

Reconstructing succession: Historical and chronosequence approaches to  
understanding the assembly of forest communities

by

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**A thesis submitted to the  
DEPARTMENT OF BIOLOGY  
FACULTY OF NATURAL SCIENCES  
UNIVERSITY OF PUERTO RICO  
RÍO PIEDRAS CAMPUS**

In partial fulfillment of the requirements for the degree of

**MASTER OF SCIENCE IN BIOLOGY**

October, 2019

San Juan, Puerto Rico

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This thesis has been accepted by the

**DEPARTMENT OF BIOLOGY  
FACULTY OF NATURAL SCIENCES  
UNIVERSITY OF PUERTO RICO  
RÍO PIEDRAS CAMPUS**

In partial fulfillment for the requirements of

**MASTER OF SCIENCE IN BIOLOGY**

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Dedicated to my mother, who introduced me to this forest as a child.

## ACKNOWLEDGEMENTS

I am grateful to Jess Zimmerman for his unwavering patience and support, and for showing me to how to read a forest. I'd like to thank my graduate committee, Drs. Nick Brokaw, Tamara Heartsill Scalley, and Mei Yu for their guidance and enthusiasm, and Dr. Miguel Acevedo for teaching me to think quantitatively. Dr. María Uriarte was a dedicated collaborator and provided the post-hurricane data. The National Science Foundation provided support for my graduate studies through the NSF DEB-1050957 to Uriarte, Zimmerman and the Luquillo Long-term Ecological Research (LTER) Program (DEB-1546686).

This thesis rests on the labor of numerous field crews, research managers, and LTER staff involved in the Chronosequence Project over the years. I am indebted to Chris Nytch, Seth Rifkin, Eda Melendez-Colom, Andrew McFadden and Wanda Ruiz for their meticulous data management and administration. I am also grateful to fellow graduate students or interns David Clark, Carlos Ortiz, Alberto Cruz, Norman Greenhawk, Melissa Salva, Benjamin Branoff and Daniela Yaffar for their help along the way.

The Smithsonian Center for Tropical Forest Research/ Forest GEO network generously provided support for four weeks of forest dynamics analytical workshops. I thank Stuart Davies, Sean McMahon, Nate Swenson, Gabriel Arellano, Jessie Needham, Natalia Umaña, Aaron Hogan, and especially Rutuja Chitra-Tarak and Mauro Lepore for their mentorship, kindness, and generosity with their time. The Organization for Tropical Studies (OTS) provided funding for coursework in Costa Rica and connected me to a passionate group of Latin American biologists. I am grateful to Jenny Stynoski and Patricia Salerno for their wisdom and support. I cannot overstate the contributions of the Forest Geo and OTS networks to the completion of my master's work.

International Institute of Tropical Forestry (IITF) staff made the historical part of this project possible. I am eternally grateful to Jorge Morales of the IITF library for procuring historical documents. Evelyn Pagán, Gisel Reyes, and Pete Weaver also assisted with historical records. Jerry Bauer drove me to historical sites in Sabana and introduced me to residents with intimate knowledge of the forest. His encouragement has inspired me to continue documenting forest history in the future. Nora Alvarez and Bill Gould of the IITF Caribbean Climate Hub provided the office space, supplies, and access to electricity I needed to continue this research after Hurricane María, and have been important research mentors. Olga Ramos and Maya Quiñones graciously provided GIS assistance and access to aerial photographs, and Sandra Soto and Jessica Castro contributed GIS support and lots of laughter. The extraordinary support of the Hub team during challenging times will always be remembered.

Finally, I'd like to acknowledge the people I've leaned on most throughout this process. Eddie Perez and Michelle Lopez-Lorenzo stuck with me throughout; Tio Japito provided history books and regular campus coffee breaks; Tio Joey and Carolina Bolivar contributed historical knowledge and homecooked meals; and Titi Anina and my brother Hector Miguel were bastions of support. I thank my parents Hector Picón and Michelle Ruiz and my partner Kris Harmon for all that they have sacrificed. To all of you: this accomplishment is yours.



## TABLE OF CONTENTS

|   |      |
|---|------|
| RECONSTRUCTING SUCCESSION: HISTORICAL AND CHRONOSEQUENCE APPROACHES TO UNDERSTANDING THE ASSEMBLY OF FOREST COMMUNITIES     |      |
| ACKNOWLEDGEMENTS  | III  |
| LIST OF TABLES  | VIII |
| LIST OF FIGURES   | X    |
| CHAPTER 1   | 2    |
| LAND USE HISTORY OF FIVE LONG-TERM FOREST RESEARCH SITES IN THE EL VERDE AND SABANA, EL YUNQUE NATIONAL FOREST, PUERTO RICO |      |
| ABSTRACT  | 2    |
| INTRODUCTION  | 4    |
| METHODS   | 5    |
| RESULTS AND DISCUSSION  | 9    |
| I. Forest age and past land use   | 10   |
| II. Reforestation era tree planting   | 19   |
| III. Timber harvest   | 27   |
| IV. Silvicultural Management  | 38   |
| CONCLUSIONS   | 56   |
| LITERATURE CITED  | 60   |
| CHAPTER 2   | 66   |
| SUCCESSIONAL TRAJECTORIES OF POST-AGRICULTURAL FORESTS AT THE BOUNDARY OF EL YUNQUE NATIONAL FOREST, PUERTO RICO            |      |
| ABSTRACT  | 66   |
| INTRODUCTION  | 68   |



|                                      |     |
|--------------------------------------|-----|
| METHODS                              | 71  |
| RESULTS                              | 77  |
| I. Stand structure                   | 77  |
| II. Species diversity and turnover   | 79  |
| III. Stand composition               | 80  |
| IV. Hurricane Irma and Maria effects | 87  |
| DISCUSSION                           | 92  |
| CONCLUSIONS                          | 110 |
| LITERATURE CITED                     | 113 |
| APPENDICES                           | 123 |

## LIST OF TABLES

### CHAPTER 1

|  |    |
|--|----|
| Table 1. Description of forest plots in the El Verde and Sabana Research Areas of El Yunque National Forest, Puerto Rico .....   | 7  |
| Table 2. Presence or absence in El Verde study plots of species reported by Marrero (1947) as planted in Tract 13 of El Yunque, Puerto Rico between 1936 and 1945 .....  | 24 |
| Table 3. Presence or absence in Sabana study plots of species reported by Marrero (1947) as planted in Tract 53 of El Yunque, Puerto Rico between 1936 and 1945 .....  | 26 |
| Table 4. Working circles for timber management in El Yunque National Forest, Puerto Rico characterized using aerial photos, low altitude aerial reconnaissance, and a ground cruise in 1948. Areas with small, inaccessible volumes of timber were not cruised. Adapted from Wadsworth (1949) .....                                    | 33 |
| Table 5. Species favored for sawtimber or polewood production in tabonuco forest type of El Yunque National Forest, Puerto Rico between 1952 and 1965. Species are listed exclusively in the highest category they occurred in during that period. Compiled from Wadsworth 1952b, Wadsworth 1955, Wadsworth 1957, and Muñoz 1965 ..... | 40 |
| Table 6. Silvicultural treatment options proposed by Wadsworth (1955) for a pilot forest management project in El Yunque National Forest, Puerto Rico. Treatments were meant to be selected depending on stand conditions .....  | 43 |
| Table 7. Forest management units in timber production areas of El Yunque National Forest, Puerto Rico in 1957 (Wadsworth 1957) and in 1965 (Muñoz 1965) timber management plans .....  | 45 |
| Table 8. Chronosequence plot locations within forest management units of El Yunque National Forest, Puerto Rico timber management areas in 1965 and factors determining order of silvicultural treatment (Muñoz 1965). Compartment (CPT) numbers before and after reorganization of management units (1964) are provided .....         | 48 |

### CHAPTER 2

|   |    |
|---|----|
| Table 1. Description of forest plots in the El Verde and Sabana Research Areas of El Yunque National Forest, Puerto Rico .....  | 74 |
| Table 2. Stand characteristics of chronosequence plots in El Yunque National Forest, Puerto Rico in census years 1 and 6 .....  | 78 |
| Table 3. Rarefied species richness ( $S$ at 1000 stems), Simpson's diversity ( $1/D$ ), and the exponent of Shannon's entropy ( $e^H$ ) of chronosequence plots in El Yunque, Puerto Rico in census years 1 and 6 ..... | 80 |
| Table 4. Annual species turnover within chronosequence plots in El Yunque National  |    |

|  |     |
|--|-----|
| Forest, Puerto Rico based on stem densities. Percent species gain, percent species loss and percent turnover (gain + loss) are relative to total species richness across two consecutive census years .....  | 81  |
| Table 5. Relative densities (RD) of the 10 most abundant stems within chronosequence plots in El Yunque National Forest, Puerto Rico in census years 1 and 6 .....   | 83  |
| Table 6. Tree mortality rates among species with $\geq 10$ individuals $\geq 10$ cm dbh across chronosequence plots EV-M, SB-M, and SB-O in El Yunque National Forest, Puerto Rico following 2017 Hurricanes Irma and María .....                          | 92  |
| Appendix A. Topographic exposure to peak hurricane winds for chronosequence plots in El Yunque National Forest, Puerto Rico during Hurricanes Hugo (1989), Irma (2017) and María (2017). Values range from 0 (no exposure) to 252 (maximum exposure) ..... | 123 |
| Appendix D. Species encountered in chronosequence plot SB-Y in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016. Nomenclature follows Gann et al. 2015-2019 .....  | 125 |
| Appendix E. Species encountered in chronosequence plot SB-M in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016 .....  | 126 |
| Appendix F. Species encountered in chronosequence plot SB-O in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016 .....  | 127 |
| Appendix G. Species encountered in chronosequence plot EV-M in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016 .....  | 128 |
| Appendix H. Species encountered in chronosequence plot EV-O in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016 .....  | 129 |

## LIST OF FIGURES

### CHAPTER 1

|   |    |
|---|----|
| Figure 1. Map of the location of El Yunque National Forest within Puerto Rico (inset) and of El Verde and Sabana research plots and field stations within El Yunque National Forest .....   | 7  |
| Figure 2. Aerial photographs of chronosequence plot EV-M in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (scale = 1:15,000) and plot (scale = 1:2,000) levels. The approximate western border of EYNF is shown in white .....  | 12 |
| Figure 3. Aerial photographs of chronosequence plot EV-O in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (scale = 1:15,000) and plot (scale = 1:2,000) levels. The approximate western border of EYNF is shown in white .....  | 14 |
| Figure 4. Aerial photographs of chronosequence plot SB-Y in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (scale = 1:10,000) and plot (scale = 1:2,000) levels. The approximate northern border of EYNF is shown in white .....   | 16 |
| Figure 5. Aerial photographs of chronosequence plot SB-M in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (scale = 1:10,000) and plot (scale = 1:2,000) levels. The approximate northern border of EYNF is shown in white .....   | 17 |
| Figure 6. Aerial photographs of chronosequence plot SB-O in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (scale = 1:10,000) and plot (scale = 1:2,000) levels. The approximate northern border of EYNF is shown in white .....   | 18 |
| Figure 7. Pizá plantation (top) and Sabana plantations (bottom) in El Yunque National Forest, Puerto Rico as drawn by Marrero (1947), shown with chronosequence study plots (small red rectangles) and the Luquillo Forest Dynamics Plot (northernmost red rectangle) .....   | 21 |
| Figure 8. Subset of the Espíritu Santo Working Circle and its compartments (8 inches: 1 mile) within El Yunque National Forest, Puerto Rico from Wadsworth (1949), shown with chronosequence study plots (small red rectangles), the Luquillo Forest Dynamics Plot (northernmost red rectangle), and the El Verde Field Station (yellow star) ..... | 35 |
| Figure 9. Subset of the Cristal Working Circle and its compartments (8 inches: 1 mile) within El Yunque National Forest, Puerto Rico from Wadsworth (1949), shown with chronosequence study plots (red rectangles) and the Sabana Field Research Station  |    |

|  |    |
|--|----|
| (yellow star) .....  | 38 |
| Figure 10. A 1965 map of El Verde Working Circle, El Yunque National Forest, Puerto Rico from Muñoz (1965) shown with chronosequence study plots (red rectangles), El Verde field station (yellow star), roads (Highway 186 in red), and rivers (blue). From North to South, study plots include the Luquillo Forest Dynamics Plot, EV-O, and EV-M .....   | 47 |
| Figure 11. Plantation establishment (yellow), plantation care (thatched), and timber stand improvement (green) conducted in fiscal years (a) 1956 and (b) 1957 in Compartment No. 2 of El Yunque National Forest, Puerto Rico. Maps from CNF (1969); shown with chronosequence study plots (left to right) SB-M and SB-Y, roads (red), and the Sabana Field Research Station (yellow star) and Climate Warming Experiment (red triangle) ..... | 51 |
| Figure 12. Timber stand improvement (green), plantation care (thatched), and timber sales (orange) in fiscal years (a) 1961 and (b) 1959 in Compartment No. 2 of El Yunque National Forest, Puerto Rico. Maps from CNF (1969); shown with chronosequence study plots (left to right) SB-M and SB-Y, roads (red), and the Sabana Field Research Field Research Station (yellow star) and Climate Warming Experiment (red triangle) .....        | 52 |
| Figure 13. A 1965 map of Sabana Working Circle, El Yunque National Forest, Puerto Rico from Muñoz (1965) shown with chronosequence study plots (red rectangles), roads (Highway 988 in red), rivers (blue), and the Sabana Field Research Station (yellow star) and Climate Warming Experiment (red triangle). From North to South, study plots include SB-Y, SB-M, and SB-O .....   | 53 |
| Figure 14. Timber stand improvement area (green) in Compartment No. 3 of El Yunque National Forest timber management area in fiscal years (a) 1961, (b) 1963 and (c) 1964. Maps from CNF (1969); shown with chronosequence plot SB-Y in red and Sabana (north-south) and Cristal (east-west) Rivers in blue .....  | 55 |

## CHAPTER 2

|   |    |
|---|----|
| Figure 1. Map of the location of El Yunque National Forest within Puerto Rico (inset) and of El Verde and Sabana research plots and field stations within El Yunque National Forest .....   | 73 |
| Figure 2. Size class distributions of chronosequence plots in El Yunque National Forest, Puerto Rico in census years 1 and 6 .....  | 78 |
| Figure 3. Mean Bray-Curtis dissimilarity between all pairs of chronosequence plots in El Yunque National Forest, Puerto Rico. Mean dissimilarity values average all available census years and are expressed as percentages ..... | 84 |

|  |     |
|--|-----|
| Figure 4. Changes in species composition within chronosequence plots in El Yunque National Forest, Puerto Rico from census year 1 to year 6. Changes are expressed as Bray-Curtis dissimilarities between year 1 composition and the composition in each other census year ..... | 85  |
| Figure 5. Changes in pairwise Bray-Curtis dissimilarity values for species composition among chronosequence plots in El Yunque National Forest, Puerto Rico from census year 1 to year 6. EV-O is excluded because of a lack of annual measurements .....                        | 86  |
| Figure 6. Predicted exposure to Hurricane Irma of chronosequence plots EV-M and EV-O and the Luquillo Forest Dynamics Plot in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white) .....                             | 87  |
| Figure 7. Predicted exposure to Hurricane María of chronosequence plots EV-M and EV-O and the Luquillo Forest Dynamics Plot in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white) .....                            | 88  |
| Figure 8. Predicted exposure to Hurricane Irma of chronosequence plots SB-Y, SB-M and SB-O in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white) .....   | 89  |
| Figure 9. Predicted exposure to Hurricane María of chronosequence plots SB-Y, SB-M and SB-O in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white) .....  | 89  |
| Figure 10. Tree mortality and damage among stems >10 cm dbh in response to 2017 Hurricanes Irma and María in three chronosequence plots in El Yunque National Forest, Puerto Rico .....  | 90  |
| Appendix B. Predicted exposure to Hurricane Hugo of chronosequence plots EV-M and EV-O and the Luquillo Forest Dynamics Plot in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white) .....                           | 124 |
| Appendix C. Predicted exposure to Hurricane Hugo of chronosequence plots SB-Y, SB-M, and SB-O in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white) .....  | 124 |



## CHAPTER 1

### **Land use history of five long-term forest research sites in the El Verde and Sabana, El Yunque National Forest, Puerto Rico**

#### ABSTRACT

Historical legacies can be important determinants of the structure, composition and dynamics of secondary forests recovering from agricultural conversion. Tracing the effects of historical processes on secondary tropical forests can lead to a better understanding of successional patterns and ecosystem states. Puerto Rico is an ideal place to study lasting legacies of human disturbance because of the widespread secondary forest growth following large-scale clearing for agriculture more than a century ago and because of the abundance of historical records produced during the recovery period. In this study we combine historical aerial photographs and land use records with tree census data from five forest plots in the El Verde and Sabana Research Areas of El Yunque National Forest differing in successional age to reconstruct forest recovery and identify land use legacies influencing secondary forest composition. We found variation in the type and intensity of land use among the forest plots and over time within agricultural disturbance and forest recovery periods that shaped local forest transformation. Enduring, localized human influences on tree communities include the presence of nonnative species planted for reforestation or silvicultural purposes that contribute to differences in species composition among plots of similar forest age. These findings can help researchers investigating the ecologies of El Verde and Sabana



areas to incorporate a historical perspective and inform our understanding and management of secondary forest stands recovering from human disturbance.

## INTRODUCTION

The majority of tropical forests worldwide are in some stage of recovery from past human disturbance (FAO 2012), yet successional patterns vary widely, and underlying processes are poorly understood (Arroyo-Rodriguez et al. 2015). Recent studies have questioned our views of secondary forest recovery as a deterministic process and called for more inquiry into sources of variation in stand dynamics, including historical contingencies (Norden et al. 2015).

While fine-scale environmental factors influencing the structure and composition of tropical forests are well-studied, the role of history is generally considered in broad strokes. This is due in part to the difficulty of tracing the sequence of historical events, both human and natural, that may have contributed to an ecosystem's present state. In temperate regions, which tend to have a greater availability of historical information, historical landscape reconstructions have provided a base of knowledge that ecologists can draw from to interpret current ecosystem patterns (Grossinger et al. 2007).

Puerto Rico is uniquely positioned to study the effects of historical processes on secondary tropical forest dynamics. Large-scale clearing for agriculture prior to the 1940's and subsequent, widespread forest recovery across the island (Rudel et al. 2000, Birdsey & Weaver 1987) has allowed the observation of ecological processes over succession (Grau et al. 2003). Frequent hurricane disturbance permits real-time observation of tree population dynamics and recovery strategies. Aerial photograph coverage dating to the 1930's provides information on past land use and landscape characteristics, and detailed records by the U.S. Forest Service provide descriptions of forest communities over a century.

Our objectives in this study are to reconstruct the recovery of secondary forests on the northern slopes of El Yunque National Forest following agricultural disturbance and to identify residual effects on present forest communities. We compile available historical information for five forest sites of varying age in the El Verde and Sabana research areas and forest census data from 2010 to 2016. Specifically, we describe the nature and spatial-temporal distribution of (i) past land cover and land use, (ii) reforestation efforts, (iii) timber extraction, and (iv) silvicultural management, and discuss links between century-scale landscape histories and the present structure and composition of forest stands.

## METHODS

### *Study site*

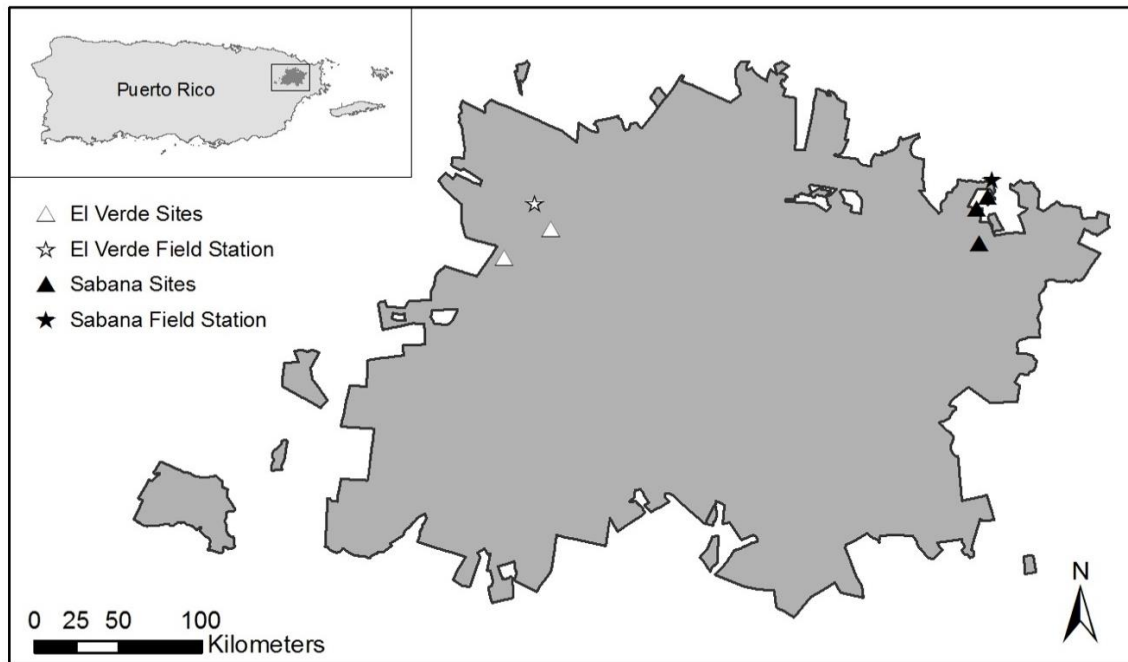
This study was conducted in two research areas along the northern border of El Yunque National Forest (also known as the Luquillo Experimental Forest) in the Luquillo Mountains of Puerto Rico (Figure 1). The Sabana Research Area (Sabana Field Research Station; 18.325, -65.730) is located in the northeastern corner of the national forest and is managed by the International Institute of Tropical Forestry (IITF) of the U.S. Forest Service. The El Verde Research Area (El Verde Field Station; 18.321, -65.820) is located in the northwestern part of the national forest and is managed by the University of Puerto Rico. Both research areas are classified as subtropical wet forest by the Holdridge life zone system (Ewel and Whitmore 1973) and fall within the tabonuco forest zone as they occur below 600 m in elevation (Brown et al. 1983). Rainfall is approximately 3500 mm/yr. The Luquillo Mountains have been affected by numerous

hurricanes over the past century that have caused defoliation, stem and branch damage, and tree mortality in parts of the forest. The most recent include Hurricane Hugo in 1989, Hurricane Georges in 1998, and Hurricanes Irma and María in September 2017. Prevailing winds and hurricane events tend to arrive from the ocean to the east; forests in north and northeast areas are considered most susceptible to hurricane winds (Van Beusekom et al. 2018).

Four forest plots differing in successional age were established to form a forest chronosequence across El Verde and Sabana Research Areas (hereafter El Verde and Sabana) (Table 1.). Plots range from 0.5 to 1 hectare (ha) in size and from 121-543 meters above sea level. Three are located in areas used for agriculture before being purchased by the U.S. Forest Service, while the fourth is located in an area of forest that to our knowledge has not been cut over or cleared for agriculture in the past century. Together the plots represent young, intermediate-aged, and old-growth forest. Estimates of forest age included in Table 1 are based on a previous study of land cover change at the periphery of El Yunque (Lugo et al. 2004).

For comparison with an additional mature forest site we include data on structure and composition from an existing plot within El Verde known as El Verde 3. El Verde 3 is a 0.72 ha plot established in 1943 by Frank Wadsworth as part of a network of 20 long-term plots to assess the growth of valuable timber species and has been censused every 1 to 12 years since, making it one of the longest continuously monitored forest lots in the Neotropics (Drew et al. 2009). Prior studies of El Verde and of this plot indicate it was forested in 1936 and that species characteristic of the tabonuco forest zone have remained dominant (Drew et al. 2009, Heartsill Scalley 2017,

Thompson et al. 2002). We refer to this plot as EV-O to indicate its old-growth structure and composition compared to the middle-aged plot EV-M.



**Figure 1.** Map of the location of El Yunque National Forest within Puerto Rico (inset) and of El Verde and Sabana research plots and field stations within El Yunque National Forest.

**Table 1.** Description of forest plots in the El Verde and Sabana Research Areas of El Yunque National Forest, Puerto Rico.

| Site            | Relative stage | ASAA (yr) | Elevation (m asl) | Aspect | Census period | Census year evaluated |
|-----------------|----------------|-----------|-------------------|--------|---------------|-----------------------|
| <u>Sabana</u>   |                |           |                   |        |               |                       |
| SB-Y            | Young          | 35-62     | 121               | E      | 2011-2016     | 2011                  |
| SB-M            | Intermediate   | >62       | 149               | E      | 2011-2016     | 2011                  |
| SB-O            | Old Growth     | Uncut     | 186               | E      | 2011-2016     | 2011                  |
| <u>El Verde</u> |                |           |                   |        |               |                       |
| EV-M            | Intermediate   | 62-76     | 543               | NW     | 2011-2016     | 2011                  |
| EV-O            | Old growth     | Uncut     | 400               | NW     | 1948-2015     | 2010                  |

*Notes:* ASAA = Age since agricultural abandonment. Census period is up to 2017. Censuses were annual except EV-O, which was intermittent until 2000 and every 5 years from 2000-2015.

### *Aerial photograph analysis*

Historical aerial photographs were used to determine the age, or time since agricultural abandonment, of each forest site. SB-O is considered old-growth forest because it was under closed-canopy forest in all aerial photographs. Even if clearing occurred in the past the closed canopy in 1936 photos suggests at least two decades of forest development had occurred, and thus at least 100 years of growth by the time of this study.

Aerial photographs from 1936 and 1951 pertaining to the four forest plots were used to evaluate changes in land cover and identify human activities in and around each plot. We acquired these photographs from the Puerto Rico Department of Natural Resources (DRNA) and the IITF Geospatial Lab. 1936 aerial photos were taken from west to east along north-south flight lines at a scale of 1:18,696, with images of the El Verde landscape taken on March 8 and of the Sabana landscape taken on April 7. The 1951 photos were taken along east-west flight lines at a scale of approximately 1:15,000, with images of both study areas taken on January 8. The photographs corresponding to our study plots were georeferenced in ArcGIS Desktop 10.5.1 using an orthorectified photomosaic published in 2010 by the Puerto Rico Planning Board (Puerto Rico Color Orthophotography, Oct 31, 2009- Jan 27, 2010, 1 square foot resolution).

### *Historical records*

We used information from historical maps, reports by foresters and land managers, and academic publications to further characterize past land use and identify human influences on the structure and composition of recovering forests. Historical

documents were obtained from U.S. Forest Service archives at the International Institute of Tropical Forestry and Catalina Service Center. These were supplemented with field observations by the authors (e.g. fence lines, ox cart trails) and conversations with local residents and U.S. Forest Service personnel. Historical information was combined with aerial imagery and tree census data to determine the spatial distribution of agricultural and forestry activities and detect legacies of prior land use on species composition.

### *Tree Census*

Tree census data allowed us to evaluate the impact of human activities on tree community composition and the distributions of particular species. Chronosequence sites were censused annually from 2011-2016 following the Center for Tropical Forest Science protocol (see Condit et al. 1998), but only data from 2011 was used in this chapter. All woody stems > 1 cm diameter at breast height (dbh) were measured, mapped, identified to species, and assessed for damage. We include in our analyses data from the 2010 census of EV-O. Census methods for EV-O are the same except that only woody stems >4 cm in diameter are measured.

## RESULTS AND DISCUSSION

El Yunque National Forest originally consisted of 5012 ha transferred to the U.S. federal government from the Spanish Crown in 1898 and declared a reserve in 1903. Its expansion to approximately 11,000 ha has occurred through donations, purchases, transfers, and exchanges of land with the Commonwealth of Puerto Rico and private landowners. A large portion of these lands were used for subsistence or commercial

agriculture before joining the reserve. The first boundary survey of El Yunque, conducted from 1915 to 1916 by the U.S. Department of the Interior (DOI), provides a record of land ownership and farm size in the areas planned for acquisition. From 1931 to 1949 the U.S. Forest Service purchased approximately 4450 ha in the Luquillo Mountains and 2400 ha in Toro Negro. The Luquillo purchases were primarily at the eastern boundary of the forest. Aerial photographs of El Yunque and surrounding areas taken by the DOI and its partners in 1936 and again in 1951, combined with maps from the 1916 boundary survey and records from the 1930's-1940's land acquisitions, provide a detailed picture of the landscapes of the El Verde and Sabana areas as forests on the flanks of the mountains began to recover from a century or more of agricultural use.

### ***I. Forest age and past land use***

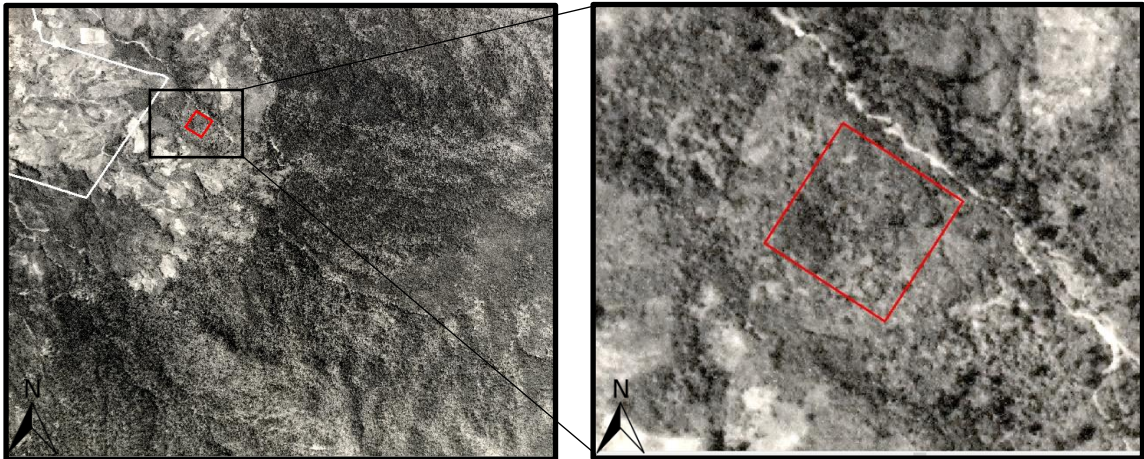
Aerial photographs from 1936 depict a partially deforested landscape in El Verde. The western part, where plot EV-M is located, is a highly transformed, agricultural landscape with little forest cover. In contrast, the landscape east of the Espíritu Santo River is densely forested and no human disturbance is visible in the photographs. To the northeast are plot EV-O and the El Verde Field Station, in a region largely forested but with canopy gaps revealing hurricane-damaged coffee plantations. The 1936 aerial photographs of Sabana reveal a heavily deforested landscape. Landcover is primarily agricultural with scattered patches of forest; plot locations range from having no forest cover (SB-Y) to having closed-canopy forest (SB-O).



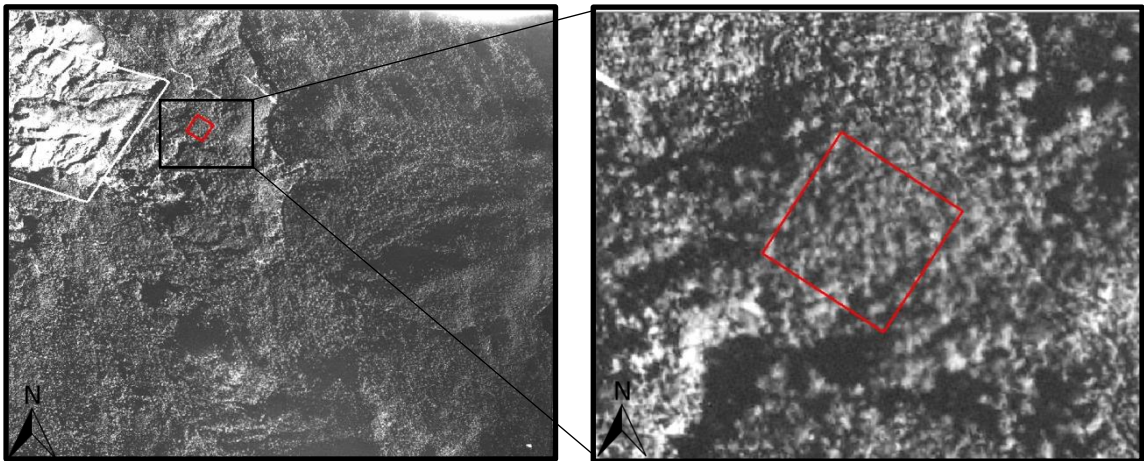
Large increases in forest area occurred in both the Sabana and El Verde areas from 1936 to 1951. Aerial photographs from 1951 demonstrate the recovery of forest cover in western El Verde from the Espiritu Santo River up to the western border of the forest, where an abrupt transition to non-forested land cover occurs. Road abandonment and roadbuilding activities are also evident. Forest recovery in Sabana from 1936-1951 was widespread but more scattered compared to El Verde. Vegetation appears in many previously cleared areas, forming a dense cover of shrubs and small trees or a sparse woodland with grass cover underneath. Natural encroachment of trees and shrubs onto former pasturelands is visible, and some smaller agricultural patches in 1936 are under a closed canopy in 1951.

Chronosequence plot EV-M is part of a parcel of land known as El Verde Tract 13 along the western border of the forest. This tract is a mid-elevation, high-rainfall area with rolling hills and heavy yellowish to red clay soils (Marrero 1947). In 1915 the tract was a 2,028-acre farm (820 ha) owned by the descendants of a man named Juan Pizá (DOI 1916). The bulk of this farm was purchased in 1938 by the U.S. Forest Service from Sagrario Aguado Rodriguez of Santurce, Puerto Rico for \$15.00. The purchase, totaling 1,951 acres (790 ha), was initiated in April of 1936 and completed in September of 1938 (CNF Acquisition Status Report). Aerial images of plot EV-M in 1936 (Figure 2) reveal shrub cover with only a few large trees. The presence of surrounding agricultural fields and a primitive road along the plot's northeast border, and the lack of a forest canopy, suggest recent agricultural or forestry activity. By 1951 a closed-canopy forest had formed over this site. Based on purchase records and signs of natural regeneration in the 1936 photos, we estimate this forest to be 75 years of age (since agricultural abandonment) at the start of this study in 2011.

1936



1951



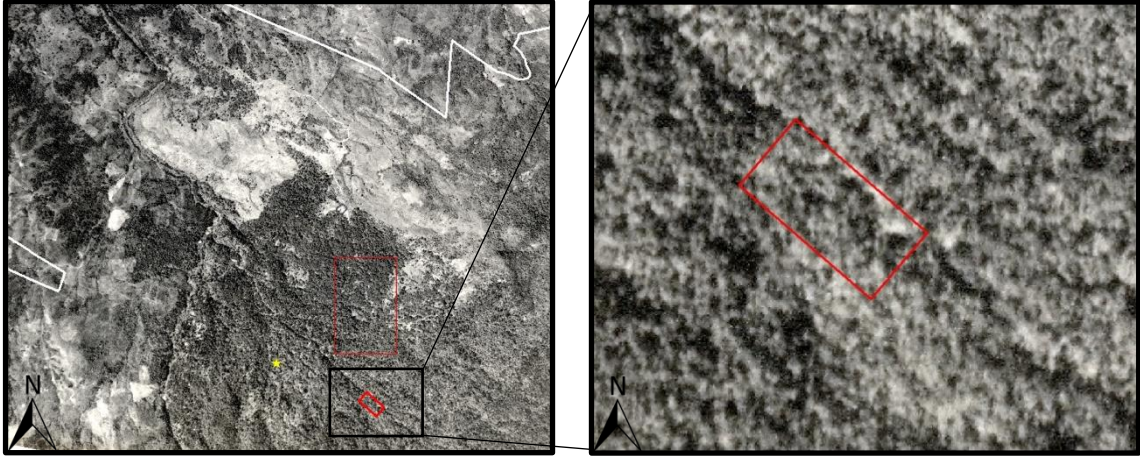
**Figure 2.** Aerial photographs of chronosequence plot EV-M in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (1:15,000) and plot (1:2,000) levels. The approximate western border of EYNF is shown in white.

Plot EV-O (or Wadsworth's Plot EV3) is located in Tract 11, another large, western parcel slightly higher in elevation and closer to the original Spanish Crownlands than Tract 13. The El Verde Field Station and 16-ha Luquillo Forest Dynamics Plot (LFDP) are also found within this tract. When it was initially surveyed in 1915, Tract 11 was a 1,071-acre farm (416 ha) called El Verde and owned by Arthur J. Harvey (DOI 1916). In September of 1934, the property (1, 027 acres or 433 ha) was purchased by the

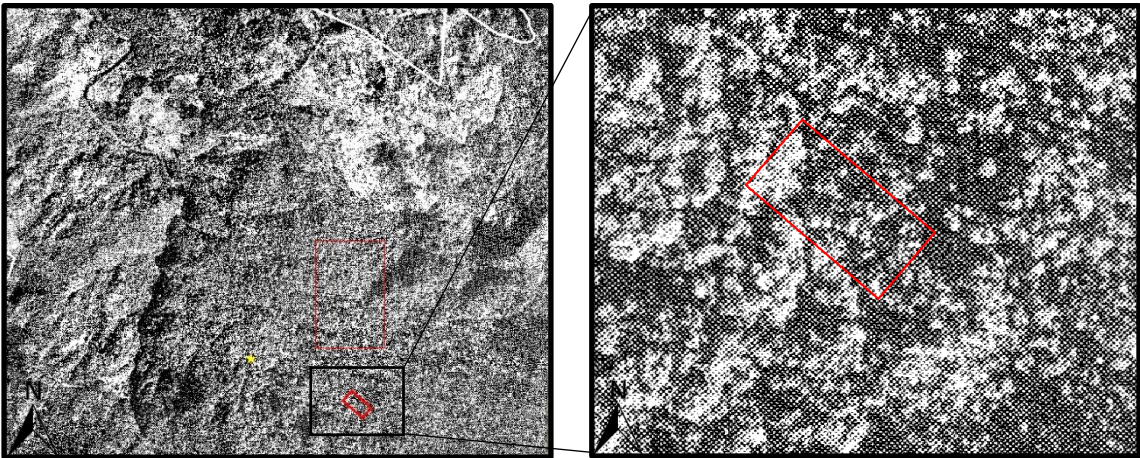
US Forest Service from the Keystone Plywood Corporation of York, Pennsylvania for a price of \$10.00 (CNF Acquisition Status Report). Previous studies of the land-use history of El Verde document that Keystone Plywood and Bliss Plywood corporations owned Tract 11 from 1924-1934 and harvested parts of it for timber and plywood in the 1920's. Cleared areas were planted with coffee or used for subsistence agriculture, until the widespread abandonment of the area after destruction by Hurricane San Felipe in 1928 (Thompson et al. 2002).

Though cultivation ceased after Tract 11's acquisition, timber harvest and management continued under U.S. Forest Service ownership (see sections III, IV). In 1943 Plot EV-O was chosen by Frank Wadsworth as a long-term site for studies of tree growth of timber species because it had not been previously cleared for agriculture, and because of its well-stocked nature and vigorous growth (Briscoe and Wadsworth 1970). Despite periodic disturbance, species characteristic of tabonuco forests (*Dacryodes-Sloanea* association) including *Dacryodes excelsa* (tabonuco), *Manilkara bidentata* (ausubo), *Sloanea berteriana* (cacao motillo), and *Prestoea montana* (sierra palm) have dominated the tree community since the plot was established (Drew 2009; Heartsill Scalley 2017). Aerial photographs of EV-O depict forest cover in both 1936 and 1951 (Figure 3). Although in 1936 gaps in the forest cover can be observed in surrounding areas, including within the LFDP, no large-scale clearing is evident within either plot. By 1951 these deforested patches have filled in and the forest edge occurs further north. This finding is consistent with prior studies on the land-use history of El Verde (Thompson et al. 2002).

1936



1951



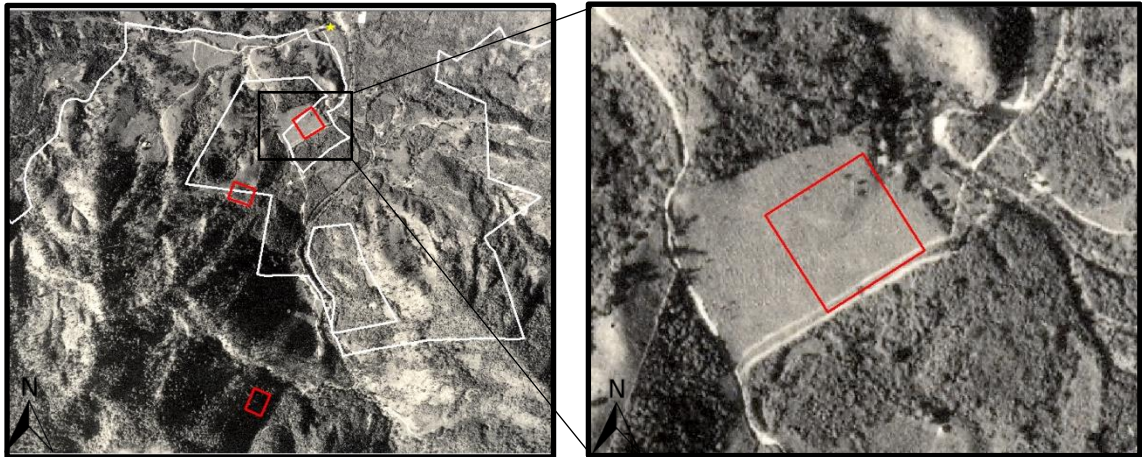
**Figure 3.** Aerial photographs of chronosequence plot EV-O in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (1:15,000) and plot (1:2,000) levels. The approximate western border of EYNF is shown in white.

All three Sabana plots form part of Sabana Tract 53, located in the northeast part of El Yunque and consisting of relatively gentle terrain along rivers and streams in valleys (Marrero 1947). In 1915, Tract 53 was a 300-acre farm (120 ha) known as “La Perla.” La Perla was owned by an American called Mr. MacFie who lived in Fajardo (DOI 1916). Tenant families or farm laborers cultivated coffee, oranges, and grapefruit on his property. Mr. MacFie left Puerto Rico around by the early 1920’s, leaving an

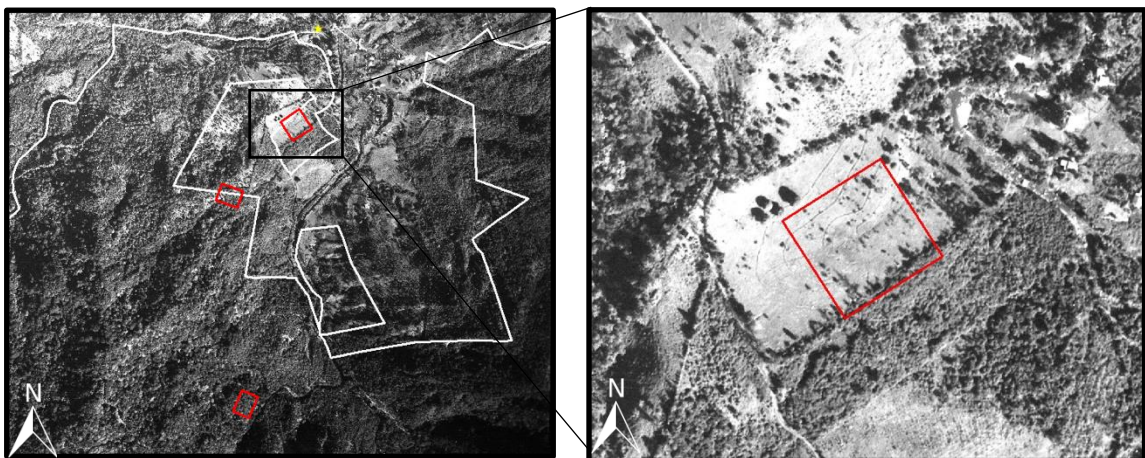
individual named Juan Cardona in charge of the farm, but his wife and children remained in the area (Angel Rosa Torres, in Robinson 1997). La Perla was likely no exception to the trend in the Sabana and Bisley area of large coffee plantations with absentee landowners where tenant families picked coffee and grew subsistence crops (García-Montiel 1994; Bauer 1987). Tract 53 was added to the national forest in 1935 by purchase from Gabriel Emmanuelli, who lived in San Juan. This 373-acre acquisition (150 ha) cost the U.S. Forest Service \$13.75 (CNF Acquisition Status Report). Though the condition of this tract at the time of purchase is unknown to us, prior land use history studies have documented heavy exploitation in the northern part of Tract 52, adjacent to and west of Tract 53, at the time of purchase. The northeast boundary of Tract 52 was in pasture and banana cultivation and the southeast area had been culled to varying extents (Scatena 1989, García-Montiel 1994).

Despite common ownership, the Sabana plots vary widely in topography and land use. The 1936 aerial photos (Figure 4) reveal that plots SB-Y and SB-M were not forested at the time of purchase. SB-Y lies within a well-maintained field, presumably pasture, with a farm road running along the southern boundary of the plot. Contour lines and a live fencerow suggest continued agricultural land use in 1951, although the farm road has been replaced by forest and a number of small trees or shrubs are scattered across the field. The forest stand that occupies this plot today is the youngest of our study plots; based on these images it was less than 60 years of age at the start of our study.

1936



1951

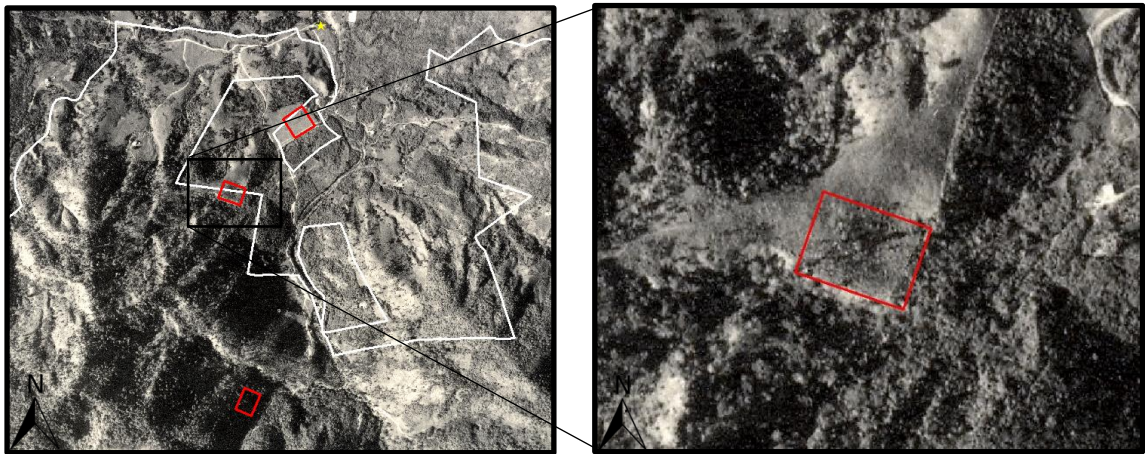


**Figure 4.** Aerial photographs of chronosequence plot SB-Y in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (scale = 1:10,000) and plot (scale = 1:2,000) levels. The approximate northern border of EYNF is shown in white.

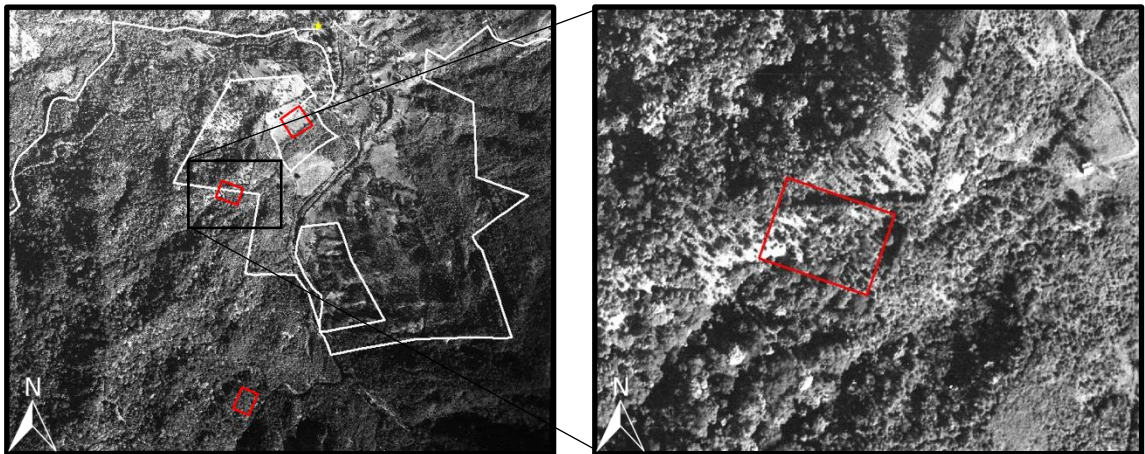
SB-M in 1936 is located in the southeastern corner of a cleared, northeast-facing hill slope, presumably also pasture (Figure 5). The southern and eastern boundaries of the plot are forested and a footpath along the eastern edge connects this field to the area of SB-Y. In 1951 SB-M consists of heterogenous, open-canopy forest, with some larger trees in the southern part and only sparse tree cover in the southwest corner of the plot.

A dense tree line trees cuts across the northern part of the plot, suggesting a property boundary. Based on these aerial photos, the tree community in this uneven-aged stand is between 60 and 75 years old.

**1936**



**1951**

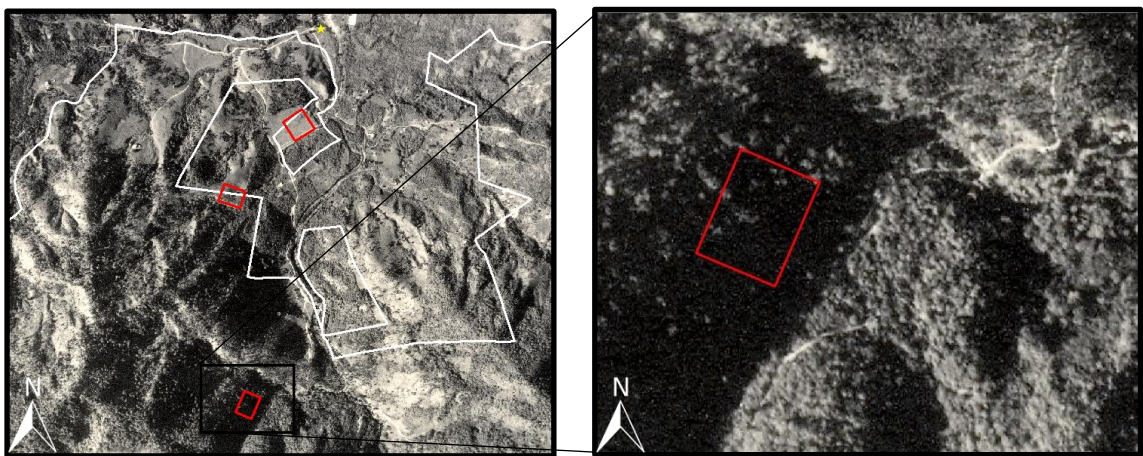


**Figure 5.** Aerial photographs of chronosequence plot SB-M in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (scale = 1:10,000) and plot (scale = 1:2,000) levels. The approximate northern border of EYNF is shown in white.

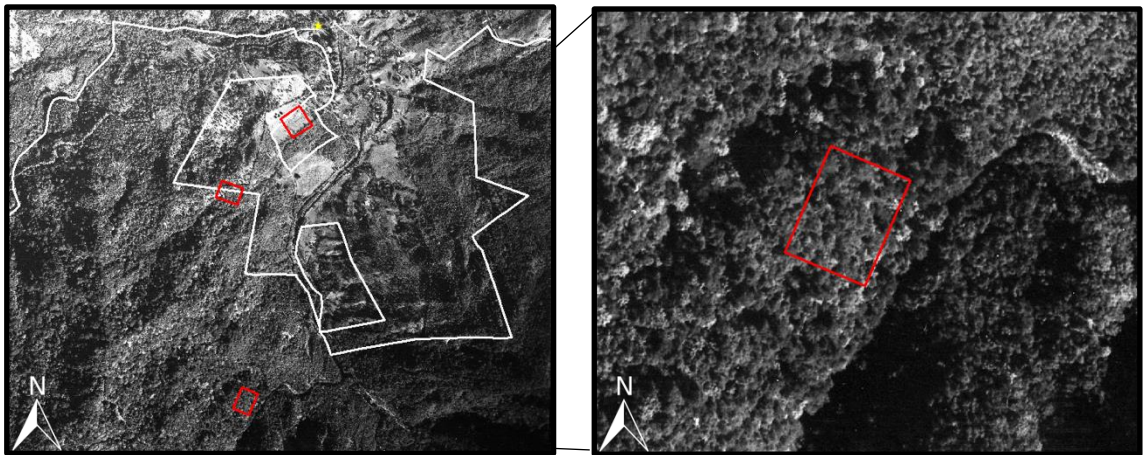
In 1936 SB-O in 1936 appears to be closed-canopy forest (Figure 6) The plot is located on a steep slope of a ridge adjacent to the Cristal River and is surrounded by

continuous forest cover. Across the Cristal River, a narrow path follows a parallel ridge, reaching flatter lands to the south or the Sabana river to the north. This path, likely a horse or ox-cart trail, is the only visible human activity in the highlands around the plot and is not visible in the 1951 photo. Based on aerial photos and field observations we consider this to be a relatively undisturbed, old-growth forest.

1936



1951



**Figure 6.** Aerial photographs of chronosequence plot SB-O in El Yunque National Forest (EYNF), Puerto Rico in 1936 and 1951, depicted at landscape (scale = 1:10,000) and plot (scale = 1:2,000) levels. The approximate northern border of EYNF is shown in white.



## ***II. Reforestation era tree planting***

### *Reforestation history*

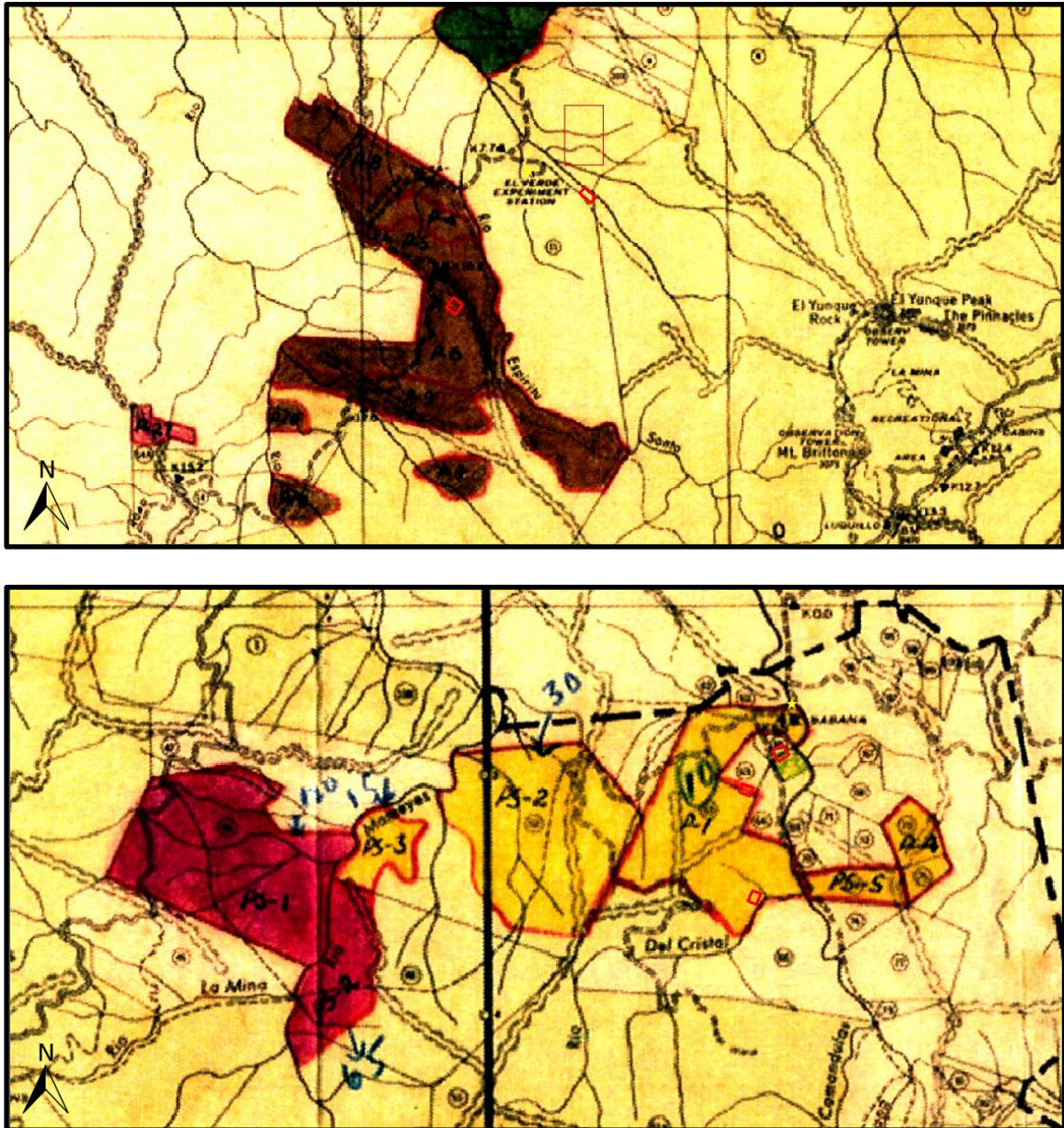
Reforestation trials with native and exotic tree species have been conducted across Puerto Rico since at least 1920 (Robinson 2014). In 1934, large-scale reforestation of federal and insular lands was initiated and included the establishment of 20,000 acres of forestry plantations. Efforts were led by the Depression-era Civilian Conservation Core (CCC) and Puerto Rico Reconstruction Administration (PRRA) programs. Lands selected for reforestation in El Yunque National Forest were grouped into six planting projects: El Verde, Pizá, Sabana, Coca Valley, Del Valle, and Ciénega Alta. Fifty-four plantations were established across these planting projects. The primary objective was timber production: land managers envisioned self-sustaining, even-aged forests composed of durable species for round timber and sawtimber production. Species were chosen that could regenerate in shady conditions under the forest canopy with little intervention beyond periodic thinning. Stands were also planted for the purpose of watershed protection, especially on steep slopes with high rainfall (Marrero 1947). Management of stands planted for timber included nearly continuous weeding, pruning, and replanting for the first 5 years, followed by pruning and thinning every 10 years. Stands would be thinned to approximately 150-200 trees per acre, with final trees being pruned up to 15 feet (Hadley 1940).

Reforestation efforts were experimental in nature, as little was known about tropical reforestation in Puerto Rico or the U.S. at the time. Many of the initial plantings failed and were later replanted, sometimes repeatedly. In 1944-45, forester Jose Marrero conducted a comprehensive survey of El Yunque's plantations to evaluate their success

and establish permanent records. He discusses plantings by tract number, rather than plantation number or area seeded, because repeated replanting over the years had altered the original distributions of plantation species substantially. The results of these studies provide information on the reforestation-era planting history of our study area (Figure 7).

*Planting history of El Verde plots:*

Tract 13 encompassed the entire Pizá plantation project, consisting of five plantations totaling 211 ha established in 1939 by the U.S. Forest Service. Timber trees were planted across most of Tract 13, but planting efforts were greatest in the northern portion which had been completely deforested. Many of the planting efforts failed, and replanting occurred until 1945. Marrero's 1944-45 survey found 265 acres to be successfully reforested, corresponding to 63% of the area where trees had been planted (169 ha). EV-M is located in the center of the former Pizá plantation project (within Plantation 6). This location is south of a dividing ridge and considered by Marrero to be a less exposed with more favorable slopes and greater natural regeneration than farther north. This portion of the tract harbored large individuals of species such as *Cordia alliodora*, *Ocotea moschata*, *Pouteria multiflora*, and *Tectona grandis* (teak), as well as the best stands of *Calophyllum antillanum*, or maría.



**Figure 7.** Pizá plantation (top) and Sabana plantations (bottom) in El Yunque National Forest, Puerto Rico as drawn by Marrero (1947), shown with chronosequence study plots (small red rectangles) and the Luquillo Forest Dynamics Plot (northernmost red rectangle).

María was by far the most successful species in Tract 13; in fact, Marrero remarked the Pizá project was “in itself a large maría plantation,” and that seeding had been most extensive there. South of the tract’s dividing ridge maría mixed with naturally regenerated forests and the stands had fewer canopy openings, leading to greater

uniformity and better tree form. *Petitia domingensis* was considered the next best species because of very high survival in all sites (Marrero 1947). A list of all species planted in Tract 13 and their presence or absence in the El Verde study plots is displayed in Table 2.

The Espíritu Santo River marks the eastern boundary of the Pizá plantations (Figure 7). No large-scale reforestation activities were conducted across the river in Tract 11 (containing EV-O), which aerial photos show was predominantly forested in the 1930's. Though localized plantings of maría were established in cut-over areas of the nearby Luquillo Forest Dynamics plot, located in the same tract (Thompson et al. 2002), it is unlikely that this occurred in EV-O which had more complete forest cover.

Six of the 13 species planted between 1936 and 1945 in Tract 13 occur in the El Verde study plots today (Table 2). María is fairly common in EV-M but not present in EV-O. María was an effective restoration species because of its ability to grow in a wide range of conditions including degraded sites, and because it produces a strong timber (Marrero 1947). This species is thought to be originally native only to moist coastal and moist limestone forest regions of northern Puerto Rico, to about 150 m in elevation (Little and Wadsworth, 1964; Weaver 1990), and to have expanded to wetter and drier sites across Puerto Rico as a result of extensive planting by foresters. Two secondary species, *Byrsonima spicata* and *Tabebuia heterophylla*, occur in both plots. Like maría, these were popular trees for reforestation of agricultural areas because of their ability to colonize eroded or nutrient-depleted soils and compete with grasses (Marrero 1950). These species also rapidly establish in abandoned pastures without human assistance (Little and Wadsworth 1964; Zimmerman et al. 2000). *Byrsonima spicata* seeds are dispersed by a variety of animals including birds, bats, and domestic and wild terrestrial

animals (Francis 1990), while *Tabebuia heterophylla* seeds wind-dispersed and can travel long distances (>100 m) from the parent tree (Weaver 1990). Though robust as colonizers, as the forest canopy recovers both species tend to decline in dominance over time due to intolerance to increased shade and to competition by faster-growing species (Francis 1990).

Two mature forest, animal-dispersed species, *Guarea guidonia* and the endemic *Ocotea moschata*, occur only in EV-O. Planting trials found that both species grow best beneath a forest canopy; plantings in open, degraded areas mostly failed (Marrero 1948). Prior coffee cultivation in parts of Tract 11 (Gerhart 1934, cited in Thompson et al. 2002) could have influenced *G. guidonia*'s abundance in EV-O, though it occurs naturally in tabonuco forest (Weaver 2012). *G. guidonia* is widely associated with coffee farms and dominant in forests growing on abandoned coffee plantations across Puerto Rico (Weaver & Birdsey 1986; Zimmerman et al. 1995; Rivera and Aide 1998; Pascarella et al. 2000) and is dispersed by bats and birds (DeVoe 1989). *Ocotea moschata*, also animal-dispersed, is an uncommon species of tabonuco and colorado forests. Successful plantings, such as below the dividing ridge of Tract 13, contained large individuals (Marrero 1947). *Ocotea moschata* forms a highly valuable timber for furniture and cabinetmaking (Little et al. 1977; Weaver 2012). This species may have been more common at lower elevations in the past but larger trees were logged, especially close to roads (Pete Weaver, personal communication). Despite heavy planting in Tract 13 (see Table 2), no *Swietenia macrophylla* (broadleaf or Honduran mahogany) is found in EV-M. A single sapling was found in EV-O. Current distributions of this species, however, are likely related to more recent timber

management including enrichment plantings, stand improvement, and selective harvest (see sections III, IV).

**Table 2.** Presence or absence in El Verde study plots of species reported by Marrero (1947) as planted in Tract 13 of El Yunque, Puerto Rico between 1936 and 1945.

| Species                        | Planted         |              | Presence    |             |
|--------------------------------|-----------------|--------------|-------------|-------------|
|                                | Seedlings (no.) | Seeds (lbs)  | EV-M (2011) | EV-O (2010) |
| <i>Byrsonima spicata</i>       | 16,200          |              | +           | +           |
| <i>Calophyllum antillanum</i>  |                 | 6,501        | +           | -           |
| <i>Casuarina equisetifolia</i> | 24,460          |              | -           | -           |
| <i>Senna siamea</i>            | 2,000           |              | -           | -           |
| <i>Cordia alliodora</i>        | 102,550         |              | -           | -           |
| <i>Guarea guidonia</i>         | 49,700          |              | -           | +           |
| <i>Pouteria multiflora</i>     |                 | 511          | -           | -           |
| <i>Ocotea moschata</i>         |                 | 500          | -           | +           |
| <i>Petitia domingensis</i>     | 4,150           |              | -           | -           |
| <i>Swietenia macrophylla</i>   | 173,425         |              | -           | +           |
| <i>Tabebuia heterophylla</i>   | 35,280          |              | +           | +           |
| <i>Tectona grandis</i>         | 18,925          |              | -           | -           |
| <i>Vitex divaricata</i>        | 3,300           |              | -           | -           |
| <b>Total</b>                   | <b>429,990</b>  | <b>7,512</b> |             |             |

*Planting history of Sabana plots:*

Sabana study plots are located within the former Sabana Planting Project, established in the Mameyes and Sabana River watersheds. The project included 7 plantations totaling 953 acres, and spanned Tracts 46, 48, 52, 53, 73, 74 and 75. Tract 53 contained the 240-acre Sabana plantation (or Plantation 1) in the Sabana River valley and surrounding hills. Low-elevation areas had been cleared for agriculture, while higher-elevation areas were generally second growth or disturbed forest (Marrero 1947). Cleared areas within the tract were initially planted in 1935-36 with alternate rows of *Cedrela odorata* and *Swietenia mahagoni*, but these species did poorly. Over the next decade, failed stands were replanted with a variety of species; successful ones included *S. macrophylla*, *Cordia alliodora*, *P. domingensis*, *C. antillanum*, and *Casuarina*

*equisetifolia*. The diverse nature of these replantings led to gaps in forest cover and non-uniform stands lacking dominant species (Marrero 1947).

Eight of the species used in the reforestation of Tract 53 are present among the Sabana plots today (Table 3). Two are among the species Marrero describes as successful plantations: *C. antillanum* (maría) and *S. macrophylla*. María is a dominant species in the tree communities of both SB-Y and SB-M. Despite no overlap in the top three most abundant species, maría ranks fourth in abundance in both sites. *S. macrophylla* is moderately abundant in SB-Y and occurs in low densities in SB-M. This species was substituted for *S. mahagoni* in Tract 53 beginning in 1939, as the conditions were too wet for the former. Marrero notes that reforestation-era plantings of *S. mahagoni* in areas of high rainfall (>2500 mm/yr) did not survive, and today this species is rarely found in El Yunque (G. Bauer, personal communication). However, the two species readily hybridize, forming fast-growing trees with high quality wood. Forest census data did not distinguish between *S. macrophylla* and hybrids in the chronosequence plots, thus we refer to both as *S. macrophylla* or Honduran mahogany in this study. As mentioned previously, this species was carefully managed for timber purposes in the ensuing years (see section IV). Though SB-O is a part of Tract 13, it is unlikely maría or mahogany were planted there as it was dense forest at the time, and neither occurs in the plot today.

The exotic tree *Senna siamea*, a fuelwood species commonly planted as windbreaks or along farm boundaries (Marrero 1947), is present in moderately low densities in SB-M. This plot is located at the northern boundary of Tract 53 and a dense tree line within the plot was observed in the 1951 aerial photos. *Tectona grandis*, an exotic and valuable timber species, is abundant and reaches large diameters in SB-Y but

those trees were likely established in later plantings for timber management (see section IV). Other planted species present in Sabana today include secondary species *B. spicata* and *T. heterophylla* and old-growth species *G. guidonia* and *M. bidentata*. It is difficult to say whether their presence in the previously agricultural sites is due to planting or to natural dispersal as the forest recovered. The remaining species described as successful plantings in Tract 53 may not have been planted within the study plots or may have been outcompeted as the forest canopy recovered. For instance, *P. domingensis* and *C. alliodora* are shade-intolerant and do not grow well or require superior drainage in areas of high rainfall (Little and Wadsworth 1964; Marrero 1947). A mixed stand of the former in El Yunque was outcompeted by faster-growing *T. grandis*, while the latter did not perform as well as other species in degraded sites and was susceptible to damage by insects and pathogens (Marrero 1947).

**Table 3.** Presence or absence in Sabana study plots of species reported by Marrero (1947) as planted in Tract 53 of El Yunque, Puerto Rico between 1936 and 1945.

| Species                        | Planted         |             | Presence (2011) |      |      |
|--------------------------------|-----------------|-------------|-----------------|------|------|
|                                | Seedlings (no.) | Seeds (lbs) | SB-Y            | SB-M | SB-O |
| <i>Albizia lebeck</i>          | 12,610          |             | -               | -    | -    |
| <i>Byrsonima spicata</i>       | 472             |             | -               | +    | +    |
| <i>Calophyllum antillanum</i>  |                 | 212         | +               | +    | -    |
| <i>Senna siamea</i>            | 5,510           |             | -               | +    | -    |
| <i>Casuarina equisetifolia</i> | 12,280          |             | -               | -    | -    |
| <i>Cedrela odorata</i>         | 135,000         |             | -               | -    | -    |
| <i>Cordia alliodora</i>        | 2,762           |             | -               | -    | -    |
| <i>Eucalyptus sp.</i>          | 4,640           |             | -               | -    | -    |
| <i>Guarea guidonia</i>         | 160             |             | +               | +    | -    |
| <i>Manilkara bidentata</i>     | 1,450           |             | +               | +    | +    |
| <i>Thespesia grandiflora</i>   | 5,983           |             | -               | -    | -    |
| <i>Petitia domingensis</i>     | 10,000          |             | -               | -    | -    |
| <i>Swietenia macrophylla</i>   | 37,710          |             | +               | +    | -    |
| <i>Swietenia mahagoni</i>      | 217,000         |             | -               | -    | -    |
| <i>Tabebuia heterophylla</i>   | 6,500           |             | +               | +    | +    |
| <i>Tectona grandis</i>         | 1,100           |             | +               | -    | -    |
| <b>Total</b>                   | <b>453,177</b>  | <b>212</b>  |                 |      |      |



### ***III. Timber harvest***

#### *Background*

Timber has been harvested from the Luquillo Mountains for centuries or longer. Spanish settlers in the early 1500's mining gold from rivers such as the Espiritu Santo and the Sabana River felled trees for, infrastructure, fuelwood, and to transport equipment. The construction of forts, walls, and colonial homes in San Juan caused a demand for timber species such as ausubo and tabonuco resin was used to caulk ship timbers (Robinson et al. 2014, Weaver 2012). In the 17<sup>th</sup> and 18<sup>th</sup> centuries, a contraband lumber trade and expeditions for firewood for sugar plantations on deforested islands drove a large demand for timber across the Caribbean (Giusti 2009). The proximity of the Luquillo Mountains to coastal ports and their abundance of large-statured trees suggests prolonged timber exploitation in accessible areas of the lower slopes.

In the 18<sup>th</sup> century the harvesting of wood for homes, furniture and charcoal rose as populations and towns grew, and in the mid-19<sup>th</sup> century timber was harvested for export from the lower slopes of the Bisley, Jimenez and Mameyes watersheds (Weaver 2012). Embarcadero Point, near the city of Luquillo, was an important port for timber exports. In the 1880's the Spanish Crown protected 10, 632 ha of the Luquillo Mountains as a public forest reserve and began controlling timber harvest. Timber from Crownlands was typically sold by auction (Wadsworth 1970). By 1903 all mountainous areas in the Sabana River Valley had been logged to some extent (Scatena 1989). Despite government protection under the Spanish and subsequently the U.S., local inhabitants continued extracting timber, producing charcoal, and mining for gold in the Luquillo Mountains in the early twentieth century. Uncontrolled timber extraction under

U.S. rule was reported in 1914 and likely continued until a resident forester (1917) and forest guards (1918) were hired and horse trails constructed (1919-26) to patrol the forest boundary.

### *Early timber extraction*

In the 1920's private sawmills operated in both the El Verde and Sabana areas, implying valuable timber was present and accessible. In the Espíritu Santo valley, a sawmill established in 1923 processed timber brought by oxen and tractor from Tract 11, where EV-O and the LFDP are located today. Though this operation was short-lived, lasting only 8 months, a variety of species were milled including *Dacryodes excelsa*, *Manilkara bidentata*, *Magnolia splendens*, *Tetragastris balsamifera*, *Ocotea moschata*, *Buchenavia tetraphylla*. Under the ownership of Bliss Plywood and Keystone Plywood Corporations, parts of Tract 11 were logged and a portable mill operated in the northern area of the tract between 1924 and 1934 (Thompson et al. 2002). In Sabana Valley, a sawmill operating from approximately 1920 to 1935 milled logs brought by oxen from tracts 18, 52, and 53 (where the three Sabana plots are located) (B. Peraza, cited in Wadsworth 1949).

Over time timber harvest shifted from dispersed and often illegal activities to centralized sales by the U.S. Forest Service, who conducted timber cruises and began operating sawmills near the reserve boundary. From 1937 to 1943 a Forest Service sawmill in Sabana Valley provided tabonuco timber for subsistence farmers residing in the forest (Hadley 1940). Approximately 4,720 m<sup>3</sup> (2,000,000 board feet) of tabonuco were cut from the Sabana and Mameyes valleys (Wadsworth 1949). Beginning in 1932 timber sales including fuelwood, polewood, and sawtimber were permitted in the

reserve, and by 1949 nearly 300,000 cubic meters of wood had been sold by the US Forest Service. By 1940, the timber production area of the national forest included 17,700 acres (7,163 h; Hadley 1940).

Most trees of value for timber were located at low elevations (<600 m) in tabonuco forest where species such as *Dacryodes excelsa*, *Manilkara bidentata*, *Sloanea berteriana*, *Homalium racemosum* (caracolillo), and *Guarea guidonia* (guaraguo) were characteristic. Higher-elevation colorado forests were far less accessible because of rough topography and an abundance of lianas. A survey of approximately 1,700 acres (688 ha) in preparation for a 1940 management plan found severe culling of low-elevation tabonuco forest had taken place and indicated that tree growth rates had slowed because of prior soil erosion and agricultural depletion in those areas (Hadley 1940).

Harvest activities in the 1930's and 1940's focused on the salvage of dead or fallen timber and the extraction of trees cut as part of silvicultural management activities. Because no logging industry or stumpage market existed, cutting was mainly carried out by the U.S. Forest Service and sold as logs or boards. Trees were also harvested by private parties for fuelwood and charcoal in more remote parts of the forest. Demand for charcoal soared during World War II fuel shortages and declined quickly with the spread of kerosene stoves after the war. Preferred trees for charcoal production included *Inga laurina* (guamá), *Inga vera* (guaba), and *Andira inermis* (moca; Garcia and Scatena 1994, Robinson 2014).

The location of the El Verde and Sabana areas at low elevations along the northern forest boundary, together with their large supplies of timber on relatively gentle terrain, have long made them attractive areas for logging activities. In 1940 timber

production areas covered 3, 677 acres (1488 ha) in three blocks: Río Grande (1, 915 acres/ 775 ha), Fajardo (1,021 acres/ 413 ha), and Naguabo (741 acres/ 300 ha), with most logging taking place in the El Verde area of the Río Grande Block and the Sabana area of the Fajardo Block. Timber in the Sabana area was accessed via a road that connected La Margarita, located on the road from Luquillo to Fajardo, to La Perla (Tract 53) to the south. This road was used to extract timber from tracts 53, 52, 48, 51, and 51A, which had the highest concentrations. Valuable timber in the El Verde-Pizá area was transported on a road crossing directly through Tract 13, beginning a kilometer east of Río Grande and leading to Ciénega Alta. In 1940 this road was still incomplete but meant to connect with a state highway from Canóvanas to Juncos. From these roads, wood was dragged out of the forest on old logging trails by tractors or by oxen, depending on soil conditions. The construction of temporary logging trails separate from the forest road system was under consideration at this time (Hadley 1940).

### *Systematic timber management*

The creation of a profitable and sustainable forest sector in Puerto Rico was a central goal of forest administrators from the start of the century until the 1980's. The first supervisor of El Yunque, Emory M. Bruner, advocated for the “slow, constant, and permanent” use of forest products by establishing small but high-value industries that could sustain nearby rural communities in perpetuity. Pursuing industries limited in both scale and scope would ensure that forest products were not consumed faster than they could be produced, and that forest cover and associated watershed protection would remain intact (Bruner 1919).

Building a forest sector first required knowledge of available timber supply. Early surveys of the supply in El Yunque between 1905 and 1922 estimated a total volume of 120,000 m<sup>3</sup> of standing timber and an average stocking of sawtimber of 30 m<sup>2</sup>/ha in tabonuco forest. The first systematic timber survey was conducted in 1930 by Forest Supervisor William Kramer, who estimated the per-acre volume of all potential timber species sampled. In 1933 Forest Supervisor William Barbour estimated stumpage values and proposed working circles to organize timber cutting. The second systematic cruise was conducted in 1937 by Forest Supervisor Evan Worth Hadley who summarized timber volumes by blocks of land, which he used as management units (Wadsworth 1949, 1970). According to Frank Wadsworth (1949), these geographic units were not useful for management a decade later and the lack of estimated volumes available for immediate cutting was problematic. In addition, many species ignored for their lack of timber value then had since acquired economic value.

Increases in sales in the 1940's led to the development of a timber budget in 1945 proposing the removal of approximately 160,000 m<sup>3</sup> of timber from 8,500 ha during a first cutting cycle and of 150,000 m<sup>3</sup> from the same area during a second cycle. A revision in 1947 reduced the area to 6,700 ha and the budget to approximately 110,000 m<sup>3</sup> (Wadsworth 1949). In 1948 a new timber cruise was carried out over the 6,700 ha designated for timber with a carefully designed sampling system was carried out to improve timber budgets and management planning, including transportation infrastructure. The results were analyzed by Wadsworth in his 1949 dissertation and combined with timber records from the past 5 years to outline a detailed timber cutting program. This inventory data and harvest plan formed the basis for silvicultural

management in El Yunque until the next forestry inventory in 1962 and served as a foundation for larger-scale forest management in the 1950's and 60's (see section IV).

Wadsworth's system organized timber harvest by geographic regions based on natural features and the locations of rural communities in valleys, which could provide a steady source of labor as long as harvest locations were near their homes. Each valley identified for timber production was managed individually as a continuously operating working circle. Within each working circle, smaller compartments specified where cutting should take place each year, beginning with the most accessible stands. Compartments were based on natural features to avoid expensive boundary maintenance and were treated as homogenous silvicultural units. Harvest activities were also divided by forest type to account for differences in stand characteristics and growth rates. Stands within each working circle were classified as tabonuco or colorado, with palm forest encompassed within the colorado type. Tabonuco stands would be harvested annually for 10 years, while slower-growing colorado forests would be harvested in 20-year cycles. Wadsworth calculated overall volumes by on working circle area (Table 4) and cubic volumes available for harvest, and published maps made during the inventory depicting each working circle and forest type (See Figures 8 and 9).

Ten working circles and approximately 85 compartments were defined, although these units would change over the ensuing decades based on updated supply volumes, accessibility for harvest, and management priorities. The El Verde area corresponds to the Espíritu Santo Working Circle, while Sabana falls within the Cristal Working Circle. These areas contained the highest and second highest total volumes of sawtimber, respectively (Table 4). To determine the precise location of the chronosequence plots within timber management areas (Figure 8, Figure 9) and relative to high-priority timber

stands, we georeferenced the maps of these two working circles (scale=8 inches) and overlaid the coordinates of each plot.

**Table 4.** Working circles for timber management in El Yunque National Forest, Puerto Rico characterized using aerial photos, low altitude aerial reconnaissance, and a ground cruise in 1948. Areas with small, inaccessible volumes of timber were not cruised. Adapted from Wadsworth (1949).

| Working Circle | Area (ha)    | Total Timber Volume (M Cu. Ft) |             |              |
|----------------|--------------|--------------------------------|-------------|--------------|
|                |              | Sawtimber                      | Polewood    | Fuelwood     |
| Cacique        | 502          | 923                            | 280         | 1190         |
| Cienega Alta   | 808          | 285                            | 660         | 910          |
| Cristal        | 499          | 1020                           | 200         | 1800         |
| Cubuy          | 289          | 67                             | 58          | 1020         |
| Espíritu Santo | 788          | 1570                           | 850         | 2590         |
| Fajardo        | 665          |                                | Not cruised |              |
| Gurabo         | 510          |                                | Not cruised |              |
| Hicaco         | 1,172        | 795                            | 360         | 4000         |
| Jimenez        | 762          | 493                            | 830         | 1200         |
| La Mina        | 732          | 990                            | 410         | 1700         |
| <b>Total</b>   | <b>6,727</b> | <b>6143</b>                    | <b>3648</b> | <b>14410</b> |

Notes: M Cu. Ft = Thousand cubic feet. Sawtimber = trees >25 cm in diameter at breast height (dbh). Trees <25 cm dbh were classified as polewood or fuelwood based on merchantability.

#### *Espíritu Santo Working Circle*

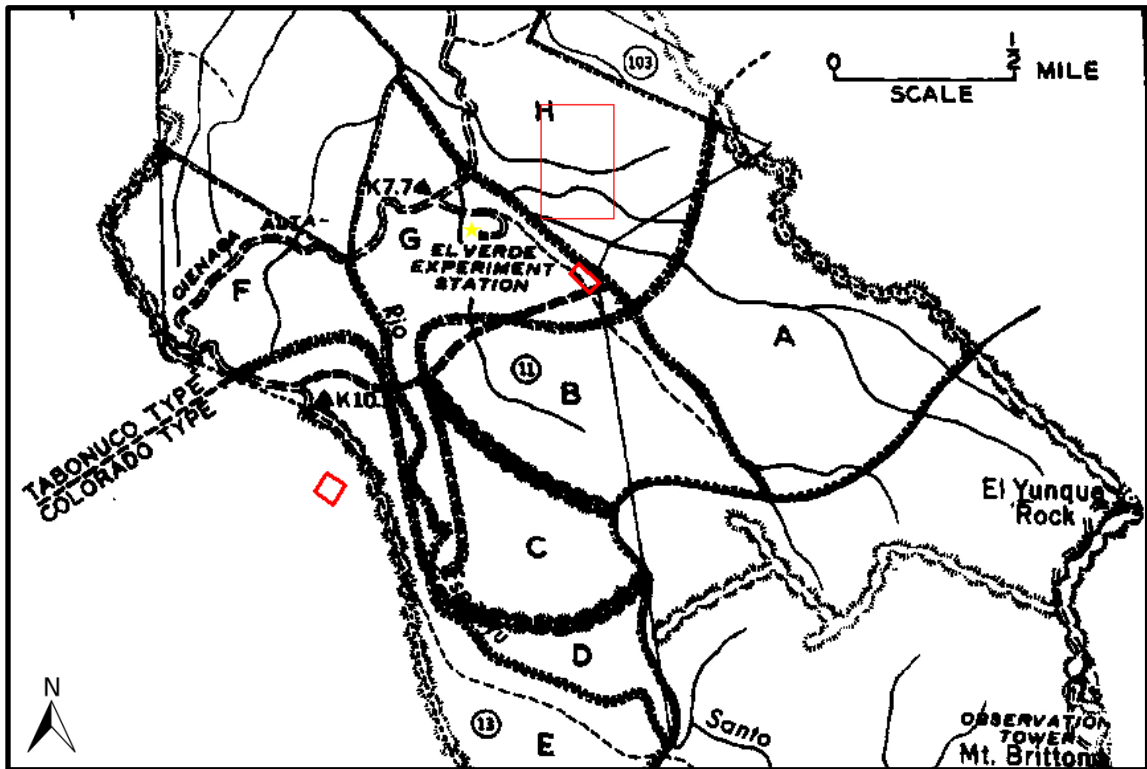
Plot EV-O is found within the Espiritu Santo Working Circle, along with the El Verde Field Station and the nearby Luquillo Forest Dynamics Plot (LFDP). Plot EV-M lies just outside the western border of this harvest area, on the other side of a north-south ridge. The working circle encompassed 1, 948 acres (788 ha) included the valley of the Espiritu Santo river, the Quebrada Sonadora, and their tributaries. In 1948, this area was 88 percent forested.

EV-O was located within compartment G, classified as Colorado forest and described as a “heavy stand of overmature timber” with high priority for timber removal (along with compartments A and C). The Field Station and LFDP were located within

tabonuco forest compartments G and H, respectively, and described as younger, more accessible timber which, as second priority, could be thinned by cutting for stand improvement. Though plot EV-M is located outside of the working circle, its close proximity (<200 m) to the production forest of colorado type in compartment E on one side and the Western boundary of the national forest on the other (<300 m) suggest timber extraction was feasible.

Management prescriptions for the Espíritu Santo Working Circle included the annual harvest of 70 acres (28 ha) per year in tabonuco forest and 15 per year (6 ha) in colorado forest. The experimental underplanting of timber species in the more accessible stands was also recommended. 120 acres of farmland existed within the working circle and would remain in use. Approximately 67 percent of the Espíritu Santo Working Circle was accessible for sawtimber and 30 percent for polewood production. Tabonuco and laurel sabino (*Magnolia splendens*) were identified as the primary sawtimber species. In the preceding 5-year cycle, approximately 1100 cubic meters per year (m<sup>3</sup>/yr) or 468,000 board feet/yr (BF) of timber were harvested from the Espíritu Santo Working Circle.





**Figure 8.** Subset of the Espiritu Santo Working Circle and its compartments (8 inches: 1 mile) within El Yunque National Forest, Puerto Rico from Wadsworth (1949), shown with chronosequence study plots (small red rectangles), the Luquillo Forest Dynamics Plot (northernmost red rectangle), and the El Verde Field Station (yellow star).

### *Cristal Working Circle*

Plots SB-Y, SB-M, and SB-O are found within the Cristal Working Circle, consisting of 1,232 acres (499 ha) of timberland in the valley of the Río Sabana and its tributaries. In 1948, this area was 96 percent forested. All three plots are within the tabonuco forest section of the working circle. SB1 and SB2 are located along northern borders of Compartment E, and SB3 is just above the Río del Cristal which forms the southern border of Compartment E. This compartment was not a high timber priority likely due to young stand age; more mature stands with larger timber volumes were found farther south in Compartments A and B. Additional experimental understory

planting was recommended for nearby compartments (F, G, H) but no such recommendations were made for compartment E. Twelve acres of farmland occurred within the working circle and would remain as such, and abundant labor for timber harvesting could be found just outside the forest boundary. High-priority timber was considered accessible with adequate transportation infrastructure, though the continuation of Sabana Ridge road was recommended for the future.

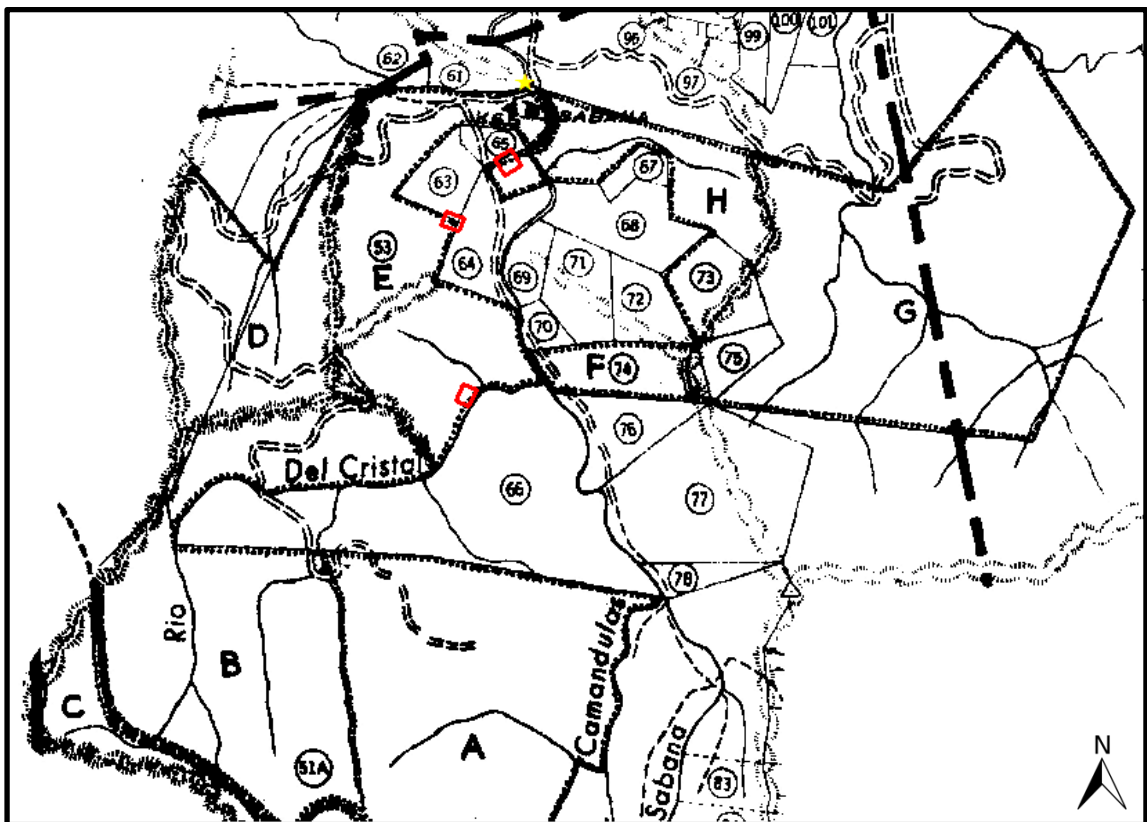
The recommended timber harvest for the Cristal Working Circle was 70 acres per year in tabonuco forest type, with a production of 115m<sup>3</sup>/yr (49,000 BF) proposed for the next 5-year cycle. Over the previous cycle approximately 1220 m<sup>3</sup>/yr (516,000 BF) were removed including 165 m<sup>3</sup>/yr (70,000 BF) of saw timber. Approximately 60 percent of the working circle area was accessible for saw timber production and 44 percent for polewood production. As in the Espíritu Santo Working Circle, the primary sawtimber species were tabonuco and *M. splendens*.

According to these maps, all of the plots except EV-M are located in areas designated and accessible for timber harvest in the 1940's and 1950's. Though we know a limited amount of harvesting took place in the preceding timber cycle and presumably for the next five years as prescribed, these data are presented at the scale of the working circle and the extent to which our study plots were affected is unknown. Descriptions of the working circles indicate widespread forest cover with small patches of farmland remaining in each, though Sabana valley was more heavily forested and Espíritu Santo valley contained a slightly larger proportion of actively grazed or cultivated lands. They also indicate the two areas had the highest volumes of sawtimber among working circles both overall and on a per-area basis.

Characterizations of the smaller compartment divisions provide insights on relative forest age and other stand characteristics. The compartment containing EV-O was marked as a stand of overmature timber, suggesting trees were reaching very large sizes impractical for forestry use (e.g. >50 cm dbh), while those containing the El Verde Field Station and LFDP were younger, denser stands with promising timber if managed over time. The depiction of the compartment containing the Sabana plots as younger and less timbered forest than the forests to the south is consistent with aerial photo results for SB1 and SB2, but surprising for SB3 which is under a closed canopy in 1936 and 1951. Whether the stand containing SB3 was lumped in with the younger forests to the north or whether it was notably younger with smaller trees than surrounding stands to the south is unclear.

*Magnolia splendens* was a highly desired furniture and cabinet wood in Puerto Rico (Bruner 1919, Little & Wadsworth 1964). This is a bird-dispersed species endemic to the Luquillo Mountains, occurring in old-growth tabonuco and colorado forests between 400 and 1,000 m (Wadsworth 1950, 1951). It is most common at higher elevations where tree growth is so slow that timber production is not economically feasible, and low germination rates make propagation difficult (Little & Wadsworth 1964). Logging until the early 1950's removed many large-sized trees in El Yunque, accentuating naturally low regeneration rates of this species by removing much of its seed source. The species appeared to Weaver (1987) to be undergoing a long-term decline but to our knowledge this trend has not been evaluated in recent years. *Magnolia splendens* did not occur in any of the chronosequence plots in this study. The Sabana plots may be too low in elevation, but its absence from the El Verde plots is plausibly related to logging given evidence of its harvest for timber in Tract 11 as early as 1923.

Records indicate this species was extracted from higher parts of the Sonadora watershed until the early 1950's (Weaver 1987). While other logged species, such as *D. excelsa* and *T. balsamifera*, are still present in the plots, *M. splendens* may have been removed at a rate faster than new individuals could be recruited into the remaining population. Long-lasting canopy closure after Hurricane San Cipriano (1932) may have contributed to population decline by eliminating gaps favorable to *M. splendens* regeneration and growth (Weaver 1987).



**Figure 9.** Subset of the Cristal Working Circle and its compartments (8 inches: 1 mile) within El Yunque National Forest, Puerto Rico from Wadsworth (1949), shown with chronosequence study plots (red rectangles) and the Sabana Field Research Station (yellow star).

#### *IV. Silvicultural Management*

### *Timber stand improvement*

As planted and natural forests grew and developed on formerly cleared lands, silvicultural management was implemented to increase their economic value. The first phase of stand improvements was carried out along with reforestation plantings by Civilian Conservation Corps workers from 1934-1939 (Wadsworth 1951, 1970). Young plantations were weeded and de-vined, valuable trees were pruned, and maturing stands were thinned to improve their structure. As crop trees developed, they were released from competition by harvesting, girdling or poisoning competitors. Trees removed for thinning or release were sold for use as posts or fuelwood.

Forest management intensified over the next few decades to improve the stock of valuable trees in timber production areas, including natural forests. Young, post-agricultural forests were characterized by a low basal area, small-diameter trees, low diversity, and few species of high forestry value. In contrast, mature forest stands tended to have many “over mature” trees that exceeded the ideal size for their most valuable timber products. Foresters envisioned an optimum stand with a basal area around 14- 23 m<sup>2</sup>/ha, straight trees less than < 50 cm dbh, an even size class distribution, and a high stand density that still provided growing room. Desirable species would regenerate naturally or else be planted underneath the canopy (Wadsworth 1949, 1952b).

A gradual transition of natural forests toward optimum structure and composition for timber was initiated through successive improvement cuttings. A first cut would adjust density in overcrowded stands and remove deteriorating trees in mature stands; subsequent cuts would remove non-useful species and competitors, opening growing space for timber trees. Over time the representation of species desirable for furniture or construction use (“crop trees”) would be maximized, and species with no foreseeable

market value would be removed from the forest (Wadsworth 1949, 1952b). Crop trees were selected based on a continuously updated list ranking species according to their value for forest products (Table 5). Only trees reaching merchantable heights (>5 m) and diameters (8-50 cm) were considered. Improvement cuttings began with dying or diseased trees, followed by the removal of all non-listed tree species and finally the girdling or poisoning of all trees within a critical distance from a crop tree. Once a maximum density of crop trees was reached, other crop trees would be removed based on their form and relative timber value.

**Table 5.** Species favored for sawtimber or polewood production in tabonuco forest type of El Yunque National Forest, Puerto Rico between 1952 and 1965. Species are listed exclusively in the highest category they occurred in during that period. Compiled from Wadsworth 1952b, Wadsworth 1955, Wadsworth 1957, and Muñoz 1965.

| Highest Priority                 | High or Medium Priority       | Lower priority                  |
|----------------------------------|-------------------------------|---------------------------------|
| <i>Buchenavia capitata</i>       | <i>Alchornea latifolia</i>    | <i>Alchorneopsis floribunda</i> |
| <i>Byrsonima spicata</i>         | <i>Andira inermis</i>         | <i>Chionanthus domingensis</i>  |
| <i>Calophyllum antillanum</i>    | <i>Beilschmiedia pendula</i>  | <i>Cupania americana</i>        |
| <i>Cordia alliodora</i>          | <i>Cecropia schreberiana</i>  | <i>Guazuma ulmifolia</i>        |
| <i>Dacryodes excelsa</i>         | <i>Ceiba pentandra</i>        | <i>Laetia procera</i>           |
| <i>Guarea guidonia</i>           | <i>Chrysophyllum cainito</i>  | <i>Matayba domingensis</i>      |
| <i>Homalium racemosum</i>        | <i>Eugenia stahlii</i>        | <i>Nectandra coriácea</i>       |
| <i>Manilkara bidentata</i>       | <i>Ficus citrifolia</i>       | <i>Nectandra hihua</i>          |
| <i>Magnolia splendens</i>        | <i>Genipa americana</i>       | <i>Nectandra membranaceae</i>   |
| <i>Micropholis garciniifolia</i> | <i>Hernandia sonora</i>       | <i>Nectandra patens</i>         |
| <i>Ocotea moschata</i>           | <i>Hymenaea courbaril</i>     | <i>Nectandra turbacensis</i>    |
| <i>Petitia domingensis</i>       | <i>Inga laurina</i>           | <i>Cinnamomum elongatum</i>     |
| <i>Pouteria multiflora</i>       | <i>Inga vera</i>              | <i>Laplacea portoricensis</i>   |
| <i>Swietenia macrophylla</i>     | <i>Mammea americana</i>       | <i>Zanthoxylum martinicense</i> |
| <i>Tabebuia heterophylla</i>     | <i>Meliosma herbertii</i>     |                                 |
| <i>Tectona grandis</i>           | <i>Micropholis guyanensis</i> |                                 |
| <i>Tetragastris balsamifera</i>  | <i>Nectandra coriacea</i>     |                                 |
|                                  | <i>Ocotea cuneata</i>         |                                 |
|                                  | <i>Ocotea leucoxylon</i>      |                                 |
|                                  | <i>Ormosia krugii</i>         |                                 |
|                                  | <i>Schefflera morototoni</i>  |                                 |
|                                  | <i>Sloanea berteriana</i>     |                                 |
|                                  | <i>Spondias mombin</i>        |                                 |
|                                  | <i>Vitex divaricata</i>       |                                 |

### *Regeneration management*

Large areas of secondary forest in El Yunque lacked regeneration of species desirable for timber (Wadsworth 1952b). Silvicultural treatments in these areas included the establishment of plantations or the planting of desirable species underneath a forest canopy (enrichment planting). The latter method was preferable to plantations because shady environments permitted the planting of species of later successional and reduced site preparation and weeding or de-vining costs (Wadsworth 1960). *Swietenia macrophylla* was found to be the best species for underplanting in El Yunque's lower slopes and valleys because of its superior timber value and form, ease of establishment, and preference for intermediate successional environments (Wadsworth 1970). *Swietenia* enrichment plantings began in the Sabana area in the 1960's (Bauer 1987) and by 1981 covered over 1200 ha in northern and western areas of secondary forest (Weaver 2012, CNF 1986). A nursery was established for mahogany seedling development in Catalina in 1976.

Plantations were reserved for deforested lands, including recently acquired farmlands or areas where natural regeneration or previous planting efforts had failed. Such lands had no forestry value and were prescribed immediate reforestation. If left to regenerate naturally, resulting forests would be dominated by hardy pioneers with low timber value, requiring very long time periods of time to recover more valuable native species. However, earlier reforestation efforts had demonstrated that high-value timber species, generally adapted to the shady conditions and more productive soils of later successional stages, tended to fail in open sites. The solution was a form of accelerated succession: short rotations were planted of species that produced low yields but were adapted to degraded sites and gradually replaced with higher-value species as site

conditions improved (Wadsworth 1952b). Sites with adequate soils could be planted with *S. macrophylla* or *T. grandis*, requiring 40-year rotations, while highly degraded sites were planted with less demanding species such as *Pinus caribae* (Caribbean pine) or *Neolamarckia cadamba* (cadam), which required 30-year rotations (Muñoz 1965).

Through improvement cuttings and reforestation treatments (see Table 6), foresters closely controlled the composition of secondary forest stands in timber production areas. These practices likely altered the nature of forest succession in the chronosequence plots located within managed stands by speeding their transition to a closed-canopy forest dominated by late-successional species, and by favoring certain species and size classes over others. Though direct and specific effects on modern stand characteristics and species communities are difficult to trace, a closer look at the types and locations of secondary forest management activities can provide insights about the nature of human disturbance on the chronosequence plots from the reforestation era until the cessation of timber management in the 1980's.



**Table 6.** Silvicultural treatment options proposed by Wadsworth (1955) for a pilot forest management project in El Yunque National Forest, Puerto Rico. Treatments were meant to be selected depending on stand conditions.

| Treatment                              | Definition   | Species (refer to Table Y)  |
|--|--|---|
| <u>Improvement</u>                     |  |   |
| Commercial improvement cutting         | Remove only sawtimber, poles or posts of sizes and species currently in demand. Goal is to minimize treatment costs.       | High, medium, and low-priority timber species favored. Marketable trees removed first.                      |
| Intensive improvement cuttings         | Eliminate trees for stand improvement without regard to their commercial value. Goal is to maximize long-term stand value. | High, medium, and low-priority timber species favored. Non-listed species removed first                     |
| <u>Regeneration</u>                    |  |   |
| Natural regeneration by shelterwood    | In stands with high overstory, manage for desirable species underneath. Later eliminate shelterwood and manage crop.       | High or medium priority and shade-tolerant timber species favored.  |
| Natural regeneration by clearcutting * | Encourage seedling reproduction of sawtimber species by clearing large trees and competitors                               | High-priority timber species favored (see Table 5). All trees > 30 cm and non-sawtimber trees >10 cm culled |
| Underplanting                          | Plant and manage desirable sawtimber species underneath stands with undesirable composition                                | <i>Swietenia macrophylla</i> (<300 m)   |
| Natural reforestation                  | Study natural stand development and composition. Improvement cuttings begin after 5 years.                                 | Native species (first 5 years)  |
| Artificial reforestation               | Establish and manage plantations on deforested sites   | <i>Tectona grandis</i> (<600 m) or <i>Eucalyptus robusta</i> (>600 m)                                       |

### *Pilot management project*

From 1943-51, 5,000 acres (2000 ha) of tabonuco and colorado forest were subject to improvement cuttings through timber sales. Within five years stands were notably denser with straight trees suitable for posts and poles. All trees with no use beyond fuelwood had been eliminated, yet the canopy remained intact (Wadsworth 1952a). Based on the results of these and other silvicultural trials, a pilot forest management project was initiated in 1956 to expand intensive management to a scale

relevant to commercial operations. Approximately 6,700 acres (2700 ha) in the northern part of the forest were set aside for this demonstration project (Tropical Forest Research Center 1956, 1957). Treatments were carried out in 5-year cycles in six working circles derived from those of Wadsworth's 1949 study, with 20 percent of each working circle treated each year. Working circles were divided into 44 compartments that would each receive the same treatment. Permanent records including area treated, yield, cost, man-hours, and stand conditions were kept on a compartment basis. These records provide detailed information about the management of our study areas on a compartment level (see Table 7).

The first cutting cycle was carried out from 1956-62 and thinned the entirety of the pilot management area. Timber sales totaled 550,000 board feet (1300 m<sup>3</sup>; Muñoz 1965). A forest inventory was conducted at the end of the cycle to evaluate stand structure and establish permanent forest monitoring plots. The inventory found that 62 percent of the project area remained understocked. Species composition had shifted but stand structure remained the same, perhaps because mature sawtimber had been depleted by earlier harvesting and because young forests were still recovering from agricultural use. The second cutting cycle, focusing again on stand conditioning, took place from 1965-70 and was preceded by a reorganization of management units. Six working circles were combined to form two, El Verde and Sabana, to reflect the increased mobility of laborers. Smaller compartments were designated to facilitate uniform and tailored stand treatments and more accurately estimate timber volumes for sales (Muñoz 1965). The reduced compartment sizes and maps to delineate them allow us to further reduce our scale of analysis concerning the effects of human disturbance in the El Verde and Sabana areas (see Table 7).

**Table 7.** Forest management units in timber production areas of El Yunque National Forest, Puerto Rico in 1957 (Wadsworth 1957) and in 1965 (Muñoz 1965) timber management plans.

| 1957 Management Units |           |             | 1965 Management Units |           |             |         |                |           |
|-----------------------|-----------|-------------|-----------------------|-----------|-------------|---------|----------------|-----------|
| Working circle        | Area (ha) | No. of CPTs | Working circle        | Area (ha) | No. of CPTs | CPT     | Valley         | Area (ha) |
| Sabana                | 570       | 9           | Sabana                | 1,452     | 26          | 150-175 | Sabana         | 570       |
| Mameyes               | 929       | 13          |                       |           | 43          | 100-142 | Mameyes        | 881       |
| Espíritu Santo        | 225       | 4           | Espíritu Santo        | 1,282     | 12          | 40-51   | Espíritu Santo | 225       |
| Jiménez               | 380       | 7           |                       |           | 19          | 60-78   | Jiménez        | 380       |
| Rio Grande            | 234       | 5           |                       |           | 13          | 20-32   | Rio Grande     | 216       |
| Cubuy                 | 373       | 6           |                       |           | 16          | 1-16    | Cubuy          | 462       |

Notes: CPTs = Compartments

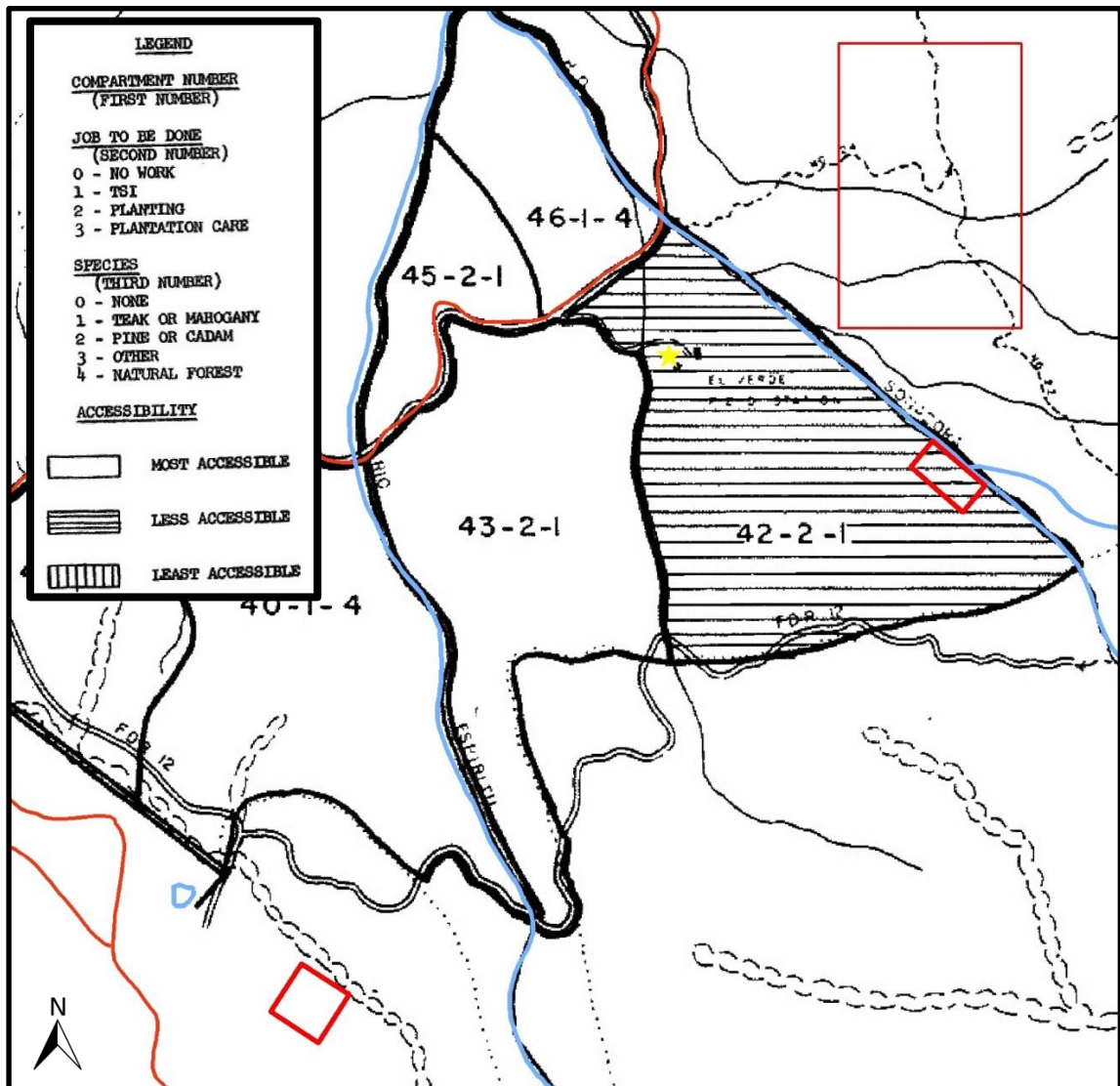
### *Stand improvement in El Verde*

Multiple maps produced as a part of the pilot project records indicate that EV-O and all three Sabana plots were included within the pilot demonstration project area. As in 1949, EV-M lies outside the western boundary of the Espiritu Santo Working Circle (Figure 10). The LFDP lies outside the eastern boundary, which is defined by the south fork of the Sonadora River. EV-O and the El Verde Field Station are located within section A of Compartment 2 of the Espiritu Santo Working Circle, measuring 214 acres (87 ha).

Previous studies report that within EV-O a selective harvest was conducted in 1937 and timber stand improvement treatment was carried out in 1958. The 1958 thinning involved the removal or poisoning of 146 stems primarily of smaller size classes (109 stems from 4-9 cm class, 26 stems from 8-16 cm class, and 11 stems >16cm). *Sloanea berteriana*, *Dacryodes excelsa*, and *Manilkara bidentata* were most commonly removed. A subsequent spike in tree mortality rates occurred and two species, *Micropholis garciniaefolia* and *Beilschmiedia pendula*, disappeared from the plot. However, secondary species did not increase in importance and the plot otherwise

continued an “unmistakable trend toward a mature forest” (Crow 1980, Drew 2009). The 1937 harvest had removed commercially over mature timber (Briscoe and Wadsworth 1970), was intentionally very light to reduce impact to the watershed (F. Wadsworth, cited by Crow 1980), and is unlikely to have had a major impact on forest characteristics.

In 1962, Compartment 2A contained 39 crop trees per acre but was not marked for silvicultural treatment. In 1964, Compartment 2A was re-defined as Compartment 42 but the area remained roughly the same (Table 8). In a 1965 timber management plan for the pilot project area (Muñoz 1965), Compartment 42 was marked as a moderately accessible stand and planting with teak or mahogany was prescribed (Figure 10). The stand was not marked for TSI, perhaps because experiments with radiation were being conducted at El Verde at the time. The compartment sections located just over the ridge from EV-M were not marked for silvicultural activities in 1962, being considered “worthless stands” for forestry (Espíritu Santo Working Circle Map, 1962). North of the plot, above Palo Hueco Road, sections of Compartment 1 were marked for intensive stand improvement. In 1965, the updated timber management area no longer included the areas bordering EV-M east of the ridge (Figure 10).



**Figure 10.** A 1965 map of El Verde Working Circle, El Yunque National Forest, Puerto Rico from Muñoz (1965) shown with chronosequence study plots (red rectangles), El Verde field station (yellow star), roads (Highway 186 in red), and rivers (blue). From North to South, study plots include the Luquillo Forest Dynamics Plot, EV-O, and EV-M.

**Table 8.** Chronosequence plot locations within forest management units of El Yunque National Forest, Puerto Rico timber management areas in 1965 and factors determining order of silvicultural treatment (Muñoz 1965). Compartment (CPT) numbers before and after reorganization of management units (1964) are provided.

| Plot | 1965 Working circle and valley | Old CPT | New CPT | Area (ha) | Accessibility (Least to Most) | Slope (%)    | Stocking | DFR   | PTR  |
|------|--------------------------------|---------|---------|-----------|-------------------------------|--------------|----------|-------|------|
| EV-O | El Verde; ESV                  | 2A      | 42      | 34        | Less                          | Not recorded |          |       |      |
| SB-Y | Sabana; SV                     | 2D      | 156     | 7         |                               | Not recorded |          |       |      |
| SB-M |                                | 2A      | 153     | 11        | Less                          | > 50 %       | 56       | 406 m | 1968 |
| SB-O |                                | 3B      | 158     | 28        | Most                          | > 50 %       | 67       | 203 m | 1967 |

*Notes:* DFR, distance from road; PTY, proposed treatment year; ESV, Espíritu Santo Valley; SV, Sabana Valley. Plot EV-M is located outside of the timber management area.

### *Regeneration management in Sabana*

Plots SB-Y and SB-M were located in in sections D and A, respectively, of Compartment 2 of the Sabana Working Circle. Compartment 2, measuring 113 acres (46 ha), corresponds to the far northern part of Tract 53 or La Perla. Both stand improvement and reforestation treatments were carried out in this compartment, indicating that forest cover was lacking in places or natural regeneration had been unsatisfactory. During the first cutting cycle (1956-62), the focus in Compartment 2 was on plantation establishment in the northern half of the compartment. In 1956 three teak (*T. grandis*) plantations were established, including one in the area where SB-Y is located (Figure 11). Teak was the preferred species for deforested areas at drier low elevations (Table 6) because of its high value for cabinetmaking. It was typically planted with 8 x 8 foot spacing (2.4 x 2.4 m), weeded annually for two years, and thinned three times within 15 years (Muñoz 1965). Nine acres of Compartment 2 were planted in teak that year, but only four were successful. Plantings at the site of a former sawmill along PR Route 988 failed twice because the site was too wet and were later replaced with *T. heterophylla* and *Cecropia schreberiana*. Teak plantations were weeded twice in 1956

and once in 1957. A maría plantation was established and thinned in 1956, along the south edge of Route 988 near the western boundary.

In 1957, 1200 teak trees were planted around the Sabana Field Research Station, covering 4.5 acres (1.8 ha) and requiring 295 man-hours of labor. Further along Route 988 a plantation of *Hernandia sonora* (mago) was established with 750 seedlings. Mago is a fast-growing, light-demanding tree easy to propagate from seed and with soft wood suitable for boxes, crates, and interior construction (Little and Wadsworth 1964). Other Compartment 2 plantings during the first 5-year management cycle included small areas of Honduran mahogany; a mixed planting of teak, mago, *Talipariti elatum* (mahoe), and *Pterocarpus officinalis* (pterocarpus) to replace failed *C. schreberiana* at the former sawmill site; an experimental planting of 100 *Pinus caribae* (Caribbean pine) trees; and an underplanting of *C. schreberiana* in a *Casuarina equisetifolia* plantation after a 1959 thinning and timber sale.

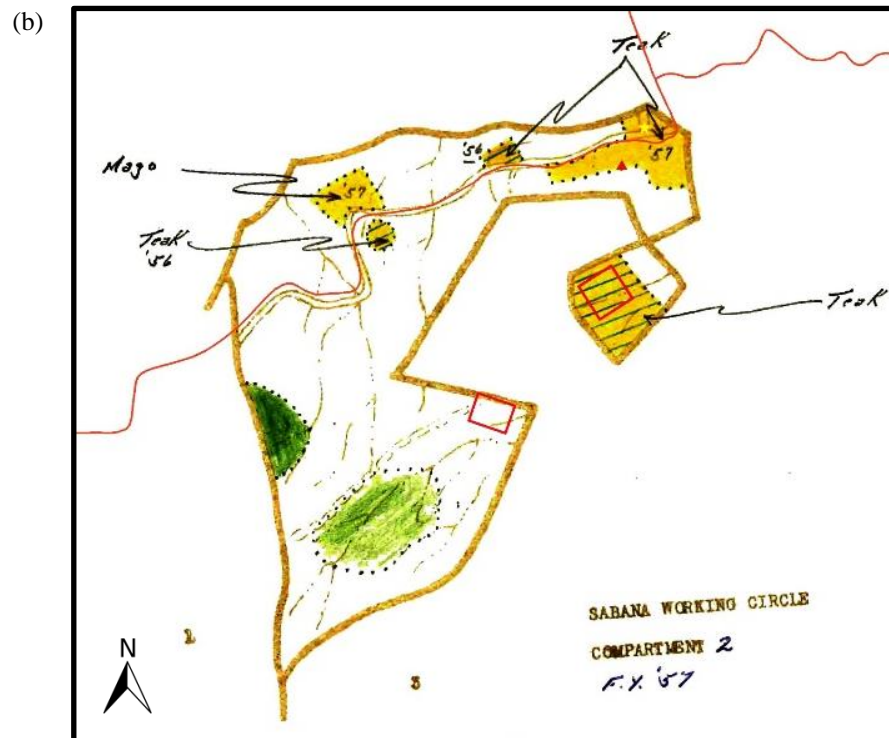
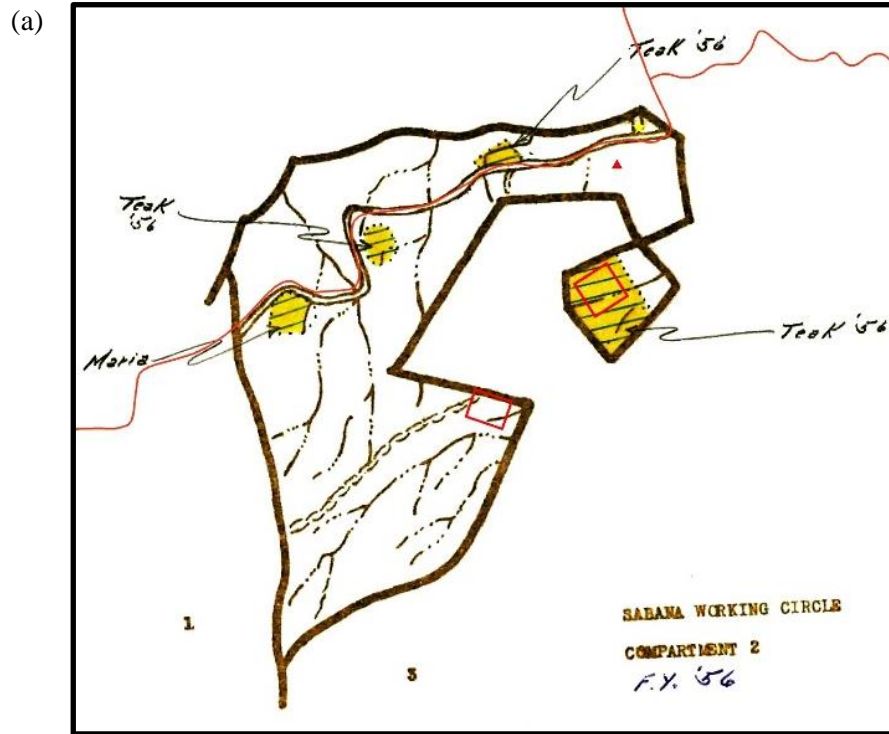
#### *Stand improvement in Sabana*

Toward the end of the first cutting cycle, forest management records demonstrate a shift from plantation management to the thinning of natural forest stands, intended to promote the growth of crop trees. Timber stand improvement (TSI) cuttings were first carried out on 14 acres (6 ha) in 1957 in the southern half of the compartment (Figure 11), and in 1959 thinning for timber sales was conducted along Route 188 and just south of the Sabana Field Research Station (Figure 12). Neither of these affected the chronosequence plots. In 1961 a TSI treatment of 107 acres thinned all but the easternmost part of Compartment 2, affecting SB-M but not SB-Y (Figure 12). Sales

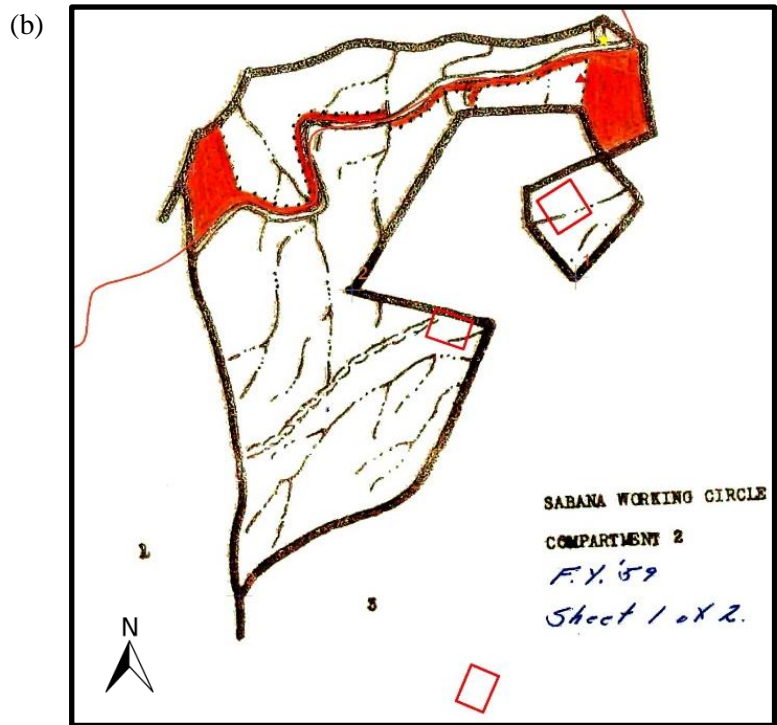
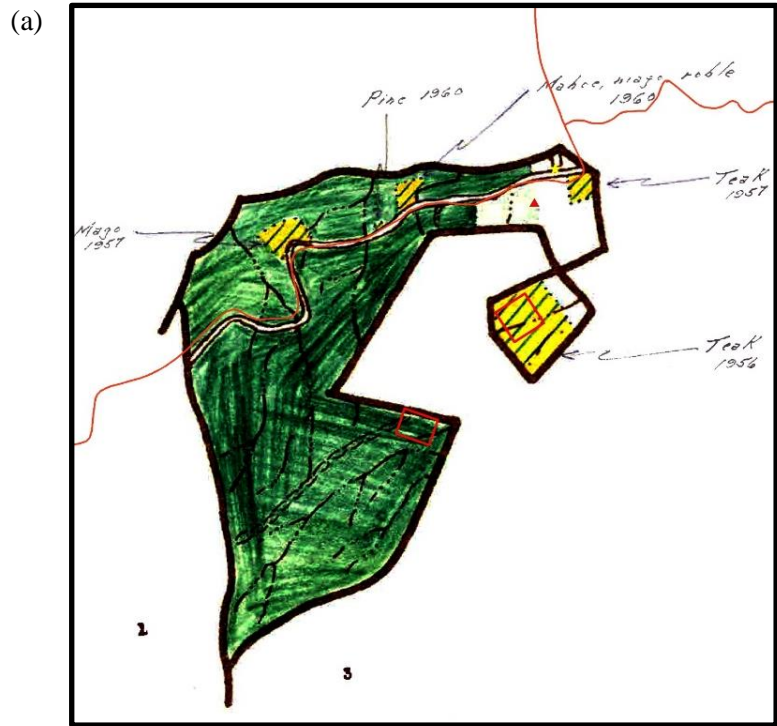
from this treatment included posts and bamboo stems. TSI in 1963 included the sale of bamboo and poles from the western area only.

In the 1965 timber management plan, the reorganization of management units placed SB-Y in compartment (CPT) 156 and SB-M in CPT 153 (Table 8) for the second cutting cycle (1966-70). The former was classified as teak plantation requiring TSI over the second cutting cycle and ranked among the most accessible sites, located only 200 m from a road (Figure 13). CPT 153 was likewise labeled natural forest requiring TSI and containing 56 crop trees per acre but considered steeper and less accessible, approximately 400 m from the closest road. More accessible and flatter sites were given priority for treatment. Subsequent management records indicate SB-Y (CPT 156) was subject to TSI in 1966 and 1967, producing posts, poles, and miscellaneous products for sale. No management records exist for SB-M (CPT 153) in the second cutting cycle, although the adjacent 44-acre (18 ha) compartment 154 received silvicultural treatments in 1965 and 1967.

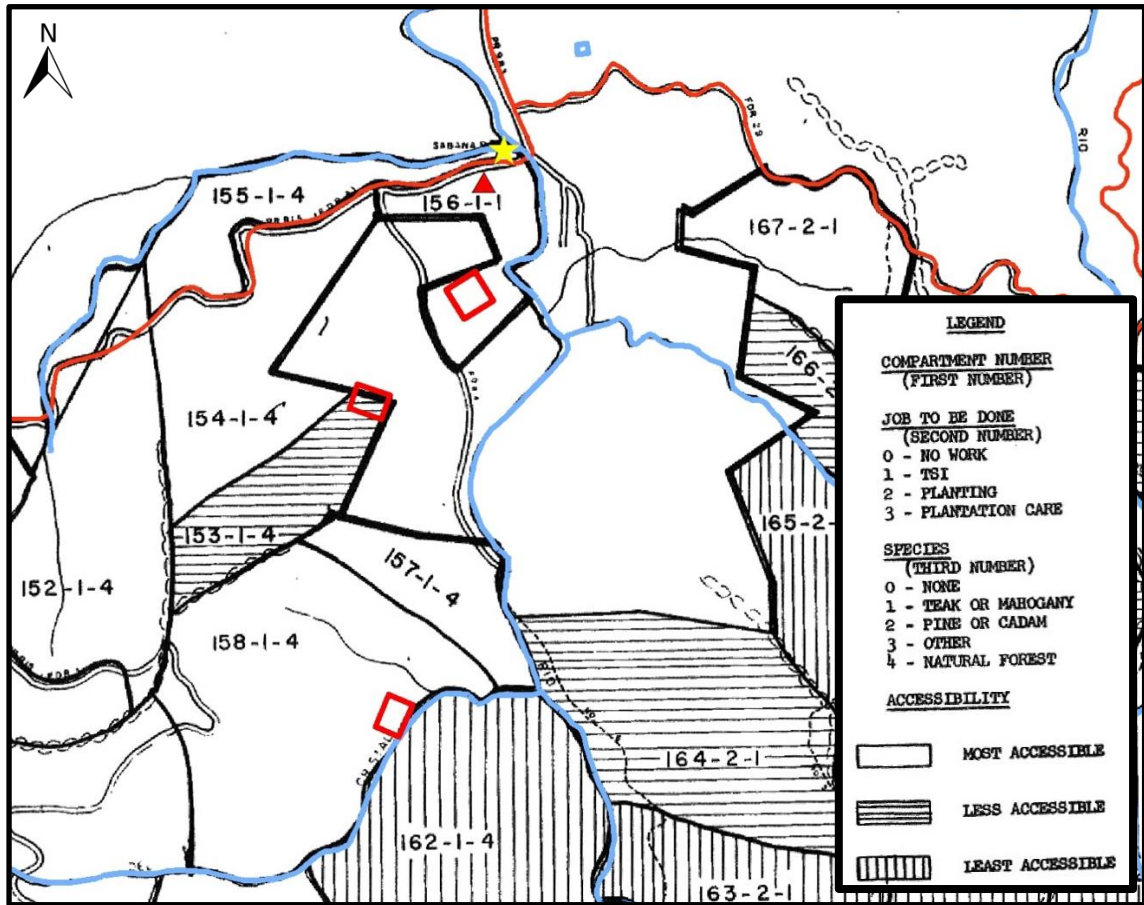




**Figure 11.** Plantation establishment (yellow), plantation care (thatched), and timber stand improvement (green) conducted in fiscal years (a) 1956 and (b) 1957 in Compartment No. 2 of El Yunque National Forest, Puerto Rico. Maps from CNF (1969); shown with chronosequence study plots (left to right) SB-M and SB-Y, roads (red), and the Sabana Field Research Station (yellow star) and Climate Warming Experiment (red triangle).



**Figure 12.** Timber stand improvement (green), plantation care (thatched), and timber sales (orange) in fiscal years (a) 1961 and (b) 1959 in Compartment No. 2 of El Yunque National Forest, Puerto Rico. Maps from CNF (1969); shown with chronosequence study plots (left to right) SB-M and SB-Y, roads (red), and the Sabana Field Research Station (yellow star) and Climate Warming Experiment (red triangle).

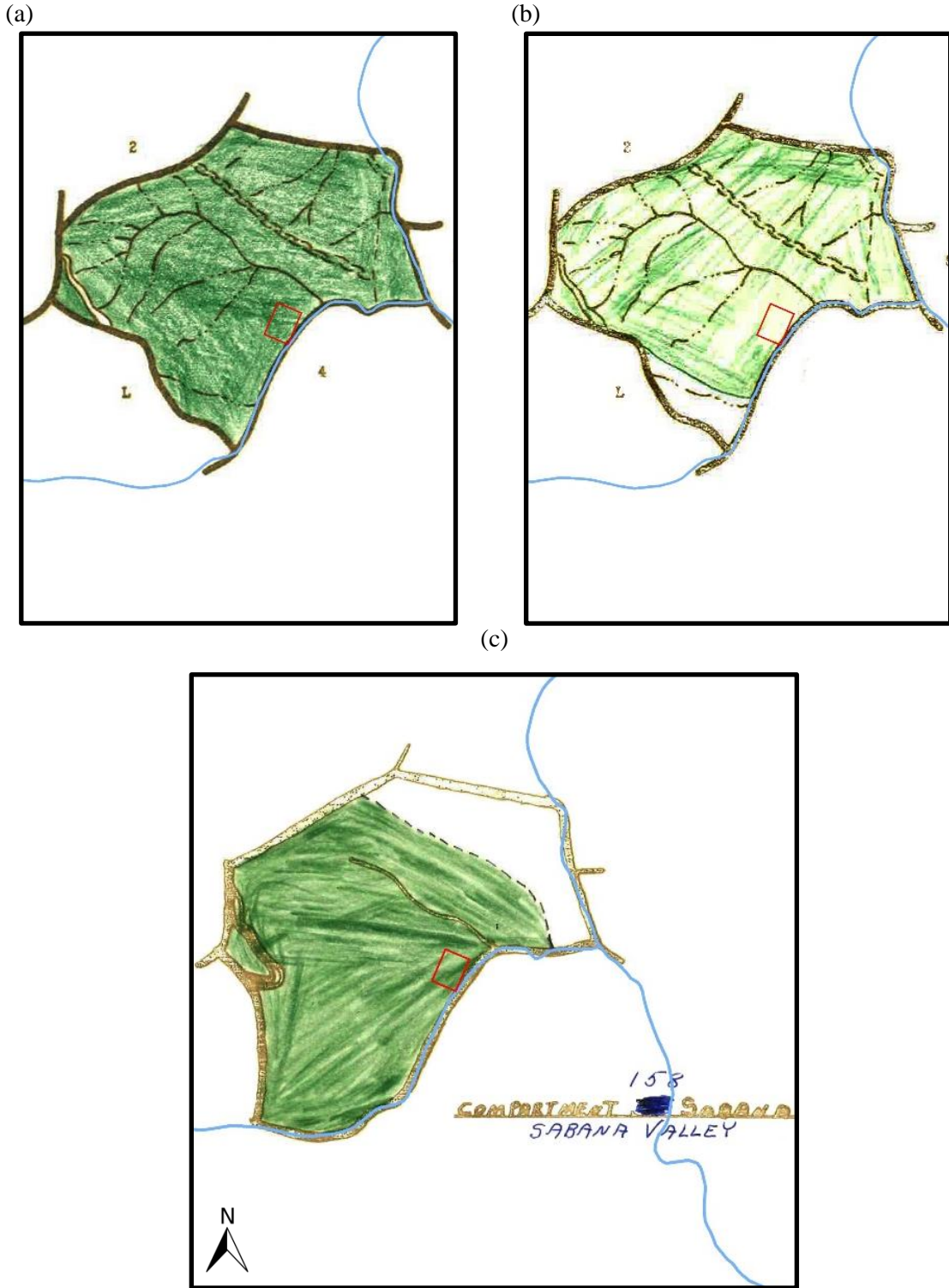


**Figure 13.** A 1965 map of Sabana Working Circle, El Yunque National Forest, Puerto Rico from Muñoz (1965) shown with chronosequence study plots (red rectangles), roads (Highway 988 in red), rivers (blue), and the Sabana Field Research Station (yellow star) and Climate Warming Experiment (red triangle). From North to South, study plots include SB-Y, SB-M, and SB-O.

Plot SB-O is encompassed within Compartment 3 of the Sabana Working Circle. This forest area first appears in pilot demonstration project records in 1959. Timber stand improvement was carried out on 88 acres (36 ha) in 1959, 1960, and 1961 and led to sales of poles, posts, crossties, cordwood, bamboo, miscellaneous forest products, and fuelwood. The total cost of the 1961 treatment was \$777.04 including 960 man-hours of labor. Project maps indicate SB-O was included in the treatment area (Figure 14) and

depict a former road at the western edge of the compartment that presumably provided timber access. The following year silvicultural treatment was limited to bamboo extraction, but in 1963 a stand improvement treatment was implemented on 80 acres, costing \$2,607.48 and involving 1132 man-hours of labor (Figure 14).

SB-O, part of the new 69-acre (28 ha) Compartment 158 beginning in 1964, was labeled a natural forest stand requiring TSI in the 1965 timber management plan. The compartment was stocked with 67 crop trees per acre. Based on its proximity (200 m) to a road, CPT 158 was ranked among the most accessible sites (Figure 13, Table 8). Records for Compartment 158 during the second cutting cycle include stand improvement of 65 acres (26 ha) in 1964 (Figure 14), the thinning of 19 acres for polewood in 1966, and stand improvement of 69 acres in 1969. The specific location of the 1966 thinning is not mentioned.



**Figure 14.** Timber stand improvement area (green) in Compartiment No. 3 of El Yunque National Forest timber management area in fiscal years (a) 1961, (b) 1963 and (c) 1964. Maps from CNF (1969); shown with chronosequence plot SB-Y in red and Sabana (north-south) and Cristal (east-west) Rivers in blue.

## CONCLUSIONS

In this study we assemble the land use histories of five forest communities important for long-term ecological research. These sites are located in the northern part of El Yunque National Forest where widespread deforestation occurred prior to 1935 and where smaller-scale disturbances continued for several decades. We characterize the processes of forest recovery and continued at varying spatial scales, including (1) the purchase of agricultural lands and details of past agricultural use at the level of individual, large farms, (2) human-assisted reforestation at the level of farms and plantations, (3) the supply and accessibility of timber at the compartment scale, and (4) extent of silvicultural management in each chronosequence plot. Forest census data reflects persistent human influences on the tree community, such as the presence of nonnative trees planted for reforestation or silvicultural purposes, confirming the presence of land use legacies in our forest research sites today.

This study adds to a set of regional forest landscape histories that underscore the long-lasting impact human actions on forest structure and composition (Scatena 1989, Garcia & Scatena 1994, Thompson et al. 2002). In North America, landscape histories have provided important implications for conservation and ecosystem restoration, such as by assessing the degree to which present forest stands resemble pre-European conditions (Gimmi & Radeloff 2013), providing baselines for the restoration of ecosystem structure and composition (Beller et al. 2005, Whipple et al. 2011), and identifying misinterpretations of previous forest conditions (Grossinger et al. 2007). Forest landscape reconstruction has also been undertaken to visualize long-term effects

of forestry activities and provide a tool for participatory forest management (Saito et al. 2007).

The locations of El Verde and Sabana on the flanks of the Luquillo Mountains and at the periphery of a protected area have made them vulnerable to human disturbance for centuries. Greater accessibility and more gentle terrain compared with the forest interior played a role in the longer duration and higher intensity of land-use activities such as logging, grazing, and cultivation. Historical aerial images provide a clear visual of the influence of topography on forest age, with steeper areas regaining forest earlier than flatter areas more valuable for agriculture. Other studies have found forests on more accessible and more arable lands to be younger than less fertile forests (Munteanu et al. 2017, Helmer et al. 2008) and suggested younger forests are more vulnerable to continued human disturbance (Kennaway & Helmer 2007). Trajectories of land use in the core of the national forest and at the periphery have converged over time, obscuring their fundamentally different histories. This result can differ where elevation and topography do not protect core areas. In one study, forest protection with differing management in core and buffer areas results in a divergence of previously similar land use trajectories (Gimmi & Radeloff 2013).

The species composition of plots SB-Y, SB-M and EV-M differ from that of interior forests, but not just because of their age since abandonment. More recently acquired lands, especially farmlands, were more likely to be reforested by humans than left to regenerate naturally. Initial tree communities in these areas were made up of species that were easy to seed and known to be hardy, as well as species able to invade and compete with those planted. As their forests recovered, SB-Y and SB-M were also managed for timber. This not only affected their species composition but also their

recovery rates, as the goal of timber management was to accelerate succession to mature stands with large, heavy-wooded trees. In combination the more intense planting and silvicultural management of SB-Y and SB-M meant that as these forests regenerated their species composition was subject to a greater degree of human control. Management decisions may have had important implications for local species pools, stand diversity, and mortality and growth rates of both desirable and undesirable trees. Consistent decisions by foresters to foster uneven-aged stands and retain a closed canopy also help define the nature of recovery of the younger forest communities.

Our ability to determine the impacts of human activities on forest communities in El Yunque is limited by the scale of analysis that different historical sources impose. The quality of spatial information improved over time as forest maps increased in precision and management units decreased in size. Land-use histories of large, heterogenous tracts of farmland were necessarily broad, while histories of timber management units were more precise and in some cases identified human activities at the level of the forest plot. Analysis of change over time was limited by the intermittent nature of historical records: our interpretations are based solely on the years for which we have aerial photographs, maps, or forest records. Conclusions about landscape change can also be affected by uncertainty generated in the georeferencing and interpretation of historical maps (Schaffer & Levin 2015, Kaim et al. 2016), which are more likely to disagree in less-accessible areas and near forest edges (Gimmi et al. 2016). We attempted to minimize uncertainty by combining historical maps and aerial photographs with forest survey data, administrative reports, and management plans to reconstruct landscape-level histories and evaluate impacts to current forest plots. Integrating multiple data sources is a common approach to addressing limitations in the



quality and extent of information available for historical reconstructions (Stäubli 2008, Trueman et al. 2013).

Despite discontinuities, historical sources provided detailed accounts of critical periods of forest transformation and chronicled the general sequence of events that led to today's forest state. This landscape history provides a foundation for future studies in El Verde and Sabana to incorporate a historical perspective, an especially important goal in research plots established to improve our understanding of long-term processes and stochastic events. Ideally, a better understanding of historical forest change will help scientists, managers and the public place future disturbances in a larger context.

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## CHAPTER 2

# **Successional trajectories of post-agricultural forests at the boundary of El Yunque National Forest, Puerto Rico**

### ABSTRACT

Forests are re-growing on abandoned agricultural lands across the tropics. Secondary forests tend to resemble much older forests in their structural attributes but not species compositions. Understanding secondary forest succession over short and long time spans and the extent to which patterns of species replacement are directional is important for predicting the nature of future forests. Here we analyze successional patterns using tree census data from a chronosequence of forest plots in El Yunque National Forest, Puerto Rico and evaluate stand vulnerability to Hurricanes Irma and María. Six years of resampling allowed us to test whether forest dynamics reflected patterns observed across the chronosequence. Stand density and basal area shifted in the direction of a mature forest, while species richness, diversity, and composition did not follow predicted patterns clearly. Past hurricane disturbance and a disease outbreak influenced the direction of structural changes. We observed an increase in the number of mature forest species as forests aged but found did not find convergence in species composition across sites. Species-specific mortality rates following two major hurricanes were highest for early-successional shrubs and small trees and lowest for large-statured, old-growth specialists. Variable successional trajectories and susceptibility to hurricanes highlight



the importance of site differences, including land-use legacies and dominant nonnative species, which can have long-lasting impacts on secondary forest communities.

## INTRODUCTION

The conversion of tropical forests to agricultural lands has caused the disappearance of much of their biodiversity as well as the goods and services forests provide (FAO 2018). Subsequent abandonment of agricultural lands has provided an opportunity for many forests to regenerate and recover. However, these secondary forests are growing in altered environmental and landscape conditions that may favor different tree communities than original forests (Lugo 2002). The extent to which secondary forests can reach a state similar to their old-growth counterparts remains a question and has important consequences for the conservation of biodiversity and maintenance of important ecosystem services (Chazdon 2014).

Studies of post-agricultural succession have demonstrated remarkable resilience in tropical forest structure. Basal area and aboveground biomass accumulate rapidly early in succession (Saldarriaga et al. 1988, Guariguata et al. 1997, Aide et al. 2000, Pascarella et al. 2000, Silver et al. 2000, Guariguata & Ostertag 2001, Peña-Claros 2003), while stand density increases with tree colonization and decreases with density-dependent mortality as the canopy closes (Van Breugel et al. 2006). Forest cover, litterfall, soil organic matter, and nutrient cycling also exhibit rapid recovery to pre-disturbance values or rates (Walker et al. 2010, Zou et al. 1995, Brown & Lugo 1990). Species tend to accumulate rapidly if seed sources and dispersal agents are available (Guariguata et al. 1997; Nicotra et al. 1999; Aide et al. 2000; Denslow and Guzman 2000; Chinea 2002) allowing species richness and diversity to reach the levels of mature forests quickly (Chazdon et al. 2007). Two competing hypothesis concerning diversity recovery patterns include a linear increase with forest age (Odum 1969, Budowski 1965)

and a peak at intermediate ages due to the coexistences of pioneer, intermediate, and shade-tolerant species as predicted by the Intermediate Disturbance Hypothesis (Huston and Smith 1987, Bongers et al. 2009). Within 20-40 years, tropical secondary forests may be indistinguishable from old-growth forests in their structure and function (Rivera & Aide 1998, Aide et al. 2000, Guariguata & Ostertag 2001, Chinea 2002).

While stand structure recovers quickly, species assemblages remain distinct for much longer and may never fully resemble those of old-growth forests (Zimmerman et al. 1995, Finegan 1996). These differing patterns have led researchers to suggest a decoupling of structural and floristic attributes during succession (Guariguata & Ostertag 2001, Chazdon et al. 2007, Letcher & Chazdon 2009) and have contributed to a poor understanding of the capacity of tropical forests to recover their pre-disturbance species compositions (Rozendaal et al. 2019). Land-use history and the initial composition at a site can determine successional pathways and rates of species turnover, as the first species that establish at site can have long-lasting influences on the emerging forest community (Chazdon et al. 2007). Less clear is whether such differences early in succession lead to permanently distinct forest communities, or whether variable successional trajectories eventually lead to the same endpoint (Walker et al. 2010). If the latter is true, we expect to see the composition of differing secondary forest communities converge on that of nearby old-growth forests. Deterministic models of succession support this pattern, predicting that sites undergoing the same biological processes will demonstrate a predictable sequence of species replacement. Neutral models give greater importance to dispersal limitations and stochastic events, suggesting communities change idiosyncratically and will not become more similar to one another over time (Norden et al. 2009, 2015).

Most of our knowledge concerning successional change in tropical forests has been inferred by comparing the characteristics of forest sites of different ages. This space-for-time substitution, or chronosequence approach, allows us to overcome the limitations posed by the longevity of trees and slow rates of change in community attributes. However, the method has been criticized because attributing differences among sites to forest age rests on the assumption that sites have the same abiotic and biotic history, which is difficult to achieve especially in heterogenous tropical landscapes (Walker et al. 2010, Quesada et al. 2009). Failure to account for the influence of site differences and stochastic processes can lead to misleading inferences about successional dynamics (Flynn et al. 2010), especially in forests with high-frequency disturbance regimes. A better approach is to combine knowledge derived from chronosequences with long-term observations of forest dynamics that can better capture the underlying processes operating over succession, for example by remeasuring chronosequence sites over time (Foster & Tilman 2000). Such tracking of sites allows the testing of deterministic assumptions and, where short-term changes deviate from chronosequence predictions, an examination of potential ecological drivers including natural disturbance (Pascarella et al. 2004).

In this study we combine chronosequence and resampling approaches to examine the recovery of stand structure and species composition over time. We evaluate changes in stand parameters with forest age, predicting that (1) stand density will decrease and basal area increase as forests self-thin over succession (2) species richness and diversity will be highest in intermediate-aged sites because of overlapping tree life histories, (3) stands will demonstrate directional change and convergence on an old-growth composition and (4) difference in species composition will influence stand-level

hurricane damage and mortality. If forest communities are converging in their composition, we expect to see a reduction over time in compositional heterogeneity among chronosequence sites.

## METHODS

### *Study site*

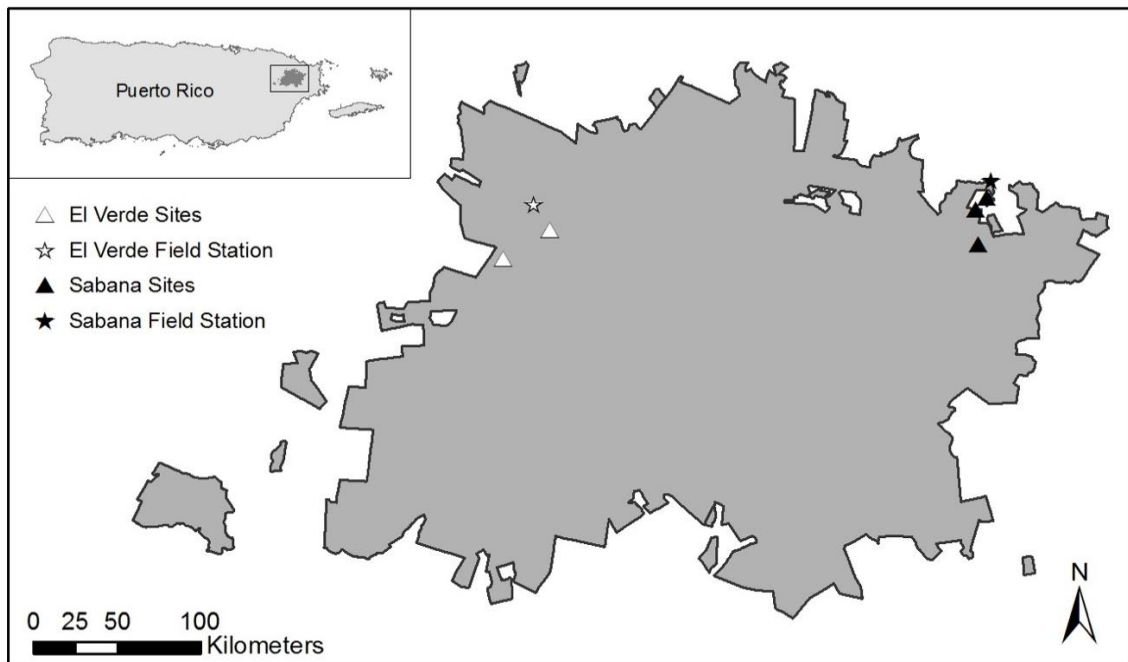
This study was conducted in two research areas along the northern border of El Yunque National Forest in the Luquillo Mountains of Puerto Rico (Figure 1). The Sabana Research Area (Sabana; 18.324, -65.730) is located in the northeastern corner of the national forest and is managed by the International Institute of Tropical Forestry (IITF) of the U.S. Forest Service. The El Verde Research Area (El Verde; 18.333, -65.816) is located in the northwestern part of the national forest and is managed by the University of Puerto Rico. Both research areas are classified as subtropical wet forest by the Holdridge life zone system (Ewel and Whitmore 1973) and fall within the lower montane forest zone life zone below 600 m in elevation (Brown et al. 1983). Rainfall is approximately 3500 mm/yr.

The predominant vegetation in the lower montane forest is the *Dacryodes-Sloanea* forest association, commonly known as tabonuco forest (Beard 1949, Crow & Grigal 1979). Older stands are typically dominated by the large-statured canopy tree *Dacryodes excelsa* (tabonuco) and the Sierra palm *Prestoea montana* as well as the shade-tolerant trees *Sloanea berteriana*, *Manilkara bidentata*, *Buchenavia tetraphylla* and *Guarea guidonia* (Briscoe & Wadsworth 1970, Wadsworth 1951). Two fast-growing and light-demanding species, *Cecropia schreberiana* and *Schefflera morototoni*, proliferate in

canopy openings following natural disturbance (Silander 1979, Brokaw 1998). In lower-elevation stands with a history of agriculture and selective logging, densities of large, heavy-wooded trees such as *D. excelsa* and *M. bidentata* are low and a different set of disturbance-adapted trees and shrubs is dominant. The wind-dispersed tree *Tabebuia heterophylla* and shrubs or small trees of the Melastomataceae and Rubiaceae families are common (Aide et al. 1995, Ostertag et al. 2005, Zimmerman et al. 1995). The Luquillo Mountains have been affected by numerous hurricanes over the past century that have caused defoliation, stem and branch damage, and tree mortality in parts of the forest. The most recent include Hurricane Hugo in 1989, Hurricane Georges in 1998, and Hurricanes Irma and María in September 2017. Prevailing winds and hurricane events tend to arrive from the ocean to the east; forests in north and northeast areas are considered most susceptible to hurricane winds (Boose et al. 1994). Hurricane Hugo caused severe damage to the forest, with greater damage reported for North-facing slopes. Hurricane Georges caused localized defoliation and damage to trees (Ostertag et al. 2005). As a result of frequent and patchy damage by hurricanes, forest structure and composition are highly dynamic with individual stands in varying stages of recovery.

Four forest plots differing in successional age were established to form a forest chronosequence across El Verde and Sabana (Table 1.). Plots range from 0.5 to 1 hectare (ha) in size and from 121-543 meters above sea level. Three are located in areas used for agriculture before being purchased by the U.S. Forest Service, while the fourth is located in an area of forest that to our knowledge has not been cut over or cleared for agriculture in the past century. Together the plots represent young, intermediate-aged, and old-growth forest. Estimates of forest age included in Table 1 are based on a previous study of land cover change at the periphery of El Yunque (Lugo et al. 2004).

For analysis we expanded the chronosequence to include data on structure and composition from an existing, mature forest plot within the El Verde research area known as El Verde 3. El Verde 3 is a 0.72 ha plot established in 1943 by Frank Wadsworth as part of a network of 20 long-term plots to assess the growth of valuable timber species and has been censused every 1 to 12 years since, making it one of the longest continuously monitored forest lots in the Neotropics (Drew et al. 2009). Prior studies of El Verde and of this plot indicate it was forested in 1936 and that species characteristic of tabonuco forest have remained dominant (Drew et al. 2009, Heartsill Scalley 2017, Thompson et al. 2002). We refer to this plot as EV-O to indicate its old-growth structure and composition compared to the middle-aged plot EV-M.



**Figure 1.** Map of the location of El Yunque National Forest within Puerto Rico (inset) and of El Verde and Sabana research plots and field stations within El Yunque National Forest.

**Table 1.** Description of forest plots in the El Verde and Sabana Research Areas of El Yunque National Forest, Puerto Rico.

| Site            | Relative stage | ASAA (yr) | Elevation (m asl) | Aspect | Census period evaluated |
|-----------------|----------------|-----------|-------------------|--------|-------------------------|
| <u>Sabana</u>   |                |           |                   |        | 2011 - 2016             |
| SB-Y            | Young          | 35-62     | 121               | E      | 2011 - 2016             |
| SB-M            | Intermediate   | >62       | 149               | E      | 2011 - 2016             |
| SB-O            | Old Growth     | Uncut     | 186               | E      | 2011 - 2016             |
| <u>El Verde</u> |                |           |                   |        | 2011 - 2016             |
| EV-M            | Intermediate   | 62-76     | 543               | NW     | 2011 - 2016             |
| EV-O            | Old growth     | Uncut     | 400               | NW     | 2010 - 2015             |

*Notes:* ASAA = Age since agricultural abandonment. Census period is up to 2017. Censuses were annual except EV-O, which was intermittent until 2000 and every 5 years from 2000-2015.

### *Tree census and hurricane damage*

The chronosequence sites were censused annually from 2011-2016 following the Center for Tropical Forest Science protocol (see Condit et al. 1998). All woody stems > 1 cm diameter at breast height (dbh) were measured, mapped, identified to species, and assessed for damage and mortality. We include in our analyses data from the 2010 and 2015 censuses of EV-O. Census methods for EV-O are the same except that only woody stems >4 cm in diameter are measured.

A survey was conducted in Feb-March 2018 to evaluate hurricane-related mortality and damage to stems and crowns of large (>10 cm dbh) trees in three of the chronosequence sites. SB-Y is not included in this analysis because of extensive damage to the plot by a utility company before the post-hurricane survey could be completed.

The relative exposures of chronosequence plots to Hurricane Irma and Hurricane María winds were examined with the simple meteorological model HURRECON and topographic exposure model EXPOS described in Boose et al. (1994). HURRECON reconstructs local wind conditions based on the track, size and intensity of a hurricane



and EXPOS uses the predicted peak wind direction and a 30-m digital elevation map to estimate exposure to strong winds at the landscape level. Minimum values denote areas most likely protected by their topographic position while maximum values indicate high exposure to peak winds.

### *Data analysis*

Parameters used to quantify differences in forest structure among sites and changes over the census period include stand density and basal area, size class distributions, relative densities and importance values of species, species richness and diversity, and species turnover. Values were calculated for initial and final census years (2011 and 2016 for chronosequence plots; 2010 and 2015 for EV-O) with the exception of species turnover which used all available census years. Density and basal area were expressed on a per hectare basis and comparisons of size class distributions grouped stems into the following DBH categories: 1–1.9, 2–4.9, 5–9.9, 10–19.9, 20–29.9, 30–39.9, 40–49.9, and  $\geq 50$  cm). Importance values were calculated by summing species relative densities, relative basal areas, and relative frequencies and range from 0-300%. Nomenclature follows Gann et al. (2015-2019). Species richness was rarefied to account for differences in stem densities among sites and was calculated for a sample of 1000 stems in the R statistical environment (R Development Core Team 2018) using the package Vegan (Oksanen et al. 2018). Diversity metrics were also calculated with Vegan and include Simpson's diversity, which places more weight on dominant species, and the exponent of Shannon's entropy which emphasizes evenness in abundance (Shannon 1948, Simpson 1949, Hill 1973). Annual species turnover was calculated with the R package

Codyn and included percent species gain, percent species lost, and percent turnover (gain + loss) across two consecutive census years relative to total species richness.

Species composition was examined in several ways as we were particularly interested in its recovery over time. This involved (1) comparing relative densities of species in each plot in the first and final census years across sites, (2) calculating mean pairwise Bray-Curtis dissimilarity values among sites and over time, and (3) calculating Bray-Curtis dissimilarity values within a site over the census period. Bray-Curtis values were based on a primary matrix of species densities (number of individuals per ha) and dissimilarities within sites were calculated by pairing census year 1 with each other census year. Plot EV-O was excluded from within-site analysis as it lacks annual measurements.

Initial mortality resulting from Hurricanes Irma and María was calculated as the proportion of stems in a site that died between the last census (fall 2016) and the damage survey (Jan-March 2018), which was completed six months after the storms. Stem damage in each site was evaluated by calculating the proportion of trees with broken stems, uprooted stems, or both. Estimates of crown damage excluded dead, broken or uprooted trees as well as palms and tree ferns as these species' hurricane-damaged crowns could have re-grown prior to the damage survey. Remaining trees in each site were grouped into three categories of damage: light ( $\geq 75\%$  crown remaining), medium (25-75% crown remaining), or heavy ( $< 25\%$  crown remaining). Species-specific mortality rates for species with at least 10 stems ( $\geq 10$  cm DBH) surveyed were calculated as the proportion of individuals across all sites found dead at the time of survey.

## RESULTS

### *I. Stand structure*

Stem density values in the first census year ranged from ~8600 stems per hectare (stems/ha) in SB-Y to only ~1500 stems/ha in EV-O (Table 2). When all sites were compared, stem density did not follow the expected pattern of a decline with forest age. El Verde site stem density values were uniformly lower than Sabana values, and values of plot SB-M (~6000 stems/ha) were double those of EV-M (~3,000 stems/ha). Within each research area, however, stem density values declined steadily with forest age. The stem density of EV-M was double that of EV-O (~1500 stems/ha) and Sabana plots declined from approximately 8600 stems/ha in SBY to 6000 in SB-M and 4000 in SB-O.

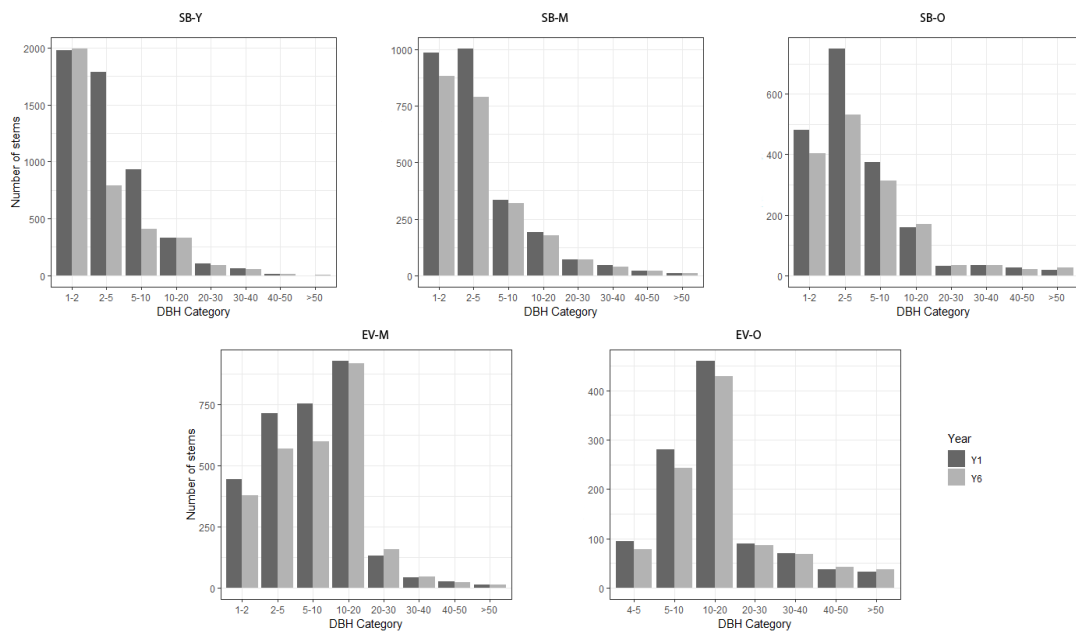
Basal area values followed a more predictable pattern, with values increasing steadily with stand age across sites. Initial values ranged from 36 m<sup>2</sup>/ha in SB-Y to 50 m<sup>2</sup>/ha in EV-O. Though SB-M had double the stand density of EV-M, these two sites were similar in basal area (39 and 38 m<sup>2</sup>/ha, respectively). The old growth plots showed more variation: from EV-M to EV-O a large jump in basal area was observed (39 to 50 m<sup>2</sup>/ha), while SB-M and SB-O exhibited similar values (39 and 41 m<sup>2</sup>/ha).

Stem losses over the six-year census period declined in magnitude with forest age within a research area, but not across all sites. The largest reductions occurred in SB-Y (29% stem loss) and SB-M (24%), followed by SB-3 (17%). Changes in El Verde were less pronounced: EV-M decreased in stem density by 11.5% while EV-O increased by 4%. Basal area showed an unexpected decrease over the census period in the youngest stand. SB-Y declined by 13.5%, while SB-M and EV-M underwent only slight

reductions (<2%). EV-O accumulated basal area (6%) while SB-O increased only slightly (<2%).

**Table 2.** Stand characteristics of chronosequence plots in El Yunque National Forest, Puerto Rico in census years 1 and 6.

| Site | Density (stems/ ha) |       | Basal area (m <sup>2</sup> / ha) |      |
|------|---------------------|-------|----------------------------------|------|
|      | Y1                  | Y6    | Y1                               | Y6   |
| SB-Y | 8,664               | 6,136 | 36.4                             | 31.5 |
| SB-M | 5,985               | 5,232 | 39.1                             | 38.8 |
| SB-O | 3,923               | 3,258 | 40.6                             | 41.3 |
| EV-M | 3,087               | 2,733 | 37.8                             | 37.1 |
| EV-O | 1,551               | 1,612 | 50.6                             | 53.5 |



**Figure 2.** Size class distributions of chronosequence plots in El Yunque National Forest, Puerto Rico in census years 1 and 6.

The distribution of stem diameter size classes across plots (Figure 2) indicate large proportions of small trees in the Sabana sites. Stems <5 cm were most abundant in all three sites, although SB-O had fewer stems in the 1-2 cm category than the younger sites. At El Verde sites the greatest proportion of stems were in the 10-20 cm size class,

followed by the 5-10 cm category. All sites had relatively few stems in large ( $\geq 20$  cm) size classes, though EV-O had a greater proportion of large trees than other sites.

Stem losses over the census period varied by size class among sites but did not shift overall patterns of size distributions. In SB-Y, the number of stems in the 2-5 cm size class and in the 5-10cm class each declined by more than half, while the 1-2 cm and large size classes remained stable. SB-M and SB-O displayed greatest reductions in the 2-5 cm class, while El Verde sites showed relatively even stem losses across small and intermediate size classes.

## ***II. Species diversity and turnover***

Species diversity (Table 3) followed the same pattern in three metrics of species richness and diversity: rarefied species richness (S at 1000 stems), Simpson's diversity ( $1/D$ ), and the exponent of Shannon's entropy ( $e^H$ ). SB-O was the most diverse site followed by EV-M, EV-O, SB-M and SB-Y, indicating diversity increased with stand age in Sabana but not in El Verde or overall across sites. Initial diversity increased by more than fourfold from SB-Y to SB-O, and roughly doubled from SB-Y to SB-M. In contrast the true diversity of EV-O was only half that of EV-M and roughly equivalent to that of SB-M.

Over the census period species richness increased or remained stable in all sites. The largest increase occurred in SB-Y (16%) followed by EV-O (5%) and SB-M (4%). In contrast diversity increased in the youngest two sites and decreased in the oldest three sites, suggesting a peak in diversity at intermediate stages of succession. SB-Y exhibited

the greatest rate of change with a 50% increase in 1/D and 60% in  $e^H$  implying a rapid accumulation of species. SB-M and SB-O displayed nearly identical rates of change (20% change in 1/D and 10% in  $e^H$ ) but in opposite directions. EV-M declined even more gradually, and EV-O showed only slight changes in 1/D and no change in  $e^H$ .

**Table 3.** Rarefied species richness (S at 1000 stems), Simpson's diversity (1/D), and the exponent of Shannon's entropy ( $e^H$ ) of chronosequence plots in El Yunque, Puerto Rico in census years 1 and 6.

| Site | $S^{1000}$ |      | 1/D  |      | $e^H$ |      |
|------|------------|------|------|------|-------|------|
|      | Y1         | Y6   | Y1   | Y6   | Y1    | Y6   |
| SB-Y | 32.9       | 38.1 | 2.96 | 4.43 | 6.06  | 9.75 |
| SB-M | 38.4       | 40.0 | 5.89 | 7.05 | 10.8  | 11.9 |
| SB-O | 53.5       | 53.9 | 17.4 | 14.0 | 26.6  | 24.1 |
| EV-M | 52.2       | 53.0 | 11.0 | 9.51 | 20.0  | 18.1 |
| EV-O | 46.5       | 48.9 | 5.80 | 5.65 | 10.2  | 10.1 |

Annual species turnover (percent of total species richness) declined with stand age (Table 4). Nonzero values ranged from 1.5% turnover (EV-M) to 11.5% turnover (SB-Y). High turnover in SB-Y was driven by species gains including a 10% gain in species from the first to the second annual census. Turnover values in other sites were more moderate (<6%), with none gaining more than 3% of species in any given year. Species losses were low in all sites (<4%) but greatest in SB-Y. EV-O lacks annual measurements but an overall turnover rate of 0.6% over the census period was calculated.

### ***III. Stand composition***

A total of 107 species were found across all plots. Fifteen of these are endemic to Puerto Rico, four are nonnative to the island and naturalized, and one (*Tectona grandis*)

is nonnative and cultivated only (Gann et al. 2015-2019). The inclusion of EV-O in the chronosequence increased the original number of species from 103 to 107 and of endemics from 13 to 15. No cultivated species and only one stem of one naturalized species, *Swietenia macrophylla*, were found in EV-O.

**Table 4.** Annual species turnover within chronosequence plots in El Yunque National Forest, Puerto Rico based on stem densities. Percent species gain, percent species loss and percent turnover (gain + loss) are relative to total species richness across two consecutive census years.

| Site | Census years | Gain (%) | Loss (%) | Turnover (%) |
|------|--------------|----------|----------|--------------|
| SB-Y | 1 – 2        | 9.62     | 1.92     | 11.54        |
|      | 2 – 3        | 0.00     | 0.00     | 0.00         |
|      | 3 – 4        | 3.77     | 3.77     | 7.55         |
|      | 4 – 5        | 3.77     | 1.89     | 5.66         |
|      | 5 – 6        | 0.00     | 3.85     | 3.85         |
| SB-M | 1 – 2        | 0.00     | 0.00     | 0.00         |
|      | 2 – 3        | 2.00     | 0.00     | 2.00         |
|      | 3 – 4        | 1.96     | 3.92     | 5.88         |
|      | 4 – 5        | 0.00     | 2.04     | 2.04         |
|      | 5 – 6        | 2.04     | 0.00     | 2.04         |
| SB-O | 1 – 2        | 3.33     | 0.00     | 3.33         |
|      | 2 – 3        | 0.00     | 0.00     | 0.00         |
|      | 3 – 4        | 0.00     | 0.00     | 0.00         |
|      | 4 – 5        | 0.00     | 3.33     | 3.33         |
|      | 5 – 6        | 0.00     | 0.00     | 0.00         |
| EV-M | 1 – 2        | 1.54     | 0.00     | 1.54         |
|      | 2 – 3        | 0.00     | 0.00     | 0.00         |
|      | 3 – 4        | 1.52     | 3.03     | 4.55         |
|      | 4 – 5        | 3.03     | 1.52     | 4.55         |
|      | 5 – 6        | 0.00     | 1.54     | 1.54         |
| EV-O | 1 – 6        | 0.06     | 0.00     | 0.06         |

### *Species densities*

Relative densities of species differed substantially across sites (Table 5). In the first census year, SB-Y was dominated by the nonnative ornamental tree *Syzygium*

*jambos* (55%) and the native early-successional tree *Psychotria brachiata* (17%). SB-M was dominated by two pioneer trees known to successfully colonize abandoned pastures in Puerto Rico, *Miconia prasina* (33%) and *Myrcia deflexa* (22%; Aide et al. 1995, Zimmerman et al. 1995), as well as the small-statured understory tree *Faramea occidentalis* (8%). SB-O also exhibited a high abundance of *F. occidentalis* (16%) and *M. prasina* (9%) but contained a more even distribution of species densities. In EV-M the most abundant species was the native palm *Prestoea montana* (22%), common at high elevations, followed by *Casearia arborea* (14%) and small endemic tree *Eugenia stahlii* (9%). *Prestoea montana* was again the most dominant species in EV-O (28%), followed by the late-successional species *Dacryodes excelsa* (24%), *Manilkara bidentata* (17%) and *Tetragastris balsamifera* (7%). The pioneer tree *Cecropia schreberiana* was common in El Verde but not in the Sabana sites.

Within sites, species composition shifted to differing extents over the six-year census period (Table 5). In EV-M and EV-O the five most abundant species retained their rank, with the exception of a decline of *M. prasina* in EV-M. The top species in SB-M likewise remained dominant but underwent larger changes in abundance. *M. prasina* and *M. deflexa* declined in abundance while *F. occidentalis* and *P. brachiata* increased. SB-O displayed more reshuffling amongst the top species, with *M. prasina* falling in rank while *S. tulae* and larger-statured species such as *D. excelsa* and *T. balsamifera* increased. *F. occidentalis* remained dominant and increased in abundance. Changes in abundance and rank were more pronounced in SB-Y, including a major increase in the relative density of *P. brachiata* which became the most abundant species, while *S. jambos* fell to the second most abundant. *M. prasina* and the shrub *Miconia*



*impetiolaris* increased in abundance and rank. Importance values by site of all species by in census years 1 and 6 can be found in Appendices D-H.

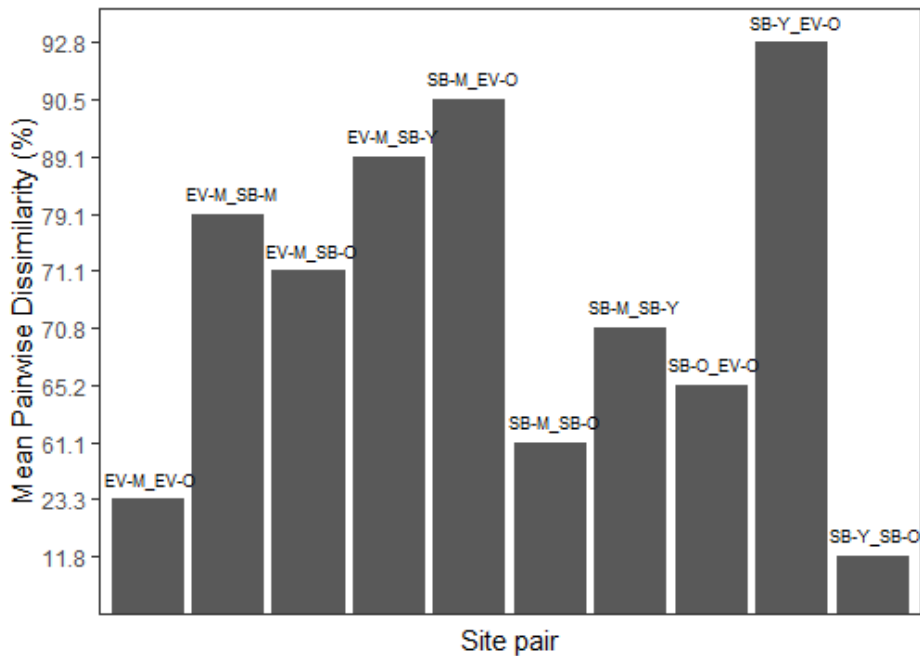
**Table 5.** Relative densities (RD) of the 10 most abundant stems within chronosequence plots in El Yunque National Forest, Puerto Rico in census years 1 and 6.

| Species                      | RD    | Species                      | RD    | Species                      | RD    | Species                      | RD    |
|------------------------------|-------|------------------------------|-------|------------------------------|-------|------------------------------|-------|
| <u>SB-Y Year 1</u>           |       | <u>SB-Y Year 6</u>           |       | <u>SB-M Year 1</u>           |       | <u>SB-M Year 6</u>           |       |
| <i>Syzygium jambos</i>       | 54.99 | <i>Psychotria brachiata</i>  | 44.39 | <i>Miconia prasina</i>       | 32.65 | <i>Miconia prasina</i>       | 28.43 |
| <i>Psychotria brachiata</i>  | 17.42 | <i>Syzygium jambos</i>       | 12.55 | <i>Myrcia deflexa</i>        | 21.51 | <i>Myrcia deflexa</i>        | 17.76 |
| <i>P. berteroaana</i>        | 3.67  | <i>Miconia prasina</i>       | 6.39  | <i>Faramea occidentalis</i>  | 7.68  | <i>Faramea occidentalis</i>  | 10.8  |
| <i>C. antillanum</i>         | 3.59  | <i>Miconia impetiolaris</i>  | 4.96  | <i>C. antillanum</i>         | 5.5   | <i>Psychotria brachiata</i>  | 9.27  |
| <i>Miconia prasina</i>       | 2.88  | <i>C. antillanum</i>         | 4.01  | <i>Psychotria brachiata</i>  | 4.33  | <i>C. antillanum</i>         | 5.59  |
| <i>Miconia impetiolaris</i>  | 1.99  | <i>Psychotria grandis</i>    | 3.3   | <i>Ocotea leucoxylon</i>     | 4.04  | <i>Ocotea leucoxylon</i>     | 4.88  |
| <i>Tectona grandis</i>       | 1.84  | <i>Prestoea montana</i>      | 2.79  | <i>Syzygium jambos</i>       | 3.9   | <i>Syzygium jambos</i>       | 2.52  |
| <i>S. macrophylla</i>        | 1.72  | <i>P. berteroaana</i>        | 2.3   | <i>Schefflera morototoni</i> | 3.31  | <i>Schefflera morototoni</i> | 2.44  |
| <i>T. heterophylla</i>       | 1.7   | <i>S. macrophylla</i>        | 2.1   | <i>T. heterophylla</i>       | 2.26  | <i>Ixora ferrea</i>          | 2.24  |
| <i>Guarea guidonia</i>       | 1.31  | <i>Guarea guidonia</i>       | 1.92  | <i>Ixora ferrea</i>          | 1.89  | <i>Manilkara bidentata</i>   | 2.15  |
| <u>SB-O Year 1</u>           |       | <u>SB-O Year 6</u>           |       | <u>EV-M Year 1</u>           |       | <u>EV-M Year 6</u>           |       |
| <i>Faramea occidentalis</i>  | 16.03 | <i>Faramea occidentalis</i>  | 20.65 | <i>Prestoea montana</i>      | 22.02 | <i>Prestoea montana</i>      | 24.66 |
| <i>Miconia prasina</i>       | 9.2   | <i>Simarouba tulae</i>       | 7.86  | <i>Casearia arborea</i>      | 13.64 | <i>Casearia arborea</i>      | 14.34 |
| <i>Simarouba tulae</i>       | 5.86  | <i>Dacryodes excelsa</i>     | 5.37  | <i>Eugenia stahlii</i>       | 8.8   | <i>Eugenia stahlii</i>       | 9.51  |
| <i>Manilkara bidentata</i>   | 4.63  | <i>T. balsamifera</i>        | 5.37  | <i>Myrcia deflexa</i>        | 6.46  | <i>Myrcia deflexa</i>        | 6.7   |
| <i>T. balsamifera</i>        | 4.63  | <i>Manilkara bidentata</i>   | 5.24  | <i>Miconia prasina</i>       | 5.94  | <i>Hirtella rugosa</i>       | 6.11  |
| <i>Dacryodes excelsa</i>     | 4.46  | <i>Miconia prasina</i>       | 4.79  | <i>Hirtella rugosa</i>       | 4.97  | <i>Ocotea leucoxylon</i>     | 3.55  |
| <i>Prestoea montana</i>      | 4.03  | <i>Ormosia krugii</i>        | 4.54  | <i>Ocotea leucoxylon</i>     | 3.22  | <i>M. guayanensis</i>        | 3.29  |
| <i>Ormosia krugii</i>        | 3.93  | <i>Prestoea montana</i>      | 4.48  | <i>M. guayanensis</i>        | 2.83  | <i>Sloanea berteriana</i>    | 2.89  |
| <i>P. berteroaana</i>        | 3.93  | <i>Tetrazygia urbanii</i>    | 3.77  | <i>Cecropia schreberiana</i> | 2.57  | <i>Miconia prasina</i>       | 2.45  |
| <i>Miconia mirabilis</i>     | 3.87  | <i>Ocotea leucoxylon</i>     | 3.13  | <i>Sloanea berteriana</i>    | 2.21  | <i>C. luquillensis</i>       | 1.87  |
| <u>EV-O Year 1</u>           |       | <u>EV-O Year 6</u>           |       |                              |       |                              |       |
| <i>Prestoea montana</i>      | 26.85 | <i>Prestoea montana</i>      | 28.49 |                              |       |                              |       |
| <i>Dacryodes excelsa</i>     | 24.98 | <i>Dacryodes excelsa</i>     | 24.26 |                              |       |                              |       |
| <i>Manilkara bidentata</i>   | 17.28 | <i>Manilkara bidentata</i>   | 17.13 |                              |       |                              |       |
| <i>T. balsamifera</i>        | 7.14  | <i>T. balsamifera</i>        | 6.85  |                              |       |                              |       |
| <i>Sloanea berteriana</i>    | 3.29  | <i>Sloanea berteriana</i>    | 3.07  |                              |       |                              |       |
| <i>C. schreberiana</i>       | 2.63  | <i>C. schreberiana</i>       | 2.52  |                              |       |                              |       |
| <i>Andira inermis</i>        | 1.5   | <i>M. guayanensis</i>        | 1.53  |                              |       |                              |       |
| <i>M. guayanensis</i>        | 1.5   | <i>Andira inermis</i>        | 1.35  |                              |       |                              |       |
| <i>Schefflera morototoni</i> | 1.03  | <i>Schefflera morototoni</i> | 0.99  |                              |       |                              |       |
| <i>Drypetes glauca</i>       | 0.94  | <i>Drypetes glauca</i>       | 0.9   |                              |       |                              |       |

Notes: *P. berteroaana*, *Psychotria berteroaana*; *C. antillanum*, *Calophyllum antillanum*; *S. macrophylla*, *Swietenia macrophylla*; *T. heterophylla*, *Tabebuia heterophylla*; *T. balsamifera*, *Tetragastris balsamifera*; *P. berteroaana*, *Psychotria berteroaana*; *M. guayanensis*, *Micropholis guayanensis*; *C. luquillensis*, *Calypranthes luquillensis*; *C. schreberiana*, *Cecropia schreberiana*.

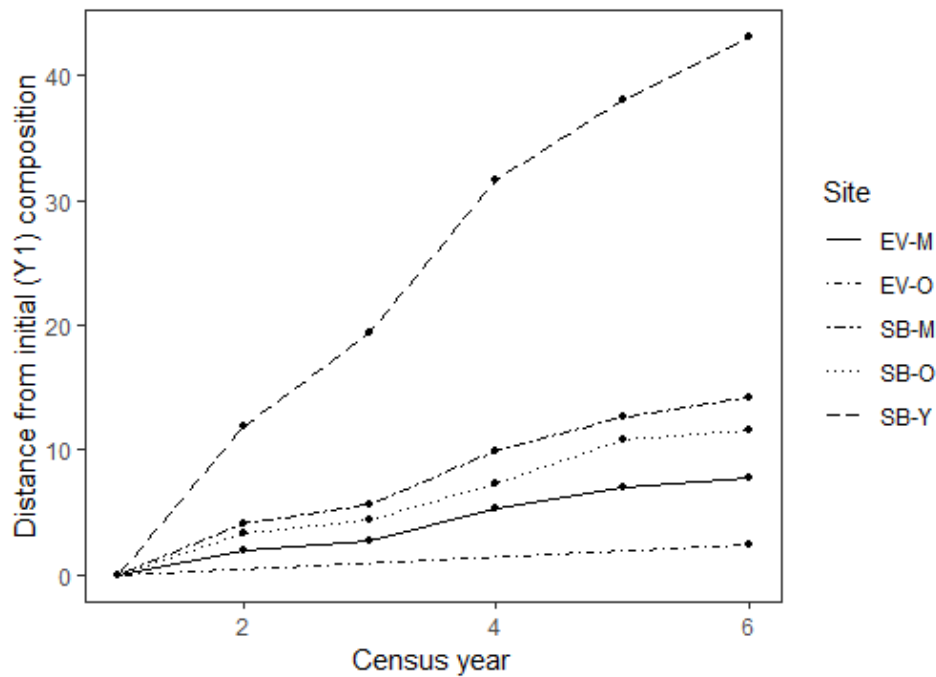
### *Dissimilarity values*

To determine the extent of overlap in species composition among sites we compared pairwise Bray-Curtis dissimilarities for all possible pairs of sites. Average dissimilarity values for each site pair were calculated from all available census years and are expressed as percentages (Figure 3). The greatest dissimilarity in species composition (least overlap in composition) occurs between SB-Y and EV-O as expected based on age and site differences. The least dissimilarity (greatest overlap in composition) occurs between SB-Y and SB-O despite large differences in age, followed by EV-M and EV-O. The two old-growth stands showed only moderate overlap in composition, further highlighting the important role of site differences.



**Figure 3.** Mean Bray-Curtis dissimilarity between all pairs of chronosequence plots in El Yunque National Forest, Puerto Rico. Mean dissimilarity values average all available census years and are expressed as percentages.

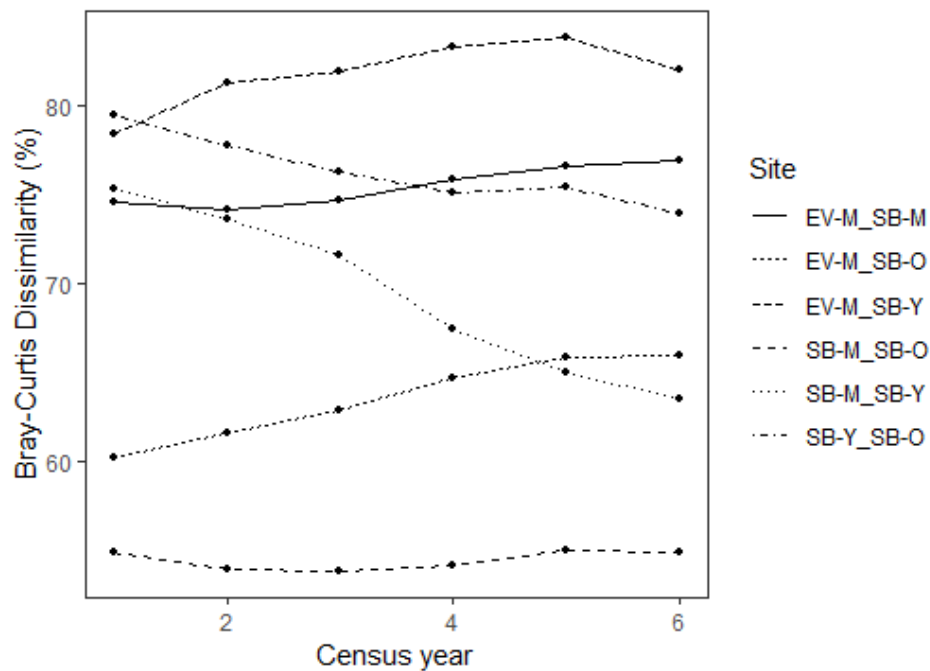
To track shifts in species composition within sites we calculated Bray-Curtis dissimilarities between initial stand composition (year 1) and each subsequent census year (Figure 4). For EV-O only year 1 and year 6 were compared. The expected pattern was of directional change over succession, with greater change in younger sites and more stability in the mature forest sites. SB-Y displayed dramatic changes in species composition from year 1 to year 6 (> 40%) while the other three chronosequence sites showed more moderate changes (<20%). EV-M showed the least compositional change over the census period, followed by SB-O. All sites showed the greatest rate of change from year 3 to year 4 (2013-2014).



**Figure 4.** Changes in species composition within chronosequence plots in El Yunque National Forest, Puerto Rico from census year 1 to year 6. Changes are expressed as Bray-Curtis dissimilarities between year 1 composition and the composition in each other census year.

We found little evidence of convergence in composition among sites. Changes in floristic similarity over the census period were evaluated by plotting pairwise trajectories

for all site pairs over time, based on Bray-Curtis dissimilarities for each year and excluding EV-O which lacks annual measurements (Figure 5). Only two site pairs, SB-Y with SB-M and SB-Y with SB-O, showed increasing overlap (decreasing dissimilarity) in composition with time. The latter pair was more similar to begin with and exhibited a greater rate of increase in shared species. Three site pairs showed an opposing trend. EV-M with SB-O and EV-M with SB-M showed similar declines in species overlap (increasing dissimilarity) throughout the census period. SB-Y with EV-M, the most distinct pair of sites, became more distinct each year until year 5 when the trend reversed.

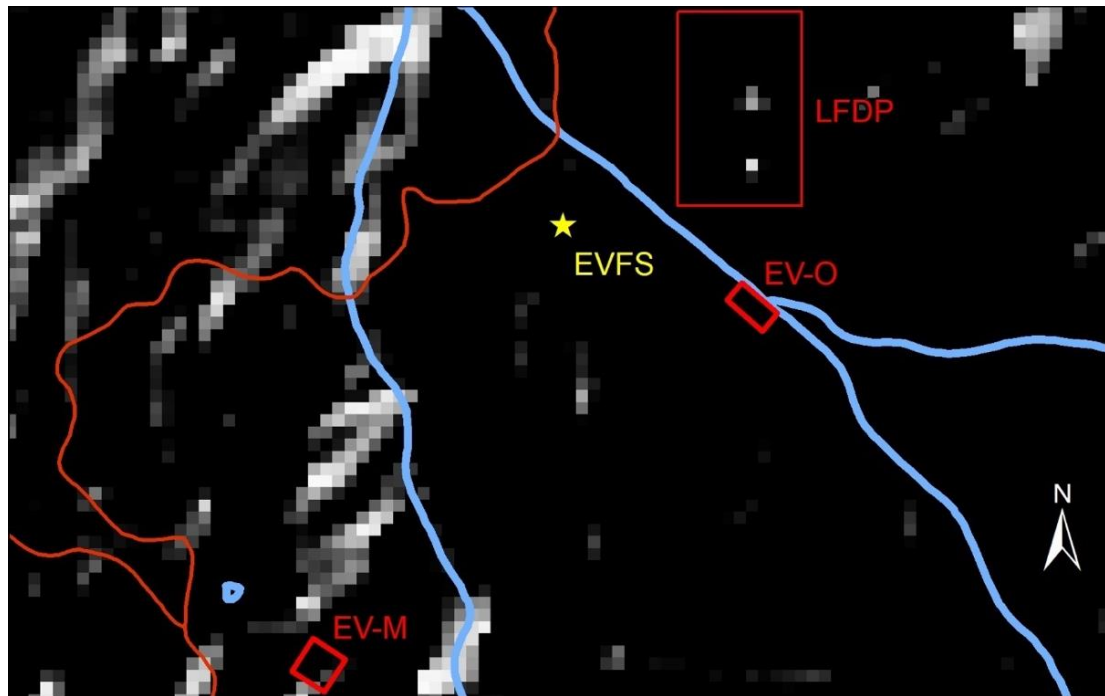


**Figure 5.** Changes in pairwise Bray-Curtis dissimilarity values for species composition among chronosequence plots in El Yunque National Forest, Puerto Rico from census year 1 to year 6. EV-O is excluded because of a lack of annual measurements.

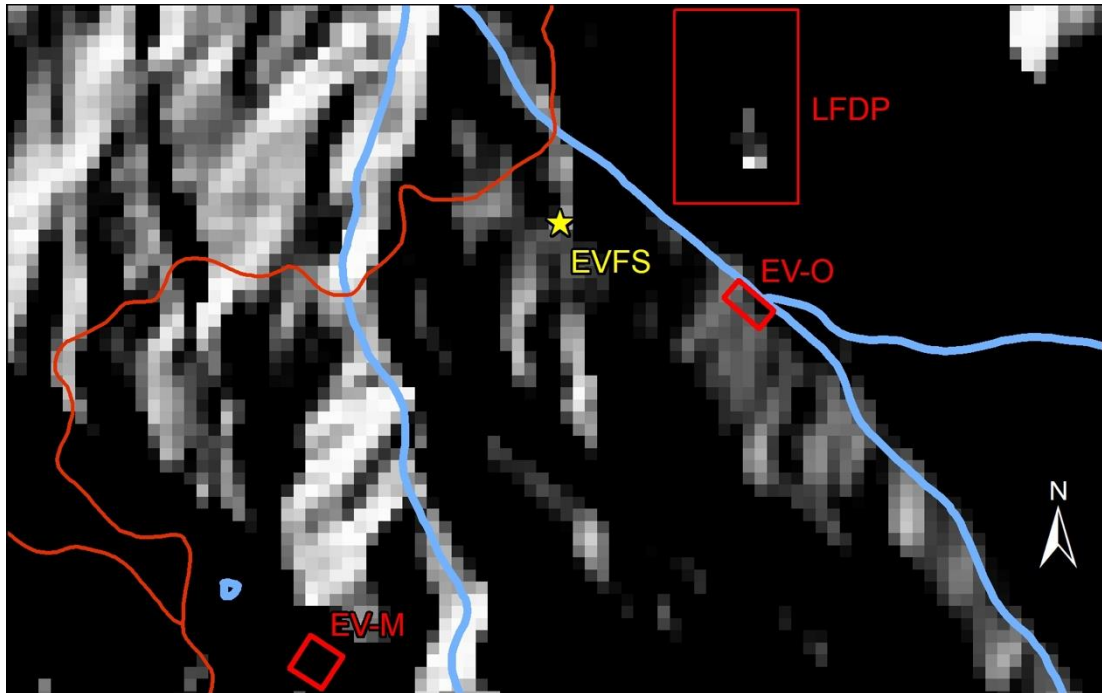
#### *IV. Hurricane Irma and Maria effects*

##### *Hurricane exposure*

Exposure models indicate large parts of the El Verde Research Area were topographically protected from Hurricane Irma. Exposure values of each site can be found in Appendix A. Plot EV-O was in a highly sheltered position in relation the direction of peak Irma winds (Figure 6) while EV-M had a low degree of exposure. This pattern reversed during Hurricane María (Figure 7): EV-M was in a highly protected position while the location of EV-O was partially exposed. Overall topographic exposure of El Verde was higher in Hurricane María than in Hurricane Irma.

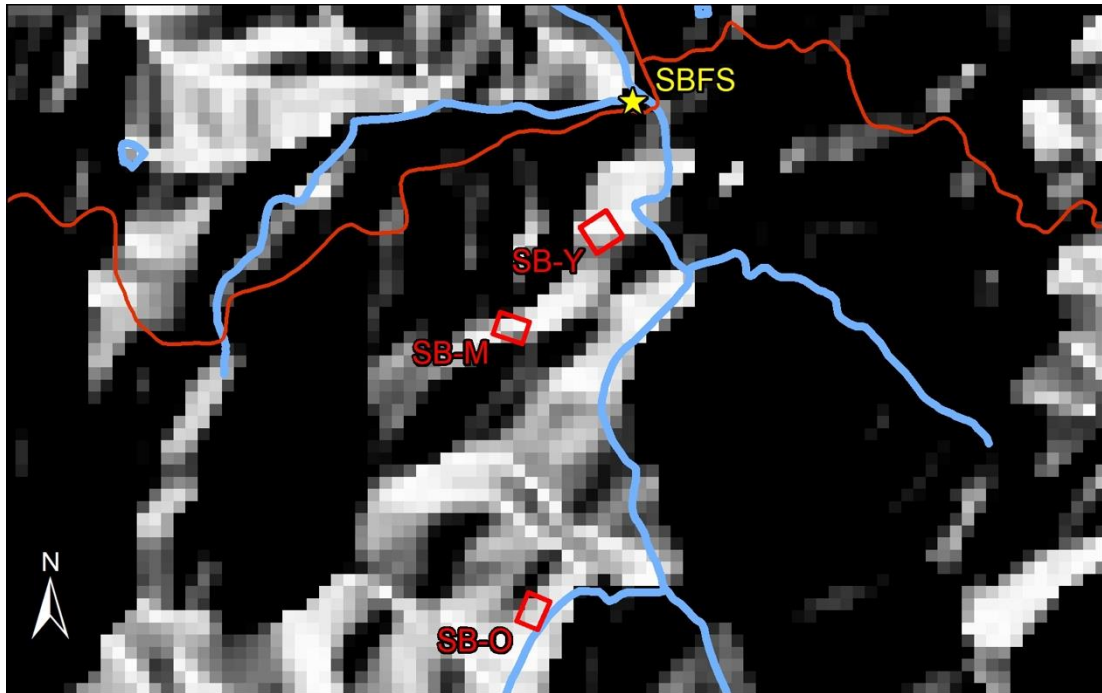


**Figure 6.** Predicted exposure to Hurricane Irma of chronosequence plots EV-M and EV-O and the Luquillo Forest Dynamics Plot in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white).

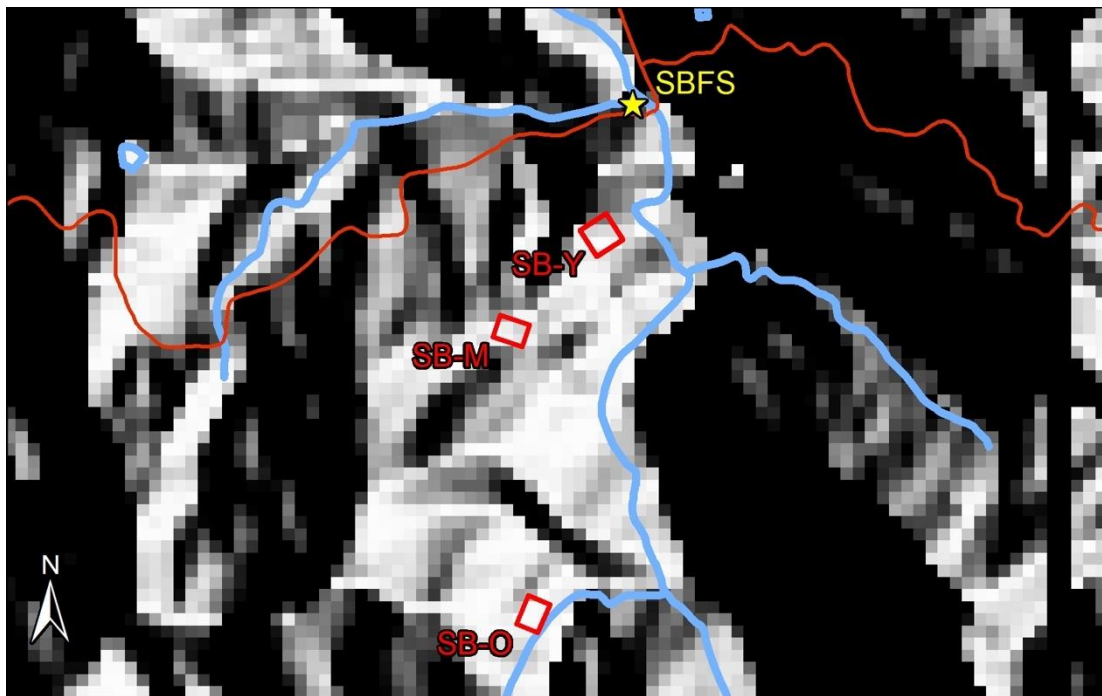


**Figure 7.** Predicted exposure to Hurricane María of chronosequence plots EV-M and EV-O and the Luquillo Forest Dynamics Plot in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white).

Sabana sites display a far greater degree of exposure than El Verde to peak wind directions during both hurricanes (Figure 8, Figure 9). All three sites were unprotected during both storms. Average exposure values indicate SB-Y was most vulnerable in topographic position to Hurricane Irma while SB-O was the least sheltered from Hurricane María.



**Figure 8.** Predicted exposure to Hurricane Irma of chronosequence plots SB-Y, SB-M and SB-O in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white).

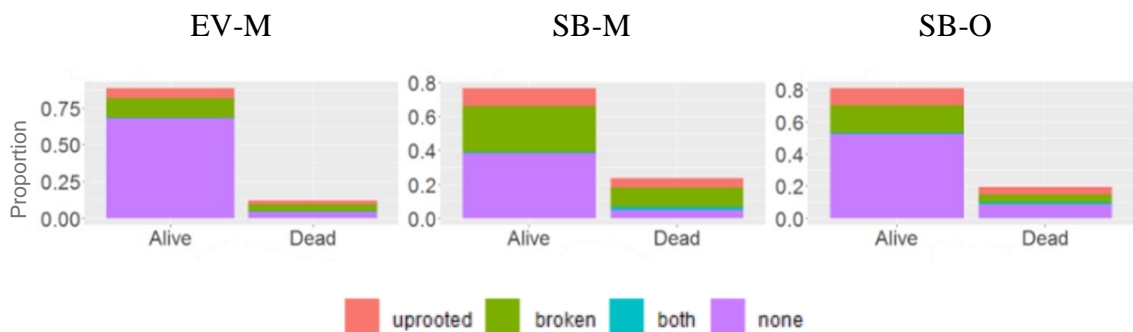


**Figure 9.** Predicted exposure to Hurricane María of chronosequence plots SB-Y, SB-M and SB-O in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white).

## Hurricane damage

Initial mortality and damage to trees as a result of Hurricanes Irma and María was evaluated for plots EV-M, SB-M and SB-O. The average mortality across plots was 15% and the average overall stem damage was 35%. A comparison of the three plots did not show a clear pattern with age (Figure 10). Mortality in SB-M (24%) was double that of EV-M (12%), with SB-O falling in between (19%). Damage to stems in the form of breakage and uprooting followed the same trend. Stem breakage showed greater variation across sites than uprooting. The highest proportion of broken stems occurred in SB-M followed by SB-O.

EV-M had the most stems with light or no crown damage (38% of stems) and the least with heavy or medium crown damage (62% of stems), while the other two sites were similar with 70-80% stems with medium or heavy crown damage. The proportion of stems with heavy crown damage (< 25% crown remaining) was 28% in EV-M, 25% in SB-M, and 23% in SB-O. The proportion with medium damage (25%-75% crown remaining) was 34% in EV-M, 48% in SB-M, and 55% in SB-O.



**Figure 10.** Tree mortality and damage among stems >10 cm dbh in response to 2017 Hurricanes Irma and María in three chronosequence plots in El Yunque National Forest, Puerto Rico.



Of the 61 species with stems  $\geq 10$  dbh surveyed, 29 had at least 10 individuals of that size for which a mortality rate could be calculated (Table 6). Mortality varied substantially among species, ranging from 0 to 85%. Late-successional species dominant in plot SB-O generally exhibited low rates of mortality. Less than 5% of *D. excelsa* and 0 of 74 *M. bidentata* trees were killed by the hurricane. In contrast the most abundant species of SB-O, *F. occidentalis* displayed one of the highest mortality rates (36%), likely due to damage from canopy branches of larger trees. The palm *P. acuminata* var. *montana*, also abundant in late-successional forests, suffered 13.5% mortality.

Secondary species common after human disturbance shared a common mortality rate of 9-10% (*Casearia arborea*, *Tabebuia heterophylla*, *Byrsonima spicata*, *Ocotea leucoxylon*). An exception to this pattern was the smaller understory tree *Myrcia deflexa* whose mortality rate was three times higher (27%). Two pioneer trees common after hurricane disturbance, *Cecropia schreberiana* and *Schefflera morototoni*, suffered 34% and 29% mortalities respectively.

The highest mortality rates occurred in two species of *Miconia*, *M. mirabilis* (85%) and *M. tetrandra* (73%) which tend to be found in early-successional habitats. Three introduced species suffered similar and relatively high mortality rates: *Syzygium jambos* (23%) and *Calophyllum antillanum* (22%), abundant in the younger sites, and *Senna siamea*, (18%), found only in SB-M.

**Table 6.** Tree mortality rates among species with  $\geq 10$  individuals  $\geq 10$  cm dbh across chronosequence plots EV-M, SB-M, and SB-O in El Yunque National Forest, Puerto Rico following 2017 Hurricanes Irma and María.

| Species                          | n   | Mortality (%) |
|----------------------------------|-----|---------------|
| <i>Miconia mirabilis</i>         | 13  | 84.6          |
| <i>Miconia tetrandra</i>         | 11  | 72.7          |
| <i>Cyathea arborea</i>           | 11  | 45.5          |
| <i>Faramea occidentalis</i>      | 14  | 35.7          |
| <i>Cecropia schreberiana</i>     | 47  | 34            |
| <i>Matayba domingensis</i>       | 12  | 33.3          |
| <i>Schefflera morototoni</i>     | 66  | 28.8          |
| <i>Myrcia deflexa</i>            | 26  | 26.9          |
| <i>Syzygium jambos</i>           | 43  | 23.3          |
| <i>Calophyllum antillanum</i>    | 123 | 22            |
| <i>Senna siamea</i>              | 11  | 18.2          |
| <i>Prestoea montana</i>          | 630 | 13.5          |
| <i>Sloanea berteriana</i>        | 33  | 12.1          |
| <i>Eugenia stahlii</i>           | 129 | 11.6          |
| <i>Byrsonima spicata</i>         | 19  | 10.5          |
| <i>Alchornea latifolia</i>       | 20  | 10            |
| <i>Casearia arborea</i>          | 154 | 9.7           |
| <i>Tabebuia heterophylla</i>     | 53  | 9.4           |
| <i>Tetragastris balsamifera</i>  | 11  | 9.1           |
| <i>Ocotea leucoxydon</i>         | 56  | 8.9           |
| <i>Andira inermis</i>            | 15  | 6.7           |
| <i>Calypranthes luquillensis</i> | 30  | 6.7           |
| <i>Micropholis guayanensis</i>   | 34  | 5.9           |
| <i>Dacryodes excelsa</i>         | 41  | 4.9           |
| <i>Alchorneopsis floribunda</i>  | 13  | 0             |
| <i>Buchenavia tetraphylla</i>    | 24  | 0             |
| <i>Coccoloba swartzii</i>        | 28  | 0             |
| <i>Homalium racemosum</i>        | 14  | 0             |
| <i>Manilkara bidentata</i>       | 74  | 0             |

## DISCUSSION

The ability of tropical secondary forests to regain the characteristics of mature forests, especially their highly diverse species compositions, is currently under debate (Rozendaal et al. 2019, Villa et al. 2018, Arroyo-Rodríguez 2017, Dent et al. 2013,

Fridley 2013, do Nascimento et al. 2014, Lebrija-Trejos et al. 2010, Norden et al. 2009).

We assessed patterns of recovery of secondary forest structure and composition along a forest chronosequence and found clear trends in structural characteristics, but not species richness, diversity, or composition, as forests aged.

### *Recovery of forest structure and diversity*

The observed structural shifts in the direction of a mature forest are typical of chronosequence studies of forest succession (e.g. Aide et al. 2000, Peña-Claros 2003, do Nascimento et al. 2014). Changes in stem density, basal area, and size classes with stand age suggest a successional shift from crowded stands of small-diameter trees to more open conditions with a greater range of tree sizes and a higher basal area. Forest structure varied among forests of the same age and patterns were more consistent within a research area (El Verde or Sabana) than across all sites. Edaphic factors, landscape composition, disturbance histories, and the dynamics of individual species could each be contributing to the variation in structure across similar-aged sites (Chazdon et al. 2007).

Longitudinal observations within sites support inferred chronosequence patterns of stand density, but not basal area. We observed consistent declines in stand density with stem losses concentrated in small size classes, implying a process of natural thinning driven by competition among small trees in an increasingly shaded environment. Basal area increased predictably with forest age across chronosequence sites. Highly consistent findings from previous studies of post-agricultural succession document increases in basal area over the first 20-40 years of recovery followed by relative stability in stand-level values (Aide et al. 2000, Chazdon et al. 2007). While

stable short-term trends within the mid-successional sites and SBO are in line with this pattern, an unexpected and sharp decline in basal area occurred in SB-Y and a steady increase took place in EV-O. These deviations signal that attributing observed structural patterns to the process of stand thinning over succession may be an oversimplification. Though large losses of small stems occurred in SB-Y, a simultaneous decrease in basal area demonstrates that mortality occurred in excess of growth and recruitment and likely affected larger trees. Causes of mortality beyond direct competition, such as drought or disease, appear to be contributing to the loss of stems in this stand. The increasing trend in the basal area of EV-O has previously been attributed to the effects of hurricane disturbance (Heartsill Scalley 2017). Long-term monitoring has revealed that EV-O is still responding to the effects of the devastating 1932 Hurricane San Ciprián, with defoliation by Hurricanes Hugo and Georges serving to reinforce the accumulation of basal area and directional shifts in species composition.

Patterns of species diversity among chronosequence sites were less clear. In Sabana sites levels increased with forest age, a trend documented by several chronosequence studies in the Amazon basin and Puerto Rico (Villa et al. 2018, Peña-Claros 2003, Aide et al. 1995, Saldarriaga 1988). A meta-analysis of tropical dry forest resilience by Derroire et al. (2016) provided broad support for this pattern: in general species richness and evenness increased over succession as species gradually accumulated. In contrast, the decline in diversity from EV-M to EV-O appears to support previous assertions of a mid-successional peak driven by temporary coexistence of pioneer and mature forest species (Bongers et al. 2009, Eggeling 1947, Huston and Smith 1987, Molino & Sabatier 2001, Sheil 2001). Comparison with other studies is

complicated by the variety of diversity metrics used, the ranges of forest ages considered, and the effects of disturbance histories and soil properties (Villa et al. 2018, Letcher & Chazdon 2009, Chazdon et al. 2007, Pascarella et al. 2000, Aide et al. 1995). Insights can be gained by examining annual changes in diversity over the census period and the life-histories of dominant species. Species richness increased or remained stable in all sites and diversity increased in the younger Sabana sites. However, diversity declined in SB-O and EV-M even as species richness and basal area remained relatively stable. Long-term studies capturing post-hurricane forest recovery in Puerto Rico have observed a peak in richness and diversity due to the arrival of pioneer and secondary species in canopy gaps, with subsequent declines in diversity as forest structure recovers and shade-tolerant species increase in dominance (Crow 1980, Weaver 1983, 1989). In EV-O the effects of Hurricane San Ciprián lasted over three decades, with diversity reaching a peak 15-20 years after the storm (Crow 1980). Following this timeline, the dynamics observed in the chronosequence plots could be related to altered conditions by the more severe Hurricane Hugo in 1989 or the more recent Hurricane Georges in 1998.

Differing patterns in El Verde and Sabana could be driven by asymmetrical impacts of past disturbances. Among the old-growth stands species diversity was higher in SB-O, despite EVO's geographic proximity to species-rich EV-M. Although differences in richness were moderate, evenness was twice as high in SB-O and declined over the census period while EV-O remained stable. It is likely that patterns in SB-O reflect increased dominance by late-successional trees following past hurricane defoliation and silvicultural activities (Chapter 1) that opened the forest canopy. Among secondary stands EV-M had far higher and more stable richness and diversity than the

Sabana sites. Short-term stand dynamics in the Sabana sites, including rapid increases in richness and evenness along with declines in basal area, indicate diversity may have been suppressed by dominant trees that are now declining. Another possible driver of differences in diversity is that the landscape position and topography of EV-M, including south and west-facing slopes, have partly protected it from the most powerful winds of one or many large storms to pass through El Yunque. This appears to have been the case in Hurricane Hugo (see Appendix B) and Hurricane María (see Figure 7 and discussion below). Low exposure to hurricane winds relative to the other sites could explain EV-M's stability in basal area, species richness, and species composition. High diversity in EV-M could also be influenced by its high elevation and closer proximity to an ecotone between lower montane and montane rainforest where habitat specialists are more common (Thompson et al. 2002, Weaver 2012). Further, reforestation of the landscape surrounding El Verde occurred earlier and more completely in El Verde than in Sabana (see Chapter 1) which likely meant greater propagule availability and diversity early in forest development. During the forest recovery period silvicultural management, including the elimination of "undesirable species," was conducted in Sabana sites and briefly in EV-O but to our knowledge was not carried out in EV-M. Greater representation of endemic species, which previous studies have shown increase with time after disturbance (De Walt et al. 2003, Endress 2002, Liebsch et al. 2008) further supports a lower frequency or intensity of historical disturbances (both human and natural) at this site.

### *Recovery of species composition*

The greatest overlap in species composition occurred in different-aged sites in close geographic proximity, rather than in sites of similar successional age. The presence and abundance of trees previously associated with certain successional stages or disturbance types provides clues toward site characteristics and histories that could be contributing to this pattern.

The prevalence of mature tabonuco forest species varied across chronosequence sites. *Dacryodes excelsa*, *Sloanea berteriana* and *M. bidentata* were abundant in all old-growth but not all secondary forest sites. Although the establishment of *D. excelsa* populations has been documented in abandoned pastures in El Verde (Zimmerman et al. 1995), in each of our three secondary sites *D. excelsa* was represented by a single tree. In EV-O *D. excelsa* was second in density to palms, while in EV-M palms were followed in dominance by *C. arborea*, a secondary species associated with past human disturbance in the nearby LFDP (Zou et al. 1995, Thompson et al. 2002). *Manilkara bidentata* and *S. berteriana* followed opposing trends across sites: the first was abundant in Sabana sites but contained only three individuals in 1-ha EV-M, while the second was common in El Verde but rare or absent in Sabana secondary forest. The success of *M. bidentata* in SB-Y and SB-M, which reverted from pasture between 35 and 75 years ago (see Chapter 1), contrasts with previous studies of forest recovery on abandoned pastures in which it was absent or scarce (Zimmerman et al. 1995, Aide et al. 2000). *Buchenavia tetraphylla* was common in EV-M but absent from Sabana secondary forest. Previous studies have reported associations between *B. tetraphylla* and *M. bidentata* (Crow & Grigal 1979) and high densities of *M. bidentata* seedlings under *B. tetraphylla*, whose

large size and sparse crown may be preferred by bat dispersers (You 1991), however in our secondary sites co-occurrence of these species was marginal. Overall patterns indicate late-successional tabonuco forest species are able to establish in these secondary forests but that species-specific barriers remain and vary by site. Their establishment could be hindered by a lack of seed dispersers or pollinators or by low seed production due to inbreeding within remaining nearby populations (Aide et al. 2000).

Differences across sites in the recovery of *M. bidentata*, one of the most valuable timber species in Puerto Rico, could be related to past land use and forest management. Populations in El Verde and Sabana were affected by selective logging and agricultural clearing prior to acquisition by the U.S. Forest Service in the 1930's (see Chapter 1). During early reforestation efforts the farm tract where Sabana sites are located was planted with over 1400 *M. bidentata* seedlings; meanwhile this species was not included on plantings in the farm tract where EV-M occurs (Marrero 1947). Further, all chronosequence sites except EV-M were managed for timber by the U.S. Forest Service from the 1930's to 1958 (EV-O) or later, including the establishment of tree plantations as late as 1956 in the younger Sabana sites (see Chapter 1). Bat dispersers would have found relatively open perches in timber crop trees, and a higher availability of light would have favored seedling survival and growth (You 1991) in managed sites. The distribution and growth of *M. bidentata* seedlings is highly related to bat behavior (You 1991). Hurricane Hugo (1989), whose trajectory passed northeast of Sabana, may have reinforced site differences in *M. bidentata* abundance through a greater release of suppressed seedlings in the more exposed Sabana sites. Previous studies suggest a high resistance to hurricane damage (e.g. Basnet 1992, Walker 1991, Zimmerman et al. 1994)



and increased seedling recruitment in post-hurricane conditions promote *M. bidentata* abundance (You & Petty 1991). A steady increase in *M. bidentata* dominance after Hurricane San Ciprián (1932) and abundance in small size classes after Hurricane Hugo were documented in long-term studies of EV-O (Crow 1980, Briscoe & Wadsworth 1970). Nearly all *M. bidentata* stems in Sabana secondary sites are in small (<10 cm) size classes while the few trees found in EV-M are >30 cm.

In contrast to the large-statured and heavy-wooded dominants, mature forest species *Prestoea montana* and *C. schreberiana* were abundant in all sites and *S. morototoni* occurred in varying densities in all sites. *Prestoea montana* is considered a late-successional species based on its conservative leaf physiology (Feng et al. 2018a) but demonstrates ecological plasticity, growing rapidly and producing more seeds in forest gaps (Gregory & Sabat 1996, Lugo & Rivera Batlle 1987) and recovering quickly from hurricane defoliation (Zimmerman & Covich 2007). Dense stands are common on floodplains and steep slopes across El Yunque, and in the LFDP occur in areas with a history of logging (Thompson et al. 2002). *Cecropia schreberiana* and *S. morototoni* are fast-growing pioneer trees also capable of rapid establishment in canopy gaps following natural disturbance (Crow 1980, Silander & Lugo 1990). Though these species are poor colonizers of abandoned pastures (Aide et al. 1995,1996; Zimmerman et al. 1995, 2000), the establishment and increase of *Cecropia schreberiana* populations have been noted in abandoned pastures after 25-40 years of forest regrowth (Aide et al. 2000).

Though mature forest species appear to be returning as the forests age, we found considerable differences across similar-aged sites. EV-M and SB-M differed in the dominance of palms and *C. arborea* versus pasture-colonizing pioneers, high densities

of several human-promoted species in SB-M (*Calophyllum antillanum*, *Syzygium jambos*, *Tabebuia heterophylla*), and high densities of three endemic species in EV-M (*Eugenia stahlia*, *Hirtella rugosa*, *Tetrazygia urbanii*). The preeminence of *P. montana* in El Verde sites could be due to their higher elevation or could stem from the impacts land use or hurricane disturbance more than 80 years ago. Drew et al. (2009) documented a steady but striking increase in palms in EV-O from a minor stand component in 1943 until replacing *D. excelsa* as the most dominant species in 2005 and attributed this trend to long-term recovery from Hurricanes San Ciprián (1932) and San Felipe (1928). Slow rates of change and competitive dominance of palms, including the ability to regenerate in a wide range of environmental conditions (Lugo and Lowe 1995, Frangi & Lugo 1998), may be contributing to the greater stability in composition of El Verde sites over the census period.

High densities of early successional shrubs and small trees in the Melastomataceae and Rubiaceae families (e.g. *Miconia prasina*, *Psychotria brachiata*, *Psychotria berteriana*) across secondary sites and of the wind-dispersed tree *Tabebuia heterophylla* in the former pasture sites are in line with previous chronosequence studies in eastern Puerto Rico (Aide et al. 1995, Pascarella et al. 2000, Zimmerman et al. 1995). *Miconia prasina* was abundant across all sites except EV-O and declined substantially over the census period in EV-M, SB-M, SB-O. This shrub is known to reach high densities after initial colonization of pastures but decline with stand age, possibly facilitating the establishment of other species (Aide et al. 2000). Growth rates are highest in young stands with sparse canopy cover and become negative with canopy closure (Pascarella et al. 2007). The prevalence of *M. prasina* in SB-O is surprising

given its structural maturity and may point to recent disturbance; *M. prasina* (bird-dispersed; DeVoe 1989) is common in nearby pastures (J.K. Zimmerman, personal observation) and could have colonized gaps created by Hurricanes Hugo (1989), Hurricane Georges (1998), or silvicultural improvements prior to 1990 (see Chapter 1). A more than 50 percent decline in density over the census period is consistent with prior observations of the disturbance-related and relatively transient presence of *M. prasina* in mature forests (Pascarella et al. 2007). High densities and substantial declines of *C. schreberiana*, *S. morototoni*, and especially *P. berteriana* (92% stem loss) support the characterization of SB-O as a stand recovering from considerable disturbance. These species were present in lower densities in EV-O with no stem losses occurring over the census period. Long-term studies in mature tabonuco forest have associated abundances of *C. schreberiana* and *S. morototoni* with extensive disturbance by hurricanes or possibly cuttings in the past (Crow 1980) and have documented the decrease of all three species over a half century following the 1932 Hurricane San Ciprián (Crow 1980, Weaver 1983).

Attributes of the youngest forest site were heavily influenced by dynamics of the dominant species *Syzygium jambos*, which experienced large die-offs (95% reduction in density; ~4,500 stems lost) from 2011-2016 due to infection by an exotic rust (Burman et al. 2017). *Syzygium jambos* is a nonnative, shade-tolerant tree that successfully colonized pastures, coffee farms, and riparian areas following agricultural abandonment in the Luquillo Mountains and has expanded into old-growth forest (Aide et al. 1996, Brown et al. 2006, Little and Wadsworth 1964, Pascarella et al. 2000). This species occurred in all three Sabana sites and densities declined with site age, consistent with

previous findings that *S. jambos* is a dominant member of secondary forests with open canopies in 1936 and reaches higher densities in young and mature secondary forests compared to old-growth stands (Brown et al. 2006). *Austropuccinia psidii* or guava rust was first detected in Puerto Rico in 2006 and has since infected stands of *S. jambos* across the island (Burman et al. 2017). Consequences of this this species' rapid decline in SB-Y include sharp drops in stand density and basal area, jumps in species richness and diversity, and increased dominance of native, early-successional shrubs although *S. jambos* remained second in relative density. Brown et al. (2006) found a strong negative correlation between *S. jambos* and plant diversity but no pattern with species richness and considered this species to be the overriding force driving community patterns in areas where it is dominant. Our findings support those of Brown et al. (2006) and strongly suggest that *S. jambos* can suppress both species richness and evenness in secondary forests. However, the rapid loss of thousands of stems to disease challenges previous assertions that this species will persist for hundreds of years and that *S. jambos*-dominated stands must be managed for native communities to recover (Aide et al. 1996, Brown et al. 2006).

Human impacts are also reflected in the abundance of a suite of introduced species in secondary sites. *Calophyllum antillanum*, native to Puerto Rico's coastal moist forests, was introduced to the Luquillo Mountains to reforest degraded sites and was planted in the farm tracts where EV-M and all Sabana sites occur 70 to 80 years before this study (see Chapter 1). Populations remain in (or have been dispersed short distances by bats to) all three sites, reaching high densities in the Sabana sites, and declined at differing rates over the census period. A plantation of the valuable tree

*Tectona grandis* established in 1956 to reforest open areas encompassed the area of SB-Y (see Chapter 1) and explains high densities of this species in SB-Y. Similarly, enrichment plantings of *Swietenia macrophylla* established in the Sabana area between the 1950's and 1980's have persisted in this plot and a few individuals <10 cm have dispersed to SB-M. While *T. grandis* declined by nearly 50 percent over the census period and does not appear to be recruiting (7 of 8 saplings <10cm died from 2011-2016), *S. macrophylla* suffered a more moderate decline and small size classes fared better.

#### *Successional trajectories in composition*

Of particular interest in the Neotropics is whether the recovery of species composition follows a deterministic trajectory toward old-growth forest communities or is governed by stochastic processes that limit the predictability of future forest composition (Norden et al. 2009, 2011). Deterministically, we expect secondary sites to approach the composition of old-growth sites over time since agricultural disturbance and since the most recent hurricane. If stochastic processes are more important, we expect species composition to follow independent trajectories over time. We observed independent directions of change in species composition, with similarity of some site pairs increasing but no general convergence on the composition of old-growth sites.

Divergence in species composition occurred between EV-M and SB-O despite concurrent declines in early-successional species, and between EV-M and Sabana secondary sites. One possibility is that mature forest compositions in Sabana and El Verde sites were inherently different before agricultural disturbance, reflecting

differences in edaphic properties, elevation and topography. The clearing or logging of nearly all low-elevation forests during the agricultural era and lower human disturbance of steeper, higher-elevation forests, precludes chronosequence studies with more homogenous site characteristics in El Yunque. Another, non-exclusive explanation is that differential impacts of natural disturbances continue to influence species communities. The effects of Hurricane Hugo, Hurricane Georges and a 2015 summer drought could have been mediated by the exposure, topography, structure, and species communities at each site which in turns has been influenced by prior land use. Previous studies have highlighted the role of interactions between land use history and hurricane disturbance in shaping successional trajectories of tabonuco forest stands (Foster 1999, Flynn et al. 2010, Hogan et al. 2016, Pascarella et al. 2004, Thompson et al. 2002, Zimmerman et al. 1995). In this study we found that differences in environment or disturbance history continue to override the influence of forest age despite decades of successional change, suggesting secondary sites with differing characteristics and legacies may never converge in their composition.

Converging trends were found between SB-Y and the older Sabana sites. Sharp declines in *S. jambos*, a gradual loss of *T. grandis* stems, increases in native shrubs and the recovery of mature forest species such as *P. montana* and *M. bidentata* in SB-Y contributed to increased similarity in composition. Several studies of neotropical secondary succession have found a decrease in the density of dominant canopy species with increasing stand age (Brown et al. 2006, do Nascimento et al. 2014, Saldarriaga et al. 1998, Pascarella et al. 2000). The declines of dominant species favored by certain land use histories or idiosyncratic events opens growing space for colonization by the

species present in nearby forests and should lead to higher species overlap among sites with similar environments. Brown et al. (2006) did not find this pattern in secondary forests with high densities of *S. jambos*, where recruitment remained high and a reduced abundance and diversity of native plants appeared to preclude a convergence on pre-disturbance species assemblages. However, their study was conducted before the widespread infection of *S. jambos* by guava rust. The convergence of SB-Y on older species communities within the same research area as a once-persistent nonnative species diminishes in abundance supports the notion that dominant species can slow deterministic successional processes (Connell & Slatyer 1977, do Nascimento et al. 2014).

Post-agricultural studies in Puerto Rico have found a lack of floristic convergence between secondary and old-growth stands along chronosequences despite similarities in structure and species richness (Aide et al. 2000, Pascarella et al. 2000, Chinea 2002, Marcano-Vega 2002, Marin-Spiotta et al. 2007). This pattern has been attributed to the colonization and persistence of exotic trees species following widespread agricultural disturbance (Brown et al. 2006, Letcher & Chazdon 2009). However, in studies considering temporal dynamics and size-class differences, dominant exotic species appear to decline as ecosystems recover and give way to native species of later successional stages (Martinez 2010, Lugo 2004). We found several nonnative species had persisted over many decades of post-agricultural succession, yet stem losses in all dominant exotics and increases in native species densities support the idea that the influence of agricultural legacies will diminish over larger time scales. The extent to which secondary forests resemble mature tabonuco forests in the future may depend

more on the ability of large-statured, shade tolerant species to establish in these new habitats. We provide mixed support for the recovery of such species and note the absence of the once-common and heavily logged endemic *Magnolia splendens* from all sites.

Elsewhere in the Neotropics studies are split as to whether secondary forests will recover the species composition of old-growth communities. In northeastern Costa Rica, secondary forests 30-42 year of age have been found to converge in composition with old-growth sites (Letcher & Chazdon 2009) and seedlings and saplings of secondary forest sites 12-29 years of age showed increasing similarity to mature forest canopies (Norden et al. 2009). In the Atlantic Forest of Brazil, do Nascimento et al. (2014) found high similarity in the species compositions of secondary forests, but low similarity between secondary and old-growth sites. On Barro Colorado Island, Panama, similarity among old-growth stands was high but neither adults nor juveniles of secondary forest stands increased in similarity to the old-growth communities over time (Dent et al. 2013). Rozendaal et al. (2019) examined this question across a large environmental gradient, compiling chronosequence data from 56 lowland forest sites in 10 countries across the Neotropics. They found that secondary forests generally consist of a wide diversity of secondary forest specialists, with old-growth species present but not abundant and delayed arrival of rare species with low dispersal capacities. While species richness resembled old-growth values in 54 years on average, predicted recovery of species composition averaged 780 years and ranged from 19 years to no recovery at all.

Our results do not support a timely convergence in the species composition of secondary and old-growth stands, but they do support a view of tropical forests as



resilient. Secondary stands were able to recuperate many species present in mature stands through natural regeneration processes, including some old-growth specialists and rare and endemic species, and abundances of nonnative species showed diminishing trends. Our secondary sites may represent ideal conditions for floristic recovery, as they are in close proximity to older forest stands with high seed availability in El Yunque. Sites in landscapes lacking remnant forest patches or with high-intensity disturbance histories may recover old-growth specialists only very slowly or not at all (e.g. Marciano-Vega 2002). Continued long-term monitoring is needed to better distinguish between idiosyncratic floristic trends and variation in successional trajectories driven by dominant species that turn out to be transient. Capturing the impacts of stochastic events such as hurricanes and pathogen outbreaks as well as gradual environmental change is crucial to making progress on these questions.

### *Hurricane effects*

Differences among sites and species point toward high levels of heterogeneity in forest damage after Hurricanes Irma and María, consistent with other recent studies (Feng et al. 2018b, Mariño et al. 2018, Van Beusekom et al. 2018). Stand-level damage and mortality did not show a pattern with forest age, likely because the effects of age were overridden by differences in exposure to hurricane winds. Older forests with large, heavy-crowned trees exhibited greater levels of damage to Hurricane Georges than younger stands when wind exposure was controlled for (Flynn et al. 2010). Although multiple interacting drivers including storm exposure, topography, forest structure and previous land use can affect hurricane damage to forest stands (Bellingham 1991, Boose

et al. 1994, 2004; Brokaw & Walker 1991, Everham & Brokaw 1996), an analysis of factors driving damage and mortality was beyond the scope of this study.

The initial mortality rate in EV-M following Hurricanes Irma and María was nearly identical to that observed in the LFDP (Uriarte et al. 2019) and at the maximum of the of the typical range of 7-12%. Background annual mortality rates average 1-2%, for trees >10cm dbh following severe wind events in island and coastal tropical forests (see Uriarte et al. 2019). Stand-level mortality in SB-M was double and SB-Y one and a half times El Verde rates despite El Verde's closer proximity to the eye of more-powerful Hurricane María. Topographic exposure models reveal that EV-M was somewhat sheltered from Irma winds and highly protected from María winds, while all Sabana sites were highly exposed to the peak winds of both storms. Following Hurricane Hugo, average mortality was much lower in El Verde (7-9%; Walker 1991, Zimmerman 1994) while in the windward Bisley watersheds a 50% loss of biomass occurred (Scatena et al. 1993). Sabana sites are in close geographic proximity to those of Bisley but their leeward, protected position in relation to primarily north-northwest Hugo winds (Boose et al. 1994) suggests effects were less severe than in Bisley (Appendix A, Appendix C).

Variation in species-specific mortality rates was substantial and appears to reflect differences in successional status and tree stature. Small-statured trees of all successional stages suffered high fatalities, presumably because of crushing by falling canopy trees and branches (e.g. Everham & Brokaw 1996, Frangi & Lugo 1991). High stem breakage and mortality in light-wooded pioneer species compared to shade tolerant species have been observed in response to past hurricanes and are considered an

important axis of life history differentiation in tropical trees (Zimmerman et al. 1994, Canham et al. 2010). High survival of *D. excelsa*, *M. bidentata* and *B. tetraphylla* and remarkably high fatality of *Miconia* trees in the chronosequence sites agree with observations after Hurricane Hugo (Basnet et al. 1992, Walker 1991, Zimmerman et al. 1994). The resistance of *D. excelsa* to hurricane winds has been attributed to its frequent occurrence in tree unions with grafted roots that anchor trees to one another and provide stability in shallow clay soils (Basnet et al. 1993). Mortality rates averaged across chronosequence plots were similar to those found in the LFDP following Irma and María for late-successional species, Sierra palms, and *S. morotoni* (Uriarte et al. 2019), while the survival of *C. schreberiana* was higher in the chronosequence plots. In contrast to our results Ostertag et al. (2005) found that introduced species did not suffer greater damage and mortality following Hurricane Georges. They note that the nonnative species in their study, which include *S. jambos*, are of Asian origin and occur in areas where typhoons are frequent. Mortality of *S. jambos* in the chronosequence plots was more than double that found by Ostertag et al. (2005) six months after Georges while mortality of *C. antillanum*, which they grouped with native species, was more similar. Though many factors influence species-level damage, it is plausible that disease-weakened *S. jambos* was unusually vulnerable to Irma and María winds.

Differences among forest stands, species, and individual trees in their ability to resist hurricane winds are important determinants of future stand structure and composition (Lugo & Scatena 1996, Ostertag et al. 2005). By altering the representation of successional groups, past human disturbance may have created forests more susceptible to hurricane damage than pre-disturbance stands. In the chronosequence

sites, greater mortality and damage among fast-growing pioneers and introduced species could increase the community similarity of secondary and old-growth stands (Flynn et al. 2010). However, the capacities of species to regenerate in post-hurricane conditions may be more important than resistance to damage in determining the composition of the future forest canopy (Putz et al. 1983, Walker 1991). High light availability in the understory could favor the regeneration and arrival of new secondary species as the canopy recovers, setting back the recovery of mature forest composition.

In this study old-growth tree species showed high resistance to the winds of the strongest hurricane to hit Puerto Rico since 1932 as well as the ability to recover and increase in dominance following large-scale human and hurricane disturbance. However, a changing disturbance regime with more frequent intense hurricanes will mean forest stands are repeatedly altered before their structure and species have recovered to pre-disturbance levels. Under this context, the capacity of mature tabonuco forest species to recover their dominance in secondary stands remains uncertain.

## CONCLUSIONS

The ability of tropical forests to recover after large-scale disturbance has major implications for the conservation of biodiversity and maintenance of ecosystem services in widespread secondary forests. Forest attributes tend to recover at differing rates with high variation in successional pathways. This study found a steady recovery of forest structure and diversity in a post-agricultural landscape at the edge of a national forest, demonstrating resilience after human and hurricane disturbance. Secondary forest

species communities exhibited directional change and recovery of mature forest species but were not found to be converging on the composition of nearby old-growth forests. The colonization of old-growth specialists was gradual and variable, and early-successional species associated with past agricultural land use continued to be dominant in secondary stands. Successional declines among introduced species had major impacts on stand structure and composition and may be part of a predictable transition over large time scales to mature forest composition. Introduced and early-successional species showed less resistance to hurricanes, but whether or not hurricane disturbance accelerates the transition to mature forest assemblages will depend on species regeneration and recovery rates.

Processes inferred from chronosequence patterns were sometimes supported, and sometimes not, by annual remeasurements. Incongruencies could reflect different processes occurring across temporal scales, with long-term responses to past land use being interrupted by pulse-like responses to natural disturbances. We found responses to past hurricanes and a current disease outbreak had important impacts on successional trajectories. Alternatively, patterns observed across chronosequence sites may be artifacts of inherent differences in environment or disturbance regimes among sites rather than the outcome of successional processes. We found successional patterns to be more predictable among sites in close geographic proximity, suggesting that for some stand attributes site differences are overriding the effects of forest age. Continuing to combine chronosequence approaches with long-term observations of forest dynamics will help clarify the limitations of chronosequence inferences and further our knowledge of the self-organizing processes occurring in regenerating forests. Improved

understanding and management of natural regeneration is important for restoring deforested landscapes and strengthening forest resilience to global change.

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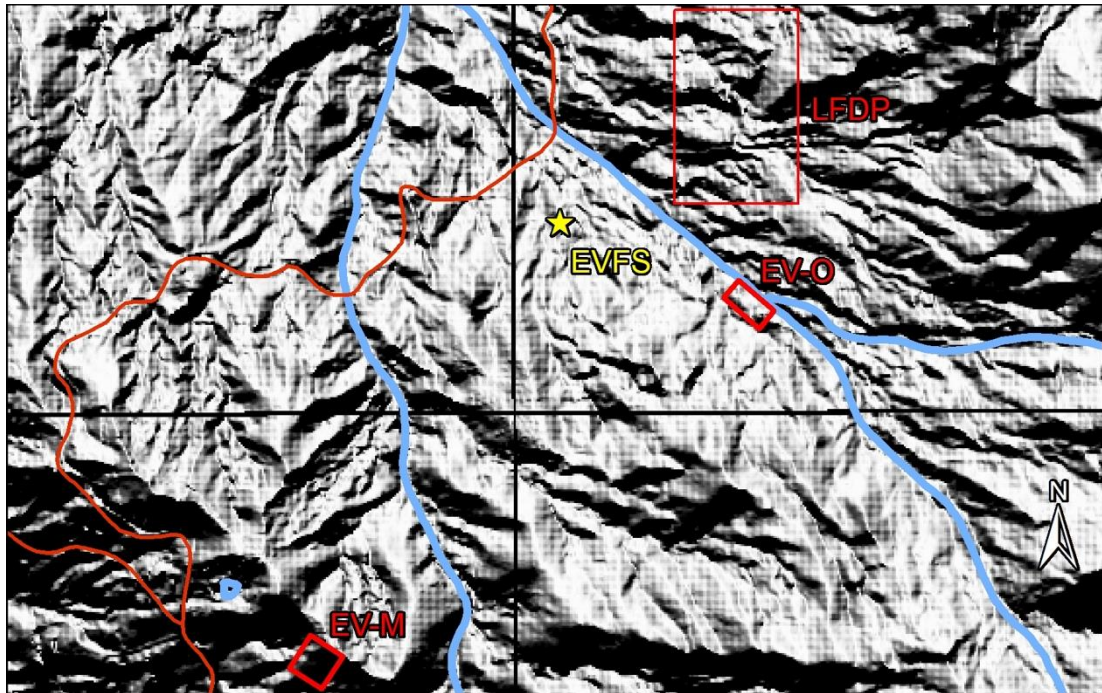
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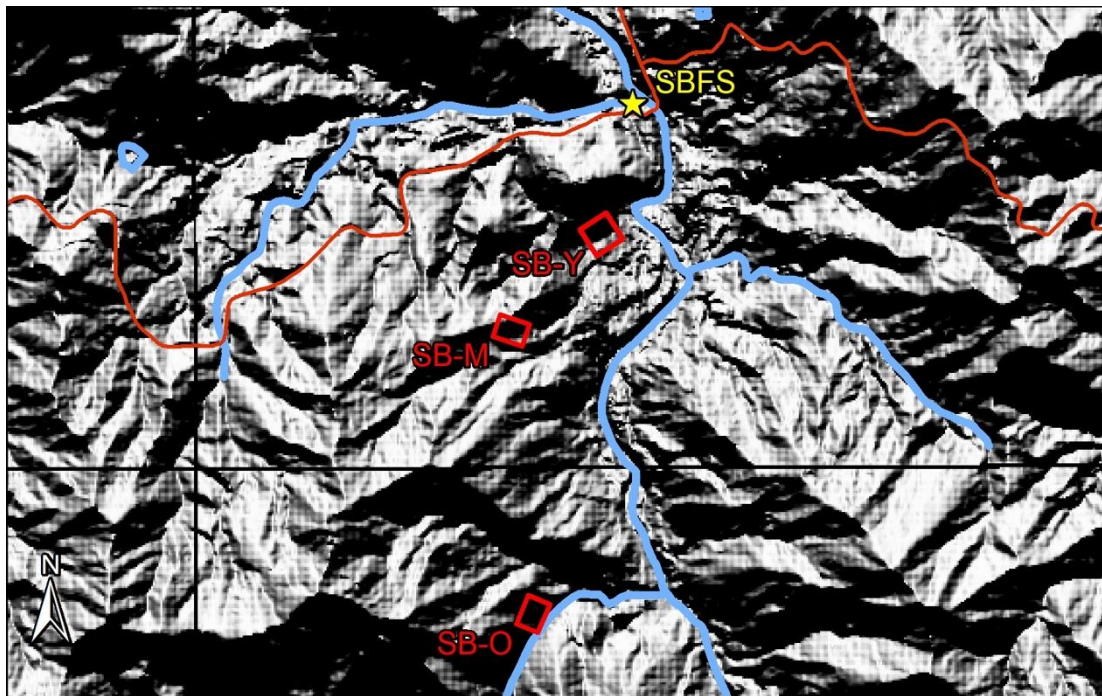
## APPENDICES

**Appendix A.** Topographic exposure to peak hurricane winds for chronosequence plots in El Yunque National Forest, Puerto Rico during Hurricanes Hugo (1989), Irma (2017) and María (2017). Values range from 0 (no exposure) to 252 (maximum exposure).

| Site                   | Minimum | Maximum | Mean   | STD   |
|------------------------|---------|---------|--------|-------|
| <u>Hurricane Hugo</u>  |         |         |        |       |
| SB-Y                   | 0       | 247     | 49.56  | 78.07 |
| SB-M                   | 0       | 252     | 31.93  | 63.93 |
| SB-O                   | 0       | 41      | 1.88   | 7.32  |
| EV-M                   | 0       | 227     | 24.19  | 49.41 |
| EV-O                   | 0       | 252     | 163.43 | 88.49 |
| <u>Hurricane Irma</u>  |         |         |        |       |
| SB-Y                   | 152     | 251     | 214    | 38.15 |
| SB-M                   | 112     | 250     | 188.25 | 57.76 |
| SB-O                   | 175     | 224     | 202.5  | 20.35 |
| EV-M                   | 0       | 71      | 7.82   | 20.24 |
| EV-O                   | 0       | 0       | 0      | 0     |
| <u>Hurricane María</u> |         |         |        |       |
| SB-Y                   | 122     | 252     | 217.57 | 41.78 |
| SB-M                   | 215     | 245     | 231.5  | 11.08 |
| SB-O                   | 247     | 252     | 249.5  | 1.8   |
| EV-M                   | 0       | 0       | 0      | 0     |
| EV-O                   | 4       | 124     | 70.86  | 35.67 |



**Appendix B.** Predicted exposure to Hurricane Hugo of chronosequence plots EV-M and EV-O and the Luquillo Forest Dynamics Plot in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white).



**Appendix C.** Predicted exposure to Hurricane Hugo of chronosequence plots SB-Y, SB-M and SB-O in El Yunque National Forest, Puerto Rico. Exposure values are shown as a gradient from low (black) to high (white).

**Appendix D.** Species encountered in chronosequence plot SB-Y in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016.

| Species                       | Family                  | IV 2011 | IV 2016 | Species                        | Family                 | IV 2011 | IV 2016 | Species                      | Family              | IV 2011 | IV 2016 |
|-------------------------------|-------------------------|---------|---------|--------------------------------|------------------------|---------|---------|------------------------------|---------------------|---------|---------|
| <i>Alchornea latifolia</i>    | <i>Euphorbiaceae</i>    | 2.99    | 3.17    | <i>Miconia impetiolaris</i>    | <i>Melastomataceae</i> | 6.01    | 9.45    | <i>Tabebuia heterophylla</i> | <i>Bignoniaceae</i> | 11.03   | 10.4    |
| <i>Andira inermis</i>         | <i>Fabaceae</i>         | 2.57    | 2.61    | <i>Miconia mirabilis</i>       | <i>Melastomataceae</i> | 0.33    | 1.1     | <i>Tectona grandis</i>       | <i>Verbenaceae</i>  | 34.97   | 24.15   |
| <i>Artocarpus altilis</i>     | <i>Moraceae</i>         |         | 0.3     | <i>Miconia prasina</i>         | <i>Melastomataceae</i> | 7.08    | 10.53   | <i>Trichilia pallida</i>     | <i>Meliaceae</i>    | 1.27    | 1.21    |
| <i>Byrsonima spicata</i>      | <i>Malpighiaceae</i>    |         | 0.3     | <i>Miconia racemosa</i>        | <i>Melastomataceae</i> | 1.53    | 0.63    |                              |                     |         |         |
| <i>Calophyllum antillanum</i> | <i>Clusiaceae</i>       | 17.16   | 19.25   | <i>Miconia serrulata</i>       | <i>Melastomataceae</i> |         | 1.24    |                              |                     |         |         |
| <i>Casearia arborea</i>       | <i>Salicaceae</i>       | 1.27    | 1.84    | <i>Miconia tetrandra</i>       | <i>Melastomataceae</i> | 0.31    | 0.3     |                              |                     |         |         |
| <i>Casearia guianensis</i>    | <i>Salicaceae</i>       | 1.02    | 1       | <i>Myrcia deflexa</i>          | <i>Myrtaceae</i>       | 4.05    | 3.8     |                              |                     |         |         |
| <i>Casearia sylvestris</i>    | <i>Salicaceae</i>       | 4.48    | 4.1     | <i>Myrcia fallax</i>           | <i>Myrtaceae</i>       | 0.31    |         |                              |                     |         |         |
| <i>Cecropia schreberiana</i>  | <i>Urticaceae</i>       | 3.34    | 3.46    | <i>Myrcia splendens</i>        | <i>Myrtaceae</i>       | 5.22    | 4.57    |                              |                     |         |         |
| <i>Cordia sulcata</i>         | <i>Boraginaceae</i>     | 1.41    | 1.13    | <i>Ocotea leucoxylon</i>       | <i>Lauraceae</i>       | 3.51    | 3.88    |                              |                     |         |         |
| <i>Cyathea arborea</i>        | <i>Cyatheaceae</i>      | 0.37    |         | <i>Ocotea sintensis</i>        | <i>Lauraceae</i>       | 2.7     | 2.89    |                              |                     |         |         |
| <i>Dacryodes excelsa</i>      | <i>Burseraceae</i>      | 0.4     | 0.47    | <i>Palicourea riparia</i>      | <i>Rubiaceae</i>       | 0.62    | 1.24    |                              |                     |         |         |
| <i>Dendropanax arboreus</i>   | <i>Araliaceae</i>       | 2.3     | 3.07    | <i>Piper glabrescens</i>       | <i>Piperaceae</i>      |         | 2.23    |                              |                     |         |         |
| <i>Faramea occidentalis</i>   | <i>Rubiaceae</i>        | 2.76    | 3.07    | <i>Piper hispidum</i>          | <i>Piperaceae</i>      | 0.64    | 0.93    |                              |                     |         |         |
| <i>Ficus trigonata</i>        | <i>Moraceae</i>         | 0.48    | 0.6     | <i>Prestoea montana</i>        | <i>Arecaceae</i>       | 3.65    | 14.56   |                              |                     |         |         |
| <i>Genipa americana</i>       | <i>Rubiaceae</i>        | 0.7     | 0.75    | <i>Psychotria berteriana</i>   | <i>Rubiaceae</i>       | 7.9     | 6.59    |                              |                     |         |         |
| <i>Gonzagalunia spicata</i>   | <i>Rubiaceae</i>        | 0.61    | 0.3     | <i>Psychotria deflexa</i>      | <i>Rubiaceae</i>       | 22.88   | 50.42   |                              |                     |         |         |
| <i>Guarea guidonia</i>        | <i>Meliaceae</i>        | 9.49    | 12.52   | <i>Psychotria grandis</i>      | <i>Rubiaceae</i>       | 3.58    | 6.91    |                              |                     |         |         |
| <i>Hirtella triandra</i>      | <i>Chrysobalanaceae</i> | 0.31    | 0.3     | <i>Roystonea borinquena</i>    | <i>Arecaceae</i>       | 2.85    | 3.12    |                              |                     |         |         |
| <i>Inga laurina</i>           | <i>Fabaceae</i>         | 14.49   | 20.59   | <i>Samyda spinulosa</i>        | <i>Salicaceae</i>      |         | 0.3     |                              |                     |         |         |
| <i>Inga vera</i>              | <i>Fabaceae</i>         | 0.7     | 0.4     | <i>Schefflera morototoni</i>   | <i>Araliaceae</i>      | 5.81    | 5.06    |                              |                     |         |         |
| <i>Ixora ferrea</i>           | <i>Rubiaceae</i>        | 1.29    | 2.05    | <i>Spathodea campanulata</i>   | <i>Bignoniaceae</i>    | 0.67    | 0.68    |                              |                     |         |         |
| <i>Mammea americana</i>       | <i>Clusiaceae</i>       | 0.31    | 0.3     | <i>Swietenia macrophylla</i>   | <i>Meliaceae</i>       | 13      | 17.64   |                              |                     |         |         |
| <i>Manilkara bidentata</i>    | <i>Sapotaceae</i>       | 5.31    | 6.08    | <i>Symplocos martinicensis</i> | <i>Symplocaceae</i>    | 0.37    |         |                              |                     |         |         |
| <i>Miconia affinis</i>        | <i>Melastomataceae</i>  |         | 1.21    | <i>Syzygium jambos</i>         | <i>Myrtaceae</i>       | 86      | 27.39   |                              |                     |         |         |

**Appendix E.** Species encountered in chronosequence plot SB-M in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016.

| Species                        | Family                  | IV 2011 | IV 2016 | Species                         | Family                 | IV 2011 | IV 2016 | Species                  | Family           | IV 2011 | IV 2016 |
|--------------------------------|-------------------------|---------|---------|---------------------------------|------------------------|---------|---------|--------------------------|------------------|---------|---------|
| <i>Alchornea latifolia</i>     | <i>Euphorbiaceae</i>    | 2.2     | 2.53    | <i>Miconia impetiolaris</i>     | <i>Melastomataceae</i> | 2.85    | 3.18    | <i>Trichilia pallida</i> | <i>Meliaceae</i> | 0.41    | 0.43    |
| <i>Andira inermis</i>          | <i>Fabaceae</i>         | 3.19    | 3.22    | <i>Miconia mirabilis</i>        | <i>Melastomataceae</i> | 1.47    | 0.95    |                          |                  |         |         |
| <i>Artocarpus altilis</i>      | <i>Moraceae</i>         | 1       | 1.08    | <i>Miconia prasina</i>          | <i>Melastomataceae</i> | 40.64   | 36.18   |                          |                  |         |         |
| <i>Byrsonima spicata</i>       | <i>Malpighiaceae</i>    | 3.45    | 2.83    | <i>Miconia racemosa</i>         | <i>Melastomataceae</i> |         | 0.55    |                          |                  |         |         |
| <i>Byrsonima wadsworthii</i>   | <i>Malpighiaceae</i>    | 0.57    | 0.72    | <i>Miconia serrulata</i>        | <i>Melastomataceae</i> | 1.35    | 0.98    |                          |                  |         |         |
| <i>Calophyllum antillanum</i>  | <i>Clusiaceae</i>       | 60.75   | 64.89   | <i>Myrcia citrifolia</i>        | <i>Myrtaceae</i>       | 0.44    |         |                          |                  |         |         |
| <i>Casearia arborea</i>        | <i>Salicaceae</i>       | 2.97    | 3.32    | <i>Myrcia deflexa</i>           | <i>Myrtaceae</i>       | 30.09   | 26.19   |                          |                  |         |         |
| <i>Casearia sylvestris</i>     | <i>Salicaceae</i>       | 1.36    | 1.33    | <i>Myrcia fallax</i>            | <i>Myrtaceae</i>       | 0.41    | 0.43    |                          |                  |         |         |
| <i>Cecropia schreberiana</i>   | <i>Urticaceae</i>       | 3.88    | 4.2     | <i>Myrcia leptoclada</i>        | <i>Myrtaceae</i>       | 0.86    | 0.9     |                          |                  |         |         |
| <i>Chione venosa</i>           | <i>Rubiaceae</i>        | 0.41    | 0.43    | <i>Myrcia splendens</i>         | <i>Myrtaceae</i>       | 3.45    | 2.46    |                          |                  |         |         |
| <i>Chrysobalanus icaco</i>     | <i>Chrysobalanaceae</i> | 0.44    | 0.47    | <i>Ocotea leucoxylon</i>        | <i>Lauraceae</i>       | 11.02   | 12.43   |                          |                  |         |         |
| <i>Cordia borinquensis</i>     | <i>Boraginaceae</i>     | 5.04    | 4.85    | <i>Palicourea riparia</i>       | <i>Rubiaceae</i>       | 0.41    | 0.64    |                          |                  |         |         |
| <i>Cyathea arborea</i>         | <i>Cyatheaceae</i>      | 1.16    | 1.21    | <i>Prestoea montana</i>         | <i>Arecaceae</i>       | 7.43    | 9.5     |                          |                  |         |         |
| <i>Dacryodes excelsa</i>       | <i>Burseraceae</i>      | 0.41    | 0.43    | <i>Psychotria berteriana</i>    | <i>Rubiaceae</i>       | 4.76    | 4.13    |                          |                  |         |         |
| <i>Dendropanax arboreus</i>    | <i>Araliaceae</i>       | 0.41    | 0.43    | <i>Psychotria deflexa</i>       | <i>Rubiaceae</i>       | 8.31    | 13.45   |                          |                  |         |         |
| <i>Faramea occidentalis</i>    | <i>Rubiaceae</i>        | 13.32   | 17.05   | <i>Psychotria grandis</i>       | <i>Rubiaceae</i>       | 0.41    | 0.9     |                          |                  |         |         |
| <i>Genipa americana</i>        | <i>Rubiaceae</i>        | 0.41    | 0.43    | <i>Samyda spinulosa</i>         | <i>Salicaceae</i>      | 0.48    |         |                          |                  |         |         |
| <i>Guarea guidonia</i>         | <i>Meliaceae</i>        | 1.09    | 0.72    | <i>Schefflera morototoni</i>    | <i>Araliaceae</i>      | 13.66   | 12.47   |                          |                  |         |         |
| <i>Henriettea fascicularis</i> | <i>Melastomataceae</i>  | 0.41    | 0.43    | <i>Senna siamea</i>             | <i>Fabaceae</i>        | 8.31    | 7.4     |                          |                  |         |         |
| <i>Hirtella triandra</i>       | <i>Chrysobalanaceae</i> | 0.41    | 0.43    | <i>Sloanea berteriana</i>       | <i>Elaeocarpaceae</i>  |         | 0.47    |                          |                  |         |         |
| <i>Homalium racemosum</i>      | <i>Salicaceae</i>       | 4.03    | 4.23    | <i>Swietenia macrophylla</i>    | <i>Meliaceae</i>       | 0.9     | 0.94    |                          |                  |         |         |
| <i>Inga laurina</i>            | <i>Fabaceae</i>         | 3.1     | 2.76    | <i>Symplocos martinicensis</i>  | <i>Symplocaceae</i>    | 2.32    | 2.14    |                          |                  |         |         |
| <i>Ixora ferrea</i>            | <i>Rubiaceae</i>        | 6.35    | 6.42    | <i>Syzygium jambos</i>          | <i>Myrtaceae</i>       | 17.86   | 13.33   |                          |                  |         |         |
| <i>Manilkara bidentata</i>     | <i>Sapotaceae</i>       | 6.35    | 6.85    | <i>Tabebuia heterophylla</i>    | <i>Bignoniaceae</i>    | 16.89   | 15.81   |                          |                  |         |         |
| <i>Miconia affinis</i>         | <i>Melastomataceae</i>  | 1.39    | 1.89    | <i>Tetragastris balsamifera</i> | <i>Burseraceae</i>     | 1.14    | 0.9     |                          |                  |         |         |

**Appendix F.** Species encountered in chronosequence plot SB-O in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016.

| Species                         | Family                | IV 2011 | IV 2016 | Species                        | Family                  | IV 2011 | IV 2016 | Species                         | Family                 | IV 2011 | IV 2016 |
|---------------------------------|-----------------------|---------|---------|--------------------------------|-------------------------|---------|---------|---------------------------------|------------------------|---------|---------|
| <i>Alchornea latifolia</i>      | <i>Euphorbiaceae</i>  | 2.08    | 1.84    | <i>Guarea glabra</i>           | <i>Meliaceae</i>        | 0.82    | 0.92    | <i>Samyda spinulosa</i>         | <i>Salicaceae</i>      | 1.33    | 1.5     |
| <i>Alchorneopsis floribunda</i> | <i>Euphorbiaceae</i>  | 0.34    | 0.38    | <i>Guatteria caribaea</i>      | <i>Annonaceae</i>       | 1.08    | 1.23    | <i>Schefflera morototoni</i>    | <i>Araliaceae</i>      | 7.04    | 6.54    |
| <i>Andira inermis</i>           | <i>Fabaceae</i>       | 3.77    | 4.17    | <i>Henriettea fascicularis</i> | <i>Melastomataceae</i>  | 1.56    | 1.68    | <i>Simarouba tulae</i>          | <i>Simaroubaceae</i>   | 8.99    | 11.3    |
| <i>Antirhea obtusifolia</i>     | <i>Rubiaceae</i>      | 0.5     | 0.5     | <i>Hirtella rugosa</i>         | <i>Chrysobalanaceae</i> | 1.51    | 1.68    | <i>Sloanea berteriana</i>       | <i>Elaeocarpaceae</i>  | 7.09    | 7.45    |
| <i>Ardisia glauciflora</i>      | <i>Myrsinaceae</i>    | 0.72    | 0.86    | <i>Hirtella triandra</i>       | <i>Chrysobalanaceae</i> | 0.34    | 0.38    | <i>Syzygium jambos</i>          | <i>Myrtaceae</i>       | 6.06    | 4.97    |
| <i>Buchenavia tetraphylla</i>   | <i>Combretaceae</i>   | 2.2     | 2.3     | <i>Homalium racemosum</i>      | <i>Salicaceae</i>       | 1.47    | 1.55    | <i>Tabebuia heterophylla</i>    | <i>Bignoniaceae</i>    | 7.88    | 8.27    |
| <i>Byrsonima spicata</i>        | <i>Malpighiaceae</i>  | 5.43    | 5.93    | <i>Ilex sideroxyloides</i>     | <i>Aquifoliaceae</i>    | 0.92    | 0.96    | <i>Tetragastris balsamifera</i> | <i>Burseraceae</i>     | 12.83   | 14.16   |
| <i>Casearia arborea</i>         | <i>Salicaceae</i>     | 3.85    | 4.21    | <i>Inga laurina</i>            | <i>Fabaceae</i>         | 0.92    | 1.01    | <i>Tetrazygia urbanii</i>       | <i>Melastomataceae</i> | 7.77    | 8.71    |
| <i>Casearia sylvestris</i>      | <i>Salicaceae</i>     | 0.93    | 0.45    | <i>Ixora ferrea</i>            | <i>Rubiaceae</i>        | 5.02    | 5.36    | <i>Trichilia pallida</i>        | <i>Meliaceae</i>       | 2.65    | 2.52    |
| <i>Cassipourea guianensis</i>   | <i>Rhizophoraceae</i> | 1.72    | 1.84    | <i>Manilkara bidentata</i>     | <i>Sapotaceae</i>       | 48.68   | 52.19   | <i>Zanthoxylum martinicense</i> | <i>Rutaceae</i>        | 0.71    |         |
| <i>Cecropia schreberiana</i>    | <i>Urticaceae</i>     | 6.39    | 2.84    | <i>Meliosma herbertii</i>      | <i>Sabiaceae</i>        | 2.82    | 2.13    |                                 |                        |         |         |
| <i>Chionanthus domingensis</i>  | <i>Oleaceae</i>       | 1.54    | 0.92    | <i>Miconia mirabilis</i>       | <i>Melastomataceae</i>  | 8.69    | 7.1     |                                 |                        |         |         |
| <i>Chione venosa</i>            | <i>Rubiaceae</i>      | 0.5     | 0.56    | <i>Miconia prasina</i>         | <i>Melastomataceae</i>  | 13.88   | 9.37    |                                 |                        |         |         |
| <i>Clusia rosea</i>             | <i>Clusiaceae</i>     |         | 0.38    | <i>Miconia tetrandra</i>       | <i>Melastomataceae</i>  | 2.2     | 1.47    |                                 |                        |         |         |
| <i>Coccoloba pyrifolia</i>      | <i>Polygonaceae</i>   | 1.41    | 1.55    | <i>Myrcia deflexa</i>          | <i>Myrtaceae</i>        | 5.06    | 5.46    |                                 |                        |         |         |
| <i>Comocladia glabra</i>        | <i>Anacardiaceae</i>  | 0.34    |         | <i>Myrcia leptoclada</i>       | <i>Myrtaceae</i>        | 4.68    | 5.83    |                                 |                        |         |         |
| <i>Cordia borinquensis</i>      | <i>Boraginaceae</i>   | 4.34    | 4.75    | <i>Myrcia splendens</i>        | <i>Myrtaceae</i>        |         | 0.38    |                                 |                        |         |         |
| <i>Cordia sulcata</i>           | <i>Boraginaceae</i>   | 0.6     | 0.53    | <i>Ocotea leucoxylon</i>       | <i>Lauraceae</i>        | 7.31    | 7.8     |                                 |                        |         |         |
| <i>Cyathea arborea</i>          | <i>Cyatheaceae</i>    | 1.07    | 0.43    | <i>Ormosia krugii</i>          | <i>Fabaceae</i>         | 7.81    | 8.73    |                                 |                        |         |         |
| <i>Dacryodes excelsa</i>        | <i>Burseraceae</i>    | 31.84   | 32.77   | <i>Piper blattarum</i>         | <i>Piperaceae</i>       | 0.5     | 0.51    |                                 |                        |         |         |
| <i>Drypetes glauca</i>          | <i>Euphorbiaceae</i>  | 5.18    | 4.73    | <i>Piper glabrescens</i>       | <i>Piperaceae</i>       | 0.72    | 0.38    |                                 |                        |         |         |
| <i>Eugenia domingensis</i>      | <i>Myrtaceae</i>      | 0.4     | 0.45    | <i>Prestoea montana</i>        | <i>Arecaceae</i>        | 11.7    | 12.16   |                                 |                        |         |         |
| <i>Eugenia stahlii</i>          | <i>Myrtaceae</i>      | 2.98    | 3.28    | <i>Pseudolmedia spuria</i>     | <i>Moraceae</i>         | 0.34    | 0.38    |                                 |                        |         |         |
| <i>Faramea occidentalis</i>     | <i>Rubiaceae</i>      | 21.89   | 26.9    | <i>Psychotria berteriana</i>   | <i>Rubiaceae</i>        | 7.61    | 1.42    |                                 |                        |         |         |
| <i>Ficus trigonata</i>          | <i>Moraceae</i>       | 0.44    | 0.48    | <i>Psychotria deflexa</i>      | <i>Rubiaceae</i>        | 1.6     | 1.44    |                                 |                        |         |         |

**Appendix G.** Species encountered in chronosequence plot EV-M in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016.

| Species                           | Family          | IV 2011 | IV 2016 | Species                         | Family           | IV 2011 | IV 2016 | Species                          | Family           | IV 2011 | IV 2016 |
|-----------------------------------|-----------------|---------|---------|---------------------------------|------------------|---------|---------|----------------------------------|------------------|---------|---------|
| <i>Alchornea latifolia</i>        | Euphorbiaceae   | 4.98    | 4.91    | <i>Drypetes glauca</i>          | Euphorbiaceae    | 0.26    |         | <i>Micropholis guayanensis</i>   | Sapotaceae       | 11.7    | 12.48   |
| <i>Alchorneopsis floribunda</i>   | Euphorbiaceae   | 4.02    | 4.26    | <i>Eugenia domingensis</i>      | Myrtaceae        | 0.2     | 0.23    | <i>Myrcia deflexa</i>            | Myrtaceae        | 11.54   | 12.18   |
| <i>Antirhea obtusifolia</i>       | Rubiaceae       | 0.3     | 0.33    | <i>Eugenia stahlia</i>          | Myrtaceae        | 22.04   | 23.72   | <i>Myrcia fallax</i>             | Myrtaceae        | 5.41    | 5.68    |
| <i>Buchenavia tetraphylla</i>     | Combretaceae    | 17.57   | 15.68   | <i>Faramea occidentalis</i>     | Rubiaceae        | 0.26    | 0.29    | <i>Myrcia splendens</i>          | Myrtaceae        |         | 0.23    |
| <i>Byrsonima spicata</i>          | Malpighiaceae   | 9.37    | 8.2     | <i>Ficus americana</i>          | Moraceae         | 1.64    | 1.75    | <i>Ocotea leucoxyton</i>         | Lauraceae        | 8.18    | 9.26    |
| <i>Byrsonima wadsworthii</i>      | Malpighiaceae   | 0.2     | 0.23    | <i>Ficus trigonata</i>          | Moraceae         | 0.6     | 0.66    | <i>Ocotea spathulata</i>         | Lauraceae        | 0.51    | 0.52    |
| <i>Calophyllum antillanum</i>     | Clusiaceae      | 7.51    | 7.44    | <i>Guarea glabra</i>            | Meliaceae        | 3.24    | 2.42    | <i>Ormosia krugii</i>            | Fabaceae         | 1.08    | 1.12    |
| <i>Calycogonium squamulosum</i>   | Melastomataceae | 0.95    | 0.67    | <i>Guettarda valenzuelana</i>   | Rubiaceae        | 0.92    | 1.01    | <i>Palicourea riparia</i>        | Rubiaceae        | 0.62    | 0.86    |
| <i>Calyptranthes luquillensis</i> | Myrtaceae       | 6.16    | 6.39    | <i>Henriettea fascicularis</i>  | Melastomataceae  | 2.76    | 2.89    | <i>Prestoea montana</i>          | Areceaceae       | 49.81   | 53.7    |
| <i>Casearia arborea</i>           | Salicaceae      | 26.08   | 28.14   | <i>Hirtella rugosa</i>          | Chrysobalanaceae | 9.16    | 10.68   | <i>Psychotria berteriana</i>     | Rubiaceae        | 4.46    | 1.78    |
| <i>Casearia sylvestris</i>        | Salicaceae      | 0.51    | 0.59    | <i>Homalium racemosum</i>       | Salicaceae       | 2.72    | 2.74    | <i>Psychotria deflexa</i>        | Rubiaceae        | 1.7     | 0.6     |
| <i>Cassipourea guianensis</i>     | Rhizophoraceae  | 0.2     | 0.23    | <i>Ilex sideroxyloides</i>      | Aquifoliaceae    | 3.37    | 3.19    | <i>Rheedia portoricensis</i>     | Clusiaceae       | 3.66    | 4.25    |
| <i>Cecropia schreberiana</i>      | Urticaceae      | 7.46    | 5.84    | <i>Inga laurina</i>             | Fabaceae         | 1.3     | 1.39    | <i>Schefflera morototoni</i>     | Araliaceae       | 4.47    | 5.55    |
| <i>Chionanthus domingensis</i>    | Oleaceae        | 0.87    | 0.98    | <i>Ixora ferrea</i>             | Rubiaceae        | 2.11    | 2.09    | <i>Sloanea berteriana</i>        | Elaeocarpaceae   | 9.73    | 9.73    |
| <i>Clusia rosea</i>               | Clusiaceae      | 0.9     | 1.95    | <i>Laetia procera</i>           | Salicaceae       | 0.31    | 0.37    | <i>Tabebuia heterophylla</i>     | Bignoniaceae     | 5.17    | 5.25    |
| <i>Coccoloba pyrifolia</i>        | Polygonaceae    | 0.87    | 1.07    | <i>Manilkara bidentata</i>      | Sapotaceae       | 1.49    | 1.71    | <i>Ternstroemia luquillensis</i> | Pentaphylacaceae | 0.28    | 0.31    |
| <i>Coccoloba swartzii</i>         | Polygonaceae    | 5.87    | 6.21    | <i>Matayba domingensis</i>      | Sapindaceae      | 4.04    | 4.17    | <i>Trichilia pallida</i>         | Meliaceae        | 0.2     | 0.23    |
| <i>Comocladia glabra</i>          | Anacardiaceae   | 0.2     |         | <i>Miconia affinis</i>          | Melastomataceae  | 0.88    |         |                                  |                  |         |         |
| <i>Cordia borinquensis</i>        | Boraginaceae    | 5.27    | 5.11    | <i>Miconia impetolaris</i>      | Melastomataceae  | 0.2     | 0.23    |                                  |                  |         |         |
| <i>Cordia sulcata</i>             | Boraginaceae    | 0.67    | 0.72    | <i>Miconia mirabilis</i>        | Melastomataceae  | 3.09    | 1.28    |                                  |                  |         |         |
| <i>Cyathea arborea</i>            | Cyatheaceae     | 1.23    | 1.03    | <i>Miconia prasina</i>          | Melastomataceae  | 10.62   | 6.37    |                                  |                  |         |         |
| <i>Cyathea borinquena</i>         | Cyatheaceae     |         | 0.23    | <i>Miconia racemosa</i>         | Melastomataceae  |         | 0.49    |                                  |                  |         |         |
| <i>Cyrilla racemiflora</i>        | Cyrillaceae     | 1.2     | 1.35    | <i>Miconia serrulata</i>        | Melastomataceae  | 2.51    | 2.23    |                                  |                  |         |         |
| <i>Dacryodes excelsa</i>          | Burseraceae     | 0.57    | 0.66    | <i>Miconia tetrandra</i>        | Melastomataceae  | 3.55    | 3.15    |                                  |                  |         |         |
| <i>Daphnopsis philippiana</i>     | Thymelaceae     | 0.2     | 0.23    | <i>Micropholis garcinifolia</i> | Sapotaceae       | 0.98    | 0.85    |                                  |                  |         |         |

**Appendix H.** Species encountered in chronosequence plot EV-O in El Yunque National Forest, Puerto Rico and their importance values (IV) in 2011 and 2016.

| Species                         | Family                  | IV 2011 | IV 2016 | Species                         | Family                 | IV 2011 | IV 2016 |
|---------------------------------|-------------------------|---------|---------|---------------------------------|------------------------|---------|---------|
| <i>Alchornea latifolia</i>      | <i>Euphorbiaceae</i>    | 0.73    | 0.7     | <i>Ilex sideroxyloides</i>      | <i>Aquifoliaceae</i>   | 0.25    | 0.18    |
| <i>Alchorneopsis floribunda</i> | <i>Euphorbiaceae</i>    | 0.33    | 0.31    | <i>Inga laurina</i>             | <i>Fabaceae</i>        | 1.03    | 1.01    |
| <i>Andira inermis</i>           | <i>Fabaceae</i>         | 2.56    | 2.49    | <i>Inga vera</i>                | <i>Fabaceae</i>        | 0.17    | 0.22    |
| <i>Buchenavia tetraphylla</i>   | <i>Combretaceae</i>     | 3.7     | 3.65    | <i>Ixora ferrea</i>             | <i>Rubiaceae</i>       | 0.72    | 0.78    |
| <i>Byrsonima spicata</i>        | <i>Malpighiaceae</i>    | 0.09    | 0.09    | <i>Laetia procera</i>           | <i>Salicaceae</i>      | 0.97    | 0.92    |
| <i>Byrsonima wadsworthii</i>    | <i>Malpighiaceae</i>    | 0.4     | 0.56    | <i>Laplacea portoricensis</i>   | <i>Theaceae</i>        | 0.09    | 0.09    |
| <i>Casearia arborea</i>         | <i>Salicaceae</i>       | 0.46    | 0.42    | <i>Manilkara bidentata</i>      | <i>Sapotaceae</i>      | 28.84   | 29.58   |
| <i>Casearia guianensis</i>      | <i>Salicaceae</i>       | 0.09    | 0.09    | <i>Matayba domingensis</i>      | <i>Sapindaceae</i>     | 0.36    | 0.47    |
| <i>Casearia sylvestris</i>      | <i>Salicaceae</i>       | 0.11    |         | <i>Meliosma herbertii</i>       | <i>Sabiaceae</i>       | 0.21    | 0.18    |
| <i>Cassipourea guianensis</i>   | <i>Rhizophoraceae</i>   | 0.3     | 0.18    | <i>Miconia tetrandra</i>        | <i>Melastomataceae</i> | 0.89    | 0.91    |
| <i>Cecropia schreberiana</i>    | <i>Urticaceae</i>       | 4.86    | 4.72    | <i>Micropholis guayanensis</i>  | <i>Sapotaceae</i>      | 1.87    | 1.92    |
| <i>Cordia borinquensis</i>      | <i>Boraginaceae</i>     | 0.72    | 0.65    | <i>Myrcia leptoclada</i>        | <i>Myrtaceae</i>       | 0.74    | 0.79    |
| <i>Cordia sulcata</i>           | <i>Boraginaceae</i>     | 0.4     | 0.34    | <i>Myrcia splendens</i>         | <i>Myrtaceae</i>       | 0.3     | 0.29    |
| <i>Croton poecilanthus</i>      | <i>Euphorbiaceae</i>    | 1.19    | 1.03    | <i>Ocotea moschata</i>          | <i>Lauraceae</i>       | 0.25    | 0.24    |
| <i>Cyathea arborea</i>          | <i>Cyatheaceae</i>      | 0.09    |         | <i>Ormosia krugii</i>           | <i>Fabaceae</i>        | 1.74    | 1.76    |
| <i>Dacryodes excelsa</i>        | <i>Burseraceae</i>      | 77.28   | 76.64   | <i>Prestoea montana</i>         | <i>Arecaceae</i>       | 39.76   | 40.54   |
| <i>Drypetes glauca</i>          | <i>Euphorbiaceae</i>    | 1.28    | 1.22    | <i>Pseudolmedia spuria</i>      | <i>Moraceae</i>        | 0.21    | 0.22    |
| <i>Eugenia stahlii</i>          | <i>Myrtaceae</i>        | 0.68    | 0.68    | <i>Psychotria berteriana</i>    | <i>Rubiaceae</i>       | 0.3     |         |
| <i>Ficus crassinervia</i>       | <i>Moraceae</i>         | 0.58    | 0.67    | <i>Schefflera morototoni</i>    | <i>Araliaceae</i>      | 1.66    | 1.53    |
| <i>Guarea glabra</i>            | <i>Meliaceae</i>        | 0.3     | 0.29    | <i>Sloanea berteriana</i>       | <i>Elaeocarpaceae</i>  | 4.74    | 4.53    |
| <i>Guarea guidonia</i>          | <i>Meliaceae</i>        | 3.14    | 3.24    | <i>Swietenia macrophylla</i>    | <i>Meliaceae</i>       | 0.09    | 0.09    |
| <i>Guetteria caribaea</i>       | <i>Annonaceae</i>       | 0.55    | 0.52    | <i>Tabebuia heterophylla</i>    | <i>Bignoniaceae</i>    | 0.44    | 0.51    |
| <i>Guettarda valenzuelana</i>   | <i>Rubiaceae</i>        | 0.21    | 0.18    | <i>Tetragastris balsamifera</i> | <i>Burseraceae</i>     | 11.9    | 11.68   |
| <i>Hirtella rugosa</i>          | <i>Chrysobalanaceae</i> | 0.78    | 0.7     | <i>Trichilia pallida</i>        | <i>Meliaceae</i>       | 0.83    | 0.79    |
| <i>Homalium racemosum</i>       | <i>Salicaceae</i>       | 0.82    | 0.89    |                                 |                        |         |         |