one of the ten most challenging problems that require spatial data from combined ground and remote observations to resolve (Rose et al. 2015). The development of methods utilizing this type of technology allows for the mapping of ecological features that were previously only feasible through ground collection. Remote sensing allows for the study of objects without direct contact, typically through the use of satellite imagery. Because of this, it can allow for broad mapping of forest extent, climate, and ecological processes at a large scale more quickly than possible solely through assessment on the ground. Ground measurements are expensive, laborious, and time consuming, as well as typically very limited spatially. Field collections have to be spatially limited due to time constraints and labor input, and remote areas may be difficult to access and sample; using imagery can allow for easier analysis of these areas without additional disturbance. Remote sensing is a practical necessity to measure and monitor forests globally. Monitoring forest biomass over regional and global scales is imperative with increasing concerns about climate change, as more attention needs to be focused on accurately estimations of carbon fluxes.

Costa Rica’s unique position, bordered on two sides by oceans and having varied topography results in many different micro-environments and niches, allowing for high levels of biodiversity and primary productivity. Understanding the dynamic nature of the vegetation growth and health may give us a better idea of how different ecosystems may be impacted by a changing climate, particularly by varied temperature and precipitation regimes. This project will utilize spaceborne passive and active sensors to effectively monitor aspects about the forests Costa Rica important to conservationists, policy-makers, and ecologists within the Neotropical country of Costa Rica.

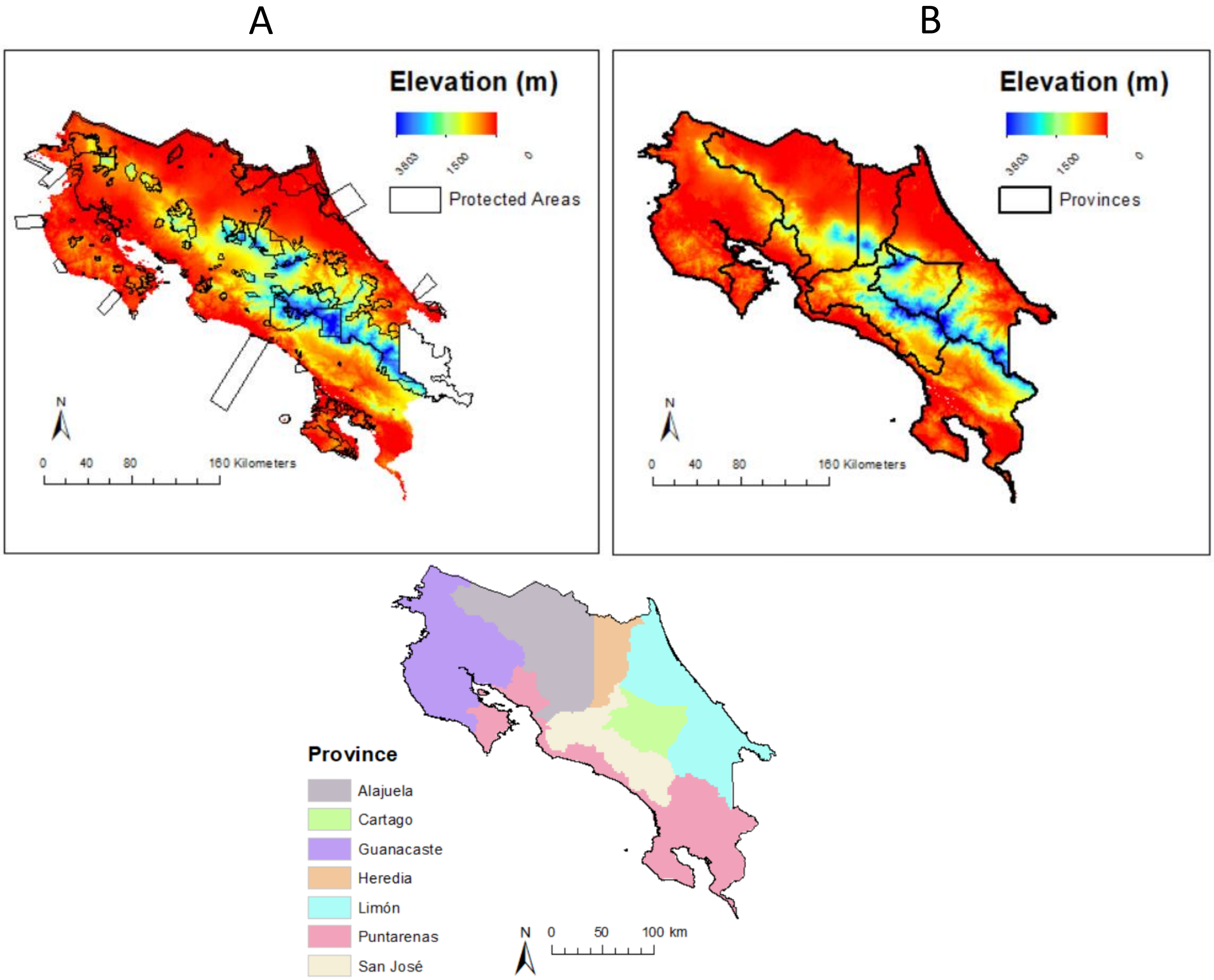
This research has four primary research objectives. First, we examine forest cover change in Costa Rica from 2000 to 2016 to assess patterns within provinces and across protected areas. Second, we identify changes in NDVI in protected areas from 2000 to 2016. Third, we identify if there are significant increases in population within the country and within protected areas. Fourth, we identify if there have been significant changes in fire frequency and extent within and outside protected areas. This project used a combination of remote sensing, GIS layers, and ground-derived products to examine how the forest in Costa Rica has changed between 2000 and 2016, particularly in terms of protected versus non-protected areas. Developing an understanding of diversity and successional stages both within and outside of protected areas may give us some insight on how to best manage tropical montane systems and may aid in developing conservation priorities, particularly in the face of climate change.

5.2 Study Site, Data, and Methods

5.2.1 Study Site: Costa Rica

This project covers the entirety of the country of Costa Rica, a country in Central America fringed by the Pacific Ocean and the Caribbean Sea, and bordered by Nicaragua and Panama, with an area of roughly 51,636 km^2 of terrestrial land area, and 576,100 km^2 marine area (IUCN 2017). Costa Rica has highly varied topography and geography which has allowed for the evolution of high levels of biodiversity: while Costa Rica encompasses only 0.03% of the terrestrial world it contains 4.8% of all described species (Kuper 2013, SINAC 2009). Elevations in Costa Rica range from sea level to ~3805m (Figure 16). According to downloaded WorldClim data annual mean temperature across the country ranges from 4 to 27° C, while total annual precipitation ranges from 0 to 272 cm (Hijmans et al. 2004). Due to the ranges of topographical and climatic variables, there are highly varied landscapes that cover many different life zones and biomes (IUCN 2017, Kuper 2013, Sanchez-Azofeifa, Harriss, and Skole 2001).

Figure 16. SRTM elevation over the country of Costa Rica. A has protected areas overlaid and B has provinces overlaid.



5.2.2 Forest coverage

This project will use a combination of remote sensing, GIS layers, and ground-derived products to examine how the forest in Costa Rica has changed between 2000 and 2016, particularly in terms of protected versus non-protected areas. For forest coverage, we used the Global Forest Change dataset, which uses Landsat-based imagery at 30 m spatial resolution annually for the years 2000-2016 (Hansen, Stehman, and Potapov 2010, Hansen et al. 2013). Each year uses a combination of Landsat scenes from that year to limit the cloud coverage, and then is processed to determine annual loss of forest (i.e. a conversion of the pixel from forest to non-forest classification), and pixels that “gained” forest over the entire 16 year period. We also calculated the Normalized Difference Vegetation Index (NDVI) derived from Landsat from the initial state image (2000) and for the final state image (2016) and performed a change detection. NDVI is an index that uses a ratio between the red and near infrared reflectance from the Earth’s surface along a standardized -1 to 1 scale to determine how “green” the surface is. The closer to 1, the greener the reflectance from the surface. This can be used to look at forest versus non-forest area, although greening up in cities, from the building of a park or golf course, can also increase the NDVI in an area.

5.2.3 Shapefiles: Administrative borders and protected areas

Vector data for country, province, and district borders of Costa Rica were downloaded from the DIVA-GIS repository. Vector datasets on protected areas within Costa Rica were obtained from the World Database on protected areas through the International Union for the Conservation of Nature (IUCN) *Protected Planet* online interface, which is the most comprehensive global database on terrestrial and marine protected areas (IUCN 2017).

According to *Protected Planet,* Costa Rica contains 187 different areas under protection, with 27.6% coverage of terrestrial areas, and just 0.83% of marine area protected. After eliminating some of the marine-only areas, we used the remaining 177 mostly terrestrial PAs to do our analysis. We assessed much of the protected area data based on their IUCN category, since the 177 protected areas are varied in type, size, and function. IUCN designates protected areas on a scale from I to VI, and then some of the protected areas are not classified nor reported. Category Ia is the most protected as a "Strict Nature Reserve" with decreasing amounts of protection as the category number increases (II, for example, are "National Parks", while those classified as VI are "Protected Areas with sustainable use of natural resources" (IUCN 2017).

5.2.4 Topography and Climate

A digital elevation model (DEM) was derived from radar data collected in 2000 by NASA's Shuttle Radar Topography Mission, at 30 m x 30 m resolution. From this DEM, topographical patterns were assessed across the country.

For climate data in current and future scenarios, WorldClim BioClim version 1.4 variables were used. WorldClim is a set of global climate layers (gridded climate data) with a spatial resolution of about 1 km^2 (Hijmans et al. 2004). Monthly averages were downloaded, and then mean annual temperature and total annual precipitation were calculated.

5.2.5 Population

Population data was collected from the LandScan project of the Oak Ridge National Laboratory. Landscan has globally gridded datasets on population 1 km^2 since 1998. Using the 2000 and 2016 datasets, we looked at patterns of population and change. A raster layer was created from the difference between the two endpoints of our time series. Generally, LandScan does not recommend using their data for change over time, but we think it can draw some interesting comparisons between near-current values of population in Costa Rica that matches up with the latest accessible forest cover datasets. These layers were assessed at the province and protected area level, both in terms of the total population count, and the densest population pixel in the region in question.

5.2.6 Fires

Fire data was collected through the Fire Information for Resource Management System (FIRMS), and utilized two different fire products. For recently-sensed fires, 2012-2016, the Visible Infrared Imaging Radiometer Suite (VIIRS) 375 m active fire product (Schroeder et al. 2014). The VIIRS sensor is aboard the joint NASA/NOAA Suomi National Polar-orbiting Partnership (Suomi-NPP) satellite. MODIS FIRMS fire data was also utilized to get an idea of the overall time period 2000-2016, although at a larger, 1 km scale (Giglio et al. 2003, Giglio, Csiszar, and Justice 2006). We assessed the MODIS fire data for the longer time scale, but the higher resolution VIIRS data is better at detecting smaller-scale fire and allows for improved detection of burn area perimeters. Because of this, the VIIRS data is useful for real-time management. We downloaded fire data for the years 2000-2016 to match our years of forest coverage.

5.2.7 Data analysis

All remote sensing layers have been processed, analyzed, and assessed in a combination of ENVI and ArcMap software. The layers were clipped to the extent of the country of Costa Rica, then processed. The data is then extracted and analyzed further in Excel, R, and Kaleidagraph (R Core Team). By comparing non-protected areas to areas under protection, we can examine the changing landscape heterogeneity, frequency of fires, and successional stages of forest diversity, health, and extent, and how this is related to the nearby human population. For data that we had multiple time slices for, like NDVI and population, we utilized paired t-tests to see if there was significant change over the regions of interest. For other data, like elevation and area that were constant over the time period, we ran regressions and calculated Pearson's correlations with other variables like population, fire frequency, and forest area lost to test the strength of relationships. In doing so, we aimed to recognize patterns unique to the Protected Areas and also derive patterns of occurrence across the country.

5.3 Results

5.3.1 Topography and Climate

Across the country of Costa Rica, topography is fairly variable, with a major mountain chain crossing the middle of the country. Many of the protected areas are along the perimeter of the country, in the lowlands, but notably much of the highlands are covered by some sort of protection (Figure 16, Figure 28A).

According to downloaded WorldClim data annual mean temperature across the country ranges from 4 to 27° C, while total annual precipitation ranges from 0 to 272 cm (Hijmans et al. 2004). Due to the ranges of topographical and climatic variables, there are highly varied landscapes that cover many different life zones and biomes. In general, precipitation is highest on the western side of the country, facing the Caribbean Sea, while the eastern side of the country tends to be drier.

5.3.2 Forest Coverage and Loss

Regional Forest Coverage and Forest Loss

The forest coverage percentage for each protected area was calculated from the Hansen dataset (Figure 17). We looked at various forest variables at the country, province, and district levels, as well as solely within the PAs. For the overall country, there was an average of 66% forest coverage, with ~2459.2 km^2 of forest loss over the 2000-2016 time period, and 452.7 km^2 of forest gain (Table 8, Table 9). This is a rough overestimation since the pixels in actuality are smaller than 30 m resolution. The number of pixels that changed are reported in Table 8. The county was then assessed at the province level and within protected areas.

At the province level, the province with the highest forest coverage was determined to be Limón on the Eastern side of the country at ~82%, while Guanacaste on the western coast had the least forest coverage at ~46% (Table 8). At the provincial level, we were able to compare with a similar dataset from Sanchez-Afofeifa *et al*., 2001, which shows that our forest coverage percentages was determined to be much higher, since all of the points fall under the 1:1 line (Supplementary Figure S2, (Sanchez-Azofeifa, Harriss, and Skole 2001).

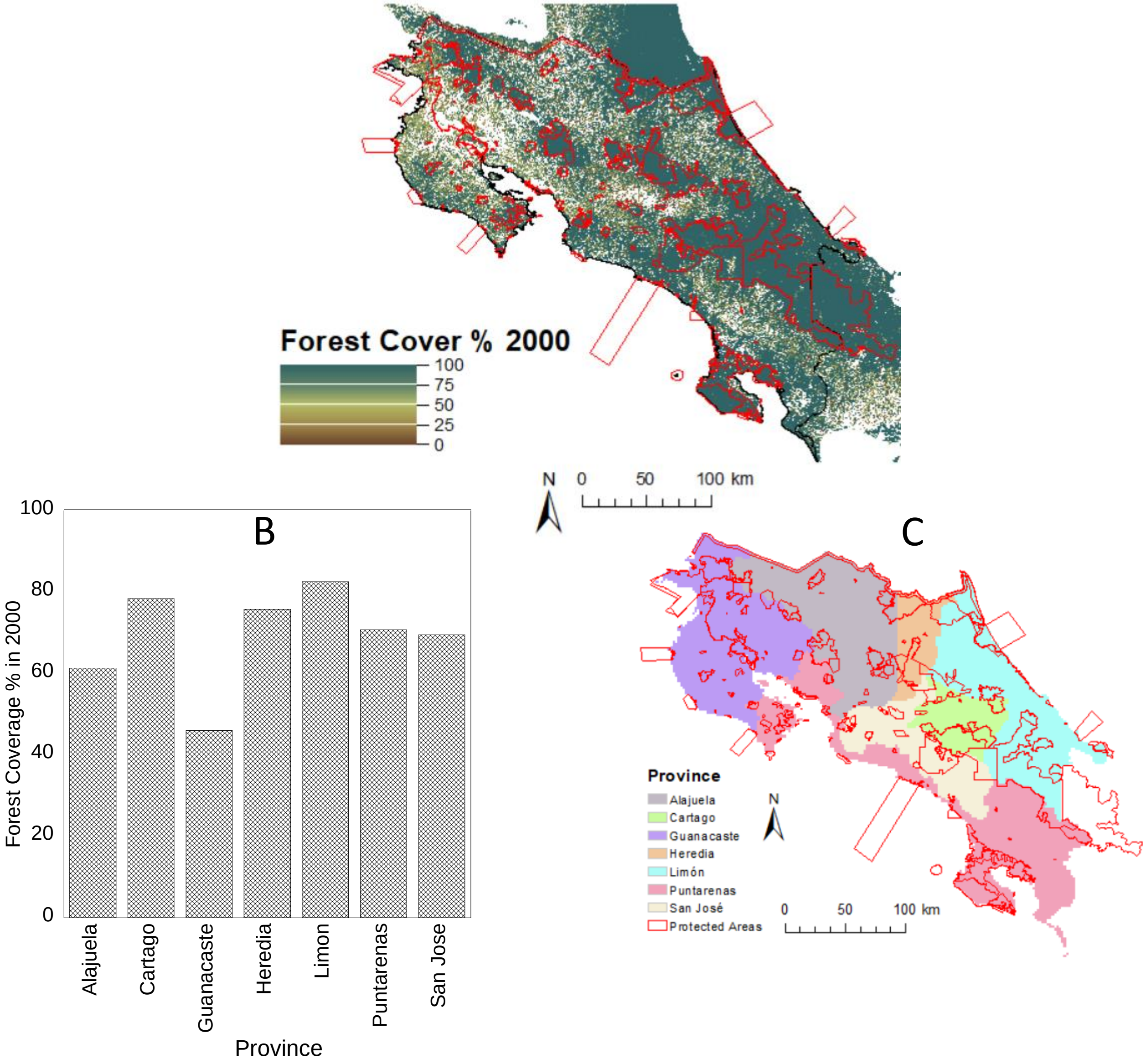
Table 8. Costa Rica Province forest data: topography, NDVI in 2000 and 2016, 2000 Forest cover percentage, and forest gain and loss over 2000-2016 in km^2 and in percentage of total province. land-area. To see the breakdown at the PA level, please see Appendix 1.

Province	Elev Max (m)	Elev Mean (m)	NDVI 2000	NDVI 2016	Forest Cover 2000 (%)	Forest Gain Pixels	Forest Loss Pixels	Forest Gain %	Forest Loss %	Pop-ulation 2000	Pop-ulation 2016
Alajuela	2706	422	0.69	0.68	61.3	94696	672899	0.74	5.26	654855	982195
Cartago	3656	674	0.76	0.74	78.4	7978	70345	0.2	1.78	424749	508586
Guanacaste	2011	272	0.61	0.63	46	73177	443933	0.56	3.41	297652	367518
Heredia	2903	634	0.71	0.74	75.8	13732	137754	0.41	4.1	261409	480280
Limón	3749	794	0.76	0.77	82.6	56938	420198	0.49	3.59	239974	434997
Puntarenas	3283	577	0.7	0.7	70.8	243551	738608	1.7	5.14	385334	445137
San José	3803	734	0.7	0.69	69.5	12941	248701	0.2	3.91	1401462	1625575
Country	3803	561	0.695	0.699	66.8	503013	2732438	0.7672	4.1677	3665435	4844288

Table 9. Entire country of Costa Rica versus just Protected Areas: NDVI in 2000 and 2016, 2000 Forest cover percentage and standard deviation.

	NDVI 2000 Mean	NDVI 2016 Mean	NDVI 2000 SD	NDVI 2016 SD	2000 Forest coverage %	2000 Forest coverage SD
Costa Rica	0.695	0.699	0.159	0.183	66.752	38.187
PAs	0.573	0.595	0.355	0.370	69.212	23.620

Figure 17. Forest Cover percentage in 2000, with darker green being more forested and browns less forest cover. Figure B shows the percentage coverage by province. Figure C shows the layout of the provinces.



In terms of forest gain and loss at the province-level, we looked at percentage of gain and loss in terms of the total province-area so as to standardize the data (Figure 18A and B, Table 8). These numbers were calculated comparing the lost forest pixels for each year 2000-2016 and comparing it to the pixels with no change or gain. In terms of forest gain, Puntarenas had the largest percentage of gain, 1.7%, with Cartago and San Jose tied for the least at 0.2% gain. For percentage lost, Alajuela had the most forest loss (5.26%) closely followed by Puntarenas (5.14%) during this time period, while Cartago had the least (1.78%) (Table 8). Figure 19 shows forest loss colored by year of occurrence, with yellow shades occurring in the early 2000s, and more blue colors occurring in recent years. Deforestation has occurred in small patches across the entirety of the country and for possibly different reasons. Subset 19C had more deforestation during the first half of the time range, and subset 19D had more change towards the second half of the time range. Statistically, the occurrence of deforestation did not have a pattern over time. However, most deforestation during this time period within the country occurred during the years of 2008-2009 (Figure 19B).

Figure 18. Province level forest change. A is forest gain as a percentage of the total area of the province. B is forest loss as a percentage of the total area of the province.

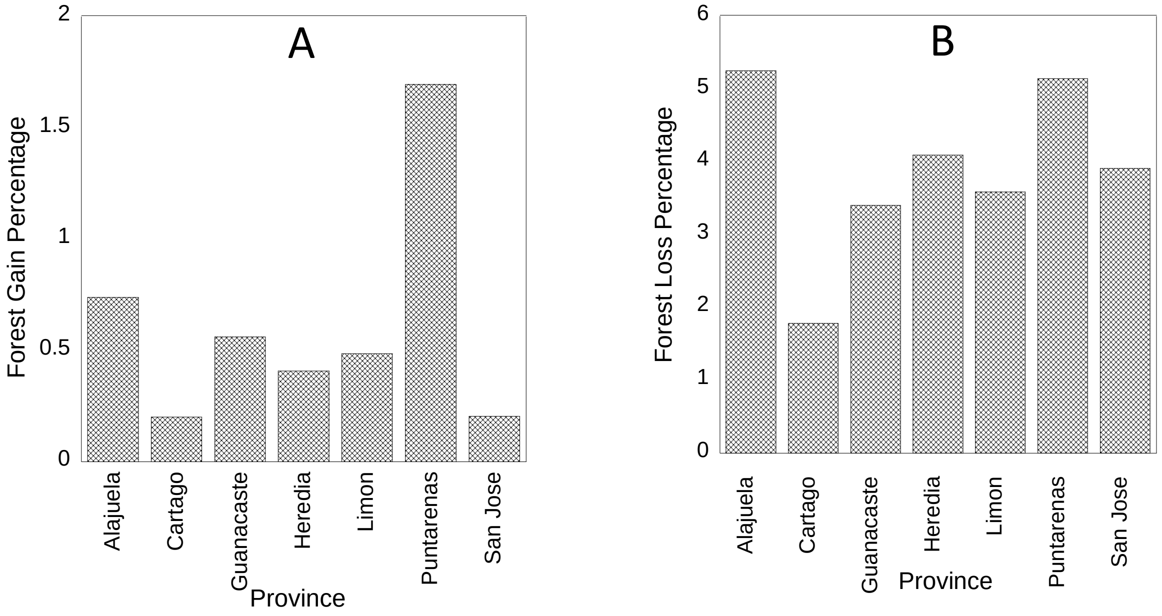
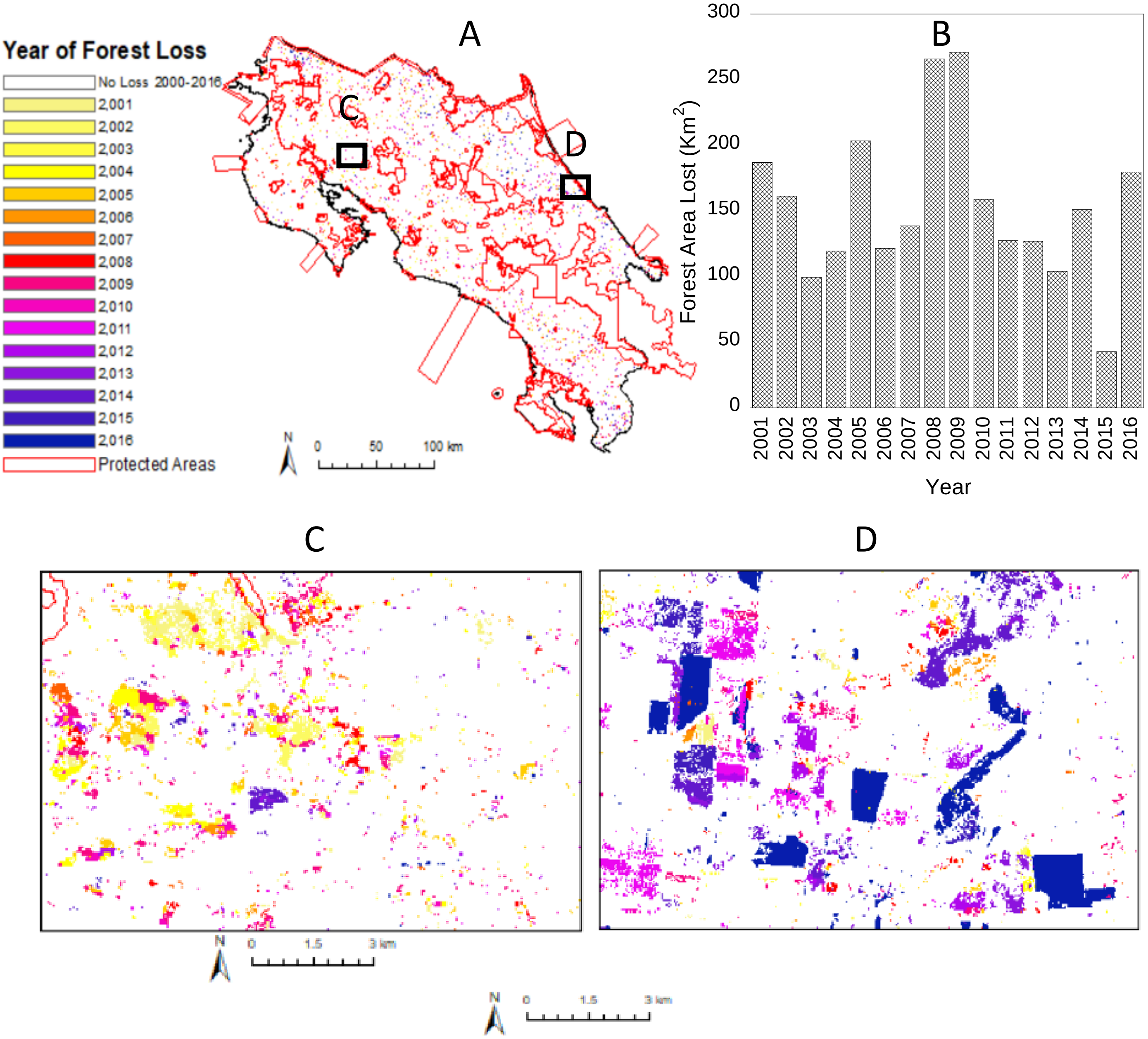


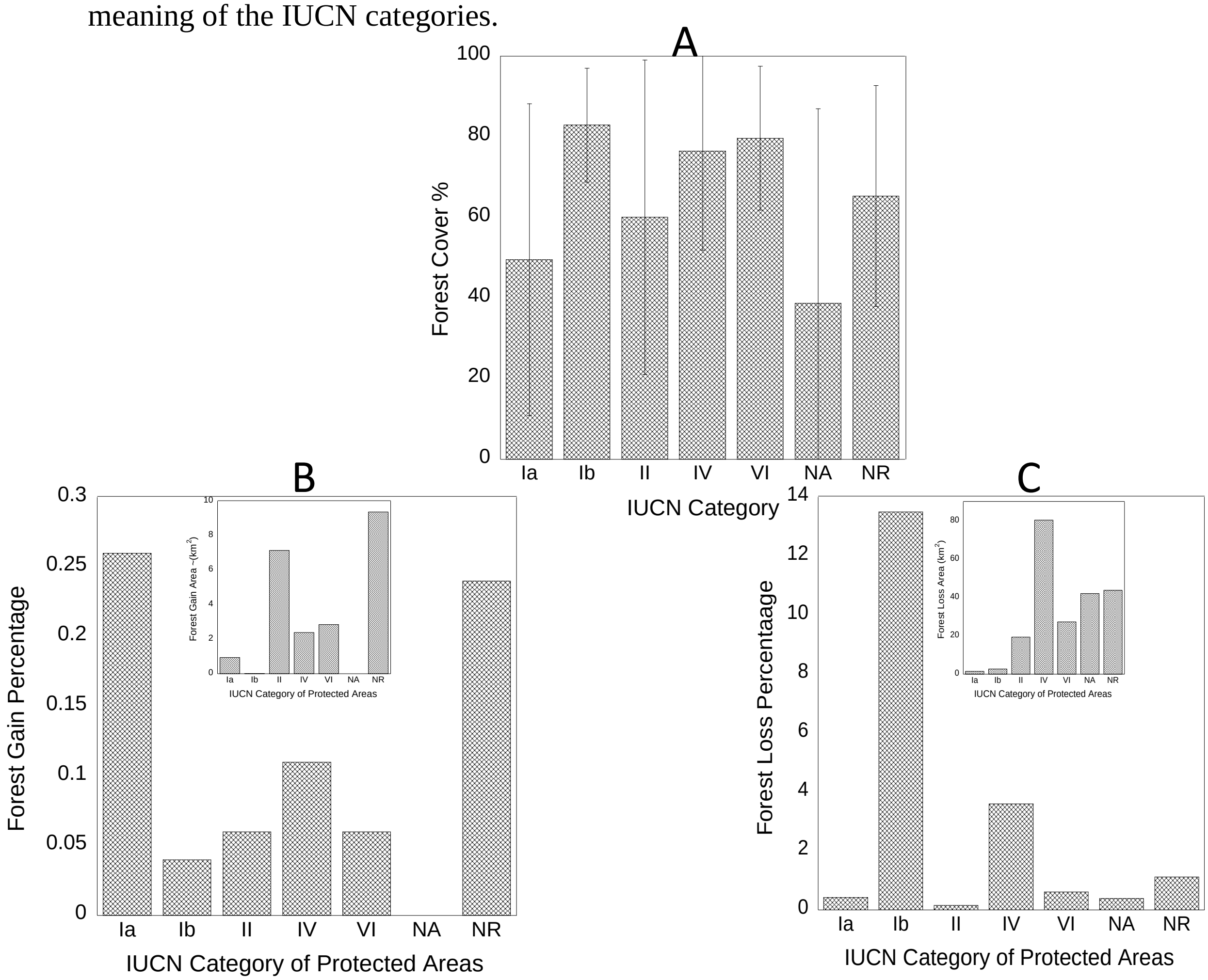
Figure 19. Forest loss from 2000-2016, colored by year. Annual pattern of forest area loss is in B. C and D are subsets of the larger image, with A having more deforestation during the first half of the time range, and B having more change towards the second half of the time range.



Protected Areas- Change in forest cover by IUCN Categories

Forest coverage varies based on IUCN designation (Figure 20A-C). IUCN designated protected areas are on a scale from I to VI, and then some of the protected areas are not classified nor reported.

Figure 20. Protected areas analyzed by IUCN categories (NA is Not Applicable and NR is Not Reported). A is Forest cover percent- error bars are one standard deviation. B is percentage of forest gain in relation to the total area of that category, and C is a similarly calculated percentage for forest loss. For B and C, the main bar graph is the percentage, while the insets are for the area of gain or loss in km^2. Please note the difference in Y-axis range for B and C, there was much more forest loss than gain across the protected areas over this 16-year period. See Table 10 for the meaning of the IUCN categories.



Category Ia is the most protected as a “Strict Nature Reserve” with decreasing amounts of protection as the category number increases (II, for example, are “National Parks”, while those classified as VI are “Protected Area with sustainable use of natural resources”).

Across the types of IUCN Categories, we have decently high numbers of forest coverage percentage, as they are afforded some type of protection (Figure 20A). Categories Ib (Wilderness Areas) and IV (Protected area with sustainable use of natural resources) had the highest percentage of forest cover in 2000, with 82.9% and 79.7% respectively (Table 10, Figure 20A). However, when we look at the total area of forest change since then, we see that IUCN category of IV (Habitat/ Species management Area) had the most forest lost at ~80.5 km^2, and category Ia has the least in total area lost at just 1.5 km^2 (Table 10, Figure 20B & C). For Figure 20B and 20C, the main bar graph is the percentage, while the insets are for the area of gain or loss in km^2.

In terms of percentage forest loss of the total area across all PAs with their particular designations, Ib (Wilderness Area) had the highest percentage loss at 13.5% of the total area of the Ib areas. In terms of total forest gain, IUCN category II (National Parks) gained ~7 km^2 of forest, and NR (non-reported) gained ~9 km^2 of forest. Percentage of total PAs with the designations, category Ia (Strict Nature Reserve) and non-reported had the highest percentage gain, with 0.26% and 0.24%, respectively. In general, across Costa Rica as a whole and within provinces and PAs, there was much more forest loss than gain over this 16 year period. Please note the difference in Y-axis range for Figure 20B and 20C, there was much more forest loss than gain across the protected areas over this 16-year period.

Table 10. Protected areas by IUCN Category: Forest gain, loss, and 2000 coverage percentage.

IUCN Category of PAs	**Description of IUCN Category**	**Gain in Pixels**	**Loss in Pixels**	**Gain Area ~(Km^2)**	**Loss Area ~(Km^2)**	**Gain %**	**Loss %**	**Forest Coverage 2000 %**	**NDVI 2000**	**NDVI 2016**
Ia	Strict Nature Reserve	1042	1676	0.938	1.508	0.26	0.42	49.53	0.528	0.562
Ib	Wilderness Area	9	2979	0.008	2.681	0.04	13.51	82.91	0.748	0.634
II	National Park	7943	21528	7.149	19.375	0.06	0.16	60.05	0.545	0.569
IV	Habitat/ Species management Area	2656	89443	2.39	80.499	0.11	3.6	76.47	0.684	0.711
VI	Protected area with sustainable use of natural resources	3163	30357	2.847	27.321	0.06	0.61	79.67	0.711	0.740
Not Applicable		0	46819	0	42.137	0	0.39	38.68	0.345	0.362
Not Reported		10417	48710	9.375	43.839	0.24	1.12	65.31	0.638	0.656

5.3.3 Normalized Difference Vegetation Index (NDVI)

NDVI has increased over the 16 year period, both at the overall country level and within the areas with a protected designation (Figure 21). For the country of Costa Rica, overall NDVI increased 0.004 from 0.6954 to 0.6994 over the time period. During this time, the NDVI within all of the PAs increased from 0.5729 to 0.5995. However, when looking at the PA's individually and utilizing a paired t-test, we found that on average they significantly decreased by roughly 0.0226, with a t-value of -6.7415 and a p-value < 0.001 (Appendix 1). However, while the mean NDVI has increased, the standard deviation of the NDVI values has also increased at both the country and PA level, meaning that the overall heterogeneity of the area has increased and the land is more variable. (Table 9). When the PAs were categorized by their IUCN categories, we generally found a decrease of -0.00499, but it was insignificant, with a t-value of -0.25034, and a p-value = 0.8107, using a paired t-test.

NDVI change over the provinces over the 16-year period revealed differences in greenness over time (Figure 22). The provinces that increased in greenness values were Heredia, Guanacaste, Limón, and Puntarenas. The provinces that decreased in greenness values were Alajuela, San Jose, and Cartago. From a paired t-test, it was determined the provinces decreased insignificantly by -0.0029, with a t-value of -0.42 and a p-value = 0.69.

However, when we compare the NDVI results to the percentage of forest cover lost or gained at the province-level, they tell different stories. The province with the most percentage lost is clearly Alajuela and Puntarenas, which also had the smallest change in NDVI, negative and positive, respectively (Figure 18 & Figure 22). Puntarenas, however, displayed the highest percentage of forest gain. Figure 21D shows a zoomed-in subset of Braulio Carrillo National park, which based on the dominance of red, generally increased in NDVI over the time period, although there are a few patches of blue, indicating a decrease in greenness in those pixels.

Figure 21. Normalized Difference Vegetation Index (NDVI) over the country. A was from 2000 data, B was calculated from 2016 data. C and D are the NDVI change over the period, a positive number or red color indicates an increase in greenness in that pixel, while a negative number of blue color indicates loss of greenness. D is a subset of C, focusing in on Braulio Carrillo National Park.

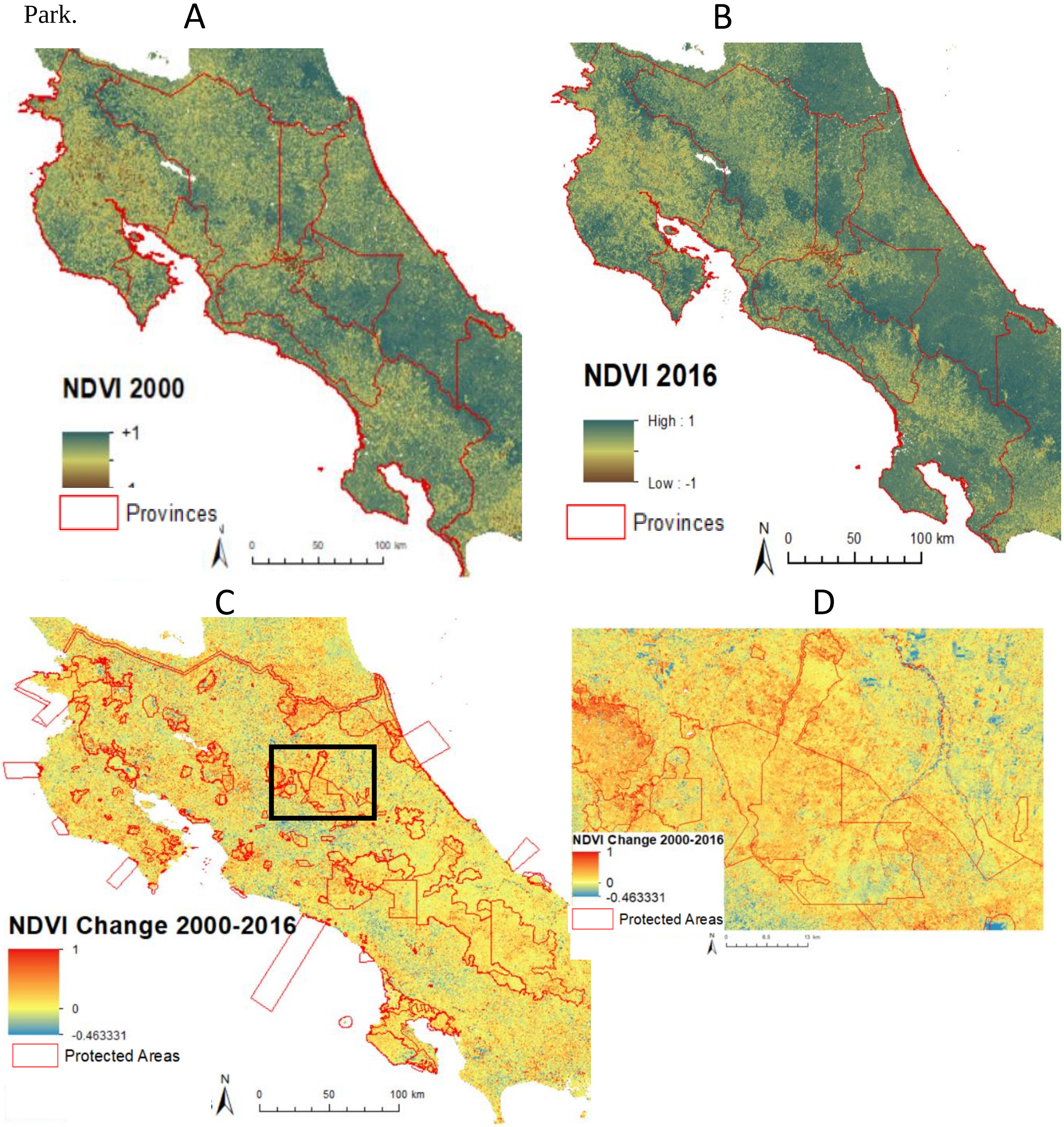
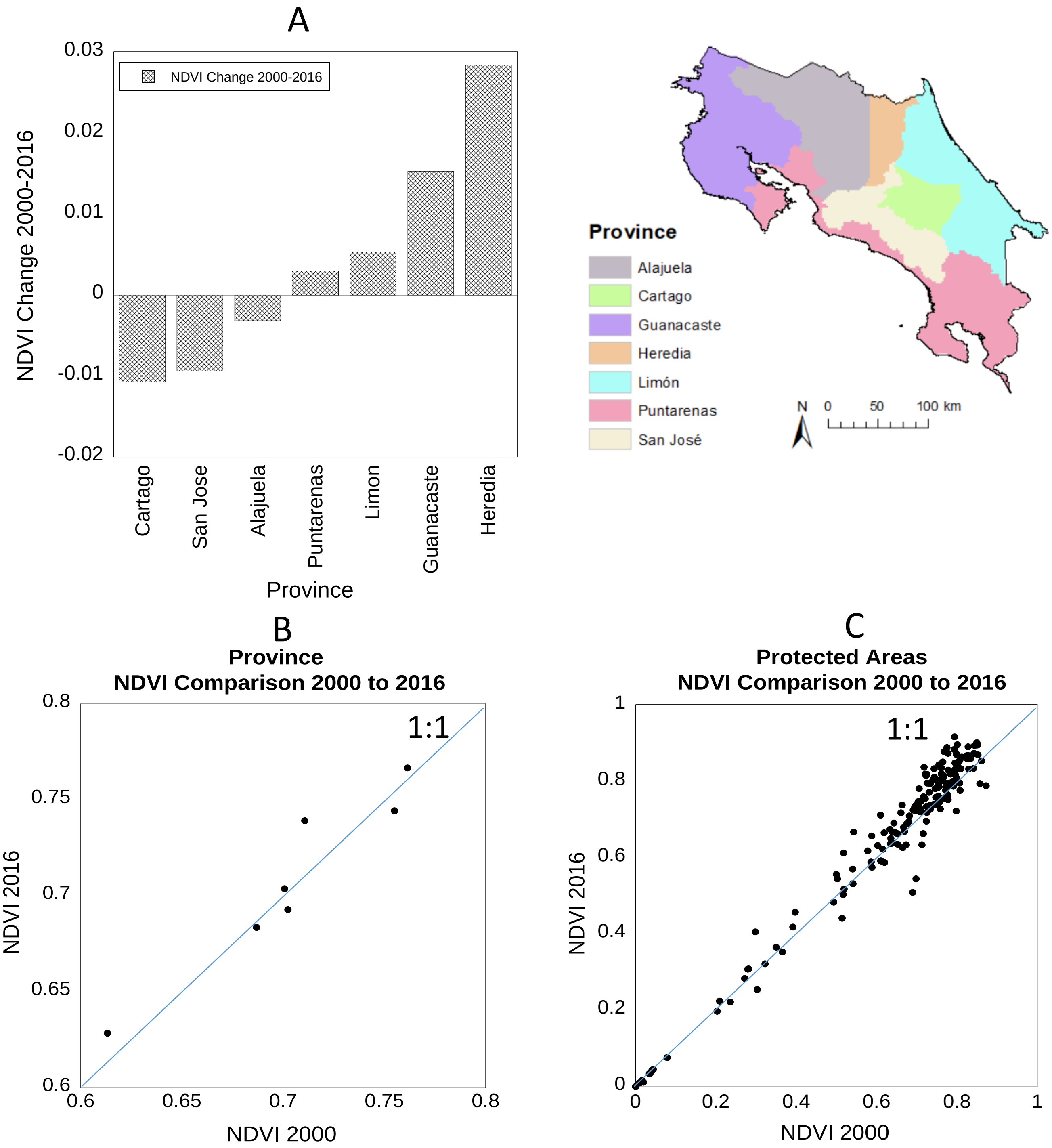


Figure 22. Normalized Difference Vegetation Index (NDVI) over the country. A has the provinces sorted by how much change in NDVI occurred. B and C compare the NDVI from 2000 to 2016, with B occurring at the province level and C at the protected area level.



5.3.4 Population

Population is highest in the central part of the country, mainly surrounding the capitol of San Jose (Figure 23). Several other clumps of higher population density occur near other major cities including Liberia, Punta Arenas, and San Isidro. In general, the protected areas tend to have low population density. Higher numbers of population were found at the higher elevations, but the provinces have large differences between the mean and maximum elevations, so there is a wide range of topography (Table 8). The provinces of San Jose and Alajuela had the highest amounts of people living within them, and Guanacaste province had the least.

Figure 27 depicts the province level relationships between 2016 population and elevation. Both plot the province using the maximum elevation within the province versus either the mean population pixel ($r^2 = 0.362$) or the total population ($r^2 = 0.3237$). In general, there are higher levels of population at higher elevations, contrary to assumptions. Looking at protected areas, very few people live in IUCN categories Ia and Ib, which are afforded the most protection under their IUCN designations, while the highest number of people living in protected areas in 2016 resided in category VI or II (Figure 23C).

Using a raster layer created from the difference between the 2016 and 2000 population, we looked at the change in population over the country. Across the whole country, population increased by 1,182,389 between 2000-2016 (Table 8). However, this was distributed unevenly across the provinces (Figure 24A, Appendix 1). The provinces that had the most increase in humans were Alajuela and San Jose, while Puntarenas, Guanacaste, and Cartago increased the least.

Figure 23. 2016 population from LandScan data. The darker the orange, the higher the population per pixel. B categorizes the population numbers by province, while C analyzes the protected areas in terms of their IUCN category.

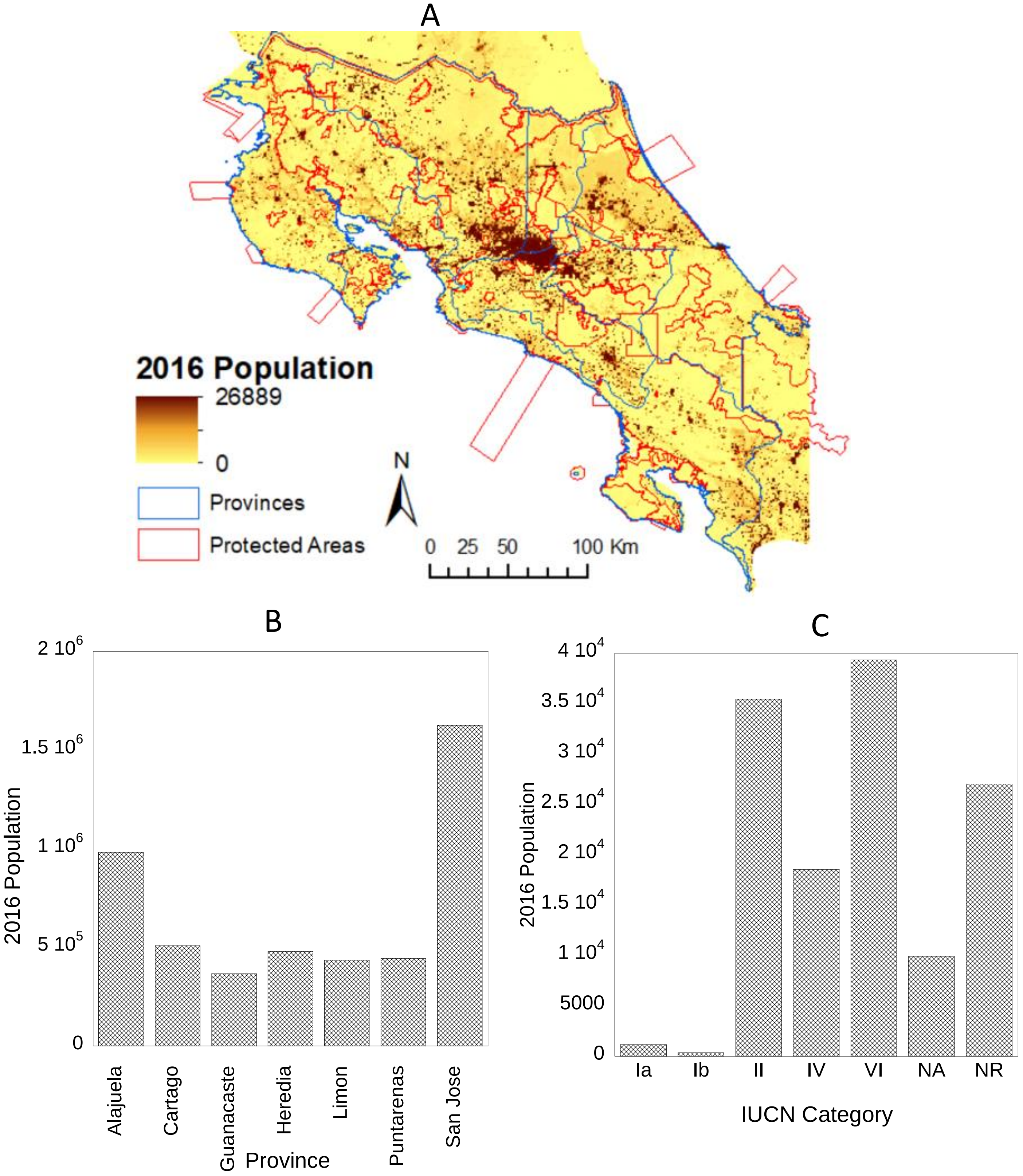
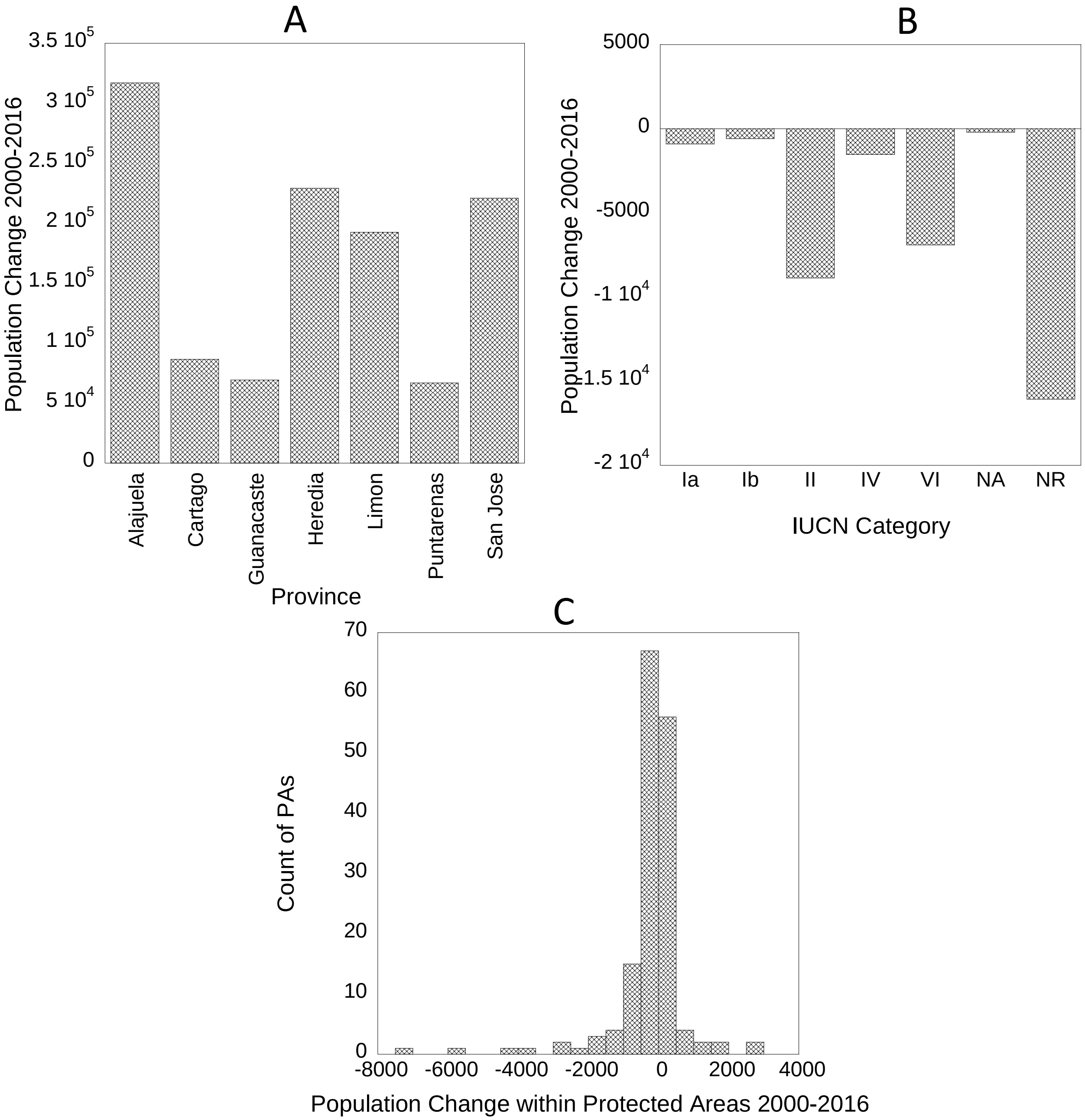


Figure 24. Population change 2000-2016. A looks across provinces, B looks across IUCN Category of the Protected Areas, and C looks at the distribution of the PAs.



Protected areas, however, behaved very differently during the years 2000-2016 (Figure 24B and 24C). In general, the PA's seem to have mostly decreased in population, although some have increased, so the distribution in Figure 24C is centered around zero change. Using a paired t-test, we found no significant change across all of the PAs (t-value 1.47, p-value = 0.144). When the

PAs are categorized into their respective IUCN categories, on average the PAs all lost many humans during this time period, particularly from IUCN category II, VI, and NR. However, while these categories seemed to have lost people over this time period, they were still the most populated IUCN categories in 2016 (Figure 23C).

5.3.5 Fires

VIIRS fire data for the period of 2012 -2016 was used for this analysis, as well as MODIS data for the full time period. It is apparent that fires are a common occurrence in Costa Rica. In Figure 25, you can see the spatial distribution of fire over the last 16 years tends to be in the lowlands and on the western, drier, side of the country, specifically in Guanacaste and Puntarenas. The eastern side of the country, bounded by the Caribbean Sea, and tends to be wetter than the leeward side of the central mountain range of the country, as well has a higher precipitation seasonality using Worldclim data. Throughout the country, there were 6,404 fires detected over the 2000-2016 year period (Table 11). In protected areas only, there were 1,175, only 18.3% of the total fires in the country during this period. At the provincial scale, Guanacaste and Puntarenas had the highest amount of fires. There was no discernible relationship between human population and the amount of fire, neither at the province level or within the protected areas (Table 11, Appendix 1). The fires predominately were focused in lowland coastal areas and rarely at high elevations. There was not a noticeable pattern of increasing or decreasing fires during this time period, but we found the years of 2009 and 2013 to have the highest fire counts across the country (Figure 26A). There was a negative correlation of -0.251 between fires detected within that year and forest area lost (Figure 26C).

The PAs with the highest fire counts during the study period were Coco's Island, the Corredor fronterizo (estatal) [Border Corridor] and multiple designations within Palos Verdes [National Park, and a non-reported RAMSAR site of International Importance].

Figure 25. Fires from A) MODIS FIRMS (2000-2016) and B) VIIRS database from (2012-2016), colored by year or categorized by a range of years. Color underlay is topography derived from SRTM displayed in Figure 16. Graphs of the number of fires from MODIS at the province level is in C and IUCN Category of protected areas in D.

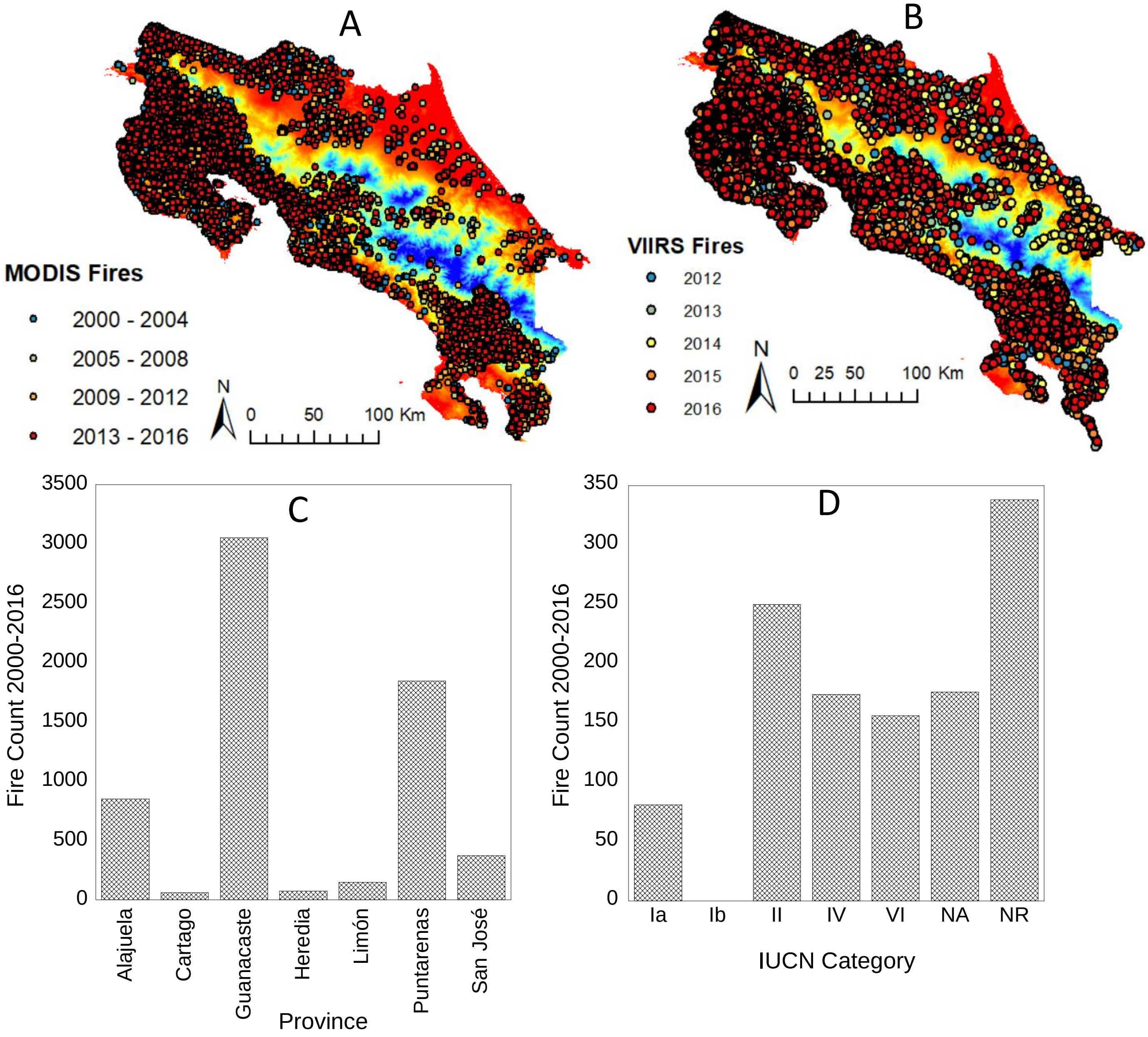


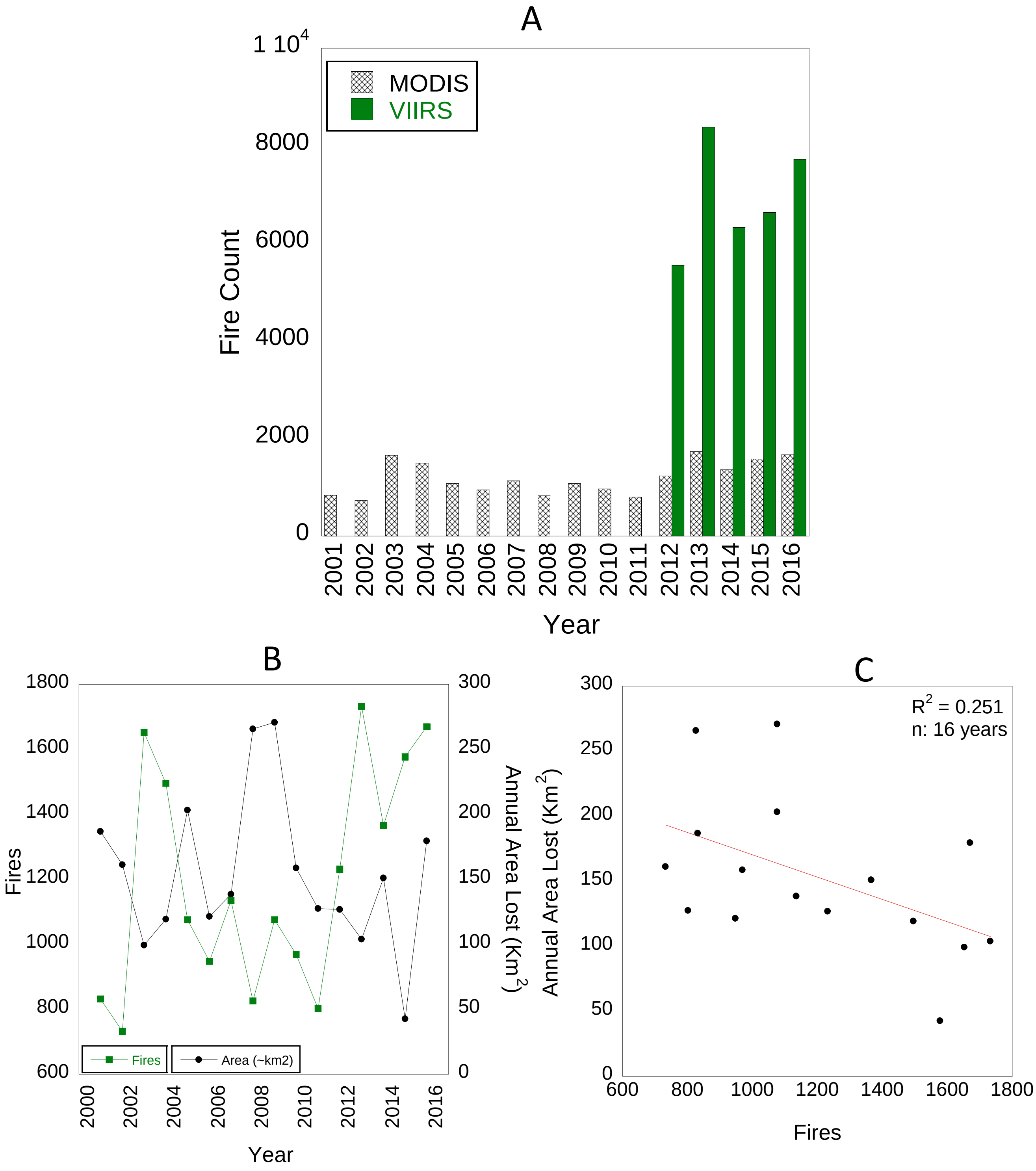
Table 11. Fire count by country, protected areas all together, and provinces. To see the breakdown at the PA level, please see Appendix 1.

	Sampling Level	**Total Fires 2012-2016**
Country	Costa Rica as a whole	6404
Protected Areas	Total in Protected Areas	1175
Province	Alajuela	852
Province	Cartago	62
Province	Guanacaste	3052
Province	Heredia	74
Province	Limón	148
Province	Puntarenas	1844
Province	San José	372

Table 12. Country level annual forest change and fire count since 2001 from MODIS. Utilized in Figure 26.

Year	**Pixels**	**Area (~km2)**	**Fires**
2001	207605	186.8445	832
2002	179274	161.3466	733
2003	110532	99.4788	1653
2004	132688	119.4192	1496
2005	225919	203.3271	1076
2006	134980	121.482	948
2007	153947	138.5523	1135
2008	295430	265.887	826
2009	301030	270.927	1076
2010	176371	158.7339	969
2011	141687	127.5183	802
2012	141135	127.0215	1232
2013	115615	104.0535	1733
2014	167793	151.0137	1366
2015	47520	42.768	1578
2016	199640	179.676	1670

Figure 26. Annual Pattern of Fires. A compares MODIS fire counts (2000-2016) to VIIRS fire counts (2012-2016). B compares Annual MODIS-sensed fire to area lost annually across the whole country. C shows the direct negative relationship between fire frequency and area lost annually within the country, with an *r* ^{2} of 0.251.



5.4 Discussion

5.4.1 Forest cover change in Costa Rica, Provinces, and Protected Areas

Deforestation has been occurring over the entirety of the country of Costa Rica since 2000. Deforestation has occurred in small patches across the entirety of the country and for possibly different reasons. Subset 19a had more deforestation during the first half of the time range, and subset 19b had more change towards the second half of the time range. If we examine the shapes of the forest loss, Figure 19C has more irregular shapes, while 19D has more regular rectangular shapes, likely cleared for agriculture or rangeland for cattle. The differing reasons for deforestation outside of protected areas makes conservation difficult to achieve. However, utilizing these GIS and remote sensing technologies makes assessments and monitoring of impact more repeatable over time.

At the province level, the province with the highest forest coverage was determined to be Limón on the Eastern side of the country at ~82%, while Guanacaste on the western coast had the least forest coverage at ~46% (Table 8). At the provincial level, we were able to compare with a similar dataset from Sanchez-Afofeifa *et al*., 2001, which shows that our forest coverage percentages was determined to be much higher, since all of the points fall under the 1:1 line (Supplementary Figure S2) (Sanchez-Azofeifa, Harriss, and Skole 2001). It is possible that since that paper was published in 2001, utilizing data from 1986-1991, the provinces all increased their percent of forest cover by 2000, when the Hansen coverage was calculated (Hansen et al. 2013).

Within protected areas, Categories Ib (Wilderness Areas) and IV (Protected area with sustainable use of natural resources) had the highest percentage of forest cover in 2000, with ~82.9% and ~79.7% respectively (Table 10, Figure 20A). However, when we look at the forest change since then, we see that Ib actually has a high percentage of forest loss and the smallest amount of gain (Figure 20B and C). But if we look at the total area lost from the subset of figure 20C, we see that it is actually a very small area in comparison to the rest of the categories. Conversely, category Ia has a small amount of actual area gained but it is actually a large percentage of the area of Ia PAs (Figure 20B). Across Costa Rica as a whole and within provinces and PAs, there was much more forest loss than gain over this 16 year period.

In a study that looked at protected areas in the Amazon, Congo, South American Atlantic Coast, and West Africa (noticeably excluding central America that includes Costa Rica), it was found that there are differences across these regions. In the Amazon and the Congo, the protected areas tended to have similar low deforestation rates around their borders, meaning that just location of the protected areas may limit human exploitation as they may be located on steep slopes or have poor soil (Joppa, Loarie, and Pimm 2008). However, they also found in West Africa and the Atlantic Coast in Brazil showed sharp boundaries in forest cover around the reserves, meaning some protected areas were actively exploited immediately outside of the zone of protection (Joppa, Loarie, and Pimm 2008). In a study based specifically in Costa Rica, they looked at the protection afforded by PAs from 1960-1997, and determined that the presence of PAs reduced deforestation and that ~10% of the forests within the PAs during this era would have been deforested if they were not protected (Andam et al. 2008, Pfaff et al. 2009). They also found that the spillover protection in boundaries nearby PAs was neglible.

In the decades since the time period covered by the Andam et al. study (2008), I think we found a combination of factors affecting the protected areas in Costa Rica. In general, there was definitely more deforestation outside of the protected areas during this time, and within the PAs, particularly along the central corridor, tended to have very high percentage of forest cover. However, this central area follows along a ridge across the country, which makes the area more inaccessible for human residence. While the count of protected areas is skewed towards the lowlands having more actual designated areas, the PAs in the highlands are much larger (Figure 27A and 27B). Figure 27A shows the distribution of the number of PAs at various elevations, and Figure 27B shows the size of the smallest PA within categories based on elevation class of the maximum elevation within the PA. Clearly, the high elevation sites above 3000 m only have large PAs. Previous studies predicted that deforestation will continue to occur, and while protected areas may be spared, surviving forests outside of protected areas will increasingly be concentrated in steep, remote, infertile, or hyper-wet areas not as ideal for human usage (Laurance, Sayer, and Cassman 2014, Sanchez-Azofeifa, Harriss, and Skole 2001). This appears to be the case in Costa Rica.

5.4.2 Changes in NDVI in Costa Rica and Protected Areas

NDVI increased over the 16 year period, both at the overall country level and within the areas with a protected designation when combined (Figure 21). For the country of Costa Rica, overall NDVI increased 0.004 from 0.6954 to 0.6994 over the time period. During this time the NDVI within all of the PAs increased from 0.5729 to 0.5995. However, when looking at the PA’s individually and utilizing a paired t-test, we see that on average they significantly decreased by roughly -0.0226. When the PAs were categorized by their IUCN categories, we generally found a decrease of -0.00499, but it was insignificant. These two results mean that the protected areas generally significantly decreased in their greenness values, but it was not specifically due to their IUCN designation. However, while the mean NDVI has increased, the standard deviation of the NDVI values has also increased at both the country and PA level, meaning that the overall heterogeneity of the area has increased and the land is more variable.

(Table 9). This could be due to forest degradation or loss of quality forest stands, possibly because of selective logging or other human impact. In addition, increases in NDVI greenness values are not always indicative of afforestation. In Figure 21, some brown areas in the 2000 NDVI colored classification changes to greener, higher NDVI value by 2016, but this likely was a conversion to agriculture. It has been suggested that while tropical nations develop economically and become increasingly urbanized, they might experience land-use transitions that allow for a partial recovery of their forest cover. However, where this forest recovery occurs, it is often based on monoculture plantations or other agriculture or secondary forest, which may have different implications on ecosystem services and fauna in the area (Lambin and Meyfroidt 2010, Laurance, Sayer, and Cassman 2014, Rudel 2005).

NDVI change over the provinces over the 16 year period revealed differences in greenness over time (Figure 21 & Figure 22), but insignificantly based on the t-test statistics. The provinces that increased in greenness values were Heredia, Guanacaste, Limón, and Puntarenas. The provinces that decreased in greenness values were Alajuela, San Jose, and Cartago. These three provinces that had decreases in their NDVI seem to be the landlocked provinces in the central part of the country of Costa Rica, while the ones that increased tended to be on the coast, with the exception of Heredia.

However, when we compare the NDVI results to the percentage of forest cover lost or gained at the province-level, they tell different stories. The province with the most percentage lost is clearly Alajuela and Puntarenas, which also had the smallest change in NDVI, negative and positive, respectively (Figure 18 & Figure 22) Puntarenas, however, displayed the highest percentage of forest gain. Figure 21D shows a zoomed-in subset of Braulio Carrillo National

Park, which based on the dominance of red, generally increased in NDVI over the time period, although these a few patches of blue, indicating a decrease in greenness in those pixels.

In general, NDVI seemed to increase over the time period of 2000-2016, but there were differences between different provinces (Table 9, Figure 21-22). At the province and protected area level, there are regions where there was increased and decreased greenness (Figure 22A-C). However, this makes them fall around the 1:1 line, so in general there is not much of a strong relationship for the provinces (Figure 22B). For protected areas, the trend is slightly above the 1:1 line, indicating a slight increase in NDVI values in a majority of the protected areas during the 2000-2016 period.

5.4.3 Population in Costa Rica and Protected Areas

Population is highest in the central part of the country, mainly surrounding the capitol of San Jose. Several other clumps of higher population density occur near other major cities including Liberia, Punta Arenas, and San Isidro. In general, the protected areas tend to have low population density. Higher numbers of population were found at the higher elevations, but the provinces have large differences between the mean and maximum elevations, so there is a wide range of topography (Table 8).

The provinces of San Jose and Alajuela had the highest amounts of people living within them, and Guanacaste province had the least (Figure 23B). Looking at protected areas, very few people live in IUCN categories Ia and Ib, which are afforded the most protection under their IUCN designations, as “Strict Nature Reserves” and “Wilderness Area” (Figure 23C). Specifically, category Ia regions are set aside to as strict protectors of biodiversity, and human visits and usage are highly managed and controlled. Category Ib contains areas that may have not been altered or only slightly, so as to retain their natural character without permanent nor significant human habitation (IUCN 2017). Some of the Costa Rican category Ia include a few of the tiny islands, like Isla del Caño and Isla Guayabo, while category Ib includes places like the Lapa Rios Reserve. There are only two category Ib protected areas in Costa Rica, so that is another reason why they have lower total population numbers than some of the other protected areas. The highest number of people living in protected areas reside in category VI, "Protected Area with sustainable use of natural resources," which allows for the conservation of habitats, along with associated cultural values and traditional natural resource management systems (IUCN 2017). Some examples of the Costa Rican category VI areas include Cordillera Volcánica Central, which takes up much of the central portion of the country, many river systems, and a portion of Tortuguero, predominately a National Park but also a popular tourist beach and reserve on the Caribbean side of the country (Appendix 1).

During the years 2000-2016, the human population increased by 1,182,389, distributed unevenly across the provinces. San Jose and Alajuela provinces had the most increase in human population, which is unsurprising as San Jose is the capitol city, while nearby Alajuela is home to the main international airport. Puntarenas, Guanacaste, and Cartago provinces had smaller increases in human population over the time period.

Protected areas, however, behaved very differently during the years 2000-2016 (Figure 24B and 24C). In general, the PA's seem to have mostly decreased in population, although some have increased, so the distribution in Figure 24C is centered around zero change. When the PAs are categorized into their respective IUCN categories, on average the PAs all lost many humans during this time period, particularly from IUCN category II, VI, and NR. However, while these categories seemed to have lost people over this time period, they were still the most populated IUCN categories in 2016 (Figure 23C).

One study that looked at human impact on IUCN categories noted that the categories do not correspond directly to some sort of gradient of "naturalness." IUCN categories Ia tended to have a higher "human footprint" than expected, while category VI tend to have low human footprint and also tend to be larger than PAs of other categories (Leroux et al. 2010). In our study, the large Cordillera Volcánica Central, category VI, has a high population of 7238, but the highest population pixel is not near the top when we look at the maximum populated pixel (Appendix 1). It covers a huge portion of land, but generally has low population density. In general, we found that within PAs, the larger the area, the higher the human population within it, with an r^2 of 0.437 (Figure 27D). We also found a pattern with generally higher human populations within PAs at higher elevations, but the relationship was not very strong, $r^2 = 0.158$ (Figure 27C).

5.4.4 Fires in Costa Rica and Protected Areas

It is apparent that fires are a common occurrence in Costa Rica. At the country level, there was not a noticeable pattern of increasing fires during this time period, but we found the years of 2009 and 2013 to have the highest fire counts (Figure 26A). The negative relationship between fires detected within that year and forest area lost, which suggests that fires are not the root cause of the deforestation (Figure 26B and 26C).

The distribution of the fires are mostly on the western side of the country and is reflected in the numbers in Table 11, specifically for the Guanacaste and Puntarenas provinces. While these two provinces had much higher fire occurrence during this period, they are also the two largest provinces, so more fire occurrence may not be so surprising. In addition, they are on the leeward side of the central Costa Rican mountain range and thus contain more dry forest than rainforest like in the western portion of the country. In Figure 25, you can see the spatial distribution of fire over the last 16 years tends to be in the lowlands and on the western, drier, side of the country, specifically in Guanacaste and Puntarenas. The eastern side of the country, bounded by the Caribbean Sea, and tends to be wetter than the leeward side of the central mountain range of the country. Past research has found that Central America seems to experience fires in dry forest at a similar rate to other dry forests globally, at roughly 20% of the area affected (Miles et al. 2006). While fire is a natural occurrence in dry forests like those on the western side of Costa Rica, this global study, they determined that fires can have a widespread and significant impact on dry forest coverage, even at the temporal scale of just a few years. When fire frequency increases, possibly due to anthropogenic reasons, the trees may not be able to regenerate and forest cover can decline over time (Miles et al. 2006). Throughout the country, there were 6,404 fires detected from 2000-2016 (Table 11). In protected areas only, there were 1,175, only 18.3% of the total fires in the country during this period. Past studies have found fewer fires or less frequent fires occur in protected areas in the Amazon (Nepstad et al. 2006). This may also apply to protected areas in Central America, like Costa Rica.

Because of this, it may be assumed that protected areas in Costa Rica are less likely to be inflicted with lots of fires. However, there is also a possibility that there are better fire management practices in effect to rapidly put out fires in these types of areas.

Figure 27. Further Population Analysis. A and B are at the province level, C and D is for Protected Areas. A utilizes the mean pixel value for population over the entirety of the province, with an r^2 of 0.362. B utilizes the total population compared to the maximum elevation of the province, with an r^2 of 0.237. C looks at population within PAs based on the maximum elevation in the PA with an r^2 of 0.158, and D looks at the PA level for population based on area of the PA, with an r^2 of 0.437.

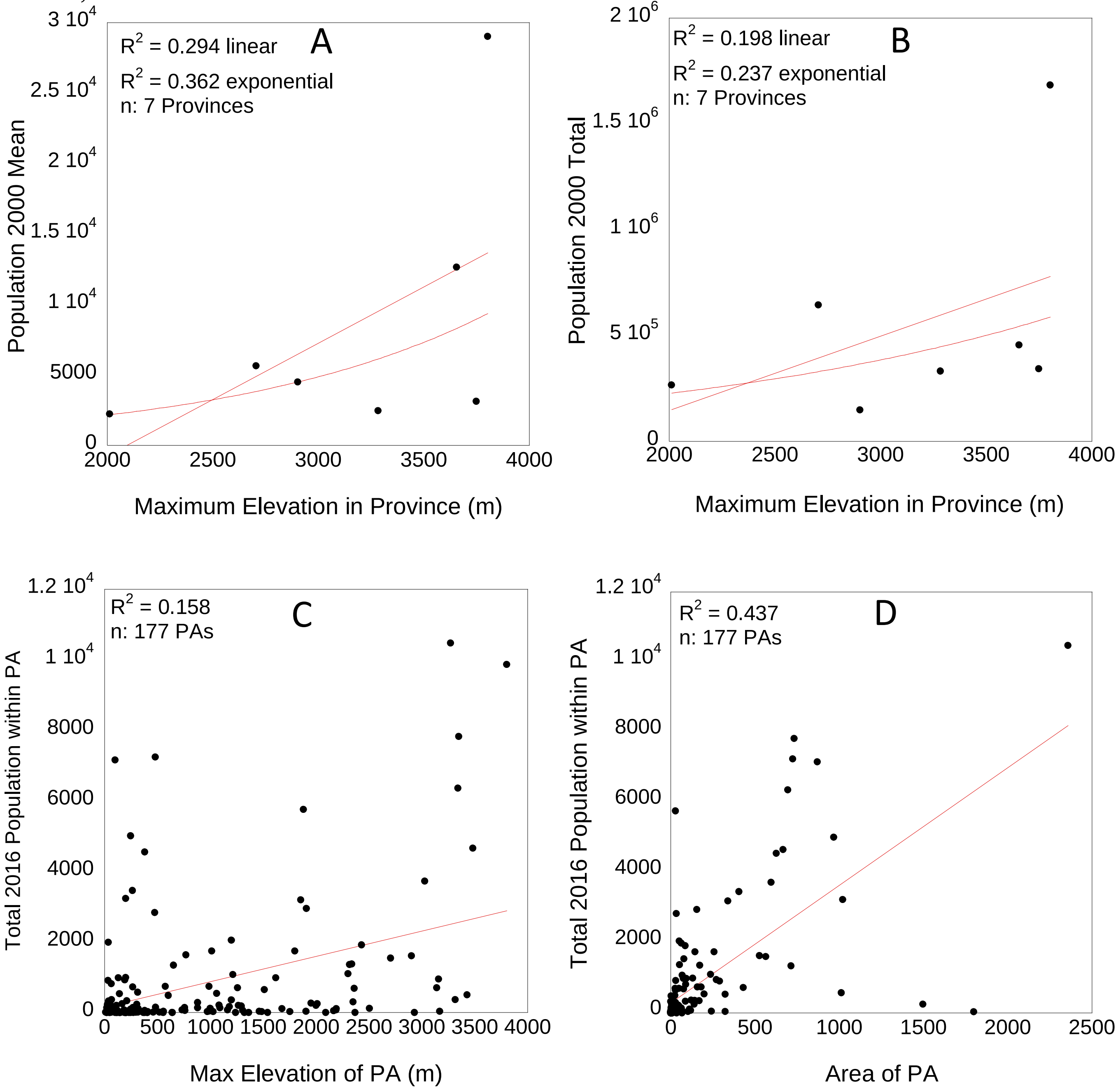
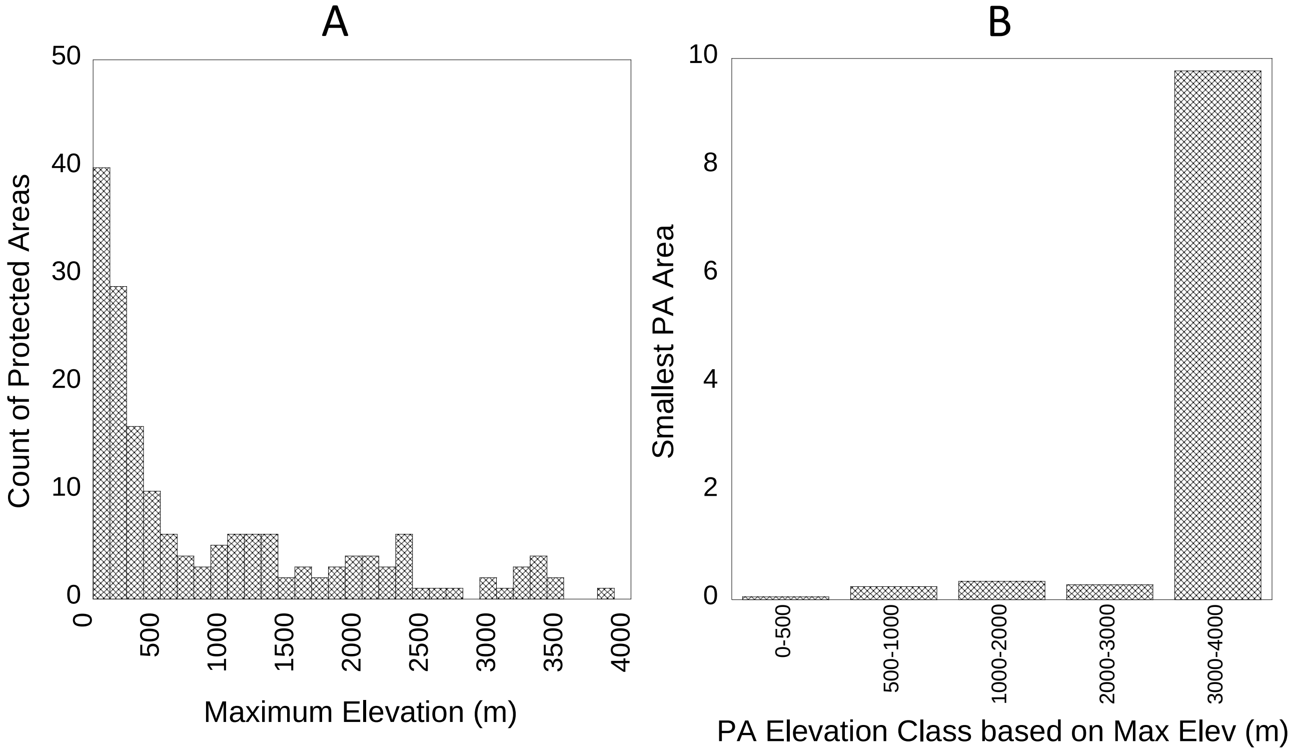


Figure 28. Distribution of protected areas (PAs). A utilizes the max elevation of the PA and looks at the count of PAs across elevation, while B separates the PAs into classes based on their maximum elevation and plots the minimum size of the PA.



5.4.5 Possible sources of error

We used shapefiles of the various protected areas to do much of the analysis, but they can be fairly small so some of the analyses may not readily apply. We tried to account for this by looking at percentage of forest gain and loss instead of just the total amount. Also, the protected areas tend to be placed in area lower than 500 m in elevation (Figure 27). However, if we look at the size of the PAs, PAs located in higher elevation regions tend to be larger in size. In addition, these protected areas span many different types of protection, besides just the IUCN classification categories we used. There also may be inherent errors in the remote sensing imagery that we would not be aware of. For example, the fire data assumes that once a pixel is above a certain temperature threshold there is a fire, but this may not always be the case. Also, the forest dataset we used does a change detection for forest to non-forest conversion for “forest loss” annually, and non-forest to forest pixel change for “gain” over the time period, but it is not corroborated with ground data and may contain errors. However, it is a fantastic global product and can readily show the use of remote sensing technologies to increase efficiency and possibility of these large-scale landscape studies.

5.5 Conclusions

This dissertation chapter had four main research objectives. First, we examined forest cover change in Costa Rica from 2000 to 2016 to assess if there had been significant changes in provinces and protected areas. Second, we identified changes in NDVI in protected areas from 2000 to 2016. Third, we identified patterns in population within the country and within protected areas. Fourth, we looked at patterns in fire frequency and extent within and outside protected areas. Future work could look at when the protected areas were established, and identify a few set up in recent years where we can assess the forest patterns before and after protection.

The first research objective found that deforestation has been occurring over the entirety of the country of Costa Rica since 2000, with Figure 19 depicting each year of forest to non-forest conversion using different colors, with yellow shades occurring in the early 2000s, and more blue colors occurring in recent years. Deforestation has occurred in small patches across the entirety of the country and for possibly different reasons. There has been some gain across the country, but very limited when you compare the gain and loss as percentages of the total land area (Figure 18). For protected areas, there has also been predominantly loss over the time period (Figure 20B-C). Our second research question examined NDVI changes. In general, NDVI seemed to increase over the time period of 2000-2016 for the entirety of the country and within the protected areas, but individually they statistically significantly decreased by -0.0226. Based on IUCN category, we generally found a decrease of -0.00499, but it was insignificant. These two results mean that the protected areas generally significantly decreased in their greenness values, but it was not specifically due to their IUCN designation. However, some provinces are doing better than others, as nearly half of them decreased in NDVI values.

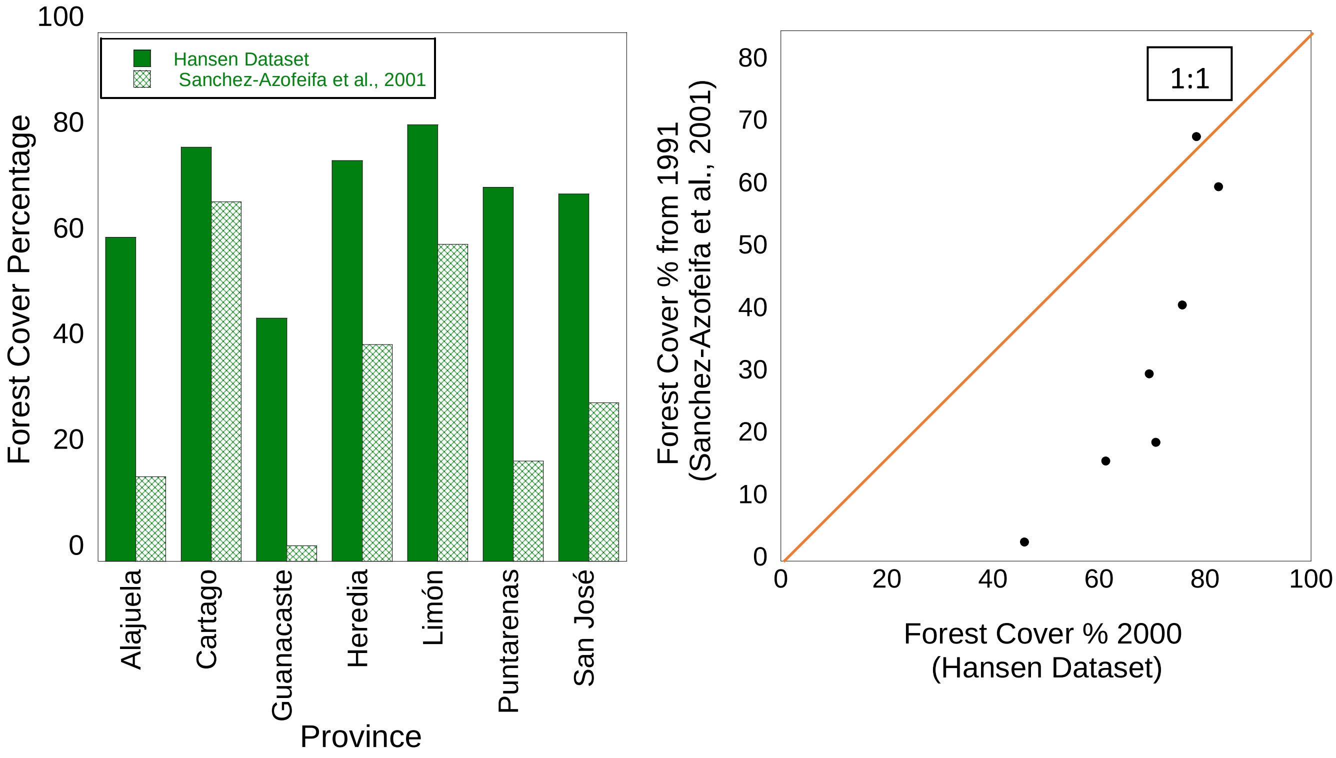
The third research objective noted that population was centered in a few major cities, specifically San Jose. The two provinces that were the most populous were San Jose and Alajuela. San Jose is the capital city and the nearby Alajuela province hosts the main international airport. For humans living in protected areas, they were mostly found in IUCN category VI, which signify “Protected Area with sustainable use of natural resources,” which allows for the conservation of habitats, along with associated cultural values and traditional natural resource management systems,” so it is unsurprising that these are the protected areas with most human presence.. In general, we found that within PAs, the larger the area, the higher the human population within it, with an r^2 of 0.437 (Figure 27D). We also found a pattern with generally higher human populations within PAs at higher elevations, but the relationship was not very strong, $r^2 = 0.158$ (Figure 27C).

The final research question looked at the pattern of fire across the country of Costa Rica. Fires during the 2000-2016 period were mainly in the lowland coastal areas, and focused on the drier western portion of the country. The incidence of fire was found to be negatively correlated with the forest area lost annually, with an r^2 of 0.25 there was less forest area lost in years with higher fire frequency. This correlation does not imply causation and instead shows that the forest loss is more likely due to forest conversion than fires.

This dissertation chapter examined the effect of protected versus non-protected status on forest loss and land conversion. Developing an understanding of diversity and successional stages both within and outside of protected areas may give us some insight on how to best manage tropical montane systems and may aid in developing conservation priorities, particularly in the face of climate change.

5.6 Supplementary Materials

Supplementary Figure S2: Comparison of province-level forest cover from 2000 to Sanchez-Azofeifa *et al*., (2001) forest cover in 1991.



Supplementary Table S1: Number of species sampled at each elevation site for wood density in Chapter 5.

Elevation (m)	**# of Species measured**
100	12
400	8
600	7
960	6
1500	9
2000	6
2400	5
2600	8
2800	8

Supplementary Table S2: Number of individuals sampled at each elevation site for wood density in Chapter 5.

Genus Species	**# Indiv sampled**
Alchornea latifolia	27
Billia colombiana	12
Brosimum lactescens	7
Brunelia costaricensis	47
Casearia arborea	42
Casearia tacanensis	3
Croton schiedeanus	4
Drimys granatensis	29
Elaeagia nitidifolia	8
Guarea guidonia	7
Guarea rhopalocarpa	5
*Hernandia ***	1
Hyeronima poasana	7
Ilex lamprophylla	17
Inga pezizifera	14
Inga thibudiana	10
Minquartia guianensis	20
Myrsine pellucidopunctata	19
Pentaclethra macroloba	17
Pourouma bicolor	33
Protium glabrum	2
Protium pittieri	25
Protium ravenii	22
Saurauia rubiformis	18
Schefflera rodriguensiana	33
Tetrochidium euryphyllum	19
Turpinia heterophylla	8
Viburnum costaricanum	34
Weinmannia pinnata	34
Total	**524**

5.7 References

Achard, F., R. DeFries, H. Eva, M. Hansen, P. Mayaux, and H. J. Stibig. 2007. "Pan-tropical monitoring of deforestation." *Environmental Research Letters* 2 (4):045022.

Andam, Kwaw S, Paul J Ferraro, Alexander Pfaff, G Arturo Sanchez-Azofeifa, and Juan A Robalino. 2008. "Measuring the effectiveness of protected area networks in reducing deforestation." *Proceedings of the National Academy of Sciences* 105 (42):16089-16094.

Asner, Gregory, Joseph Mascaro, Helene Muller-Landau, Ghislain Vieilledent, Romuald Vaudry, Maminiaina Rasamoelina, Jefferson Hall, and Michiel van Breugel. 2012a. "A universal airborne LiDAR approach for tropical forest carbon mapping." *Oecologia* 168 (4):1147-1160. doi: 10.1007/s00442-011-2165-z.

Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski. 1994. "CARBON POOLS AND FLUX OF GLOBAL FOREST ECOSYSTEMS." *Science* 263 (5144):185-190. doi: 10.1126/science.263.5144.185.

Edenhofer, Ottmar, Ramon Pichs-Madruga, Youba Sokona, Kristin Seyboth, Patrick Matschoss, Susanne Kadner, Timm Zwickel, Patrick Eickemeier, Gerrit Hansen, and Steffen Schlömer. 2011. "IPCC special report on renewable energy sources and climate change mitigation." *Prepared By Working Group III of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK.*

Fagan, Matthew, and Ruth S DeFries. 2009. *Measurement and Monitoring of the World's Forests: A Review and Summary of Remote Sensing Technical Capability, 2009-2015*: Resources for the Future.

FAO. 2010. "Global Forest Resource Assessment, Main report." *FAO Forestry Paper* 163:340.

Giacomo, Grassi, Monni Suvi, Federici Sandro, Achard Frederic, and Mollicone Danilo. 2008. "Applying the conservativeness principle to REDD to deal with the uncertainties of the estimates." *Environmental Research Letters* 3 (3):035005.

Giglio, Louis, Ivan Csiszar, and Christopher O Justice. 2006. "Global distribution and seasonality of active fires as observed with the Terra and Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) sensors." *Journal of Geophysical Research: Biogeosciences* 111 (G2).

Giglio, Louis, Jacques Descloitres, Christopher O Justice, and Yoram J Kaufman. 2003. "An enhanced contextual fire detection algorithm for MODIS." *Remote sensing of environment* 87 (2-3):273-282.

Grainger, Alan. 2008. "Difficulties in tracking the long-term global trend in tropical forest area." *Proceedings of the National Academy of Sciences* 105 (2):818-823.

Groombridge, Brian, Martin D Jenkins, and Martin Jenkins. 2002. *World atlas of biodiversity: earth's living resources in the 21st century*: Univ of California Press.

Hansen, Matthew C, Peter V Potapov, Rebecca Moore, Matt Hancher, SAa Turubanova, Alexandra Tyukavina, David Thau, SV Stehman, SJ Goetz, and TR Loveland. 2013. "High-resolution global maps of 21st-century forest cover change." *science* 342 (6160):850-853.

Hansen, Matthew C., Stephen V. Stehman, and Peter V. Potapov. 2010. "Quantification of global gross forest cover loss." *Proceedings of the National Academy of Sciences* 107 (19):8650-8655. doi: 10.1073/pnas.0912668107.

Hijmans, RJ, SE Cameron, JL Parra, PG Jones, and A Jarvis. 2004. The WorldClim interpolated global terrestrial climate surfaces. Version 1.3.

Houghton, R. A. 2003. "Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850-2000." *Tellus Series B-Chemical and Physical Meteorology* 55 (2). doi: 10.1034/j.1600-0889.2003.01450.x.

IUCN, UNEP-WCMC and. 2017. "Protected Planet: Costa Rica, Latin America & Caribbean ". UNEP-WCMC and IUCN. Accessed January 1. Available at: www.protectedplanet.net.

Jantz, Samuel M., Brian Barker, Thomas M. Brooks, Louise P. Chini, Qiongyu Huang, Rachel M. Moore, Jacob Noel, and George C. Hurtt. 2015. "Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation." *Conservation Biology* 29 (4):1122-1131. doi: 10.1111/cobi.12549.

Joppa, Lucas N, Scott R Loarie, and Stuart L Pimm. 2008. "On the protection of "protected areas"." *Proceedings of the National Academy of Sciences* 105 (18):6673-6678.

Kuper, Joe. 2013. "REDD in Costa Rica." Global Canopy Programme Consultant. http://theredddesk.org/countries/costa-rica.

Lambin, Eric F, and Patrick Meyfroidt. 2010. "Land use transitions: Socio-ecological feedback versus socio-economic change." *Land use policy* 27 (2):108-118.

Laurance, William F, Jeffrey Sayer, and Kenneth G Cassman. 2014. "Agricultural expansion and its impacts on tropical nature." *Trends in ecology & evolution* 29 (2):107-116.

Leroux, Shawn J, Meg A Krawchuk, Fiona Schmiegelow, Steven G Cumming, Kim Lisgo, Lee G Anderson, and Mirela Petkova. 2010. "Global protected areas and IUCN designations: do the categories match the conditions?" *Biological conservation* 143 (3):609-616.

Miles, Lera, Adrian C Newton, Ruth S DeFries, Corinna Ravilious, Ian May, Simon Blyth, Valerie Kapos, and James E Gordon. 2006. "A global overview of the conservation status of tropical dry forests." *Journal of Biogeography* 33 (3):491-505.

Nepstad, Daniel, Stephan Schwartzman, Barbara Bamberger, Marcio Santilli, D Ray, Peter Schlesinger, P Lefebvre, Ane Alencar, Elaine Prinz, and Greg Fiske. 2006. "Inhibition of Amazon deforestation and fire by parks and indigenous lands." *Conservation Biology* 20 (1):65-73.

Pfaff, A., S. Kerr, L. Lipper, R. Cavatassi, B. Davis, J. Hendy, and G. A. Sanchez-Azofeifa. 2007. "Will buying tropical forest carbon benefit the poor? Evidence from Costa Rica." *Land Use Policy* 24 (3):600-610. doi: 10.1016/j.landusepol.2006.01.003.

Pfaff, Alexander, Juan Robalino, G Arturo Sanchez-Azofeifa, Kwaw S Andam, and Paul J Ferraro. 2009. "Park location affects forest protection: Land characteristics cause differences in park impacts across Costa Rica." *The BE Journal of Economic Analysis & Policy* 9 (2).

R Core Team. "R: A Language and Environment for Statistical Computing." In. Vienna, Austria. https://www.R-project.org.

Rose, R. A., D. Byler, J. R. Eastman, E. Fleishman, G. Geller, S. Goetz, L. Guild, H. Hamilton, M. Hansen, R. Headley, J. Hewson, N. Horning, B. A. Kaplin, N. Laporte, A. Leidner, P. Leinagruber, J. Morisette, J. Musinsky, L. Pintea, A. Prados, V. C. Radeloff, M. Rowen, S. Saatchi, S. Schil, K. Tabor, W. Turner, A. Vodacek, J. Vogelnaann, M. Wegmann, and D. Wilkie. 2015. "Ten ways remote sensing can contribute to conservation." *Conservation Biology* 29 (2):350-359. doi: 10.1111/cobi.12397.

Rudel, Thomas. 2005. *Tropical forests: paths of destruction and regeneration*: Columbia University Press.

Saatchi, Sassan S., Nancy L. Harris, Sandra Brown, Michael Lefsky, Edward T. A. Mitchard, William Salas, Brian R. Zutta, Wolfgang Buermann, Simon L. Lewis, Stephen Hagen, Silvia Petrova, Lee White, Miles Silman, and Alexandra Morel. 2011. "Benchmark map of forest carbon stocks in tropical regions across three continents." *Proceedings of the National Academy of Sciences* 108 (24):9899-9904. doi: 10.1073/pnas.1019576108.

Sanchez-Azofeifa, G. A., G. C. Daily, A. S. P. Pfaff, and C. Busch. 2003. "Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover change." *Biological Conservation* 109 (1):123-135.

Sanchez-Azofeifa, G. A., A. Pfaff, J. A. Robalino, and J. P. Boomhower. 2007. "Costa Rica's payment for environmental services program: Intention, implementation, and impact." *Conservation Biology* 21 (5):1165-1173. doi: 10.1111/j.1523-1739.2007-00751.x.

Sanchez-Azofeifa, G., R. C. Harriss, and D. L. Skole. 2001. "Deforestation in Costa Rica: A quantitative analysis using remote sensing imagery." *Biotropica* 33 (3):378-384. doi: 10.1646/0006-3606(2001)033[0378:dicraq]2.0.co;2.

Sandbrook, C., F. Nelson, W. M. Adams, and A. Agrawal. 2010. "Carbon, forests and the REDD paradox." *Oryx* 44 (3):330-334. doi: 10.1017/s0030605310000475.

Schroeder, Wilfrid, Patricia Oliva, Louis Giglio, and Ivan A Csiszar. 2014. "The New VIIRS 375 m active fire detection data product: Algorithm description and initial assessment." *Remote Sensing of Environment* 143:85-96.

SINAC, Sistema Nacional de Áreas de Conservación. 2009. IV Informe de País al Convenio sobre la Diversidad Biológica. In *Mimeografiado*. San Jose, Costa Rics: GEF-PNUD.

Solomon, Susan. 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*. Vol. 4: Cambridge University Press.

Van der Werf, Guido R, Douglas C Morton, Ruth S DeFries, Jos GJ Olivier, Prasad S Kasibhatla, Robert B Jackson, G James Collatz, and James T Randerson. 2009. "CO 2 emissions from forest loss." *Nature geoscience* 2 (11):737.

Chapter 6: Conclusions

6.1 Rationale for these types of studies

The scope of this Ph.D. dissertation spans a range of topics from field ecological questions to extrapolation mapping and quantitative ecology. The topics covered are temporally relevant and will directly address important goals outlined in UN-REDD+ scientific plans. Developing an understanding of diversity and successional stages both within and outside of protected areas may give us some insight on how to best manage tropical montane systems and may aid in developing conservation priorities, particularly in the face of climate change.

Costa Rica harbors high levels of biodiversity and endemism. While Costa Rica does tend to have good conservation policies in place, understanding the patterns of plant diversity, forest loss or conversion, human impact, and incidence of fires can allow for better management priorities. Current technologies utilizing spaceborne or airborne remotely sensed imagery could be very useful to study terrestrial processes and allow for better monitoring of patterns of forests, both spatially and temporally. The ability of remotely sensed imagery to evaluate various attributes of forest cover allows for larger spatial scales and finer temporal scales than possible solely through ground collections. In addition, the standardization of data allows for systematic assessment of land cover change. However, there are still limitations with current technology at the global scale. Airborne data has had success with certain aspects at the local and regional scale, but improvements need to be made for spaceborne satellites in order to improve measurement accuracies. Additionally, the development of standardized protocols of field collected training data is necessary globally in order to develop relationship and test accuracies.

Anticipated future advances in remote sensing will improve these challenging aspects of land cover monitoring, including an increase in hyperspectral satellites, which have high sensitivity within the electromagnetic spectrum, improved temporal and spatial resolution of spaceborne passive and active sensors, as well as increased computing algorithms to process such large amounts of imagery. These improvements will allow for greater accuracy and smaller time scales of changes in forest extent, impacts from disturbance like fires, and improved monitoring of terrestrial aboveground carbon sequestration. In light of climate modeling predictions and the added economic value of biomass due to UN-REDD+, forest biomass and diversity needs to be assessed more accurately and monitored at various temporal scales to see relevant changes.

Improvements in relating forest structure to plant diversity in highly complex and diverse forest environments are critical to the science goals of the UN-REDD+ program as well as national policies and for tropical forest research in general. This dissertation covered six chapters across distinct but interrelated topics concerning the forest of Costa Rica, and sought to improve the existing methodologies and compare results to other datasets. Ideally, this research will be applicable to other environments with both field-collected tree inventory data and appropriate remote sensing products, but some of the results did not even require ground truth data and relied solely on available remotely sensed imagery.

6.2 Recap of results

The first chapter introduced the importance of understanding tropical forest diversity, biomass, and carbon dynamics, as well as some specific to the country of Costa Rica. The second chapter outlined the specific study area covered in Chapters 3 and 4 within Costa Rica’s Braulio Carrillo National Park (BCNP), which protects a large elevational gradient from 55 to 2814 m above sea level, and the adjacent La Selva Biological Station (LSBS). In addition, this study area chapter also discussed the country of Costa Rica in general, specifically in terms of forest policies and protection. The middle three chapters cover methodologies that coupled remote sensing imagery, GIS data, and field data to recognize patterns in tree growth, forest stand dynamics, tree diversity, deforestation, human impact, and fire data. These three middle chapters gave rise to several defined results, which will be mentioned below.

Chapter 3 utilized field inventory data coupled with large footprint (20 m) airborne lidar data over plots over the BCNP elevational gradient in order to quantify variations in topography and three-dimensional structure across plots and landscapes. A mid-elevation bulge in multiple diversity indices was observed within the plots and landscape, which supports much of the literature, as discussed above. Species richness and diversity were negatively correlated with elevation, while the two tallest relative height metrics (rh100, rh75) derived from lidar were both significantly positively correlated with species richness and diversity. The best lidar-derived topographical and three-dimensional forest structural models showed a strong relationship with the Shannon diversity index ($r^2 = 0.941$, $p < 0.01$), with ten predictors; conversely, the best species richness model was weaker ($r^2 = 0.599$, $p < 0.01$), with two predictors.

Chapter 4 analyzed wood density from 29 stand-dominant collected along the BCNP elevational gradient. The patterns of species wood density and aboveground biomass from field measured (tree cores) and database wood density values were assessed to examine how wood density and biomass are affected by changing elevations, both intraspecifically and at the stand-level. We found that wood density databases tended to have inflated values of wood density. The patterns of species wood density and aboveground biomass from field measured (tree cores) and database wood density values were assessed to examine how wood density and biomass are affected by changing elevations. At the species-level, individual tree species did not exhibit significant changes in wood density along elevational gradients. At the stand-level, we found wood density did not show a linear pattern with increasing elevations, but instead was highest at both the lowest and highest elevations with a decline at mid-elevations. We found that TEAM database values (0.60 g/cm^3) were significantly higher than field measured wood density for 58% of the species sampled, and that and estimates from the Global Wood Density Database had significantly higher wood density for 50% of the same species. If we expand to just within 1 standard deviation from the mean, TEAM values were significantly different then 80% of the species, and 69% of the Global Wood Density Database. Separating the individuals by diameter class and selecting 10% of each of the classes resulted in the best method ($r^2 = 0.98$) for reasonably capturing stand-level wood density. Our results suggest that there are decreases in wood density at mid-elevations and that we are currently overestimating carbon storage in montane forests in the tropics. We also suggested a method to collect estimates of wood density for plots and carbon storage in other tropical forests.

Chapter 5 scaled the remote sensing analysis up to entirety of the country of Costa Rica looking at general forest loss and conversion within and outside of protected areas at the 30 m scale. In this chapter, I assessed the spatial patterns driving deforestation and afforestation across Costa Rica and protected areas during 2000-2016. This analysis of forest change utilized multiple remote sensing layers, including a Landsat-based dataset on forest coverage, Normalized Difference Vegetation Index (NDVI), fire data, and human population. In addition, I compared IUCN categories of protected areas to the country as a whole and by different provinces. This project had four different main findings.

First, we found that deforestation has been occurring over the entirety of the country of Costa Rica since 2000. There has been some gain across the country, but very limited when you compare the gain and loss as percentages of the total land area. For protected areas, there has also been predominantly loss over the time period, but less so than in non-protected regions. Second, NDVI increased slightly over the time period of 2000-2016 for the entirety of the country and within the protected areas when averaged together (0.573 to 0.5995). When the PA change was analyzed individually using a paired t-test found a significant decrease of -0.0226, with a t-value of -6.7415 ($p < 0.001$). At the province level, it was determined the provinces decreased insignificantly by -0.0029. On average, some provinces increased in NDVI while other decreased. The third research objective noted that population was centered in a few major cities, specifically San Jose. The country as a whole increased in population during this time, and all provinces showed an increase in population. The two provinces that were the most populous were San Jose and Alajuela, and they also increased the most during this time period. For humans living within protected areas, they were mostly found in IUCN category VI, which signify "Protected Areas with sustainable use of natural resources," which allows for the conservation of habitats, along with associated cultural values and traditional natural resource management systems," so it is unsurprising that these are the protected areas with most human presence. In general, the PAs seem to have experienced a loss of human population during these years, though it was found to be insignificant. The final research question of this chapter looked at the pattern of fire across the country of Costa Rica. Fires during the 2000-2016 period were mainly in the lowland coastal areas, and focused on the drier western portion of the country. The incidence of fire was found to be negatively correlated with the forest area lost annually (r^2 = 0.25) there was less forest area lost in years with higher fire frequency. This correlation does not imply causation and instead shows that the forest loss is more likely due to forest conversion than fires. This chapter provided a good overview of the status of the Costa Rican forest from 2000-2016.

6.3 Future Work

A large part of this project relies on remote sensing and GIS technologies, which allow for the study of objects without direct contact. Because of this, it can allow for broad mapping of forest extent, diversity, and ecological processes at a large scale more quickly than possible solely through assessment on the ground. Ground measurements are expensive, laborious, and time consuming as well as typically very limited spatially. Field collections have to be spatially limited due to time constraints and labor input, and remote areas may be difficult to access and sample; using imagery can allow for easier analysis of these areas without additional disturbance. Because of this, remote sensing is a practical necessity to measure and monitor forests globally. Monitoring forest biomass over regional and global scales is imperative with increasing concerns about climate change, as more attention needs to be focused on accurately estimations of carbon fluxes.

The methodology used within these chapters, particularly Chapter 5, can be replicated across many other regions across the globe. Chapter 5 specifically uses all freely available, on-demand data that is available at ~ 30 m resolution worldwide, from spaceborne satellites with good coverage. This imagery can be downloaded and new analyses can be made for nearly every terrestrial surface in the world. With more readily available data, like the fire data, which is available every 24 hours with new detected fires or farther back in time reaching back to 2012, or 2000, depending on the sensor and the spatial resolution desired (Giglio et al. 2003, Giglio, Csiszar, and Justice 2006, Schroeder et al. 2014).

Unfortunately, lots of the forest in Costa Rica has already been lost, particularly in premontane forest that is easily accessible to human impact. According to Sanchez-Azofeifa and Quesada-Mateo (1995, Sanchez-Azofeifa, Harriss, and Skole 2001), there are several factors that could continue to help mitigate rates of deforestation in Costa Rica. These possible improvements include: 1) increased harvest efficiency to limit landscape degradation and waste; 2) more efficiency at the industrial level to increase yields at the sawmill; 3) increased aspirations from rural populations to organize to protect forests; 4) increase in private reserves (mainly for ecotourism reasons); 5) national government financial incentives to conserve forests; and 6) joint conservation strategies for carbon sequestration purposes like those suggested through the Framework Convention for Climate Change and the Kyoto Protocol.

In the decades since the Sanchez-Azofeifa *et al*. study (2001) that covered the time period 1986-1991, remotely-sensed imagery has become much more common and freely available, as well as with increased spatial, spectral, and temporal resolutions and new technologies like fire detection available every 24 hours. An increase in these different resolutions of available datasets can allow for more systematic and accurate monitoring of forests globally. In addition, it allows for more frequent analysis of the status of forests, at nearly real-time, within the country of Costa Rica, regionally, and even globally. With more active monitoring of things like deforestation, forest fires, patches of high diversity, areas of high carbon sequestration, may be able to more quickly inform policy makers or be able to provide quick reports on the impact of newly implemented policies.

6.4 References

Giglio, Louis, Ivan Csiszar, and Christopher O Justice. 2006. "Global distribution and seasonality of active fires as observed with the Terra and Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) sensors." *Journal of Geophysical Research: Biogeosciences* 111 (G2).

Giglio, Louis, Jacques Descloitres, Christopher O Justice, and Yoram J Kaufman. 2003. "An enhanced contextual fire detection algorithm for MODIS." *Remote sensing of environment* 87 (2-3):273-282.

Sanchez-Azofeifa, G., R. C. Harriss, and D. L. Skole. 2001. "Deforestation in Costa Rica: A quantitative analysis using remote sensing imagery." *Biotropica* 33 (3):378-384. doi: 10.1646/0006-3606(2001)033[0378:dicraq]2.0.co;2.

Sánchez-Azofeifa, Gerardo Arturo, and Carlos A Quesada-Mateo. 1995. "Deforestation, carbon dynamics, and sustainable mitigation measures in Costa Rica-The Puerto Viejo de Sarapiquí case study. Deforestación, dinámica del carbono y medidas sostenibles de mitigación en Costa Rica-Estudio de caso de Puerto Viejo de Sarapiquí." *Interciencia.* 20 (6):396-400.

Schroeder, Wilfrid, Patricia Oliva, Louis Giglio, and Ivan A Csiszar. 2014. "The New VIIRS 375 m active fire detection data product: Algorithm description and initial assessment." *Remote Sensing of Environment* 143:85-96.

Appendix 1: Extracted information for 177 protected areas.

Protected Area	IUCN Cat.	IUCN Designation	Max Elev. (m)	Mean Elev. (m)	Elev. SD (m)	Total Area (Km2)	Forest Loss (Km2)	Forest Gain (Km2)	Forest Cover % 2000	Forest Cover % SD	2016 Pop	Pop Change 16-00	Fires 00-16	NDVI 2000	NDVI 2016
Acuíferos Guácimo y Pococí	VI	Protective Zone	1200	723	222	51.16	0.093	0.034	96.76	9.21	2050	1177	0	0.796	0.798
Aguabuena (privado)	IV	National Wildlife Refuge	544	209	118	2.26	0.248	0.011	79.11	29.08	8	-8	5	0.713	0.635
Alberto Manuel Brenes	Ia	Biological Reserve	1621	1069	197	93.24	0.239	0.002	95.24	7.75	985	324	0	0.765	0.852
Ara Macao (mixto)	NR	National Wildlife Refuge	272	93	59	1	0.005	0.000	84.18	32.95	6	0	0	0.704	0.748
Area de Conservación Guanacaste	NA	World Heritage Site	1906	292	380	1798.22	10.525	0.110	23.29	39.43	35	-18	1	0.210	0.224
Areas anexas a ASP	NR	Other Reserve	1061	510	171	197.8	1.887	0.665	84.09	21.57	541	-588	44	0.779	0.829
Arenal	II	National Park	1799	917	270	144.77	0.621	0.036	85.86	25.2	1745	-3956	8	0.721	0.821
Arenal-Monteverde	VI	Protective Zone	1857	1212	304	338.87	0.737	0.039	94.51	7.12	3196	266	0	0.812	0.865
Aviarios del Caribe (privado)	IV	National Wildlife Refuge	33	16	6	0.7	0.001	0.001	98.27	1.97			0	0.799	0.810
Bahía Junquillal (estatal)	IV	National Wildlife Refuge	298	125	69	5.37	0.182	0.004	85.69	19.2	8	-41	5	0.758	0.752
Barbilla	II	National Park	1199	676	275	142.54	0.224	0.001	97.48	6	363	-914	0	0.801	0.802
Barra del Colorado (mixto)	IV	National Wildlife Refuge	249	27	22	966.98	23.529	0.577	77.74	34.13	5012	-727	10	0.691	0.726
Barra Honda	II	National Park	559	258	107	27.74	0.436	0.011	76.03	22.52	31	-68	8	0.711	0.750
Boracayán (privado)	NR	National Wildlife Refuge	1163	658	225	4.75	0.068	0.056	80.33	28.61	75	49	0	0.717	0.761
Bosque Alegre (mixto)	IV	National Wildlife Refuge	1002	742	85	10.33	0.053	0.012	87.45	27.9	119	-959	0	0.733	0.795
Bosque Escondido (privado)	NR	National Wildlife Refuge	642	240	102	8.63	0.041	0.008	78.72	19.66	4	-43	3	0.777	0.786
Braulio Carrillo	II	National Park	2903	1199	581	563.95	0.266	0.013	94.82	7.97	1609	-2794	0	0.799	0.839
Cabo Blanco	Ia	Nature Reserve	403	74	111	35.06	0.139	0.013	38.78	47.24	4	-450	0	0.635	0.651
Cacyra (privado)	IV	National Wildlife Refuge	265	223	21	0.52	0.023	0.000	96.5	3.52		-69		0.634	0.675
Cahuita	II	National Park	34	1	3	290.67	0.027	0.005	4.22	19.87	909	-68	1	0.350	0.366

Caletas-Arío (mixto)	NR	National Wildlife Refuge	31	0	2	242.38	0.074	0.194	0.9	8.85	53		3	0.794	0.918
Camaronal (mixto)	NR	National Wildlife Refuge	201	77	56	2.93	0.002	0.101	69.05	41.16	1	278	0	0.036	0.035
Caño Negro	NR	Ramsar Site, Wetland of International Importance	65	46	5	87.78	1.413	0.357	62.8	39.26	816	-10	4	0.010	0.010
Caño Negro (mixto)	IV	National Wildlife Refuge	67	43	7	121.44	4.405	0.062	49.24	40.4	369	-24	11	0.695	0.725
Caraigres	VI	Protective Zone	2507	1865	241	38.25	0.737	0.039	68.76	35.44	118	94	4	0.725	0.719
Carara	II	National Park	759	289	170	63.32	0.176	0.019	95.95	9.39	148	10	10	0.793	0.885
Carate(mixto)	NR	National Wildlife Refuge	317	144	85	2.33	0.001	0.006	94.51	14.78	104	89	0	0.791	0.788
Cataratas Cerro Redondo (privado)	IV	National Wildlife Refuge	1324	977	202	7.89	0.038	0.001	96.3	3.43	2	-24	0	0.795	0.849
Cerro Atenas	VI	Protective Zone	1083	787	122	10.99	0.202	0.011	52.74	38.75	211	192	4	0.652	0.636
Cerro Dantas (privado)	IV	National Wildlife Refuge	2093	2000	41	0.61	0.000	0.000	91.85	4.43	0	-1	0	0.844	0.896
Cerro de Escazú	VI	Protective Zone	2431	1649	326	85.94	1.475	0.026	78.2	28.57	1920	1697	4	0.747	0.759
Cerro El Chompipe	NR	Protective Zone	639	512	69	1.21	0.004	0.000	74.63	31.77	3	-10	2	0.734	0.728
Cerro La Cruz	VI	Protective Zone	409	284	52	2.48	0.006	0.002	46.94	29.86	22	-40	2	0.603	0.633
Cerro Las Vueltas	Ia	Biological Reserve	3169	3013	97	9.77	0.002	0.002	88.99	5.65	32	11	0	0.827	0.869
Cerro Nara	VI	Protective Zone	1093	561	205	28.16	0.066	0.000	96.68	9.36	135	-47	0	0.804	0.852
Cerros de la Carpintera	VI	Protective Zone	1882	1511	155	28.86	0.752	0.049	72.43	33.65	5759	2782	1	0.716	0.664
Cerros de Turrubares	VI	Protective Zone	1754	671	359	34.13	0.194	0.008	95.82	8.9	26	-37	2	0.801	0.897
Chenailles (privado)	NR	National Wildlife Refuge	270	210	74	5.81	0.114	0.001	57.74	28.99	148	63	5	0.653	0.663
Chirripó	II	National Park	3028	2235	553	596.13	0.673	0.186	81.99	22.53	3725	1480	2	0.790	0.802
Cipanci (estatal)	NR	National Wildlife Refuge	57	6	8	43.2	0.137	0.001	21.02	36.52	227	-63	28	0.282	0.309
Cocos Island National Park	NA	World Heritage Site				2192.93	0.000	0.000	0	0			163	0.000	0.000
Corcovado	II	National Park	769	182	161	527.11	0.752	0.073	91.9	21.55	1636	732	1	0.731	0.732
Cordillera Volcánica Central	VI	Forest Reserve	3350	1481	666	732.52	2.125	0.245	89.38	17.61	7823	-4008	1	0.759	0.807

Corredor fronterizo (estatal)	IV	National Wildlife Refuge	482	58	59	723.79	47.791	4.100	63.15	41.12	7240	-365	114	0.680	0.695
Costa Esmeralda (privado)	IV	National Wildlife Refuge	110	40	28	0.29	0.000	0.000	55.75	38.39			2	0.518	0.613
Cuenca del Río Abangares	VI	Protective Zone	1181	680	224	52.43	1.655	0.014	62.65	39.65	164	-112	2	0.702	0.726
Cuenca del Río Siquírres	VI	Protective Zone	761	499	113	8.19	0.277	0.000	92.32	19.45	57	3	0	0.771	0.777
Cuenca del Río Banano	VI	Protective Zone	1679	707	286	111.53	0.408	0.010	96.37	9.46	110	-859	0	0.761	0.821
Cuenca del Río Tuis	VI	Protective Zone	2000	1428	260	49.03	0.051	0.000	91.93	8.42	198	-400	0	0.857	0.795
Cueva del Murciélago (privado)	NR	National Wildlife Refuge	248	153	59	1.17	0.000	0.000	95.2	5.16	0	-1	0	0.851	0.897
Curi Cancha	IV	National Wildlife Refuge	1674	1532	47	0.9	0.000	0.000	92.91	6.15			0	0.843	0.874
Curu (estatal)	IV	National Wildlife Refuge	206	64	50	1.28	0.000	0.001	74.24	35.66	3	-29	0	0.661	0.719
De San Vito	NR	Wetland	993	981	4	0.24	0.037	0.000	64.42	29.46	46	38	0	0.724	0.697
Diría	NR	National Park	973	430	174	65.24	0.396	0.032	82.77	21.39	29	-59	26	0.767	0.816
Donald Peter Hayes (privado)	IV	National Wildlife Refuge	483	392	39	2.58	0.000	0.000	94.55	9.47	152	95	0	0.779	0.830
Dr.Archie Carr (estatal)	IV	National Wildlife Refuge	19	10	5	0.58	0.005	0.000	50.27	45.29	0	-9	0	0.514	0.442
Duaru (privado)	NR	National Wildlife Refuge	73	47	8	4.35	0.430	0.006	40.81	41.11	56	16	2	0.674	0.635
El Chayote	VI	Protective Zone	2189	1942	128	9.26	0.007	0.006	63.89	38.82	79	41	0	0.707	0.730
El Rodeo	VI	Protective Zone	1259	860	157	25.34	0.400	0.007	77.05	31.02	705	575	5	0.682	0.710
Estación Exp. Horizontes	NR	Other Reserve	212	203	8	87.52	0.548	1.613	39.7	26.42	331	-576	46	0.588	0.658
Estero Puntarenas y manglares	NR	Wetland	36	9	7	62.82	0.599	0.010	58.19	44.29	1991	-640	26	0.540	0.571
Fernando Castro C. (mixto)	IV	National Wildlife Refuge	1028	464	227	17.34	0.455	0.002	94.45	12.48	27	-27	1	0.768	0.880
Finca Baru del Pacífico (mixto)	IV	National Wildlife Refuge	320	76	73	4.27	0.032	0.036	93.26	17.55	107	53	0	0.755	0.787
Finca Hda. La Avellana (privado)	IV	National Wildlife Refuge	189	90	43	6.23	0.297	0.213	53.59	35.32	6	-134	8	0.635	0.638
Forestal Golfito S.A. (privado)	IV	National Wildlife Refuge	381	173	82	1.09	0.015	0.004	90.67	19.38	2	1	1	0.778	0.794

Gandoca-Manzanillo	NR	Ramsar Site, Wetland of International Importance	130	44	26	74.91	0.266	0.053	68.96	44.2	986	-266	1	0.588	0.576
Gandoca-Manzanillo (mixto)	IV	National Wildlife Refuge	200	16	28	129.7	0.818	0.090	23.54	41.46	993	-386	0	0.203	0.198
Golfito (mixto)	IV	National Wildlife Refuge	476	172	98	33.95	0.042	0.006	94	16.05	2832	2673	0	0.766	0.812
Golfo Dulce	VI	Forest Reserve	653	194	120	713.59	11.374	4.838	90.81	20.92	1345	-1280	35	0.753	0.763
Grecia	VI	Forest Reserve	2351	1900	191	27.61	0.023	0.006	84.93	24	300	-396	0	0.805	0.854
Guanacaste	II	National Park	263	230	26	404.12	3.781	0.435	69.34	32.15	3460	-995	50	0.706	0.735
Hacienda Copano (privado)	IV	National Wildlife Refuge	297	172	46	3.12	0.069	0.008	91.63	15.51	9	-21	1	0.724	0.736
Hitoy Cerere	Ia	Biological Reserve	735	443	178	118.76	0.527	0.008	97.63	5.34	76	-510	0	0.841	0.835
Humedal Caribe Noreste	NR	Ramsar Site, Wetland of International Importance	100	17	11	870.36	10.365	0.131	91.6	20.53	7158	351	4	0.721	0.756
Iguanita (estatal)	IV	National Wildlife Refuge	121	33	29	1.36	0.001	0.000	75.81	23.96	0	-3	2	0.763	0.808
Internacional La Amistad	II	National Park	3272	1427	798	2357.86	2.983	0.334	92.17	5.85	10473	-1266	7	0.834	0.861
Isla Chora (estatal)	NR	National Wildlife Refuge	1	0	0	0.06	0.000	0.000	46.09	42.69			0	0.516	0.504
Isla del Caño	Ia	Biological Reserve	116	4	18	65.81	0.006	0.000	4.83	20.72	0		0	0.044	0.045
Isla del Coco	II	National Park				1808.19	0.000	0.000	0	0			0	0.000	0.000
Isla Guayabo	Ia	Biological Reserve	44	19	11	0.09	0.000	0.000	5.87	18.79	0	-1	0	0.279	0.308
Isla Pajaros	Ia	Biological Reserve	0	0	0	0.06	0.000	0.000	7	19.85			63	0.298	0.407
Isla San Lucas (estatal)	NR	National Wildlife Refuge	105	20	26	11.27	0.125	0.070	31.55	39.42	13	-147	0	0.322	0.322
Islas Negritos	Ia	Biological Reserve	101	30	33	1.81	0.003	0.000	45.62	47.28	0	-3	0	0.392	0.419
Jaguarundi (privado)	IV	National Wildlife Refuge	2168	2069	42	1.59	0.000	0.000	91.16	3.8	51	46	0	0.799	0.872
Jardines de la Catarata (privado)	NR	National Wildlife Refuge	1542	1492	25	0.34	0.002	0.000	86.48	20.87	1	0	0	0.794	0.832

Joseph Steve Friedman (privado)	IV	National Wildlife Refuge	2371	2307	30	0.28	0.000	0.000	89.96	1.81	2	-59	0	0.861	0.855
Juan Castro Blanco	II	National Park	2318	1486	417	171.4	0.306	0.069	91.7	14.04	1359	-607	0	0.775	0.890
La Cangreja	NR	National Park	1295	713	231	30.13	0.644	0.002	83.54	27.91	185	163	2	0.761	0.836
La Ceiba (privado)	IV	National Wildlife Refuge	557	240	104	3.35	0.015	0.001	91.59	9.84	4	-91	1	0.755	0.845
La Ensenada (mixto)	IV	National Wildlife Refuge	135	28	27	5.95	0.149	0.014	54.5	38.23	29	-120	3	0.639	0.640
La Marta (privado)	IV	National Wildlife Refuge	1953	1305	321	16.11	0.001	0.000	93.33	3.79	270	37	0	0.872	0.790
La Nicoyana (privado)	NR	National Wildlife Refuge	151	88	26	0.47	0.006	0.000	91.59	9.75	2	-5	0	0.765	0.756
La Selva	VI	Protective Zone	882	176	195	29.86	0.160	0.132	93.95	17.62	284	88	0	0.725	0.820
La Tirimbina (privado)	NR	National Wildlife Refuge	233	192	16	3.59	0.005	0.000	97.46	7.8	33	-69	0	0.800	0.873
Lacustrino Bonilla-Bonillita	NR	Wetland	462	390	25	0.64	0.019	0.003	27.8	43.14	8	-34	0	0.236	0.222
Lacustrino Pejeperrito	NR	Wetland	53	6	9	0.84	0.000	0.000	35.76	45.43	2	0	0	0.366	0.353
Laguna Las Camelias (estatal)	IV	National Wildlife Refuge	53	45	2	0.74	0.055	0.005	81.29	22.61	2	-43	0	0.610	0.713
Laguna Madrigal	NR	Wetland	23	10	5	0.64	0.162	0.000	50.91	40.86	0	-11	3	0.689	0.510
Lagunazul (privado)	NR	National Wildlife Refuge	97	36	20	0.2	0.000	0.000	74.15	39.86			0	0.616	0.623
Lapa Rios Reserve	Ib	Conservation Easement	366	212	78	4.81	0.015	0.002	92.91	14.7			0	0.798	0.723
Las Baulas de Guanacaste	II	National Park	217	1	10	323.82	0.039	0.011	1.48	11.04	43	-41	5	0.016	0.017
Las Tablas	VI	Protective Zone	2304	1161	805	237.28	0.162	0.001	93.28	6.07	1102	462	2	0.852	0.871
Limoncito (mixto)	IV	National Wildlife Refuge	28	10	5	13.25	1.418	0.049	92.47	18.2	230	-590	2	0.757	0.747
Lomas Barbudal	Ia	Biological Reserve	186	121	32	31.72	0.593	0.059	61.8	21.57	76	-277	18	0.670	0.669
Los Quetzales	NR	National Park	3143	2686	318	49.53	0.025	0.008	89.37	8.1	705	-1667	1	0.849	0.903
Los Santos	VI	Forest Reserve	3484	1778	697	666.72	8.681	0.722	85.85	22.7	4659	878	11	0.784	0.820
Manglar Térraba-Sierpe	NR	Wetland	142	11	10	323.5	2.298	0.738	66.45	40.68	534	-1398	32	0.587	0.590
Manuel Antonio	II	National Park	168	0	5	1496.34	0.407	0.306	1.08	10.02	252	69	7	0.010	0.010
Maquenque (mixto)	NR	National Wildlife Refuge	381	83	59	626.27	19.923	1.063	90.55	21.32	4554	413	11	0.723	0.817

Marino Ballena	II	National Park	64	0	3	64.13	0.006	0.014	1.32	10.86	93	12	0	0.012	0.012
Marino Playa Blanca	NR	Wetland	94	29	28	0.14	0.001	0.000	24.15	37.24			0	0.303	0.255
Mata Redonda (estatal)	IV	National Wildlife Refuge	13	3	2	4.62	0.066	0.002	3.79	13.86	15	-46	5	0.500	0.557
Miravalles	VI	Protective Zone	2011	1100	313	139.58	0.840	0.151	79.61	29.95	249	-97	8	0.778	0.753
Montaña El Tigre (privado)	NR	National Wildlife Refuge	519	413	42	3.44	0.003	0.000	93.02	17.79	14	-19	4	0.753	0.795
Monte Alto	NR	Protective Zone	881	618	104	11.08	0.113	0.023	74.31	33.38	133	-114	2	0.726	0.797
Montes de Oro	VI	Protective Zone	1486	1155	188	22.32	0.224	0.003	74.4	34.89	28	-19	2	0.731	0.772
Monumento Nal. Guayabo	NR	Other Reserve	1307	1149	90	2.85	0.019	0.000	78.26	31.76	64	-55	0	0.746	0.782
Nacional Cariari	NR	Wetland	31	7	5	12.96	0.121	0.001	57.06	44.71	85	-23	0	0.541	0.532
Nicolás Wessberg	NR	Nature Reserve	131	61	36	0.77	0.000	0.000	82.97	35.09			0	0.743	0.741
No protegida	NR	NR	40	16	11	0.5	0.008	0.001	45.55	35.29	328	-859	0	0.493	0.484
Nogal (privado)	NR	National Wildlife Refuge	68	48	8	1.43	0.039	0.001	63.94	41.19	15	12	0	0.502	0.545
Osa (mixto)	NR	National Wildlife Refuge	382	166	92	20.97	0.126	0.060	94.12	12.71	63	-109	1	0.751	0.739
Ostional (estatal)	IV	National Wildlife Refuge	90	1	4	102.3	0.028	0.032	3.04	16.18	48	-846	3	0.034	0.034
Pacuare-Matina	VI	Forest Reserve	24	14	4	5.78	0.003	0.000	94.17	20.99	131	-6	0	0.807	0.856
Palo Verde	NR	Ramsar Site, Wetland of International Importance	206	13	17	212.19	1.335	0.590	41.93	38.42	633	54	64	0.758	0.729
Palo Verde	II	National Park	266	21	30	219.42	1.218	0.590	41.93	38.42	97	-2355	90	0.611	0.593
Palustrino Corral de Piedra	NR	Wetland	35	6	4	29.06	0.020	0.002	11.01	26.75	186	-201	10	0.611	0.593
Palustrino Lag. del Paraguas	NR	Wetland	1465	1438	12	0.62	0.005	0.000	57.21	35.72	34	18	0	0.397	0.458
Páramo (pivado)	NR	National Wildlife Refuge	2931	2436	262	6.89	0.006	0.002	88.8	11.74	1	28	0	0.667	0.681
Parque Natural Recreativo de Liberia	NR	Other Reserve	148	145	1	0.14	0.000	0.000	15.37	24.34			1	0.519	0.519
Pejeperro (mixto)	NR	National Wildlife Refuge	33	8	6	7.23	0.133	0.022	45.7	46.82	30	26	3	0.708	0.721
Peñas Blancas (mixto)	IV	National Wildlife Refuge	1511	1096	254	28.9	0.495	0.002	62.32	40.64	652	-6	0	0.578	0.619
Península de Nicoya	VI	Protective Zone	1014	321	149	256.65	3.816	0.851	80.8	25.65	1740	-1759	46	0.744	0.812

Piedras Blancas	II	National Park	576	183	140	180.23	0.352	0.581	87.07	30.03	740	288	0	0.701	0.741
Portalón (mixto)	IV	National Wildlife Refuge	307	64	68	5.63	0.177	0.083	81.85	32.64	232	167	0	0.734	0.739
Preciosa Platanares (mixto)	NR	National Wildlife Refuge	32	9	7	2.83	0.040	0.016	69.79	38.67	52	37	0	0.648	0.666
Punta Leona (privado)	IV	National Wildlife Refuge	146	104	17	0.45	0.021	0.004	77.69	33.13	4	0	0	0.718	0.838
Punta Río Claro (mixto)	IV	National Wildlife Refuge	145	86	34	3.99	0.015	0.004	92.41	20.27	3	1	0	0.752	0.784
Pya Hermosa -Pta Mala (estatal)	NR	National Wildlife Refuge	63	1	5	33.56	0.018	0.007	8.16	26.21	29	-96	4	0.078	0.076
Quebrada Rosario	VI	Protective Zone	2078	1985	43	0.38	0.006	0.000	82.1	30.06			0	0.810	0.834
Quillotro (mixto)	NR	National Wildlife Refuge	140	86	44	0.98	0.023	0.000	82.19	35.2	3	1	0	0.643	0.692
Quitirrisí	VI	Protective Zone	1239	1068	94	1.38	0.007	0.000	86.96	20.34	0	0	0	0.706	0.782
Rancho La Merced (mixto)	IV	National Wildlife Refuge	249	40	45	5.02	0.053	0.038	84.39	31.03	89	42	0	0.711	0.723
Rancho Mastatal (privado)	NR	National Wildlife Refuge	356	293	35	1.02	0.003	0.000	96.65	3.15	27	23	0	0.828	0.892
RHR Bancas (privado)	IV	National Wildlife Refuge	278	175	50	0.78	0.000	0.000	96.01	2.96	45	-13	0	0.620	0.588
Riberino Zapandi	NR	Wetland	114	33	18	9.26	0.046	0.005	44.03	32.5	202	8	0	0.806	0.797
Rincón de la Vieja	II	National Park				168.78	1.140	0.050	86.69	21.72	350	129	3	0.665	0.627
Río Cañas	NR	Wetland	103	20	9	8.01	0.094	0.010	42.29	33.25	74	-2540	5	0.829	0.833
Río Dantas (privado)	NR	National Wildlife Refuge	318	253	41	1.19	0.004	0.000	98.6	6.64	12	-1505	0	0.790	0.791
Río Grande	VI	Protective Zone	1266	951	106	18.1	0.722	0.014	59.98	34.47	201	-1	1	0.020	0.012
Río Macho	VI	Forest Reserve	3159	1622	884	270.83	1.384	0.031	92.07	9.92	949	-70	1	0.772	0.786
Río Navarro-Río Sombrero	VI	Protective Zone	2361	1758	214	76.75	0.683	0.109	81.12	26.51	683	-6	0	0.761	0.802
Río Oro (estatal)	NR	National Wildlife Refuge	19	0	2	21.15	0.004	0.012	1.51	11.53	16	-868	0	0.777	0.757
Río Pacuare	VI	Forest Reserve	989	423	159	157.34	2.824	0.042	93.87	17.93	740	237	0	0.743	0.834
Río Piro (privado)	NR	National Wildlife Refuge	197	120	31	0.41	0.002	0.001	97.16	5.78	2	38	0	0.804	0.837
Río Tiribi	VI	Protective Zone	2193	1877	146	8.48	0.090	0.002	77.38	31.36	113	-13	0	0.543	0.668
Río Toro	VI	Protective Zone	2339	1810	173	52.96	0.158	0.195	76.7	32.16	1374	24	0	0.802	0.835
Romelia (mixto)	NR	National Wildlife Refuge	125	51	34	2.89	0.014	0.010	75.37	40.64	52	-4	0	0.619	0.666

Saimiri (mixto)	NR	National Wildlife Refuge	231	83	49	1.62	0.001	0.002	96.86	6.7	3	1	0	0.776	0.766
Santa Rosa	II	National Park	202	0	1	1021.09	3.812	0.482	24.3	35.12	3231	-1186	57	0.271	0.284
Santuario Ecológ (privado)	NR	National Wildlife Refuge	367	142	90	4.05	0.033	0.005	94.74	14.4	2	0	0	0.740	0.806
Surtubal (privado)	NR	National Wildlife Refuge	1364	1021	173	1.47	0.045	0.000	95.37	5.27	0	0	0	0.778	0.874
Taboga	VI	Forest Reserve	136	45	28	3.64	0.006	0.007	73.87	26.8	15	-14	6	0.696	0.736
Talamanca Range-La Amistad Reserves / La Amistad National Park	NA	World Heritage Site	3803	1300	1063	6855.7	16.797	0.263	92.75	8.01	9866	-189	12	0.827	0.861
Tamarindo	NR	Ramsar Site, Wetland of International Importance	26	11	4	5.35	0.040	0.007	61.3	36.57	20	-174	1	0.639	0.668
Tapantí-Macizo Cerro la Muerte	NR	National Park	3341	1952	799	694.82	0.248	0.009	90.36	5.22	6357	-5626	0	0.825	0.861
Tenorio	VI	Protective Zone	1215	818	154	67.6	0.542	0.023	85.7	25.16	1077	411	0	0.699	0.725
Tivives	VI	Protected Zone	191	63	52	29.83	1.025	0.123	59.6	37.2	922	-7019	17	0.675	0.690
Tortuguero	VI	Protective Zone	47	20	6	67.37	1.809	0.012	4.28	19.4	380	162	0	0.041	0.043
Tortuguero	II	National Park	316	11	28	944.73	0.455	0.012	4.28	19.4	199	-167	1	0.041	0.043
Transilvania (privado)	VI	National Wildlife Refuge	407	246	78	0.81	0.004	0.000	93.22	16.09	1	0	0	0.807	0.777
Volcán Irazú	II	National Park	3429	3010	227	24.07	0.058	0.127	76.84	28.75	502	208	0	0.663	0.739
Volcán Poás	II	National Park	2706	2092	361	78.59	0.476	0.127	84.18	24.18	1543	703	0	0.775	0.797
Volcán Tenorio	II	National Park	1908	872	318	154.63	1.168	0.050	90.59	16.43	2950	1918	0	0.754	0.744
Volcán Turrialba	Ib	National Park	3318	2927	181	15.03	2.666	0.012	72.92	30.68	366	-583	0	0.698	0.545
Werner Sauter (mixto)	VI	National Wildlife Refuge	199	98	28	2.31	0.024	0.000	91.44	19.62	3	-16	1	0.796	0.818
Zona Emerg Volc Arenal	VI	Forest Reserve	603	503	43	2.89	0.088	0.000	74.38	35.56	484	208	1	0.695	0.735

REFERENCES

Achard, F., R. DeFries, H. Eva, M. Hansen, P. Mayaux, and H. J. Stibig. 2007. "Pan-tropical monitoring of deforestation." *Environmental Research Letters* 2 (4):045022.

Achard, Frédéric, Giacomo Grassi, Martin Herold, Maurizio Teobaldelli, and Danilo Mollicone. 2008. "Use of satellite remote sensing in LULUCF sector." Background paper at the IPCC Expert Meeting.

Acharya, Bhoj Kumar, Basundhara Chettri, and Lalitha Vijayan. 2011. "Distribution pattern of trees along an elevation gradient of Eastern Himalaya, India." *Acta Oecologica-International Journal of Ecology* 37 (4):329-336. doi: 10.1016/j.actao.2011.03.005.

Andam, Kwaw S, Paul J Ferraro, Alexander Pfaff, G Arturo Sanchez-Azofeifa, and Juan A Robalino. 2008. "Measuring the effectiveness of protected area networks in reducing deforestation." *Proceedings of the National Academy of Sciences* 105 (42):16089-16094.

Asner, Gregory, Joseph Mascaro, Helene Muller-Landau, Ghislain Vieilledent, Romuald Vaudry, Maminiaina Rasamoelina, Jefferson Hall, and Michiel van Breugel. 2012a. "A universal airborne LiDAR approach for tropical forest carbon mapping." *Oecologia* 168 (4):1147-1160. doi: 10.1007/s00442-011-2165-z.

Asner, Gregory P, Joseph Mascaro, Helene C Muller-Landau, Ghislain Vieilledent, Romuald Vaudry, Maminiaina Rasamoelina, Jefferson S Hall, and Michiel van Breugel. 2012b. "A universal airborne LiDAR approach for tropical forest carbon mapping." *Oecologia* 168 (4):1147-1160.

Austin, M. P., J. G. Pausas, and A. O. Nicholls. 1996. "Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia." *Australian Journal of Ecology* 21 (2):154-164. doi: 10.1111/j.1442-9993.1996.tb00596.x.

Aynekulu, Ermias, Raf Aerts, Pieter Moonen, Manfred Denich, Kindeya Gebrehiwot, Tor-Gunnar Vagen, Wolde Mekuria, and Hans Juergen Boehmer. 2012. "Altitudinal variation and conservation priorities of vegetation along the Great Rift Valley escarpment, northern Ethiopia." *Biodiversity and Conservation* 21 (10):2691-2707. doi: 10.1007/s10531-012-0328-9.

Bergen, K. M., S. J. Goetz, R. O. Dubayah, G. M. Henebry, C. T. Hunsaker, M. L. Imhoff, R. F. Nelson, G. G. Parker, and V. C. Radeloff. 2009. "Remote sensing of vegetation 3-D structure for biodiversity and habitat: Review and implications for lidar and radar spaceborne missions." *Journal of Geophysical Research-Biogeosciences* 114:13. doi: 10.1029/2008jg000883.

Bertrand, Romain, Jonathan Lenoir, Christian Piedallu, Gabriela Riofrio-Dillon, Patrice de Ruffray, Claude Vidal, Jean-Claude Pierrat, and Jean-Claude Gegout. 2011. "Changes in plant community composition lag behind climate warming in lowland forests." *Nature* 479 (7374):517-520. doi: 10.1038/nature10548.

Bhattarai, Khem Raj, and Ole R. Vetaas. 2006. "Can Rapoport's rule explain tree species richness along the Himalayan elevation gradient, Nepal?" *Diversity and Distributions* 12 (4):373-378. doi: 10.1111/j.1366-9516.2006.00244.x.

Bhuyan, Putul, ML Khan, and RS Tripathi. 2003. "Tree diversity and population structure in undisturbed and human-impacted stands of tropical wet evergreen forest in Arunachal Pradesh, Eastern Himalayas, India." *Biodiversity & Conservation* 12 (8):1753-1773.

Blair, J. B., and M. A. Hofton. 1999. "Modeling laser altimeter return waveforms over complex vegetation using high-resolution elevation data." *Geophysical Research Letters* 26 (16):2509-2512. doi: 10.1029/1999gl010484.

Blair, J. Bryan, Michelle Hofton, and David Lloyd Rabine. 2006. Processing of NASA LVIS elevation and canopy (LGE, LCE and LGW) data products, version 1.01. edited by Code 694 NASA Goddard Space Flight Center.

Borchert, R. 1998. "Responses of tropical trees to rainfall seasonality and its long-term changes." *Climatic Change* 39 (2-3):381-393. doi: 10.1023/a:1005383020063.

Brodie, Jedediah, Eric Post, and William F. Laurance. 2012. "Climate change and tropical biodiversity: a new focus." *Trends in Ecology & Evolution* 27 (3):145-150. doi: 10.1016/j.tree.2011.09.008.

Brown, Sandra. 1997. *Estimating biomass and biomass change of tropical forests: a primer*. Vol. 134: Food & Agriculture Org.

Burnett, Michael R, Peter V August, James H Brown, and Keith T Killingbeck. 1998. "The Influence of Geomorphological Heterogeneity on Biodiversity I. A Patch-Scale Perspective." *Conservation Biology* 12 (2):363-370.

Cardelus, C. L., R. K. Colwell, and J. E. Watkins. 2006. "Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak." *Journal of Ecology* 94 (1):144-156. doi: 10.1111/j.1365-2745.2005.01052.x.

Carpenter, C. 2005. "The environmental control of plant species density on a Himalayan elevation gradient." *Journal of Biogeography* 32 (6):999-1018. doi: 10.1111/j.1365-2699.2005.01249.x.

Cayuela, L., J. M. Benayas, A. Justel, and J. Salas-Rey. 2006. "Modelling tree diversity in a highly fragmented tropical montane landscape." *Global Ecology and Biogeography* 15 (6):602-613. doi: 10.1111/j.1466-822x.2006.00255.x.

Chambers, Jeffrey Q., Gregory P. Asner, Douglas C. Morton, Liana O. Anderson, Sassan S. Saatchi, Fernando D. B. Espírito-Santo, Michael Palace, and Carlos Souza. 2007. "Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests." *Trends in Ecology & Evolution* 22 (8):414-423.

Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Diaz. 2000. "Consequences of changing biodiversity." *Nature* 405 (6783):234-242. doi: 10.1038/35012241.

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Folster, F. Fromard, N. Higuchi, T. Kira, J. P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riera, and T. Yamakura. 2005. "Tree allometry and improved estimation of carbon stocks and balance in tropical forests." *Oecologia* 145 (1). doi: 10.1007/s00442-005-0100-x.

Chave, J., H. C. Muller-Landau, T. R. Baker, T. A. Easdale, H. ter Steege, and C. O. Webb. 2006a. "Regional and phylogenetic variation of wood density across 2456 Neotropical tree species." *Ecol Appl* 16 (6):2356-67.

Chave, Jerome, Maxime Réjou-Méchain, Alberto Búrquez, Emmanuel Chidumayo, Matthew S Colgan, Welington BC Delitti, Alvaro Duque, Tron Eid, Philip M Fearnside, and Rosa C Goodman. 2014. "Improved allometric models to estimate the aboveground biomass of tropical trees." *Global change biology* 20 (10):3177-3190.

Chave, Jérôme;, Helene C; Muller-Landau, Timothy R; Baker, Tomás A; Easdale, Hans; ter Steege, and Campbell Webb. 2006b. "Regional and phylogenetic variation of wood density across 2456 neotropical tree species." *Ecological applications* 16 (6):2356-2367.

Churchill, SP, H Balslev, E Forero, and et al. 1995. "Biodiversity and conservation of neotropical Montane Forests - Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium, The New York Botanical Garden, 21-26 June 1993 - Introduction." *Biodiversity and Conservation of Neotropical Montane Forests*:R11-R14.

Clark, David B, and Deborah A Clark. 2000. "Landscape-scale variation in forest structure and biomass in a tropical rain forest." *Forest ecology and management* 137 (1):185-198.

Clark, David B., Johanna Hurtado, and Sassan S. Saatchi. 2015. "Tropical rain forest structure, tree growth and dynamics along a 2700-m elevational transect in Costa Rica." *PloS one* 10 (4):e0122905.

Condit, R., S. P. Hubbell, J. V. Lafrankie, R. Sukumar, N. Manokaran, R. B. Foster, and P. S. Ashton. 1996. "Species-area and species-individual relationships for tropical trees: A comparison of three 50-ha plots." *Journal of Ecology* 84 (4). doi: 10.2307/2261477.

Connell, Joseph H. 1978. "Diversity in tropical rain forests and coral reefs." *Science* 199 (4335):1302-1310.

Deutsch, Curtis A, Joshua J Tewksbury, Raymond B Huey, Kimberly S Sheldon, Cameron K Ghalambor, David C Haak, and Paul R Martin. 2008. "Impacts of climate warming on terrestrial ectotherms across latitude." *Proceedings of the National Academy of Sciences* 105 (18):6668-6672.

Dijkstra, T. K. 2014. "Ridge regression and its degrees of freedom." *Quality & Quantity* 48 (6):3185-3193. doi: 10.1007/s11135-013-9949-7.

Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler, and J. Wisniewski. 1994. "CARBON POOLS AND FLUX OF GLOBAL FOREST ECOSYSTEMS." *Science* 263 (5144):185-190. doi: 10.1126/science.263.5144.185.

Doumenge, C., D. Gilmour, M. R. Perez, and J. Blockhus. 1995. "TROPICAL MONTANE CLOUD FORESTS - CONSERVATION STATUS AND MANAGEMENT ISSUES." *Tropical Montane Cloud Forests* 110:24-37.

Drake, Jason B., Ralph O Dubayah, Robert G. Knox, David B. Clark, and J.B. Blair. 2002. "Sensitivity of large-footprint lidar to canopy structure and biomass in a neotropical rainforest." *Remote Sensing of Environment* 81 (CHECK).

Drake, Jason B., Ralph O. Dubayah, David B. Clark, Robert G. Knox, J. Bryan Blair, Michelle A. Hofton, Robin L. Chazdon, John F. Weishampel, and Steve Prince. 2002. "Estimation of tropical forest structural characteristics using large-footprint lidar." *Remote Sensing of Environment* 79 (2):305-319.

Dubayah, R. O., and J. B. Drake. 2000. "Lidar remote sensing for forestry." *Journal of Forestry* 98 (6):44-46.

Dubayah, R. O., S. L. Sheldon, D. B. Clark, M. A. Hofton, J. B. Blair, G. C. Hurtt, and R. L. Chazdon. 2010. "Estimation of tropical forest height and biomass dynamics using lidar remote sensing at La Selva, Costa Rica." *Journal of Geophysical Research: Biogeosciences* 115 (G2).

Edenhofer, Ottmar, Ramon Pichs-Madruga, Youba Sokona, Kristin Seyboth, Patrick Matschoss, Susanne Kadner, Timm Zwickel, Patrick Eickemeier, Gerrit Hansen, and Steffen Schlömer. 2011. "IPCC special report on renewable energy sources and climate change mitigation." *Prepared By Working Group III of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK.*

Fagan, Matthew, and Ruth S DeFries. 2009. *Measurement and Monitoring of the World's Forests: A Review and Summary of Remote Sensing Technical Capability, 2009-2015*: Resources for the Future.

FAO. 2010. "Global Forest Resource Assessment, Main report." *FAO Forestry Paper* 163:340.

Favrichon, Vincent. 1994. "Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise."

FCPF-CF, FOREST CARBON PARTNERSHIP FUND – CARBON FUND. 2013. "Chair's Summary Online." Seventh Meeting (CF7). Paris, France.

Fearnside, Philip M. 1997. "Wood density for estimating forest biomass in Brazilian Amazonia." *Forest ecology and management* 90 (1):59-87.

Feeley, K. J., T. W. Gillespie, and J. W. Terborgh. 2005. "The utility of spectral indices from Landsat ETM+ for measuring the structure and composition of tropical dry forests." *Biotropica* 37 (4):508-519. doi: 10.1111/j.1744-7429.2005.00069.x.

Feeley, Kenneth J, Miles R Silman, Mark B Bush, William Farfan, Karina Garcia Cabrera, Yadvinder Malhi, Patrick Meir, Norma Salinas Revilla, Mireya Natividad Raurau Quisiyupanqui, and Sassan Saatchi. 2011. "Upslope migration of Andean trees." *Journal of Biogeography* 38 (4):783-791.

Feeley, Kenneth J., Johanna Hurtado, Sassan Saatchi, Miles R. Silman, and David B. Clark. 2013. "Compositional shifts in Costa Rican forests due to climate-driven species migrations." *Global Change Biology* 19 (11):3472-3480. doi: 10.1111/gcb.12300.

Feeley, Kenneth J., and Miles R. Silman. 2010. "Biotic attrition from tropical forests correcting for truncated temperature niches." *Global Change Biology* 16 (6):1830-1836. doi: 10.1111/j.1365-2486.2009.02085.x.

Fernandez-Ordonez, Yolanda, Brigitte Leblon, and Jesus Soria-Ruiz. 2009. *Forest Inventory using Optical and Radar Remote Sensing*: INTECH Open Access Publisher.

FONAFIFO, CONAFOR. 2012. "Ministry of Environment." *Lessons Learned for REDD+ from PES and Conservation Incentive Programs. Examples from Costa Rica, Mexico, and Ecuador*.

Fricker, G. A., J. A. Wolf, S. S. Saatchi, and T. W. Gillespie. 2015. "Predicting spatial variations of tree species richness in tropical forests from high-resolution remote sensing." *Ecological Applications* 25 (7):1776-1789. doi: 10.1890/14-1593.1.

Friedman, J., T. Hastie, and R. Tibshirani. 2010. "Regularization Paths for Generalized Linear Models via Coordinate Descent." *Journal of Statistical Software* 33 (1):1-22.

GEF, GLOBAL ENVIRONMENTAL FACILITY. 2005. Project Executive Summary: Mainstreaming Market-Based Instruments for Environmental Management.

Gentry, A. H. 1988. "CHANGES IN PLANT COMMUNITY DIVERSITY AND FLORISTIC COMPOSITION ON ENVIRONMENTAL AND GEOGRAPHICAL GRADIENTS." *Annals of the Missouri Botanical Garden* 75 (1):1-34. doi: 10.2307/2399464.

Ghalambor, Cameron K, Raymond B Huey, Paul R Martin, Joshua J Tewksbury, and George Wang. 2006. "Are mountain passes higher in the tropics? Janzen's hypothesis revisited." *Integrative and Comparative Biology* 46 (1):5-17.

Giacomo, Grassi, Monni Suvi, Federici Sandro, Achard Frederic, and Mollicone Danilo. 2008. "Applying the conservativeness principle to REDD to deal with the uncertainties of the estimates." *Environmental Research Letters* 3 (3):035005.

Giglio, Louis, Ivan Csiszar, and Christopher O Justice. 2006. "Global distribution and seasonality of active fires as observed with the Terra and Aqua Moderate Resolution

Imaging Spectroradiometer (MODIS) sensors." *Journal of Geophysical Research: Biogeosciences* 111 (G2).

Giglio, Louis, Jacques Descloitres, Christopher O Justice, and Yoram J Kaufman. 2003. "An enhanced contextual fire detection algorithm for MODIS." *Remote sensing of environment* 87 (2-3):273-282.

Gillespie, T. W., S. Saatchi, S. Pau, S. Bohlman, A. P. Giorgi, and S. Lewis. 2009. "Towards quantifying tropical tree species richness in tropical forests." *International Journal of Remote Sensing* 30 (6):1629-1634. doi: 10.1080/01431160802524552.

Girardin, Cecile A. J., William Farfan-Rios, Karina Garcia, Keneth J. Feeley, Peter M. Jorgensen, Alejandro Araujo Murakami, Leslie Cayola Perez, Renate Seidel, Narel Paniagua, Alfredo F. Fuentes Claros, Carla Maldonado, Miles Silman, Norma Salinas, Carlos Reynel, David A. Neill, Martha Serrano, Carlos J. Caballero, Maria de los Angeles La Torre Cuadros, Maria J. Macia, Timothy J. Killeen, and Yadvinder Malhi. 2014. "Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects." *Plant Ecology & Diversity* 7 (1-2):161-171. doi: 10.1080/17550874.2013.820806.

Giraud, Christophe. 2015. *Introduction to High-Dimensional Statistics*. Boca Raton, Florida: Chapman & Hall/CRC.

Giriraj, A., M. S. R. Murthy, and B. R. Ramesh. 2008. "VEGETATION COMPOSITION, STRUCTURE AND PATTERNS OF DIVERSITY: A CASE STUDY FROM THE TROPICAL WET EVERGREEN FORESTS OF THE WESTERN GHATS, INDIA." *Edinburgh Journal of Botany* 65 (3):447-468. doi: 10.1017/s0960428608004952.

Givnish, T. J. 1999. "On the causes of gradients in tropical tree diversity." *Journal of Ecology* 87 (2):193-210. doi: 10.1046/j.1365-2745.1999.00333.x.

GOC, Government of Costa Rica. 2009. IV Informe de País sobre el Convenio de la Diversidad Biológica. San José, Costa Rica.

GOC, Government of Costa Rica. 2011. "Propuesta para la Preparación de Readiness R-PP. Submitted to FCPF April 2011."

GOC, Government of Costa Rica. 2013. "Emissions Reduction Program Idea Note (ER-PIN). ."

Goetz, Scott, Daniel Steinberg, Ralph Dubayah, and Bryan Blair. 2007. "Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA." *Remote Sensing of Environment* 108 (3):254-263. doi: 10.1016/j.rse.2006.11.016.

Gotelli, N. J., and R. K. Colwell. 2001. "Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness." *Ecology Letters* 4 (4):379-391. doi: 10.1046/j.1461-0248.2001.00230.x.

Grainger, Alan. 2008. "Difficulties in tracking the long-term global trend in tropical forest area." *Proceedings of the National Academy of Sciences* 105 (2):818-823.

Grieve, I. C., J. Proctor, and S. A. Cousins. 1990. "SOIL VARIATION WITH ALTITUDE ON VOLCAN BARVA, COSTA-RICA." *Catena* 17 (6):525-534. doi: 10.1016/0341-8162(90)90027-b.

Groombridge, Brian, Martin D Jenkins, and Martin Jenkins. 2002. *World atlas of biodiversity: earth's living resources in the 21st century*: Univ of California Press.

Guo, Qinfeng, Douglas A Kelt, Zhongyu Sun, Hongxiao Liu, Liangjun Hu, Hai Ren, and Jun Wen. 2013. "Global variation in elevational diversity patterns." *Scientific reports* 3:3007.

Hansen, Matthew C, Peter V Potapov, Rebecca Moore, Matt Hancher, SAa Turubanova, Alexandra Tyukavina, David Thau, SV Stehman, SJ Goetz, and TR Loveland. 2013. "High-resolution global maps of 21st-century forest cover change." *science* 342 (6160):850-853.

Hansen, Matthew C., Stephen V. Stehman, and Peter V. Potapov. 2010. "Quantification of global gross forest cover loss." *Proceedings of the National Academy of Sciences* 107 (19):8650-8655. doi: 10.1073/pnas.0912668107.

Hijmans, RJ, SE Cameron, JL Parra, PG Jones, and A Jarvis. 2004. The WorldClim interpolated global terrestrial climate surfaces. Version 1.3.

Hofton, M. A., L. E. Rocchio, J. B. Blair, and R. Dubayah. 2002. "Validation of Vegetation Canopy Lidar sub-canopy topography measurements for a dense tropical forest." *Journal of Geodynamics* 34 (3-4):491-502. doi: 10.1016/s0264-3707(02)00046-7.

Holdridge, LR. 1966. "The life zone system." *Adansonia* 6 (2):199-203.

Homeier, Juergen, Siegmar- W. Breckle, Sven Guenter, Ruetger T. Rollenbeck, and Christoph Leuschner. 2010. "Tree Diversity, Forest Structure and Productivity along Altitudinal and Topographical Gradients in a Species-Rich Ecuadorian Montane Rain Forest." *Biotropica* 42 (2):140-148. doi: 10.1111/j.1744-7429.2009.00547.x.

Houghton, R. A. 2003. "Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850-2000." *Tellus Series B-Chemical and Physical Meteorology* 55 (2). doi: 10.1034/j.1600-0889.2003.01450.x.

http://www.teamnetwork.org/. 2015. "Tropical Ecology Assessment & Monitoring Network: Early Warning System for Nature." http://www.teamnetwork.org.

Hurlbert, Stuart H. 1971. "The Nonconcept of Species Diversity: A Critique and Alternative Parameters." *Ecology* 52 (4):577-586. doi: 10.2307/1934145.

Huston, Michael. 1979. "A general hypothesis of species diversity." *American naturalist*:81-101.

Hutchinson, G Evelyn. 1953. "The concept of pattern in ecology." *Proceedings of the Academy of Natural Sciences of Philadelphia* 105:1-12.

IUCN, UNEP-WCMC and. 2017. "Protected Planet: Costa Rica, Latin America & Caribbean ". UNEP-WCMC and IUCN. Accessed January 1. Available at: www.protectedplanet.net.

Jantz, Samuel M., Brian Barker, Thomas M. Brooks, Louise P. Chini, Qiongyu Huang, Rachel M. Moore, Jacob Noel, and George C. Hurtt. 2015. "Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation." *Conservation Biology* 29 (4):1122-1131. doi: 10.1111/cobi.12549.

Janzen, Daniel H. 1967. "Why mountain passes are higher in the tropics." *The American Naturalist* 101 (919):233-249.

Joppa, Lucas N, Scott R Loarie, and Stuart L Pimm. 2008. "On the protection of "protected areas"." *Proceedings of the National Academy of Sciences* 105 (18):6673-6678.

Kreft, Holger, and Walter Jetz. 2007. "Global patterns and determinants of vascular plant diversity." *Proceedings of the National Academy of Sciences of the United States of America* 104 (14):5925-5930. doi: 10.1073/pnas.0608361104.

Kuper, Joe. 2013. "REDD in Costa Rica." Global Canopy Programme Consultant. http://theredddesk.org/countries/costa-rica.

Kuper, W., H. Kreft, J. Nieder, N. Koster, and W. Barthlott. 2004. "Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests." *Journal of Biogeography* 31 (9):1477-1487. doi: 10.1111/j.1365-2699.2004.01093.x.

La Torre-Cuadros, Mdla, S. Herrando-Perez, and K. R. Young. 2007. "Diversity and structural patterns for tropical montane and premontane forests of central Peru, with an assessment of the use of higher-taxon surrogacy." *Biodiversity and Conservation* 16 (10):2965-2988. doi: 10.1007/s10531-007-9155-9.

Lambin, Eric F, and Patrick Meyfroidt. 2010. "Land use transitions: Socio-ecological feedback versus socio-economic change." *Land use policy* 27 (2):108-118.

Larjavaara, Markku, and Helene C Muller-Landau. 2012. "Temperature explains global variation in biomass among humid old-growth forests." *Global Ecology and Biogeography* 21 (10):998-1006.

Laurance, William F, Jeffrey Sayer, and Kenneth G Cassman. 2014. "Agricultural expansion and its impacts on tropical nature." *Trends in ecology & evolution* 29 (2):107-116.

Lawton, Robert O. 1984. "Ecological constraints on wood density in a tropical montane rain forest." *American Journal of Botany*:261-267.

Lefsky, Michael A., Warren B. Cohen, Geoffrey G. Parker, and David J. Harding. 2002. "Lidar remote sensing for ecosystem studies: Lidar, an emerging remote sensing technology that directly measures the three-dimensional distribution of plant canopies, can accurately estimate vegetation structural attributes and should be of particular interest to forest, landscape, and global ecologists." *BioScience* 52 (1):19-30.

Lenoir, Jonathan, Jean-Claude Gegout, Antoine Guisan, Pascal Vittoz, Thomas Wohlgemuth, Niklaus E. Zimmermann, Stefan Dullinger, Harald Pauli, Wolfgang Willner, and Jens-Christian Svenning. 2010. "Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate." *Ecography* 33 (2):295-303. doi: 10.1111/j.1600-0587.2010.06279.x.

Leroux, Shawn J, Meg A Krawchuk, Fiona Schmiegelow, Steven G Cumming, Kim Lisgo, Lee G Anderson, and Mirela Petkova. 2010. "Global protected areas and IUCN designations: do the categories match the conditions?" *Biological conservation* 143 (3):609-616.

Levin, Simon A. 1992. "The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture." *Ecology* 73 (6):1943-1967.

Liang, Jingjing, Joseph Buongiorno, Robert A Monserud, Eric L Kruger, and Mo Zhou. 2007. "Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality." *Forest Ecology and Management* 243 (1):116-127.

Lieberman, D., M. Lieberman, R. Peralta, and G. S. Hartshorn. 1996a. "Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica." *Journal of Ecology* 84 (2):137-152. doi: 10.2307/2261350.

Lieberman, Diana, Milton Lieberman, Rodolfo Peralta, and Gary S Hartshorn. 1996b. "Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica." *Journal of Ecology*:137-152.

Livingstone, David N. 1993. *The Geographical Tradition*: Wiley-Blackwell.

Lomolino, M. V. 2001. "Elevation gradients of species-density: historical and prospective views." *Global Ecology and Biogeography* 10 (1):3-13. doi: 10.1046/j.1466-822x.2001.00229.x.

Lumley, Thomas. 2017. "R package: leaps. Regression Subset Selection. Thomas Lumley based on Fortran code by Alan Miller."

Macarthur, R., and P. H. Klopfer. 1961. "POPULATION EFFECTS OF NATURAL SELECTION." *American Naturalist* 95 (885):195-&. doi: 10.1086/282175.

MacArthur, Robert H. 1965. "Patterns of species diversity." *Biological reviews* 40 (4):510-533.

MacArthur, Robert H. 1972. *Geographical ecology; patterns in the distribution of species*. New York: Harper & Row.

MacDonald, Glen M. 2003. *Biogeography: Space, Time and Life*: John Wiley & Sons Inc.

Magurran, Anne E., and Brian J. McGill. 2011. *Biological Diversity: frontiers in measurement and assessment*: Oxford University Press.

McCain, C. M. 2004. "The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica." *Journal of Biogeography* 31 (1):19-31.

McCain, Christy M. 2009. "Vertebrate range sizes indicate that mountains may be 'higher'in the tropics." *Ecology letters* 12 (6):550-560.

McCain, Christy M, and John-Arvid Grytnes. 2001. "Elevational gradients in species richness." *e LS*.

Miles, Lera, Adrian C Newton, Ruth S DeFries, Corinna Ravilious, Ian May, Simon Blyth, Valerie Kapos, and James E Gordon. 2006. "A global overview of the conservation status of tropical dry forests." *Journal of Biogeography* 33 (3):491-505.

Moser, Gerald, Dietrich Hertel, and Christoph Leuschner. 2007. "Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in Ecuador and a pan-tropical meta-analysis." *Ecosystems* 10 (6):924-935.

Muenchow, Jannes, Henrik von Wehrden, Eric Frank Rodriguez, Rodolfo Arismendiz Rodriguez, Fabian Bayer, and Michael Richter. 2013. "WOODY VEGETATION OF A PERUVIAN TROPICAL DRY FOREST ALONG A CLIMATIC GRADIENT DEPENDS MORE ON SOIL THAN ANNUAL PRECIPITATION." *Erdkunde* 67 (3):241-248. doi: 10.3112/erdkunde.2013.03.03.

Muller-Landau, Helene C. 2004. "Interspecific and Inter-site Variation in Wood Specific Gravity of Tropical Trees1." *Biotropica* 36 (1):20-32.

NASA. "Land, Vegetation, and Ice Sensor." Goddard Space National Aeronautics and Space Administration http://lvis.gsfc.nasa.gov.

Nelson, Bruce W, Rita Mesquita, Jorge LG Pereira, Silas Garcia Aquino De Souza, Getulio Teixeira Batista, and Luciana Bovino Couto. 1999. "Allometric regressions for improved estimate of secondary forest biomass in the central Amazon." *Forest ecology and management* 117 (1-3):149-167.

Nepstad, Daniel, Stephan Schwartzman, Barbara Bamberger, Marcio Santilli, D Ray, Peter Schlesinger, P Lefebvre, Ane Alencar, Elaine Prinz, and Greg Fiske. 2006. "Inhibition of Amazon deforestation and fire by parks and indigenous lands." *Conservation Biology* 20 (1):65-73.

Nicolson, M. 1996. "Humboldtian plant geography after Humboldt: The link to ecology." *British Journal for the History of Science* 29 (102):289-310.

Niklas, Karl J. 1992. *Plant biomechanics: an engineering approach to plant form and function*: University of Chicago press.

Nogueira, Euler Melo, Philip Martin Fearnside, and Bruce Walker Nelson. 2008. "Normalization of wood density in biomass estimates of Amazon forests." *Forest Ecology and Management* 256 (5):990-996.

Nogues-Bravo, D., M. B. Araujo, T. Romdal, and C. Rahbek. 2008. "Scale effects and human impact on the elevational species richness gradients." *Nature* 453 (7192):216-U8. doi: 10.1038/nature06812.

Olivares, Ingrid, Jens-Christian Svenning, Peter M. van Bodegom, and Henrik Balslev. 2015. "Effects of Warming and Drought on the Vegetation and Plant Diversity in the Amazon Basin." *Botanical Review* 81 (1):42-69. doi: 10.1007/s12229-014-9149-8.

Pau, S., T. W. Gillespie, and E. M. Wolkovich. 2012. "Dissecting NDVI-species richness relationships in Hawaiian dry forests." *Journal of Biogeography* 39 (9):1678-1686. doi: 10.1111/j.1365-2699.2012.02731.x.

Pfaff, A., S. Kerr, L. Lipper, R. Cavatassi, B. Davis, J. Hendy, and G. A. Sanchez-Azofeifa. 2007. "Will buying tropical forest carbon benefit the poor? Evidence from Costa Rica." *Land Use Policy* 24 (3):600-610. doi: 10.1016/j.landusepol.2006.01.003.

Pfaff, Alexander, Juan Robalino, G Arturo Sanchez-Azofeifa, Kwaw S Andam, and Paul J Ferraro. 2009. "Park location affects forest protection: Land characteristics cause differences in park impacts across Costa Rica." *The BE Journal of Economic Analysis & Policy* 9 (2).

Pires, Joao Murca, and Ghillean T Prance. 1985. *The vegetation types of the Brazilian Amazon*. New York, USA: Pergamon Press.

R Core Team. "R: A Language and Environment for Statistical Computing." In. Vienna, Austria. https://www.R-project.org.

Rahbek, C. 1995. "THE ELEVATIONAL GRADIENT OF SPECIES RICHNESS - A UNIFORM PATTERN." *Ecography* 18 (2):200-205. doi: 10.1111/j.1600-0587.1995.tb00341.x.

Rahbek, C. 2005. "The role of spatial scale and the perception of large-scale species-richness patterns." *Ecology Letters* 8 (2):224-239. doi: 10.1111/j.1461-0248.2004.00701.x.

Reyes, Gisel, Sandra Brown, Jonathan Chapman, and Ariel E Lugo. 1992. "Wood densities of tropical tree species." *Gen. Tech. Rep. SO-88. New Orleans, LA: US Dept of Agriculture, Forest Service, Southern Forest Experiment Station. 15 p.* 88.

Robinson, Chelsea, Sassan Saatchi, David Clark, Johanna Hurtado Astaiza, Anna Hubel, and Thomas Gillespie. 2018. "Topography and Three-Dimensional Structure Can Estimate Tree Diversity along a Tropical Elevational Gradient in Costa Rica." *Remote Sensing* 10 (4):629.

Rohde, K. 1992. "LATITUDINAL GRADIENTS IN SPECIES-DIVERSITY - THE SEARCH FOR THE PRIMARY CAUSE." *Oikos* 65 (3):514-527. doi: 10.2307/3545569.

Rose, R. A., D. Byler, J. R. Eastman, E. Fleishman, G. Geller, S. Goetz, L. Guild, H. Hamilton, M. Hansen, R. Headley, J. Hewson, N. Horning, B. A. Kaplin, N. Laporte, A. Leidner, P. Leinagruber, J. Morisette, J. Musinsky, L. Pintea, A. Prados, V. C. Radeloff, M. Rowen, S. Saatchi, S. Schil, K. Tabor, W. Turner, A. Vodacek, J. Vogelnaann, M. Wegmann, and D. Wilkie. 2015. "Ten ways remote sensing can contribute to conservation." *Conservation Biology* 29 (2):350-359. doi: 10.1111/cobi.12397.

Rosenzweig, M. L. 1992. "SPECIES-DIVERSITY GRADIENTS - WE KNOW MORE AND LESS THAN WE THOUGHT." *Journal of Mammalogy* 73 (4):715-730. doi: 10.2307/1382191.

Rudel, Thomas. 2005. *Tropical forests: paths of destruction and regeneration*: Columbia University Press.

Saatchi, Sassan, Miriam Marlier, Robin L. Chazdon, David B. Clark, and Ann E. Russell. 2011. "Impact of spatial variability of tropical forest structure on radar estimation of aboveground biomass." *Remote Sensing of Environment* 115 (11). doi: 10.1016/j.rse.2010.07.015.

Saatchi, Sassan S., Nancy L. Harris, Sandra Brown, Michael Lefsky, Edward T. A. Mitchard, William Salas, Brian R. Zutta, Wolfgang Buermann, Simon L. Lewis, Stephen Hagen, Silvia Petrova, Lee White, Miles Silman, and Alexandra Morel. 2011. "Benchmark map of forest carbon stocks in tropical regions across three continents." *Proceedings of the National Academy of Sciences* 108 (24):9899-9904. doi: 10.1073/pnas.1019576108.

Sanchez-Azofeifa, G. A., G. C. Daily, A. S. P. Pfaff, and C. Busch. 2003. "Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover change." *Biological Conservation* 109 (1):123-135.

Sanchez-Azofeifa, G. A., A. Pfaff, J. A. Robalino, and J. P. Boomhower. 2007. "Costa Rica's payment for environmental services program: Intention, implementation, and impact." *Conservation Biology* 21 (5):1165-1173. doi: 10.1111/j.1523-1739.2007-00751.x.

Sanchez-Azofeifa, G., R. C. Harriss, and D. L. Skole. 2001. "Deforestation in Costa Rica: A quantitative analysis using remote sensing imagery." *Biotropica* 33 (3):378-384. doi: 10.1646/0006-3606(2001)033[0378:dicraq]2.0.co;2.

Sánchez-Azofeifa, Gerardo Arturo, and Carlos A Quesada-Mateo. 1995. "Deforestation, carbon dynamics, and sustainable mitigation measures in Costa Rica-The Puerto Viejo de Sarapiquí case study. Deforestación, dinámica del carbono y medidas sostenibles de mitigación en Costa Rica-Estudio de caso de Puerto Viejo de Sarapiquí." *Interciencia.* 20 (6):396-400.

Sandbrook, C., F. Nelson, W. M. Adams, and A. Agrawal. 2010. "Carbon, forests and the REDD paradox." *Oryx* 44 (3):330-334. doi: 10.1017/s0030605310000475.

Schroeder, Wilfrid, Patricia Oliva, Louis Giglio, and Ivan A Csiszar. 2014. "The New VIIRS 375 m active fire detection data product: Algorithm description and initial assessment." *Remote Sensing of Environment* 143:85-96.

Simonson, William D., Harriet D. Allen, and David A. Coomes. 2012. "Use of an airborne lidar system to model plant species composition and diversity of Mediterranean oak forests." *Conservation Biology* 26 (5):840-850.

SINAC, Sistema Nacional de Áreas de Conservación. 2009. IV Informe de País al Convenio sobre la Diversidad Biológica. In *Mimeografiado*. San Jose, Costa Rics: GEF-PNUD.

Slik, J. W. F., G. Paoli, K. McGuire, I. Amaral, J. Barroso, M. Bastian, L. Blanc, F. Bongers, P. Boundja, C. Clark, M. Collins, G. Dauby, Y. Ding, J. L. Doucet, E. Eler, L. Ferreira, O. Forshed, G. Fredriksson, J. F. Gillet, D. Harris, M. Leal, Y. Laumonier, Y. Malhi, A. Mansor, E. Martin, K. Miyamoto, A. Araujo-Murakami, H. Nagamasu, R. Nilus, E. Nurtjahya, A. Oliveira, O. Onrizal, A. Parada-Gutierrez, A. Permana, L. Poorter, J. Poulsen, H. Ramirez-Angulo, J. Reitsma, F. Rovero, A. Rozak, D. Sheil, J. Silva-Espejo, M. Silveira, W. Spironelo, H. ter Steege, T. Stevart, G. E. Navarro-Aguilar, T. Sunderland, E. Suzuki, J. W. Tang, I. Theilade, G. van der Heijden, J. van Valkenburg, T. Van Do, E. Vilanova, V. Vos, S. Wich, H. Woll, T. Yoneda, R. G. Zang, M. G. Zhang, and N. Zweifel. 2013. "Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics." *Global Ecology and Biogeography* 22 (12):1261-1271. doi: 10.1111/geb.12092.

Solomon, Susan. 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC*. Vol. 4: Cambridge University Press.

Stadtmüller, Thomas. 1987. *Cloud forests in the humid tropics: a bibliographic review*: The United Nations University.

Sun, G., K. J. Ranson, D. S. Kimes, J. B. Blair, and K. Kovacs. 2008. "Forest vertical structure from GLAS: An evaluation using LVIS and SRTM data." *Remote Sensing of Environment* 112 (1):107-117. doi: 10.1016/j.rse.2006.09.036.

Suzuki, Eizi. 1999. "Diversity in specific gravity and water content of wood among Bornean tropical rainforest trees." *Ecological Research* 14 (3):211-224.

Tang, Hao, Ralph Dubayah, Anu Swatantran, Michelle Hofton, Sage Sheldon, David B. Clark, and Bryan Blair. 2012. "Retrieval of vertical LAI profiles over tropical rain forests using waveform lidar at La Selva, Costa Rica." *Remote Sensing of Environment* 124:242-250.

Tilman, David. 1988. *Plant strategies and the dynamics and structure of plant communities*: Princeton University Press.

Trumbore, S, P Brando, and Henrik Hartmann. 2015. "Forest health and global change." *Science* 349 (6250):814-818.

Turner, Ian Mark. 2001. *The ecology of trees in the tropical rain forest*: Cambridge University Press.

Unger, Malte, Juergen Homeier, and Christoph Leuschner. 2013. "Relationships among leaf area index, below-canopy light availability and tree diversity along a transect from tropical lowland to montane forests in NE Ecuador." *Tropical Ecology* 54 (1):33-45.

Van der Werf, Guido R, Douglas C Morton, Ruth S DeFries, Jos GJ Olivier, Prasad S Kasibhatla, Robert B Jackson, G James Collatz, and James T Randerson. 2009. "CO 2 emissions from forest loss." *Nature geoscience* 2 (11):737.

Vazquez, J. A., and T. J. Givnish. 1998. "Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan." *Journal of Ecology* 86 (6):999-1020.

Whittaker, R. H. 1972. "EVOLUTION AND MEASUREMENT OF SPECIES DIVERSITY." *Taxon* 21 (2-3). doi: 10.2307/1218190.

Whittaker, R. J., K. J. Willis, and R. Field. 2001. "Scale and species richness: towards a general, hierarchical theory of species diversity." *Journal of Biogeography* 28 (4). doi: 10.1046/j.1365-2699.2001.00563.x.

Whittaker, Robert H, and William A Niering. 1975. "Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient." *Ecology* 56 (4):771-790.

Wiens, J. A. 1989. "SPATIAL SCALING IN ECOLOGY." *Functional Ecology* 3 (4):385-397. doi: 10.2307/2389612.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. "Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis." *Annual Review of Ecology Evolution and Systematics* 34:273-309. doi: 10.1146/annurev.ecolsys.34.012103.144032.

Wolf, J. H. D., and F. Alejandro. 2003. "Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico." *Journal of Biogeography* 30 (11):1689-1707. doi: 10.1046/j.1365-2699.2003.00902.x.

Wolf, Jeffrey A, Geoffrey A Fricker, Victoria Meyer, Stephen P Hubbell, Thomas W Gillespie, and Sassan S Saatchi. 2012. "Plant species richness is associated with canopy height and topography in a neotropical forest." *Remote Sensing* 4 (12):4010-4021.

Wright, S Joseph, Helene C Muller-Landau, Richard Condit, and Stephen P Hubbell. 2003. "Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees." *Ecology* 84 (12):3174-3185.

Yackulic, Charles B, Matthew Fagan, Meha Jain, Amir Jina, Yili Lim, Miriam Marlier, Robert Muscarella, Patricia Adame, Ruth DeFries, and Maria Uriarte. 2011. "Biophysical and socioeconomic factors associated with forest transitions at multiple spatial and temporal scales." *Ecology and Society* 16 (3):15.

Zanne, Amy E, G Lopez-Gonzalez, David A Coomes, Jugo Ilic, Steven Jansen, Simon L Lewis, Regis B Miller, Nathan G Swenson, Michael C Wiemann, and Jerome Chave. 2009. "Global wood density database."