Hurricane disturbance effects on tropical forests; structure, plant dynamics, and carbon storage

By

Hervé Chevalier

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Thesis submitted and accepted by:
Department of Environmental sciences, College of Natural Sciences
University of Puerto Rico, Rio Piedras Campus

Thesis committee:

Nicholas Brokaw, Ph.D.
Advisor UPR-RP - Department of Environmental Sciences

Jess K. Zimmerman, Ph.D.
Co-Advisor UPR-RP - Department of Environmental Sciences

Giong Gao, Ph.D., Committee member
UPR-RP - Department of Environmental Sciences

Shawn Fraver, Ph.D., Committee member
University of Maine - School of Forest Resources

Tana Wood, Ph.D., Committee member
USDA Forest Service, International Institute of Tropical Forestry (IITF)

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DEDICATION

I dedicate this thesis to my wife Fernande Fenelon for her love and unconditional support, to my beloved children Disrally Stein and Annoa Gracey who are my source of motivation, and to my parents Anne Marie Buteau and Lincio Chevalier who gave me all their love and support.

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ABBREVIATIONS

AH	After Hurricane Hugo
AM	After Hurricane Maria
ASL	Above Sea Level
BCI	Barro Colorado Island
BH	Before Hurricane Hugo
BM	Before Hurricane Maria
CTE	Canopy Trimming Experiment
DBH	Diameter breast height
DEGI	Decanato de Estudios Graduados e Investigación
EVFS	El Verde Field Station
LEF	Luquillo Experimental Forest
LFDP	Luquillo Forest Dynamic Plot
LTER	Luquillo Long Term Ecological Research
MCN	Mean Canopy Height
NSF	National Science Foundation
UPR	University of Puerto Rico

ABSTRACT

Hervé Chevalier. Hurricane effects on tropical forest structure, structure effects on plant dynamics, and plant effects on carbon storage

Tropical cyclones are likely to increase in intensity, cause increased rainfall, and have larger storm surges. Changes in intensity and strength of tropical cyclones potentially have considerable effects on tropical forests. In the research presented in this dissertation, the hurricane disturbance effects on tropical rain forest structure, plant populations, and carbon storage were investigated in the Luquillo Experimental Forest (LEF), Puerto Rico. The overarching goal is to assess the effects of hurricanes on tropical rainforest by using El Yunque National Forest of Puerto Rico as example. It is articulated around three main objectives. 1) measure the forest canopy change through time and on the elevation gradient to see how hurricanes affect forest structure, 2) measure the effect of the canopy opening on the understory plant populations, using two pioneer species, 3) measure the hurricane disturbance effects on aboveground carbon through time in a simulation plot to see how the canopy openness and plant recruitment influence aboveground carbon.

I had three working hypothesizes for the respective objectives. 1) My first hypothesis was that forests will differ in resistance and/or resilience because of presumed climate differences associated with the elevation gradient. To test that, I used canopy height data, from before Hurricane Hugo to after Hurricane Maria, in three hectare-sized plots at 350, 750, and 1000 m asl, respectively. I compared the maximum canopy heigh through time, made triangulated irregular network before and after hurricanes, plotted standard deviation and coefficient of variations

through time for each plot. Then, I computed resistance and resilience through time for each plot and compared the values among the plots. Results indicated the Tabonuco forest seemed to be more resilient. The forest recovered at 91 percent in 2013, 24 years after Hurricane Hugo. They also showed that the Dwarf forest was the least resistant to Hugo, but the most resistant to Hurricane Maria. It seems to be the least resilient among the three plots. 25 years after Hurricane Hugo, measured in 2014, it showed only 48 percent of recovery. 2) My second hypothesis, regarding colonizing pioneer plants, was that average maximum canopy height in 2019 will be more strongly correlated with abundance in 2019 than in 2021 because of the direct overhead light. This early correlation with light is expected because the canopy recovers and shades the understory. I found that plant recruitment relative to canopy height was stronger in 2019 two years after the hurricane than in 2021, four years after the storm. 3) My third hypothesis was that forest regrowth after a simulated hurricane (experimental trimming) would compensate for carbon loss in the period of the study. If this is not true it implies that a predicted increase in frequency of intense hurricanes could eventually reduce aboveground carbon in forests subjected to strong cyclonic storms. I expected that during the 14-year period after canopy trimming, regrowth of branches and stems and stem recruitment stimulated by increased light and trimmed debris would help restore biomass and carbon loss due to trimming. Compared to control plots, in the trimmed plots recruitment of palms and dicot trees increased markedly after trimming, and stem diameters of standing trees increased. This response restored pre-treatment biomass and carbon in the experimental period. However, the data showed that recruitment of small trees adds little to aboveground carbon, compared to the amount in large trees.

Climate change is likely to alter forest processes. More hurricanes and other disturbances are projected to happen by the middle of the century in tropical regions. In the LEF, the 31-year data set shows substantial effects of hurricanes on forest structure, mainly reduction in the canopy height, and canopy surface damage. The created-gap radically changes light, temperature, soil moisture, and available nutrients to create an environment which favors many species to grow to replace the dead ones. Over the long term, a continued loss of large trees could eventually result in less aboveground carbon stored in this Puerto Rican Forest and in other hurricane-affected tropical forests.

Key words: Tropical Forest, Aboveground carbon, Forest canopy, Puerto Rico, Luquillo, Hurricanes

Author’s name in full Hervé Chevalier
Candidate for the degree of Ph.D Date: November 2022
Major Professor Dr. Nicholas Brokaw
Faculty of Natural Sciences, University of Puerto Rico, Rio Piedras
Department of Environmental Science, Rio Piedras, San Juan
Signature of Major Professor ____
Nicholas Brokaw

CHAPTER 1

GENERAL INTRODUCTION

1.1 Tropical Forest disturbance, structure, regrowth, and aboveground carbon storage

Tropical forests are defined as forested landscapes located between 23º North and South of the Equator. Variation in regional soil, precipitation, and seasonality characterize the forest systems of this area, which are responsible for half of the total terrestrial gross primary productivity (Viswanath 2019). Tropical forests play an important role in regulating climate features by absorbing carbon dioxide and producing oxygen which facilitate a balance in the maintenance of oxygen and carbon dioxide in the atmosphere. They are possibly the most important biomes on the earth, representing one-third of land-surface productivity and evapotranspiration, and are valued to host over half of the global terrestrial biodiversity (Malhi et al. 2014).

Tropical forests are habitats for many animals on earth. From the canopy top to the forest floor, they directly influence distribution of animals that eat plants (Brokaw and Lent 1999). They provide food and a repository for them. They are rich in carbon. Nearly 20% of the CO_2 currently produced globally by industrial emissions and land conversion is absorbed by the tropical forests (Lewis et al. 2009, Viswanath 2019). They contain about 553 Peta-gram (Pg.) of carbon, which accounts for 40% of the total carbon in the terrestrial biosphere, with 58% in their vegetation, 41% in soil, and 1% in litter (Soepadmo 1993).

However, tropical forests face major disturbances such as fires, typhoons, human presence, and hurricanes. Disturbances play important roles in succession of plant communities because they kill or remove organisms from the community (Krohne 2000). They cause changes in the physical environment that affect the biota. Among these disturbances hurricanes constitute one of the major disturbances influencing the tropical forest dynamics. They shape the forest structure, which refers to how the physical attributes of trees and other plants are distributed within a forest ecosystem, by creating individual and multiple treefall gaps and thereby initiating regrowth (Walker 1991). They also cause catastrophic sudden tree mortality during or after the hurricanes (Lugo and Scatena 1996) and contribute to heterogeneity in structure and floristics of forested landscapes (Crausbay and Martin 2016).

(Boose *et al*. 2004)

In Puerto Rico, forests have been affected by many cyclonic storms. Hurricanes strike Puerto Rico on average every 22 years and have significant effects on ecosystems processes, vegetation, and animals (Pascarella et al. 2004). Puerto Rican forests experience one of the highest frequencies of Hurricanes of any island in the Caribbean (Boose et al. 2004). In September 1989, Hurricane Hugo crossed Puerto Rico and the Luquillo Experimental Forest with a maximum sustained wind of 166 kph and gusts to 194 kph (Uriarte et al. 2005, Hogan et al. 2016). Later, Hurricane George struck Puerto Rico in 1998 but with less damage to the Luquillo Experimental Forest (Hogan et al. 2016, Canham et al. 2010). Recently, Hurricanes Irma and Maria, category 4 and 5 storms hit the island in 2017 (Zimmerman et al. 2018). Their impact on the forest was immense. It is predicted that climate change into the next century with increasing global warming will increase the temperatures 4.6–9°C with potential decline in precipitation of 49.7% (Henereh et al. 2016). In addition, evidence suggests that atmospheric warming will lead to more intense hurricanes of categories 4 and 5 on the Saffir-Simpson scale (Knutson et al. 2010). Therefore, the need to assess the effects of hurricane disturbances on forest canopy, plant recruitment, biomass and carbon storage is crucial. Puerto Rico, given its location in the hurricane pathway is an ideal location to conduct such a project. Findings will be improved our ability to predict forest future in relation to carbon storage as one of its greatest functions. It will also help in prediction of forest structure and plant populations in hurricanes prone areas

1.2 Study area

The study area was the Luquillo Mountains at 18° N latitude and 66° W longitude in northeastern Puerto Rico. It is also designated administratively as the Luquillo Experimental Forest (LEF) and covers an area of 11,310 ha (Weaver 2012). At only 8 km from the ocean, these mountains rise abruptly to 1075 m and become gradually zoned with elevation: a quarter of land is between 120 and 300 m, about half from 300 to 600 m, another quarter between 600 to 900 m and 3 percent from 900 to 1075 m (Weaver 1983). Five subtropical life zones are represented: wet forest, rain forest, lower montane wet forest, lower montane rain forest, and a small tract of land in the southwest portion that falls within the moist forest live zone (U.S. Department of Agriculture 2012). The soils are mostly acid clays, deep, red (Weaver 1983).

The LEF experiences major hurricanes once every 50-60 years, on average (based on records 1769-1989, Scatena and Larsen 1991), and every 39-44 years 1766-2017 (Nicholas Brokaw, personal communication); nevertheless, just nine years separated two recent hurricanes:

Hugo in 1989 (category 3) and Georges (category 2) and 1998 (Shiels et al. 2015), and the most recent severe hurricane passing over our site was Hurricane María (category 4, Saffir–Simpson hurricane scale) in September 2017.

1.3 OBJECTIVES OF THIS RESEARCH

Hurricanes break up the forest canopy which changes plant dynamics due to more sunlight and nutrient availability in the understory. Because hurricanes knock down big trees, they reduce carbon storage but hurricane effects on the canopy make room for seedlings and saplings, which leads to carbon restoration through plant dynamics. Therefore, the overarching goal of this research is to assess the effects of hurricanes on tropical rainforest, using the Luquillo Experimental Forest of Puerto Rico as example. This generalized goal correlates with the following specific objectives: 1) measure the forest canopy change through time and on the elevation gradient, 2) measure the effect of the canopy opening on the understory using two pioneer species, 3) measure the hurricane disturbance effects on aboveground carbon through time in a simulation plot. Although this dissertation discusses the potential influence of climate change on forest structure, plant regeneration, and carbon dynamics, because climate change may increase the frequency of strong cyclonic storms, it does not discuss climate change per se nor cyclonic storms. Fig 1.1 presents the conceptual framework for the dissertation. The top box is climate change, or global change. The next row of the boxes are manifestations of climate change (drought, stronger storms, sea level rise).

As depicted in Fig. 1, I believe that stronger storms will affect forest structure by snapping down or uprooting big trees, defoliating them, or by just killing them immediately or weeks later. The increasing loss of the big trees that will result from the increase in frequency of strong storms may, as a result, reduce carbon storage. But the loss of big trees allows more sunlight to reach the forest floor. The availability of more sunlight couple with dead or defoliated of big trees facilitate the upcoming of small woody plants that can potentially compensate for the loss of big trees.

1.4 DISSERTATION OUTLINE

The dissertation contains 5 chapters. Chapter 1 presents the importance of this study, an introduction to the main goals of this study and a general description of the study site. In chapter 2, I present a 31-year dataset related to the forest canopy height for 3 different plots that span a gradient of elevation in the LEF to measure changes in the canopy and the resilience of the forest. This allows us to see how hurricanes influenced forest structure overtime. Most of this data has been collected by Dr. Brokaw since 1989 before Hurricane Hugo to 2021. In chapter 3, I present results related to the effects of canopy opening on the understory. I use *Cecropia schreberiana* and *Heliconia caribaea* as two pioneer species as an example. In chapter 4, I present results of a 15-year dataset from the canopy trimming experiment. Through this chapter, I show how plant recruitment resulted from the canopy opening influences aboveground carbon. I also demonstrate which hurricane effect – canopy trimming or debris deposition – has more impact on aboveground carbon. And chapter 5 presents a summary of all preceding chapters and perspectives for possible future research in the LEF.

1.5 Literature cited

Boose, E.R., M.I. Serrano, and D.R. Foster. 2004. Landscape and regional impacts of hurricanes in Puerto Rico. *Ecological Monographs*, **74**, 335–352.

Brokaw, N.V. L., and R. A. Lent. 1999. Vertical structure. In *Maintaining biodiversity in forest ecosystems*, 372-399. N.p.: Cambridge University Press.

Brokaw, N.V. L., and J.S. Grear. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains. *Source: Biotropica* 23 (4), 386. https://doi.org/10.2307/2388256.

Canham, C. D., J. Thompson, J.K. Zimmerman, And, and M. Uriarte. 2010. Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica* 42:87-94.

Crausbay, S.D., and P. H. Martin. 2016. Natural disturbance, vegetation patterns and ecological dynamics in tropical montane forests. *Journal of Tropical Ecology* 32 (5): 384–403. https://doi.org/10.1017/S0266467416000328.

Ewel, J.J. and J.L. Whitmore. 1973. Ecological life zones of Puerto Rico and US Virgin Islands. United States Forest Service Research Paper. ITF-18. Institute of Tropical Forestry, Rio Piedras, Puerto Rico.

Frangi, J.L., and A.E. Lugo. 1985. Ecosystem dynamics of a subtropical floodplain forest. *Ecological Monographs* 55:351-369. https://www.jstor.org/stable/1942582?seq=1.

Henereh, K. A., W. A. Gould, E. Harmsen, A. Terando, M. Quinones, and J. A. Collazo. 2016. Climate change implications for tropical islands: Interpolating and interpreting statistically downscaled GCM projections for management and planning. Journal of Applied Meteorology and Climatology 55:265–282.

Hogan, J.A., J.K. Zimmerman, J. Thompson, C.J. Nytch, and M. Uriarte. 2016. The interaction of land use legacies and hurricane disturbance in subtropical wet forest: twenty-one years of change. Ecosphere 7(8):e01405. 10.1002/ecs2.1405

Knutson, T.R., J.L. Mcbride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J.P Kossin, A.K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. *Nature Geoscience*, 3(3), 157-163. https://doi.org/10.1038/ngeo779.

Lewis, S.L., L.G. Gabriela, B. Sonke et al. (2009). Increasing carbon storage in intact African tropical forests. Noture, 457: 1 003-1 006.

Lugo, A.E., and F.N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* 28:585-589.

Malhi, Y., T.A. Gardner, G.R. Goldsmith, M.R. Silman, and P. Zelazowski. Tropical forests in the anthropocene. *Annu. Rev. Environ. Resour. 39:125-159*, 2014.

Pascarella, J.B., T.M. Aide, J.K. Zimmerman. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA, *199*, 379–393. doi:10.1016/j.foreco.2004.05.041.

Scatena, F.N., M.C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica* 23:317-323.

Shiels, A.B., G. González, D.J. Lodge, M.R. Willing, and J.K. Zimmerman. 2015. Cascading effects of canopy opening and debris deposition from a large-scale hurricane experiment in a tropical rain forest. *BioScience 65: 871–81.*

Shiels, A.B., J.K. Zimmerman, D.C. Garcia-Montiel, I. Jonckheere, J. Holm, D. Horton, and N.V.L. Brokaw. 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *J. Ecol.*, 659–73.

Soepadmo, E. 1993. Tropical rain forests as carbon sinks. *Chemosphere* 27:1025-1039.

Soil Survey Staff. 1995. Order 1 Soil Surveys of Luquillo Long-Term Ecological Research Grid, Puerto Rico. United States Department of Agriculture, Natural Resource Conservation Service.

Uriarte, M., C.D. Canham, J. Thompson, J.K. Zimmerman, and N.V.L Brokaw. 2005. Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-dependence and the spatial distribution of parent trees. *Journal of Ecology 93, 291–304.* https://doi.org/10.1111/j.1365-2745.2005.00984.x.

U.S. Department of Agriculture. 2012. *Luquillo experimental forest: research history and opportunities*. Edited by Tamara Heartsill Scalley, Nancy L. Harris, Ariel E. Lugo, Sandra Brown.

Viswanath, S., and S. Sandeep. 2019. Carbon dynamics in tropical forest ecosystems. Pages 1-16 in Institute of Wood Science and Technology, editors. 14th National Sylviculture Conference. Forest and sustainability: securing a common future. Indian Consul of Forestry Research and Education, Dehradun. 18th Cross, Malleswaram, Bengaluru-560003, Karnataka, India.

Weaver, P.L., and A.J.R. Gillespie. 2017. Tree biomass equations for the forests of the Luquillo Mountains, Puerto Rico. *The Commonwealth Forestry Review* 71:35-39.

Weaver, P. L. 2012. *The Luquillo Mountains: forest resources and their history*. Jardin Botanico Sur, 1201 Calle Ceiba, San Juan, PR 00926-1119.

Weaver, P.L. 2010. Tree species distribution and forest structure along environmental gradients in the Dwarf forest of the Luquillo Mountains of Puerto Rico. *Bois et Forets des Tropiques* 306: 33-44.

Weaver, P.L. 1983. Tree growth and stand changes in the subtropical life zones of the Luquillo Mountains of Puerto Rico. *Institute of Tropical Forestry* 190: 14-16

Zimmerman, J.K., J.A. Hogan, C.J.N. Nytch, and J.E. Bithorn. 2018. Effects of hurricanes and climate oscillations on annual variation in reproduction in wet forest, Puerto Rico. *Ecology,* 99 (6): 1402-1410. https://doi.org/10.1002/ecy.2236.

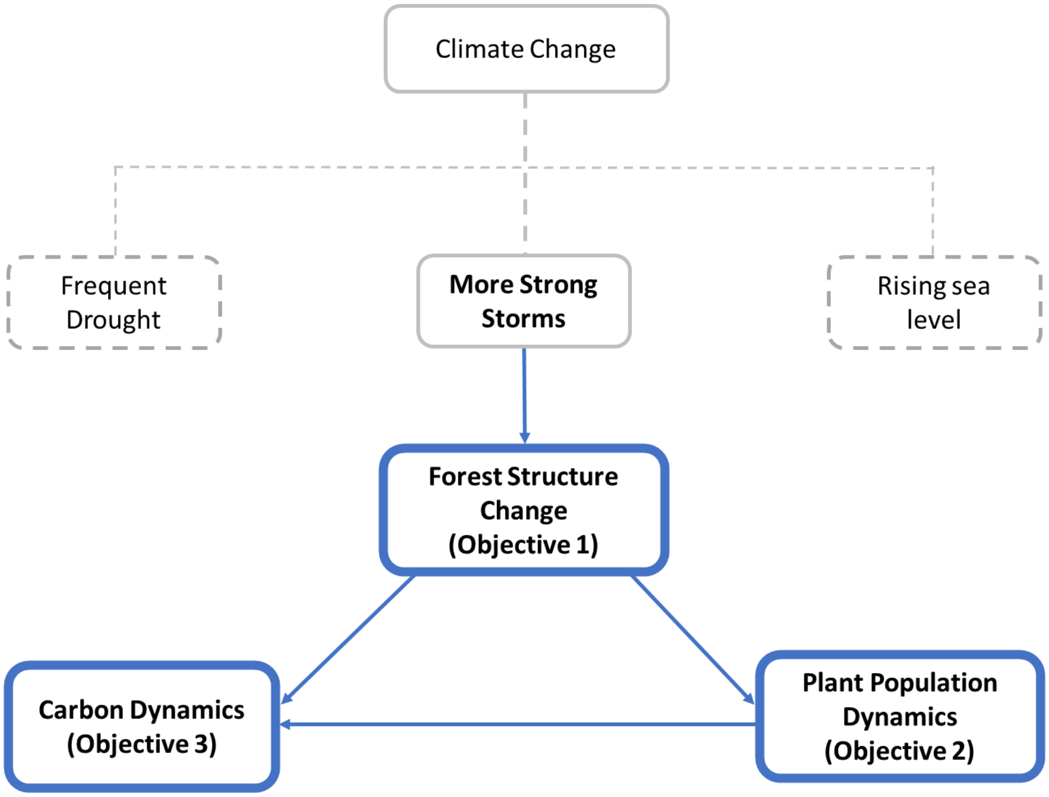

Figure 1.1. The conceptual framework of the dissertation. The top box is climate change, or global change. The next row of the boxes are manifestations of climate change (drought, stronger storms, sea level rise). I mainly focused on three areas of forest impacted by cyclonic storms: forest structure, plant population dynamics, and carbon storage. Stronger storms affect forest structure, which affects plants, and then affect carbon storage. The three objectives are respectively discussed in chapter 2, 3, and 4.

CHAPTER 2

FOREST CANOPY HEIGHT, RESISTANCE, AND RESILIENCE UNDER HURRICANE DISTURBANCES AT THREE ELEVATIONS

Abstract

The horizontal and vertical distribution of limbs and foliage in a forest, including the trees, shrubs, and ground cover, comprise three-dimensional forest structure. Hurricanes are among the factors influencing forest structure. My goal was to describe the effects of strong hurricanes on forest canopy height in forests at three elevations in the Luquillo Experimental Forest (LEF), Puerto Rico: Tabonuco forest at 350 m asl, Colorado forest at 750 m asl, and Dwarf forest at 1000 m asl. Using data collected over 31 years, during which there were three strong hurricanes, I describe changes in mean canopy height, canopy smoothness, and resistance and resilience of canopy height. The particular purpose of looking at the differences in resistance and resilience of these forests is to be able to predict which forests will be more affected than others by a change in the number of strong hurricanes. I hypothesize that forests will differ in resistance and/or resilience because of climate differences associated with the elevation gradient. For instance, Dwarf forest will be the least resilient because of climate differences such temperature, wind velocity, solar radiation, and cloud cover. To test the hypothesis, I sampled vertical forest structure using the "vegetation height profile" technique. I recorded the presence or absence of live vegetation in height intervals along an imaginary vertical line above 451 to 475 points in hectare-sized plot grids at 350 m asl (Tabonuco forest), 750 m asl (Colorado forest), and 1000 m asl (Dwarf forest). The hurricanes significantly changed canopy surface from a relatively smooth to a rough surface and decreased maximum canopy height in all plots. Tabonuco forest canopy height for instance was reduced 51% by Hurricane Hugo while Colorado was decreased by 25% and Dwarf forest by 62%. Thus, Dwarf forest was relatively less resistant to Hurricane Hugo. It was the least resilient before the passage of Hurricane Maria. Colorado Forest response was more similar to Tabonuco response than to Dwarf forest response. The frequency of strong hurricanes has increased (based on 300 years of records) in the past 30 years, and Hurricane Maria in 2017 was the strongest and had greater impacts on forests (evident in the Tabonuco forest) than did the previous hurricanes (the ones that have been studied), suggesting that stronger hurricanes and elevational differences in resistance and resilience will result in long-term, differential impacts on forests at different elevations in the Luquillo Experimental Forest. Dwarf forest may remain permanently shorter with lots of grasses and small woody plants.

Key words: Climate change, ecosystem change, elevation gradient, forest structure, hurricane, Luquillo Experimental Forest, Puerto Rico

2.1 INTRODUCTION

Forests are among the most diverse terrestrial ecosystems (Bisquit 2012), in part because they are strongly three-dimensional systems (Spies1998). Their structure refers to how the physical attributes of trees and other plants are distributed within a forest ecosystem. Its basic qualities are size, shape, and spatial distribution (vertical or horizontal) of components. Their three-dimensional structure plays major roles in ecosystem function and diversity (Spies 1998), and the three dimensions especially reflect the creation of, and regrowth in, tree and branch fall gaps. It has many components that are essential to the functioning and diversity of ecosystems: (a) tree size/age distribution, (b) vertical foliage distributions, (c) horizontal canopy distribution, and (d) dead wood (Spies 1998). Forest canopies for instance play an important role in intercepting radiation, controlling microclimates, and determining wildlife habitat, both vertically and horizontally. It affects animals and plants directly. For instance, the vertical disposition of flowers, fruits, and foliage is the vertical arrangement of food for some animals, as well as the arrangement of sites for nesting, rest, perching, basking, and mating (Bell 1991; Brokaw and Lent 1999).

Large-scale natural disturbances such as hurricanes, fires, insect outbreaks and others can cause long-term changes on forest structure and composition (Chazdon 2003, Weishampel et al. 2007). They dramatically change light, temperature, soil moisture, and available nutrients by killing nearby trees (Muscolo et al. 2014). Thus, they shape the forest structure (Spies 1998). In addition to these natural forces, forest structure is also controlled by forest management where the structure is manipulated to maximize timber outputs (Spies 1998). The created-gaps in the forest canopies by natural disturbances are ideal conditions for rapid plant reproduction and growth (Muscolo et al. 2014).

In the tropics, these large-scale disturbances, especially hurricanes, are recurrent and their distribution and frequency are likely to be altered by climate change (add citation). It is projected that, by the end of the century, maximum sustained hurricane wind speeds will increase by 6 to 15%, with an increase of 20% in precipitation within 100 km of the storm center because of the sea surface temperature rises in most regions of tropical-cyclone formation during the past decades in the North Atlantic basin (Knutson et al. 2010). As a result, forest structure in hurricane areas will be altered with a possibility of shorter forests with few or no emergent trees as opposed to non-hurricane prone areas (Fig. 2.1). In addition to canopy height, the canopy surface, which is the area of the forest that contributes to the exchange of water and carbon with the atmosphere through photosynthesis (Meyer et al. 2018), will also be altered. The alteration in size, shape, and disposition of this surface will affect, among other things, how the heat is distributed, how much turbulent mixing occurs, and how the illuminated foliage will be distributed (Geoffrey and Mary 2004). Since the canopy forest is important for the forest's hydrometeorological properties, and light absorption (Danson et al. 2006), its alteration will influence the microclimate by rising the temperature, modifying the humidity and the amount of light reaching the forest floor. Thus, variation in the microclimate will have direct and indirect effects on animals because many of them find refuge in canopy surface (horizontal and vertical layer) either for nesting, rest, perching, basking, and mating (Bell et al.1991, Brokaw and Lent 1999). The changes in the canopy surface indicate how the forest have developed.

This study focused on canopy height (mainly) and structure at three sites on the elevation gradient in the Luquillo Experimental Forest, I analyzed a thirty-year data set from before Hurricane Hugo (1989) to after Hurricane Maria (2019) to see how the hurricanes influenced forest structure over time. I addressed three questions: 1. How canopy height varies among the three forest plots before Hurricane Hugo, 2. How hurricanes have affected canopy height and smoothness over time in the plots, and 3. How canopy height resistance and resilience vary within and among the three plots from 1989 to 2019? I hypothesize that forests will differ in resistance and/or resilience because of climate differences associated with the elevation gradient. Climate on the elevation gradient will affect canopy height because of relative humidity, wind velocity, cloud cover, temperature, atmospheric saturation deficit, and solar radiation. In high elevation, it is foggy and cloudy and that reduce the amount of light received per unit area of ground (Fahey et al. 2015). The temperature is also lower because it decreases with elevation (Weaver 2012). It varies from about 24 to 27 °C in the lower part of the LEF to 17 to 20 °C at the top of the mountain (Brown et al.1983). Temperature, light, and humidity are important factors in the environment of plants because they participate in the photosynthetic process (Went 1953). Temperature alters the chemical process at high light intensities and a diffusion process at low light intensities when the photochemical process becomes limiting (Went 1953), which decreases the rate of photosynthesis per leaf area which results in less carbon fixation (Fahey et al. 2015). In order words, less carbon fixation, less evapotranspiration from leaves mean less nutrients to the leaves that lead to low plant growth overall. Differences in resistance and resilience may become apparent because the frequency of strong hurricanes has increased (based on 30 years of records, 1766-1989, Scatena and Larsen 1991, and every 39-44 years 1766-2017, Nicholas Brokaw personal communication) in the past 30 years, and Hurricane Maria in 2017 was the strongest and had greater impacts on forests (evident in the Tabonuco forest) than did the previous hurricanes, suggesting that stronger hurricanes and elevational differences in resistance and resilience will result in long-term, differential impacts on forests at different elevations in the Luquillo Experimental Forest. I will also use my data to see if they support the hypothesis of inverse relationship between resistance and resilience which suggests that relatively resistant systems are thought to be relatively not resilient while resilient systems are thought to be less resistant (Patrick et al. 2022).

I define resistance as the ability of a community to remain unchanged when challenged by disturbances (Derose and Long 2014), and I define resilience as the capacity of an ecosystem to return to the precondition state following a perturbation, including maintaining its essential characteristics taxonomic composition, structures, ecosystem functions, and process rates (Holling 1973). In other words, resilience is how much forest MCH grew back after a certain time, as a percentage of its original MCH, after enduring disturbances. The purpose of looking at the difference in resistance and resilience of these plots is to be able to predict which forests will be more affected than others by a change in the number of strong hurricanes, knowing that these forests are different because of climate differences associated with the elevation gradient (Weaver and Murphy 1990). For instance, the Dwarf forest may be less resilient but more resistant among the three plots because of the lower temperature and light to make photosynthesis.

2.2 METHODS

2.2.1 Study area

The study area was the Luquillo Mountains, at 18° N latitude and 66° W longitude in northeastern Puerto Rico. Most of the Luquillo Mountains are designated administratively as the Luquillo Experimental Forest, which covers an area of 11,310 ha (Weaver 2012). At only 8 km from the ocean, the mountains rise abruptly to 1075 m. Five subtropical life zones are represented: wet forest, rain forest, lower montane wet forest, lower montane rain forest, and a small tract of land in the southwest portion that falls within the moist forest live zone (U.S. Department of Agriculture 2012). At the Luquillo Experimental Forest a quarter of the land is between 120 and 300 m, about half from 300 to 600 m, another quarter between 600 to 900 m and 3 percent from 900 to 1075 m (Weaver 1983). Ascending the Luquillo Experimental Forest, the average tree height and DBH, number of tree species, and basal area per ha tend to decrease (Fig. 2.2 and 2.3), while stem density increases (White 1963). Temperature also varies from about 24 to 27 °C at the base of the LEF to 17 to 20 °C at the summits (Brown et al. 1983). May to December are usually the rainiest months and January to April are typically drier (Zimmerman et al. 2007). El Yunque experiences major hurricanes once every 50–60 years, on average (based on records 1769-1989, Scatena and Larsen 1991); nevertheless, just nine years separated two hurricanes: Hugo in 1989 (category 3, Saffir–Simpson hurricane scale) and Georges (category 2, Saffir–Simpson hurricane scale) and 1998 (Shiels et al. 2015), and the most recent severe hurricane passing over our site was Hurricane María (category 4, Saffir–Simpson hurricane scale) in September 2017 (Fig. 2.4).

Study sites

Three permanent plots were established in the LEF in 1989 (Fig. 2.5). Our first study site was in “Tabonuco” forest (named for the dominant “Tabonuco” tree [*Dacryodes excelsa* Vahl, Burseraceae]), qualified as *subtropical wet forest* in the Holdridge System (Ewel & Whitmore 1973). Our plot partly overlapped with the old-growth section of the Luquillo Forest Dynamics Plot (Thompson et al. 2002), near El Verde Field Station (EVFS; 18°20’ north, 65°49′ west), a principal research site of the Luquillo Long-Term Ecological Research Program (LTER). Our study plot was at 350 m asl. The terrain is steep (24% average slope) and rocky (25% of the soil surface covered by boulders [Soil Survey Staff 1995]). Soils at EVFS are mainly Zarzal clay series, which are deep Oxisols and Ultisols that originated from volcaniclastic parent material (Soil Survey Staff, 1995).

The second study site is in Colorado forest (named for the Colorado tree [*Cyrilla racemiflora*, Cyrillaceae]) and located at 750 m asl in the “Colorado forest”. Forest at this elevation is in the *lower montane wet* life zone (Ewel and Whitmore 1973). The mean annual rainfall averages from 2000-4000 mm yr^{-1}. The vegetation is characterized by open-crowned trees, many with dark, reddish-brown, coriaceous leaves, grouped toward the ends of branches (Weaver 1983). Our permanent plot in this study was located near the Tradewinds Trail, at 750 m elevation (Brokaw and Grear 1991). The soils, mainly clays or silty clay loams, are saturated most of the year (Weaver 1983).

The third study site is in Dwarf forest, in the *lower montane rain* life zone. Trees that commonly range from 1 to 6 meters (m) in height, are branchy and their trunks are seldom straight (Weaver 2010). The leaves are generally small, thick, and concentrated at the ends of branches. Roots are superficial; aerial roots are common, and grasses, sedges, and ferns occupy openings. The mean annual rainfall is over 4000 mm yr^{-1}. The Dwarf forest association is encountered on exposed peaks and summits. Our permanent plot was located near East Peak, at 980 to 1000 m elevation. The soil of Pico del Oeste appears to contain the necessary qualities for an oxic horizon, and it was classified as an Oxisol by the USDA in 1965 (Walter 1969).

Among my three working sites on the elevation gradient, ranging from 350 to 1000 m asl, the Dwarf forest is the plot where the trees are the shortest, the basal area is the lowest, while stem density is the highest (Fig. 2.2 and 2.3).

2.2.2 Experimental design

At each site I established one permanent plot, with grid points every 5 m. The Tabonuco forest was 1.08 ha (90 x 120 m), with 475 grid points; the other plots were each 1.0 ha (50 x 200 m), each with 451 grid points. I selected the Tabonuco plot at a site where there was already a 30 x 30 m grid and interpolated our 5 x 5 m grid within that other grid; as mentioned, it also includes a section of the LFDP. I selected our Colorado and Dwarf forest study sites in areas that were good representatives of those forest types (Peter Weaver, personal communication,). Each plot included variation in topography and exposure.

2.2.3 Plant measurements

Canopy structure: I sampled vertical forest structure using the "vegetation height profile" technique (Karr 1971; Brokaw and Grear 1991). The profile displays the percent cover of vegetation in different height intervals above ground. I recorded the presence or absence of live vegetation (leaves or wood, live trunks fallen or upright) along an imaginary vertical line above each point in the grids within the following height intervals: 0-0.5, 0.5-1, 1-1.5, 1.5-2, 2-2.5, 2.5-3, 3-4, 4-6, 6-8, 8-10, 10-12, 12-15, 15-20, 20-25, 25-30, and >30 m above-ground. Using a 2.5 cm diameter pole held vertically and marked at 0.5 m intervals to 3 m, I documented vegetation intercepts on the line. I estimated the height interval of intercepts above 3 m using a rangefinder. The pole was used to sight the imaginary vertical line as it extended higher into the forest. The percent vegetation cover for each height interval was computed as the number of intercepts documented for that height interval divided by the total number of grid points on the plot.

Due to the difficulty of determining the exact path of the imaginary vertical line above the grid points (especially where I moved to see around obscuring vegetation) I made repeated judgments to make sure I collected accurate data. To accommodate the increasing difficulty of judging the path of the line and the height interval of vegetation intercepts I used height intervals of gradually expanded breadth above the 3 m pole. The breadth of these higher intervals reduced uncertainty of judgments about presence or absence of vegetation along the imaginary line. So, I am assured that errors in judgment cancel out, eliminating bias, and that the data produce accurate comparisons of vegetation height distributions among the sites and at different points in time.

The first height measurements in the Tabonuco plot beginning were recorded on 30 May 1989, in Colorado forest on 12 June 1989, and in Dwarf forest on 5 September 1989. Subsequently, on 18 September 1989, Hurricane Hugo struck the LEF with wind speeds of 166 km/hr (Scatena and Larsen 1991). Post-Hurricane Hugo measurements in the Tabonuco forest were made on 24 October 1989, in Colorado forest on 15 February 1990, and in Dwarf forest on 27 November 1989. Additional sets of measurements were made in the three plots over the next 31 years, during which several hurricanes struck the LEF, including measurements before and after Hurricane Maria in 2017 (Table 2.1). Hurricane Maria had the most extreme effect on the forest of the several hurricanes (Uriarte et al. 2019). I used the same methods throughout the 31 years; N. Brokaw made most of the measurements in that period.

2.2.4 Data analysis

To describe how the forest structure changes through time and on the elevation gradient, I selected two reference points (strong hurricanes) within the 30-year study period: before and after Hurricane Hugo, and before and after Hurricane María. I used maximum canopy height (MCH) as an index of change. For the MCH, I took the average of the upper limit recorded above each point. I evaluated the effects of each hurricane by (1) comparing the MCH before and after Hugo to the MCH before and after Maria, and (2) plotting maximum canopy height against time for each plot. Then, I monitored changes in canopy smoothness over time by making triangulated irregular networks (TIN) for each plot. The triangular irregular network (TIN) model is an alternative to the grid-based model and geometric model as it shows the original shape of objects and predicts the values in an unsampled location (Liu and Wu 2019). I also used standard deviation of forest canopy height to show how the degree of variation in canopy surface (Lewontin 1966) changed through time. I compared the periods before and after the hurricanes within and between plots to see which hurricane had greater impact on the forest structure. I also calculated percent cover for the tree height interval (vegetation height profiles) before and after Hurricane Hugo, and Maria to evaluate changes in the maximum canopy height. I made Anova tests for each time period chosen to see if the changes were significant.

To evaluate forest resistance and resilience among the plots on the elevation gradient, I used the canopy height data from Hugo to Maria. The MCH was used as our index for measuring resistance and resilience. I qualified as resistant a plot that remained significantly unchanged in MCH, despite undergoing different natural disturbances, and as resilient the forest that was trimmed by hurricane Hugo but regained pre-hurricane MCH before Hurricane Georges, and then trimmed by Georges and regained MCH before Maria. In other words, resistance is how much the forest MCH changed as a percentage of its pre-disturbance MCH and resilience is how much forest MCH grew back, as a percentage of its original MCH, after enduring disturbances. For example, the canopy was 21.09 m high before Hugo and 9.3 m after Hugo. So, I divide 9.3 by 21.09, the forest was then 44% resistant to Hurricane Hugo. To calculate resilience, I divided the MCH obtained for a period of 5 to 30 years after a disturbance by the MCH height before the disturbance. For instance, in 2013, the Tabonuco plot canopy reached 19.1 m MCH, the forest was then 90% resilient by that time, (19.1/21.09). I calculated resistance and resilience in a similar way for this 31-year period, then, I compared the results across our sites using ANOVA.

2.3 RESULTS

2.3.1 Forest height and profile

In 1989 before the passage of Hurricane Hugo, the Luquillo Experimental Forest had had a long recovery time, after being hit 61 years before by one of the strongest hurricanes, San Felipe II, in 1928 (a category 5 hurricane on the Saffir-Simpson scale, Boose 2004). In 1989 vegetation profiles in the Tabonuco, Colorado, and Dwarf forest showed that the MCH (height interval with highest percent coverage) was respectively 12 - 20 m, 4 - 8 m, and 3 - 6 m (Fig. 2.6), Hurricane Hugo in 1989 lowered by 50% the main upper canopy which means the upper height intervals where cover had been the highest in all three plots. For instance, in the Tabonuco forest, before the hurricane, the dominant height tree classes, representing 60 to 80 percent cover were from 12 to 20 m (Fig. 2.7A). Many trees in these classes were snapped down, uprooted and or defoliated during the hurricane to represent just 15 to 25 percent cover after the hurricane (Fig. 2.7B). Then, 28 years later, Hurricane Maria struck the Tabonuco recovered forest in which the dominant height tree classes remained the same since Hugo, 12 – 20 m (Fig. 2.7C), nevertheless the percent cover was highly decreased, 38 – 60 % (Fig. 2.7D) in comparison to the situation before Hugo. Both hurricanes, Hugo and Maria, substantially reduced the forest canopy height. The mean maximum canopy height was 21.09 m before Hurricane Hugo and 19.1 m before Maria; they went down to 9.1 m and 7.4 m respectively after Hurricanes Hugo and María (Fig. 2.8A).

In Colorado forest, the dominant height tree classes were 4 – 8 m before Hurricane Hugo (Fig. 2.10A). These height classes represented 55 – 70% cover and dropped to 20 – 30 % after the hurricane (Fig. 2.10B). The dominant height tree classes were still the same at the time that Hurricane Maria struck the forest, but the percent cover was 35 – 50 %. However, after the hurricane the dominant height tree classes dropped to 0.5 – 1.5 m and had a percent cover of about 35 (Fig. 2.10C and 2.10D). The maximum canopy height was 10.01 m before Hurricane Hugo (Fig. 8B). When the hurricane passed over, the forest canopy height dropped to 7.59 m. In 2017, Hurricane Maria lowered the recovery forests and the maximum canopy height registered was 5.44 m (Fig.2.8B).

The same observations were made in the Dwarf forest. The dominant height tree classes were 3 – 6 m before Hurricane Hugo (Fig. 2.12A). These height classes represented 35 – 50% cover and dropped to 15 – 20% after the hurricane (Fig. 2.12B). The dominant height tree classes did not change before Hurricane Maria, 3 – 6 m but the percent cover was diminished, 10 – 20 percent. Hurricane Maria lowered the dominant height tree classes to 0.5 – 3 m for a percent cover of about 25 – 50 percent (Fig. 2.12C and 2.12D). Both hurricanes, Hugo and Maria, lowered the maximum canopy height. For instance, the forest height was 7.59 m before Hugo and dropped to 2.44 m in 1989. In 2017, Hurricane Maria lowered the recovery forests and the maximum canopy height dropped from 2.67 m to 2.47 m (Fig. 2.8C).

2.3.2 Forest canopy surface

Besides the forest height reduction in all three plots, hurricanes also changed the canopy surface. In the Tabonuco forest, before Hurricane Hugo and then again, before Hurricane Maria, the canopy surface was relatively smooth, the tallest trees were approximately the same height. The canopy was dense and there were few small woody plants, and grasses in the understory

(Fig. 2.9A and 2.9C). The hurricanes changed the canopy surface and consequently increased the forest canopy roughness (Fig. 2.9B and 2.9D). The coefficient of variation of canopy surface height changed from 25% before Hurricane Hugo to 87% after the hurricane. In Colorado forest, compared to Tabonuco, the canopy surface was more open before Hurricane Hugo and Hurricane maria, and presence of understory vegetation, and shrubs was more apparent (Fig. 2.11A and 2.11C). The coefficient of variation before Hurricane Hugo was 38% and changed to 76% after the Hurricane. However, the hurricanes disrupted the canopy surface and subsequently increased more than before the forest canopy roughness (Fig. 2.11B and 2.11D). In the Dwarf forest, compared to Tabonuco and Colorado, canopy surface was less dense before Hurricane Hugo and Hurricane Maria, and presence of grasses, small woody plants and shrubs was more apparent (Fig. 2.13A and 2.13C). The hurricanes hardly hit the canopy surface and increased the forest canopy roughness (Fig. 2.13B and 2.13D). The coefficient of variation was 47% before hurricane Hugo and changed to 98% after the hurricane

Overall, the changes registered in the forest profiles indicate that Tabonuco forest was more affected by the hurricanes. The average maximum canopy height dropped more than 50% after being hit by Hurricanes Hugo and Maria. As a result, the canopy surface underwent more changes than the other plots. It became extremely rough, based on the coefficient of variation mentioned earlier in the above paragraph and the standard deviation of the MCH of the plots. The hurricanes harshly decreased the mean canopy height whereas greatly increased its coefficient of variation (CV). Colorado and Dwarf forest followed the same trend with the Tabonuco where canopy height decreased, and CV increased (Fig. 2.14). However, the canopy surface of the Dwarf forest was less varied among the 3 plots from Hurricane Hugo to Hurricane

Maria when compared with the standard deviation of the three plots from before Hurricane Hugo to after Hurricane Maria (2.15).

2.3.3 Resistance and resilience

Hurricane Hugo and Hurricane Maria did not affect all the three elevation gradient plots in the same way. Some plots were more resistant to Hugo and others were more resistant to Maria. The Tabonuco forest for instance was significantly more resistant to Hugo, 44% (9.3/21.09), than to Maria, 39% (7.43/19.01; *P*=0.001, Fig. 2.16A). However, it showed great resilience. Nine years later after Hurricane Hugo, our results showed 72% recovery of mean canopy height and 91% recovery in 2013, 24 years later.

Colorado forest showed high resistance to both Hurricane Hugo and Hurricane Maria. But it was significantly more resistant to Hugo, (75%, 7.59/10.1) than to Maria, (53%, 7.44/10.27; *P*=0.001, Fig. 2.16B). It also showed a high level of resilience. In 1998, nine years after Hugo, the forest had recovered at 58% and 66% in 2011, 22 years after Hurricane Hugo.

In contrast to the Colorado forest, Dwarf forest was very low in resistance to Hugo. It showed just 38% resistance (2.44/5.56). However, it was significantly more resistant to Hurricane Maria than to Hugo, (92%, 2.47/2.67; *P*=0.001, Fig. 2.16C). As for resilience, Dwarf forest recovered by 57% in 1994, 5 years after Hugo and 48% in 2014, 25 years later.

To summarize, the Tabonuco and Dwarf forest were the plots that underwent the greatest disturbance from Hurricane Hugo among the three elevation gradients. However, Tabonuco forest seems to be more resilient. The forest recovered at 91 percent in 2013, 24 years after Hurricane Hugo despite suffering a greater level of damage. The Dwarf forest was the least resistant to Hugo, but the most resistant to Hurricane Maria. Dwarf forest seems to be the least resilient. 25 years after Hurricane Hugo, measured in 2014, it showed only 48 percent of recovery. The Tabonuco forest canopy surface seems to undergo more changes within this 31-year study (Fig.2.16).

2.4 DISCUSSION

2.4.1 Forest canopy height

The forest profiles indicated major changes that happened in the forest after Hurricane Hugo and Hurricane Maria. Hurricane Hugo opened the forest by uprooting or snapping the big trees facilitating the uprising of pioneer species. The results indicated that Tabonuco forest was more affected by Hugo compared to Colorado and Dwarf forest. This might be explained by the height of the trees in the Tabonuco forest. Based on our data the average maximum canopy height was 21 m before the hurricane while it was 10.1 m for Colorado and 8 m for Dwarf forest. Big trees are more vulnerable to wind damage because they offer larger areas of resistance. In Puerto Rico, Wadsworth and Englerth (1959) have observed an increased risk for wind damage to larger trees. Many other studies have found a positive correlation between stem size and catastrophic wind damage (Everham and Brokaw 1996). In addition, the big trees cause more damage when they fall.

Tabonuco forest seemed to be more affected by Hurricane Hugo, but in the Colorado and Dwarf forest plots the lowest height interval after the hurricane seemed to be slightly greater than in Tabonuco forest and even greater before the hurricane. This apparent increase might be due to the initial situation of these plots before the hurricane. They were more open than the Tabonuco plot. Another reason might be trees that have fallen but did not die and occasionally resprouting as well as growth of newly establishing plants (Brokaw and Grear 1991). Another possible reason that could explain the difference in the lowest class height is the time of the measurement after the hurricane. Colorado and Dwarf forest were respectively measured 9 and 20 weeks after the hurricane while it was just 5 weeks for Tabonuco forest (Brokaw and Grear 1991). I made the same observation for our three plots after Hurricane Maria. Tabonuco was also the most affected plot probably because the tree height before the hurricane was 19 m on average. However, Colorado and Dwarf forest lowest class height was higher after the hurricane. The time of measurement can be one of the main factors explaining the difference. A second factor might be the tree height before the hurricane. The forest was more open in Dwarf and Colorado forest before the hurricanes which increased more light availability on the ground. The results for the lowest height interval were similar to what was found by Brokaw and Grear (1991) who did previous work in these plots.

2.4.2 Canopy surface change

The hurricanes disturbed the canopy surface and created gaps in the forest vertical structure. In the Tabonuco plot, the canopy was relatively smooth before the passage of the Hurricanes Hugo and Maria. The upper canopy trees were approximately the same height. It was denser and smoother before Hurricane Hugo than before Hurricane Maria. One possible reason is that the LEF was a late second-growth forest before the passage of Hurricane Hugo, the trees were approximately even-aged that were recovered from the severe hurricane of 1932 or after human disturbance (Brokaw et al. 2004). It was a period of approximately 60 years without any major hurricanes. However, before Maria, the LEF was still a second-growth forest which was recovering from Hurricanes Hugo and Georges that struck the forest respectively 28 and 19 years before our measurements. Thus, the forest had less recovery time before Hurricane Maria and did not become as smooth as it had become before Hurricane Hugo. Another possibility is that the forest is not second growth (in the sense of a forest that has grown up from an area where forest has been removed) but is merely recovering from trimming by hurricane winds, which might also produce a smooth canopy.

Hurricane Maria had a greater effect on the canopy surface in the Tabonuco forest despite the forest being on average 2 m shorter, but Hurricane Maria was stronger than Hurricane Hugo. More gaps were created, as it is apparent in the post-hurricanes 3-D graphs (Fig. 2.9). In the Colorado forest, Hurricane Maria lowered the canopy surface by 47% while Hurricane Hugo lowered it by 25%. Thus, Hurricane Maria had greater impact on the Colorado Forest than Hurricane Hugo. In the Dwarf forest plot, in contrast to Colorado, Hurricane Hugo lowered the canopy surface by 62% while Hurricane Maria lowered it by only 8%. Thus, Hurricane Hugo had a greater impact on Dwarf forest canopy surface than did Hurricane Maria.

The canopy smoothness either before Hurricanes Hugo or Maria was expected because forest stands experiencing so many disturbances may be unable to develop large crowns with big and old trees to begin dying, thus creating a rough canopy (Dahir and Lorimer 1996). In Barro

Colorado Island in Panama for instance, most of the canopy gaps are created by background tree mortality which causes instantaneous mortality to younger ones in the stand. The largest gap encountered in the Tabonuco forest at El Verde before hurricane Hugo was 117 m^2 while in Barro Colorado Island (BCI) in Panama was 452 m^2 (Brokaw et al. 2004).

2.4.3 Forest resistance and resilience

Tabonuco was significantly less resistant to Hurricane Hugo than Maria when I compared the mean canopy height before and after the hurricanes. I expected that Hurricane Hugo would have had a greater effect on Tabonuco because the Luquillo Experimental Forest spent approximately 60 years without being hit by big hurricanes before Hugo. The forest was taller and denser and could consequently undergo greater damage. It is believed that taller and bigger trees tend to experience more damage to hurricanes because they offer with their branches greater surface of resistance and as a result destroy more. However, Hurricane Maria was a stronger hurricane (category 4) and found a forest of 91% of recovery from Hurricane Hugo. It lowered the mean maximum canopy height from 19.1 m to 7.4 m, more than before. It was 9.1 m after Hugo.

Colorado forest experienced the same pattern as the Tabonuco forest. Perhaps for the same reason mentioned previously. However, in Dwarf forest, Hurricane Hugo lowered the mean maximum canopy height more than did Hurricane Maria. It was the least resistant to Hurricane Hugo among the three plots, 38 percent resistant, but the most resistant to Hurricane Maria 92%. This greater resistance as shown in our results may be due to the time that I collected the data, almost four years after Maria (see table 1). The forest had more time to recover compared to the

Tabonuco. Another reason that makes Dwarf forests look more resistant is the height of the trees. The mean maximum canopy height was 5.56 m and 2.67 m respectively before hurricane Hugo and Hurricane Maria. Its low resilience after the passage of hurricane Hugo helped it to be less affected by Hurricane Maria. That is also the reason explaining the lowest height class to be slightly greater than in the other plots.

Among the three plots at different elevations, Tabonuco forest seems to be the most resilient while Dwarf forest seems to be the most resistant (as already explained why earlier). Tabonuco forest takes less time to recover after the hurricanes. Walker (1991) observed that leaves had regrown on some affected trees in 2 weeks and on most by 7 weeks; one year and 2 weeks later, all trees had leaves and just 7 percent were leafless. Elevation might be the possible explanation for the forest's recovery. It plays a fundamental role in plant growth because of the environmental conditions such as temperature, light, and humidity. They participate in the photosynthetic process (Went 1953). As mentioned from the beginning, temperature alters the chemical process at high light intensities and a diffusion process at low light intensities when the photochemical process becomes limiting (Went 1953). Thus, in Dwarf forest, the low temperature causes the forest to be less resilient (46%), the pants grow slowly, but more resistant (92%) compared to the other plots. Tabonuco for instance showed low resistance (31%) but high resilience (91%). It always grows back fast after being struck by hurricanes. This might be the reason why it is less resistant. Therefore, my data support the idea of the inverse relationship hypothesis which suggests that relatively resistant systems are thought to be relatively not resilient while resilient systems are thought to be less resistant.

2.5 CONCLUSION

Climate change is likely to affect a range of ecosystem processes related to forest growth, and potentially resistance and recovery from major disturbances. With the rising temperatures, rising atmospheric carbon dioxide, increased precipitation variability, more hurricanes and other disturbances are projected to happen by the middle of the century in tropical regions. In Puerto Rico, forests are subjected to hurricane disturbances because of the island's geographical position in the Atlantic Ocean. Our 31-year data set shows substantial effects of hurricanes on forest structure of the LEF, mainly reduction in the canopy height, and canopy surface damage which would have boosted light and temperature on the forest floor (Fernández and Fetcher 1991).

Despite the significant changes of disturbance on the forest, this 31-year study period has shown how resistant and resilient LEF forests are. After each hurricane, the canopy surface underwent modification consequently the forest became shorter, but years after, our measurements indicate that the forest nearly reached the stage before being struck by Hurricane Hugo in terms of percent cover and canopy height.

However, in the LEF, all the plots did not respond the same way. The Dwarf forest for instance shows great resistance capacity but very low in resilience. This suggests that stronger hurricanes couple with elevational differences in resistance and resilience will result in long-term, differential impacts on forests at different elevations in the Luquillo Experimental Forest. Among the differential impacts, the Dwarf forest may remain permanently shorter with lots of grasses and small woody plants. Hurricane Hugo opened the forest by uprooting or snapping the big trees facilitating the uprising of pioneer species.

In this chapter, I have shown how hurricanes change canopy height and cover. How does change in canopy affect plants? In the next chapter, I will show how post-hurricane changes in canopy are correlated with the population dynamics of two indicator pioneer species in the LEF.

2.6 LITERATURE CITED

Bell, S.S, E.D. McCoy, and H.R. Mushinsky. 1991. *Habitat structure: the physical arrangement of objects in space*. London: Chapman and Hall.

Bisquit, A.L., Boris Patentreger, and D. Tarrier. 2012. Textes pour Web Envol Vert. *Envol Vert*, September 1, 2012. http://envol-vert.org/wp-content/uploads/2012/08/Publication-n%C2%B01_Services-rendus-par-les-for%C3%AAts.pdf.

Boose, E.R., M.I. Serrano, and D.R. Foster. 2004. Landscape and regional impacts of hurricanes in Puerto Rico. Ecol. Monogr. 74, 335–352.

Boucher, D.H. 1989. Growing back after hurricanes: catastrophes may be critical to rain forest dynamics. *Biol. Digest* 16:11-18.

Brokaw, N.V.L., S. Fraver, J.S. Grear, J. Thompson, J.K. Zimmerman, R.B. Waide, E.M. Everham III, S.P. Hubbell, and R.B. Foster. 2004. Disturbance and canopy structure in two tropical forests. In *tropical forest diversity and dynamism*, edited by Elizabeth C. Losos; and Egbert G. Leigh Jr, 177–95. Chicago and London: The University of Chicago Press.

Brokaw, N.VL., and R.A. Lent. 1999. “Vertical structure.” In *Maintaining biodiversity in forest ecosystems*, 372-399. N.p.: Cambridge University Press.

Brokaw, N.V.L., 1998. Cecropia Schreberiana in the Luquillo Mountains of Puerto Rico. *The Botanical Review* 64: 91–120.

Brokaw, N.V.L., and J.S. Grear. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains. *Source: Biotropica* 23(4), 386-392. https://doi.org/10.2307/2388256.

Brown, S.; A.E. Lugo, S. Silander, L.H. Liegel. 1983. Research history and opportunities in the Luquillo Experimental Forest. Gen. Tech. Rep. SO-44. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 128 p.

Canham, C.D., J. Thompson, J. K. Zimmerman, And, and M. Uriarte. 2010. Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica* 42:87-94.

Chazdon, R.L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6 (1-2): 0-71. https://doi.org/10.1078/1433-8319-00042.

Chazdon, R.L. and N. Fetcher. 1984. Photosynthetic light environments in a lowland rain forest in Costa Rica. Journal of Ecology 72: 553-564.

Crausbay, S.D., and P.H. Martin. 2016. Natural disturbance, vegetation patterns and ecological dynamics in tropical montane forests. *Journal of Tropical Ecology* 32 (5): 384-403. https://doi.org/10.1017/S0266467416000328

Cremer, K.W., B. J. Myers, F. Van der Duys and I. E. Craig. 1977. Silvicultural lessons from the 1974 windthrow in radiata pine plantations near Canberra. *Austral. Forest.* 40: 274-29.

Dahir, S., and C.G. Lorimer. 1996. Variation in canopy gap formation among developmental stages of northern hardwood forests. *Canadian Journal of Forest Research* 26: 1875-92.

Danson, M., D. Hetherington, and F. Morsdorf, B. Koetz, B. Allgöwer, T. Koukal, W. Schneider (2006). Three-dimensional forest canopy structure from terrestrial laser scanning. *Forestry*, 61-65. doi:10.5167/uzh-77859

Derose, Robert J.; Long, James N. (2014). *Resistance and Resilience: A Conceptual Framework for Silviculture. Forest Science, 60(6), 1205–1212.* doi:10.5849/forsci.13-507

Denslow, S.J. 2013. Gap Partitioning among Tropical Rainforest Trees. *Biotropica* 12(2), 47-55.

Dossa, Gbadamassi G. O.; E. Paudel, J. Fujinuma, H. Yu, W. Chutipong, Y. Zhang, S. Paz, R.D. Harrison, N.G. Swenson. 2013. *Factors determining forest diversity and biomass on a Tropical Volcano, Mt. Rinjani, Lombok, Indonesia. PLoS ONE, 8(7), e67720-.* doi:10.1371/journal.pone.0067720

Everhan, E. M. III, and Brokaw, N.V. L. 1996. Forest damage and recovery from catastrophic wind. *The Botanical Review* 62(2):113-85.

Ewel, J.J., J.L. Whitmore. 1973. Ecological life zones of Puerto Rico and US Virgin Islands. United States Forest Service Research Paper. ITF-18. Institute of Tropical Forestry, Rio Piedras, Puerto Rico.

Fahey, T. J., R.E. Sherman, E.V.J. Tanner. 2015. Tropical montane cloud forest: environmental drivers of vegetation structure and ecosystem function. Journal of Tropical Ecology, 32(05), 355–367. doi:10.1017/s0266467415000176

Fernández D.S. and N. Fetcher. 1991. Changes in light availability following Hurricane Hugo in a Subtropical Montane Forest in Puerto Rico. *Biotropica* 23(4a):393 399

Geoffrey, G.P., M.E. Russ. 2004. The canopy surface and stand development: assessing forest canopy structure and complexity with near-surface altimetry. *Forest Ecology and Management* 189(1-3), 0-315. doi:10.1016/j.foreco.2003.09.001

Hogan, J.A., J.K. Zimmerman, J. Thompson, C.J. Nytch, and M. Uriarte. 2016. The interaction of land use legacies and hurricane disturbance in subtropical wet forest : twenty-one years of change. *Ecosphere*, 7(8):e01405. Doi:10.1002/ecs2.1405.

Holling, C.S. 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.*, 4:1-23.

Knutson, T.R., J.L. Mcbride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J.P. Kossin, A.K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. *Nature Geoscience,* 3(3), 157-163. https://doi.org/10.1038/ngeo779.

Lewontin, R.C. 1966. *On the Measurement of Relative Variability. Systematic Biology, 15(2), 141-142.* doi:10.2307/sysbio/15.2.141

Liu, H., W. Changshan. 2019. Developing a scene-based Triangulated Irregular Network (TIN) technique for individual tree crown reconstruction with LiDAR data. *Forests,* 11(1), 28-. doi:10.3390/f11010028

Lugo, A.E., and F.N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica 28:585-589*.

Lugo, A.E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecol.* 33, 368-39.

María, U., J. Thompsonn and J.K. Zimmerman. 2019. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. *Nature Communications* 10:1362.

Meléndez-Ackerman, E., C. Calisto-Perez, M. Morales-Vargas, and J. Fumero-Caban. 2003. Post-Hurricane recovery of a herbaceous understorey plant in a tropical rain forest in Puerto Rico. Journal of Topical Ecology, 19(6), 677–84. https://doi.org/10.1017/S0266467403006072.

Meyer, V., S. Saatchi, D.B. Clark, M. Keller, G. Vincent, A. Ferraz, F. Espírito-Santo, V.N. Marcus d'Oliveira, D. Kaki, J. Chave. 2018. Canopy area of large trees explains aboveground biomass variations across neotropical forest landscapes. *Biogeosciences, 15(11), 3377-3390.* doi:10.5194/bg-15-3377-2018

Muscolo, A., S. Bagnato, M. Sidari, and R. Mercurio. 2014. A review of the roles of forest canopy gaps. *Journal of Forestry Research* 25(4), 725-736. https://doi.org/10.1007/s11676-014-0521-7

Nelson, B.W., V. Kapos, J.B. Adams, W.J. Oliveira, O.P.G. Braun, and I.L. do Amaral. 1994. Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology 75: 853-858.*

Odum, H.T. 1970. Rainforest structure and mineral cycling homeostasis. pages H3-H52 in Odum, H. T., and R. F. Pigeon (eds.) *A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. U.S. Atomic Energy Commission*, N.T.I.S., Springfield, Virginia.

Pascarella, J.B., T.M. Aide, and J.K. Zimmerman. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico , USA 199: 379-93. https://doi.org/10.1016/j.foreco.2004.05.041

Patrick, J.C., K.S. John, M.H. William, B. Benjamin, L. David, L. Miguel, H. Enie, H.J.S. Marc, S.A. Bradley, A.T. Mitchell, A. Anna, M. Campos-Cerqueira, C.M. Victoria, C.A. Todd, D.J. Donna, D. Sarah, E.E. Brad, A.F. Rusty, G.J. Simon, H.S. Nathan, H.K. Amber, H.R. Michael, H.J. Aaron, H.J. Derek, K. Sean, K.J. Jeremy, L. Teng-Chiu, L. Kaijun, M.J. Christopher, M.A. Paul, O'C.S. Christine, P.C. Edward, R.K. Brandi, R.W Joseph, R.L. Kelly, R.A. Scott, O.S. Rolando, S. Astrid, S.L. Delbert, S.S. Rachel, S. Gregory, S.A. Beth, W.M. Lily, W.A. Carolyn, W.S. Michael, W.R. Elizabeth, W.S. Sara, X. Jianhong, Z. Xiaoming. 2022. A general pattern of trade-offs between ecosystem resistance and resilience to tropical cyclones. *Science Advances* 8, eabl9155.

Sánchez, O.S., and G.A. Islebe. 1999. Hurricane Gilbert and structural changes in a tropical forest in South-Eastern Mexico. *Global Ecology and Biogeography*. 8, 29-38.

Scatena, F.N., M.C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica* 23, 317-323.

Shiels, A.B., G. González, D.J. Lodge, M.R. Willing, and J.K. Zimmerman. 2015. 2015. Cascading effects of canopy opening and debris deposition from a large-scale hurricane experiment in a tropical rain forest. *BioScience 65: 871-81*.

Shiels, Aaron B, Jess K Zimmerman, Diana C Garcia-Montiel, Inge Jonckheere, Jennifer Holm, David Horton, and Nicholas Brokaw. 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *Journal of Ecology*, 98(3), 659-673. doi:10.1111/j.1365-2745.2010.01646.x

Soil Survey Staff. 1995. Order 1 Soil Surveys of Luquillo Long-Term Ecological Research Grid, Puerto Rico. United States Department of Agriculture, Natural Resource Conservation Service.

Spies, T.A. 1998. Forest Structure: A Key to the ecosystem. *Northwest Science* 72(2), 34-39.

Thompson, J., N.V.L. Brokaw, J.K. Zimmerman, R.B. Waide, E.M. III Everham, D.J. Lodge, C.M. Taylor, D. García-Montiel, and M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. Ecological Applications: 12(5): 1344-1363.

Uriarte, M., J. Thompson, and J.K. Zimmerman. 2019. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. *Nature Communications*, 10(1), 1362-. https://doi.org/10.1038/s41467-019-09319-2

Uriarte, M., C.D. Canham, J. Thompson, J.K. Zimmerman, and N.V.L Brokaw. 2005. Seedling recruitment in a hurricane-driven tropical forest : light limitation , density-dependence and the spatial distribution of parent trees. *Journal of Ecology 93, 291–304.* https://doi.org/10.1111/j.1365-2745.2005.00984.x.

U.S. Department of Agriculture. 2012. *Luquillo Experimental Forest: research history and opportunities*. Edited by Tamara Heartsill Scalley Nancy L. Harris, Ariel E. Lugo, Sandra Brown.

Wadsworth, F.H. and G.H. Englerth. 1959. Effects of the 1956 Hurricane on Forests in Puerto Rico. *Carib. Forester* 20, 38–51.

Walker, L.R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23(4), 379-385.

Walter, L.H. 1969. The ecology of an elfin forest in Puerto Rico, 7. Soil, root, and earthworm relationships. *Journal of the Arnold Arboretum* 50:210-224.

Weaver, P.L. 2012. *The Luquillo Mountains: forest resources and their history*. Jardin Botanico Sur, 1201 Calle Ceiba, San Juan, PR 00926-1119.

Weaver, P.L. 2010. Tree species distribution and forest structure along environmental gradients in the Dwarf forest of the Luquillo Mountains of Puerto Rico. *Bois et Forets des Tropiques* 306: 33-44.

Weaver, P.L., and P.G. Murphy. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* 22(1), 69-82.

Weaver, P.L. 1983. Tree growth and stand changes in the subtropical life zones of the Luquillo Mountains of Puerto Rico. *Institute of Tropical Forestry* 190: 14-16

Weishampel, J.F., J.B. Drake, A. Cooper, J.B. Blair, and M. Hofton. 2007. Forest canopy recovery from the 1938 hurricane and subsequent salvage damage measured with Airborne LIDAR. *Remote sensing of environment* 109, 142-1.

Went, F.W. 1953. *The Effect of Temperature on Plant Growth. Annual Review of Plant Physiology, 4(1), 347–362.* doi:10.1146/annurev.pp.04.060153.002023

White, H.H. 1963. Variation of stand structure correlated with altitude in the Luquillo Mountains. *Carib. J. For.* 1: 46-52.

Whitmore, T.C. 1974. Change with time and the role of cyclones in tropical rain forests on Kolombangara, Solomon Islands. *Journal of Ecology* 63 (2): 723-24.

Zimmerman, J.K., E.M. Everham III, R.B. Waide, D.J. Lodge, C.M. Taylor and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology*, 82: 911-92.

Zimmerman, J.K., S.J Wright, O. Calderon, M.A. Pagan, and S. Paton. 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance. *Journal of Tropical Ecology* 23, 231-251.

Zimmerman, J.K., J.A. Hogan, C.J.N. Nytch, and J.E. Bithorn. 2018. Effects of hurricanes and climate oscillations on annual variation in reproduction in wet forest, Puerto Rico. *Ecology*, 99 (6): 1402-1410. https://doi.org/10.1002/ecy.2236.

Table 2.1. Canopy measurement for the three forest plots in the Luquillo Experimental Forest. Some data sets are incomplete, I did not use them. The blank spaces are also for the period that data was not collected for such a plot. The table shows only the data I used.

Plot	**Tabonuco 350 m asl**	**Colorado 750 m asl**	**Dwarf 1000 m asl**
Measurement dates	1989 pre-Hugo	1989 pre-Hugo	1989 pre-Hugo
	1989 post-Hugo	1990 post-Hugo	1989 post-Hugo
	1991	1991	1991
	1993	1993	1993
	1994	1994	1994
	1997	…	…
	1998 post-Georges	1998 pre-Georges	…
	2000	…	…
	2008	2011	2009
	2013-2014 Pre-H. Maria	2014-2015 Pre-H. Maria	2014-2015 Pre-H. Maria
	2017-2018/ Post-María	…	…
	2019	…	…
	…	2020 Post-H. Maria	2020 post-H. Maria
Measurement sets	**12**	**9**	**8**

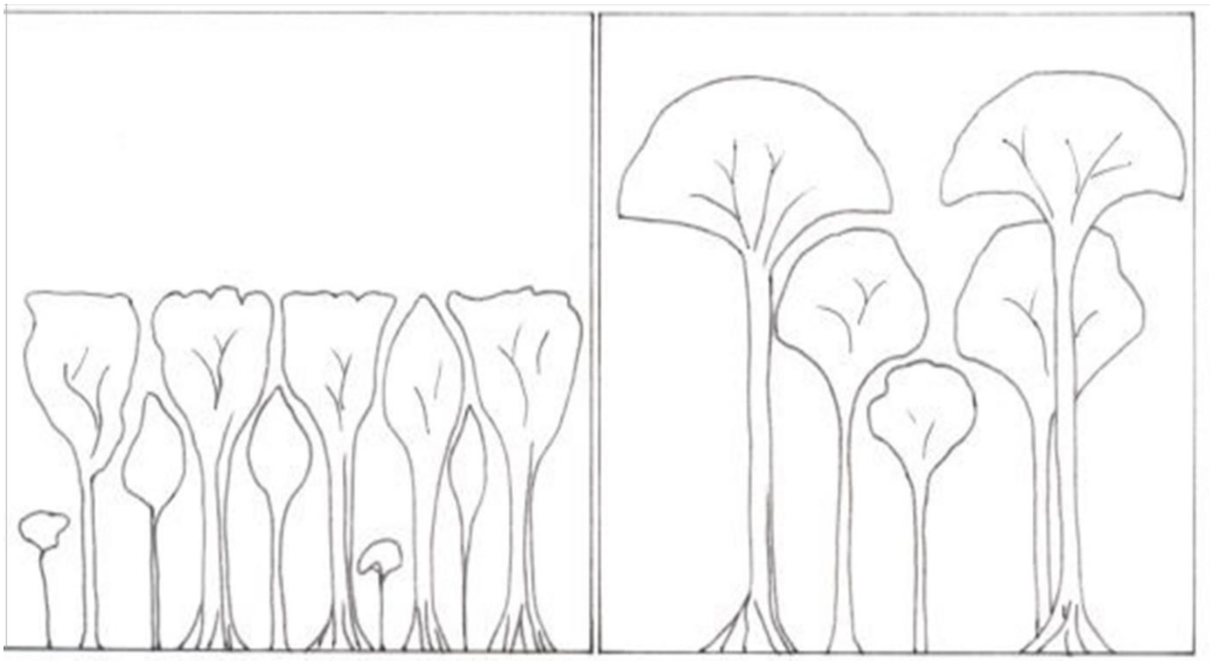

Figure 2.1. Profiles of an idealized "hurricane forest" (on the left) and an idealized "non-hurricane forest" (on the right), Odum, H. T. 1970.

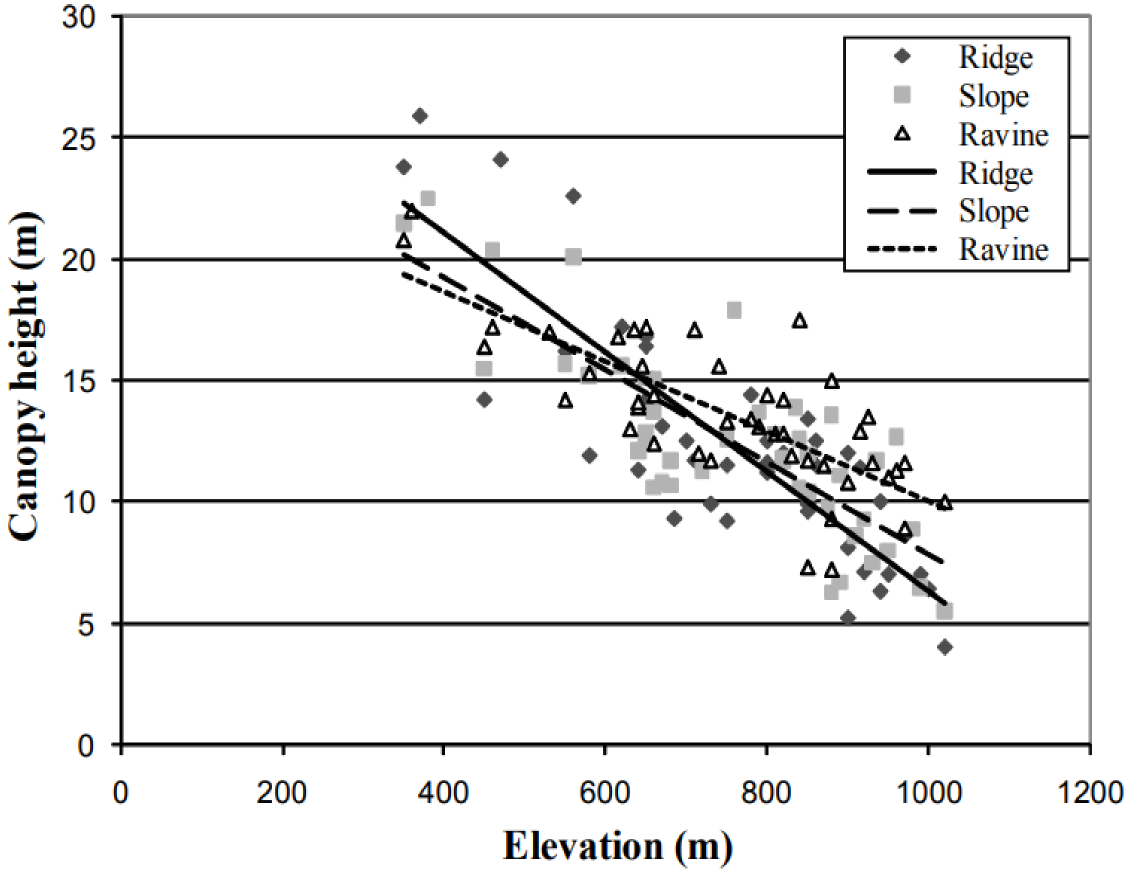

Figure 2.2. Mean canopy heights per plot by elevation in the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine; Weaver 2012).

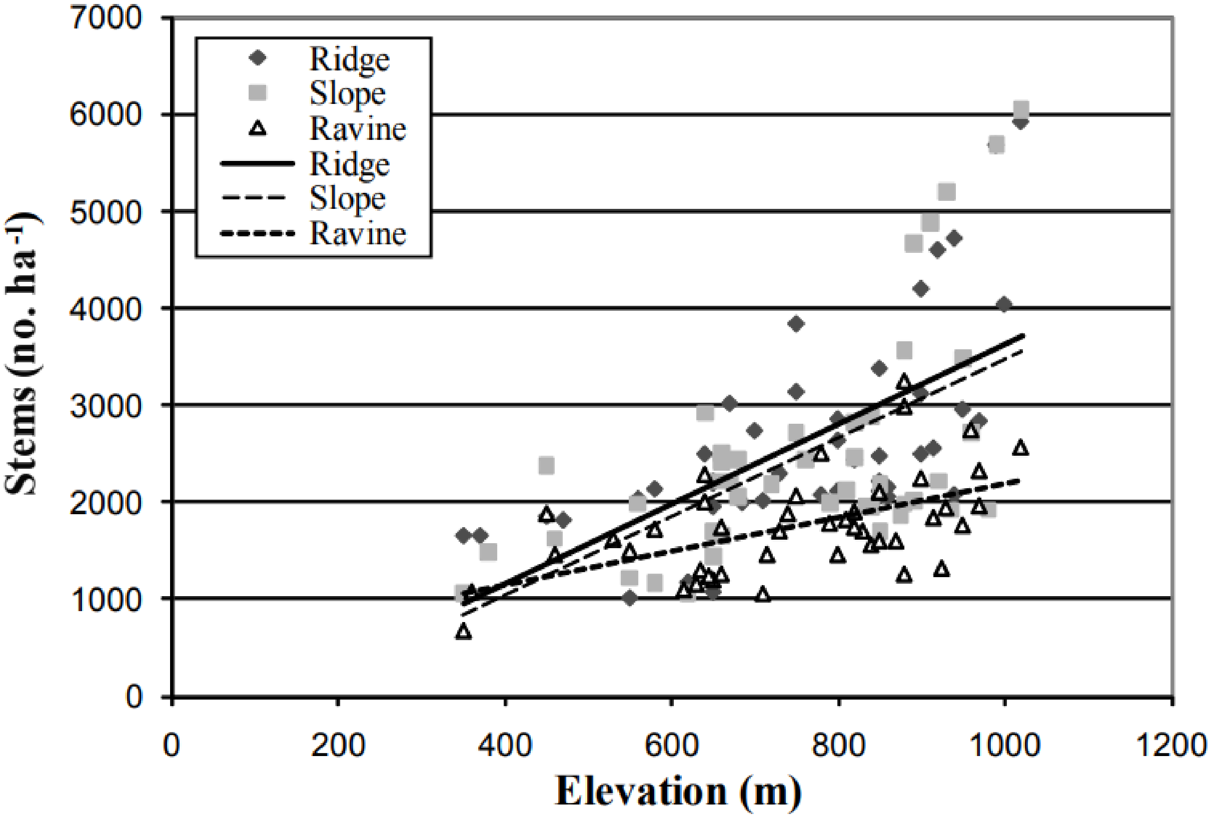

Figure 2.3. Mean density of stems ≥4 cm DBH per plot by elevation in the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine; Weaver 2012)

Figure 2.4. Photograph of Luquillo Experimental Forest 1-2 month after H. Maria in Colorado forest near Route 191 in EYNF. This was taken by Nicholas Brokaw.

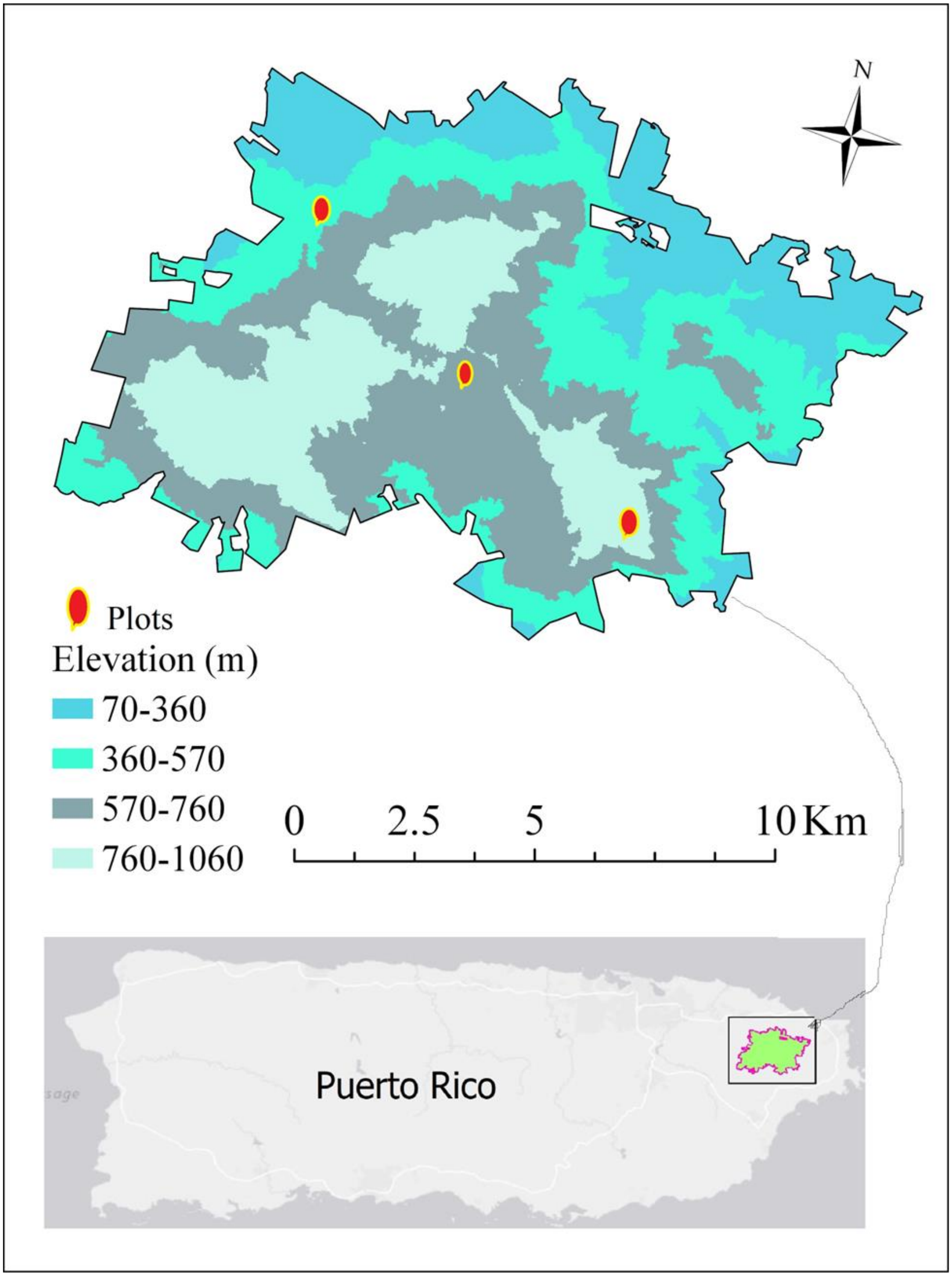

Figure 2.5. Map of 3 sites studied in the Luquillo Experimental Forest, Puerto Rico.

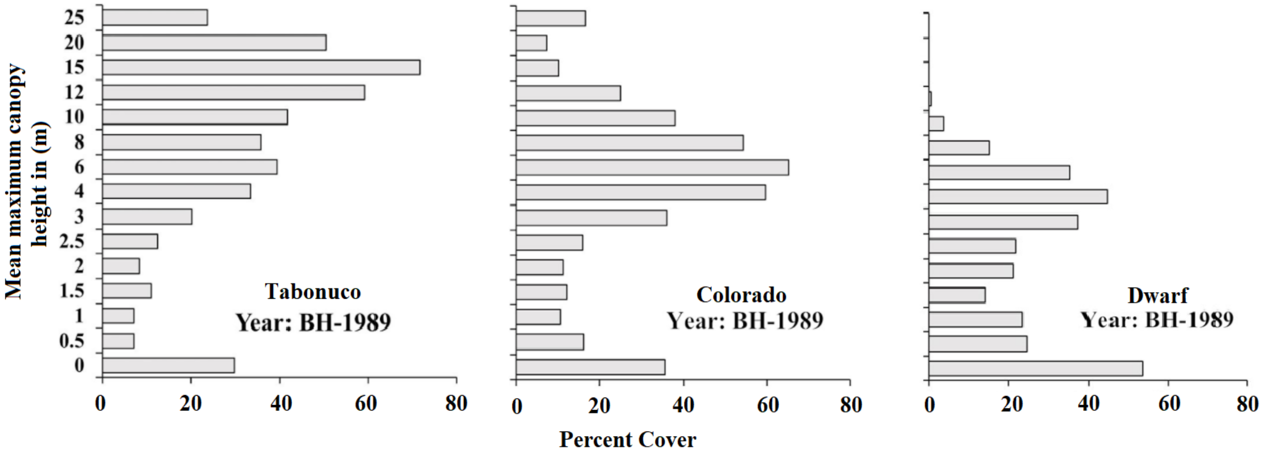

Figure 2.6. Vegetation height profiles of Tabonuco, Colorado, and Dwarf forest respectively 350 m elevation (475 points), 750 m elevation (451 points), and 1000 m elevation (451) in a ha plot before Hurricane Hugo in 1989. Horizontal scale shows total points with cover as percent of total number of grid points in each plot. Vertical scale is graduated and shows the upper limit of each height interval.

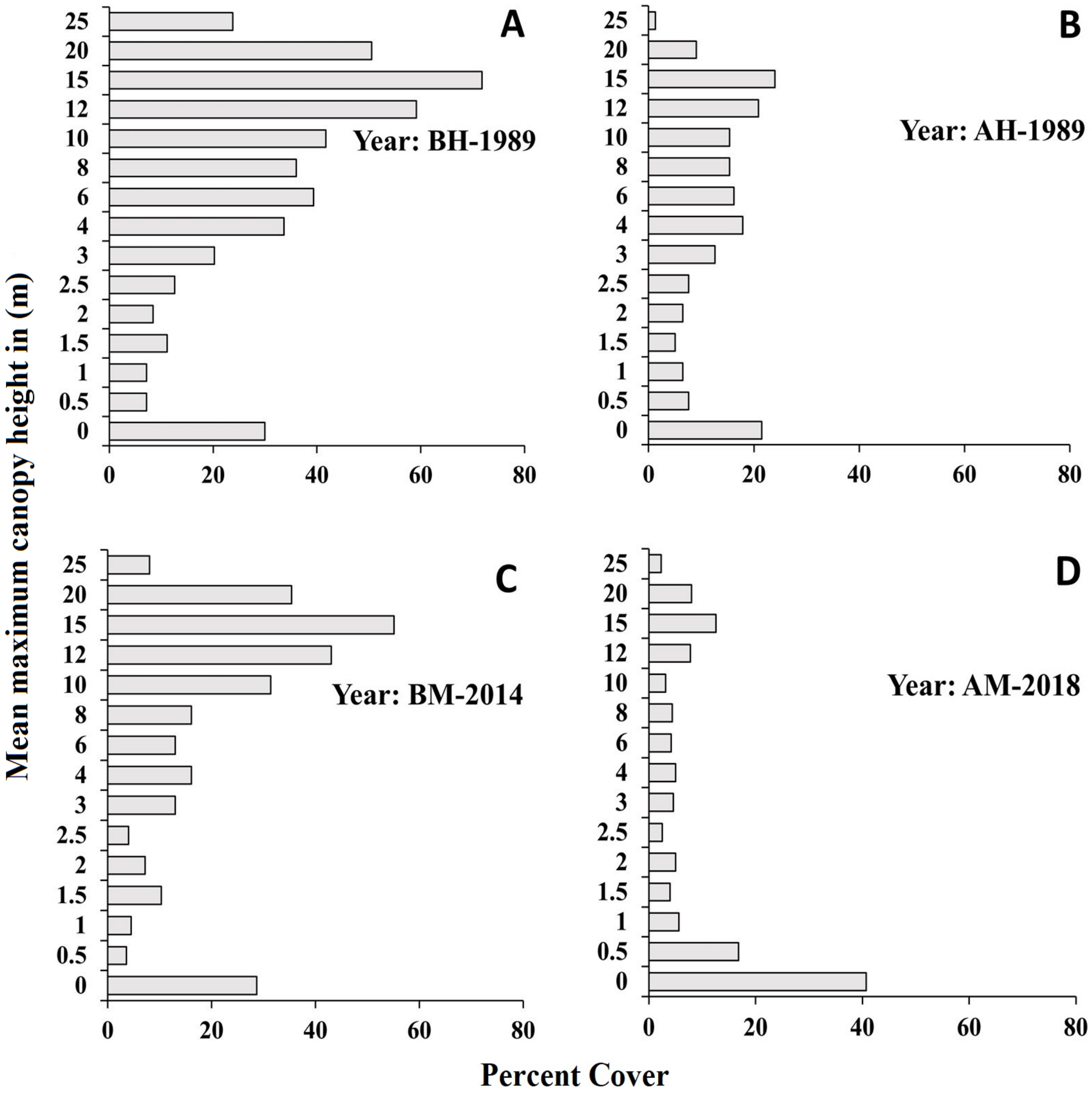

Figure 2.7. Vegetation height profiles in Tabonuco (350 m elevation) forest plots in the Luquillo Experimental Forest, Puerto Rico (BH = Before Hurricane Hugo, AH = After Hurricane Hugo, BM = Before Hurricane Maria, AM = After Hurricane Maria). Horizontal scale shows total points with cover as percent of total number of grid points in each plot. Vertical scale is graduated and shows the upper limit of each height interval. Data are from measurements at 475 points in a 1.08 ha plot.

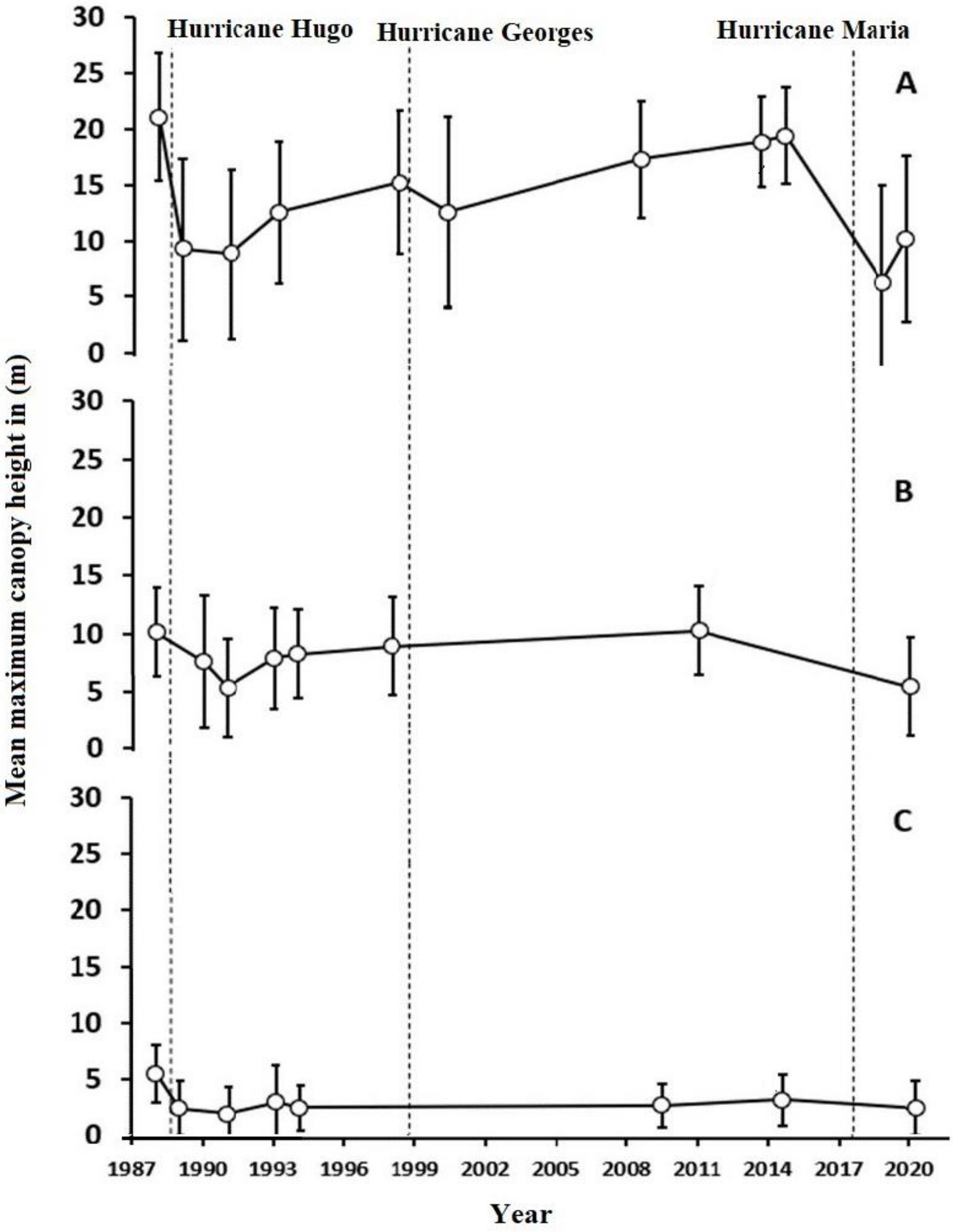

Figure 2.8. Mean and standard deviation of height of upper surface of forest canopy from 1989 to 2020, in Puerto Rico. A= Tabonuco forest, at 360 m asl; B= Colorado forest at 700 m asl.; and C= Dwarf forest, at 1000m asl. Hurricane events are indicated in the relevant intervals between measurements.

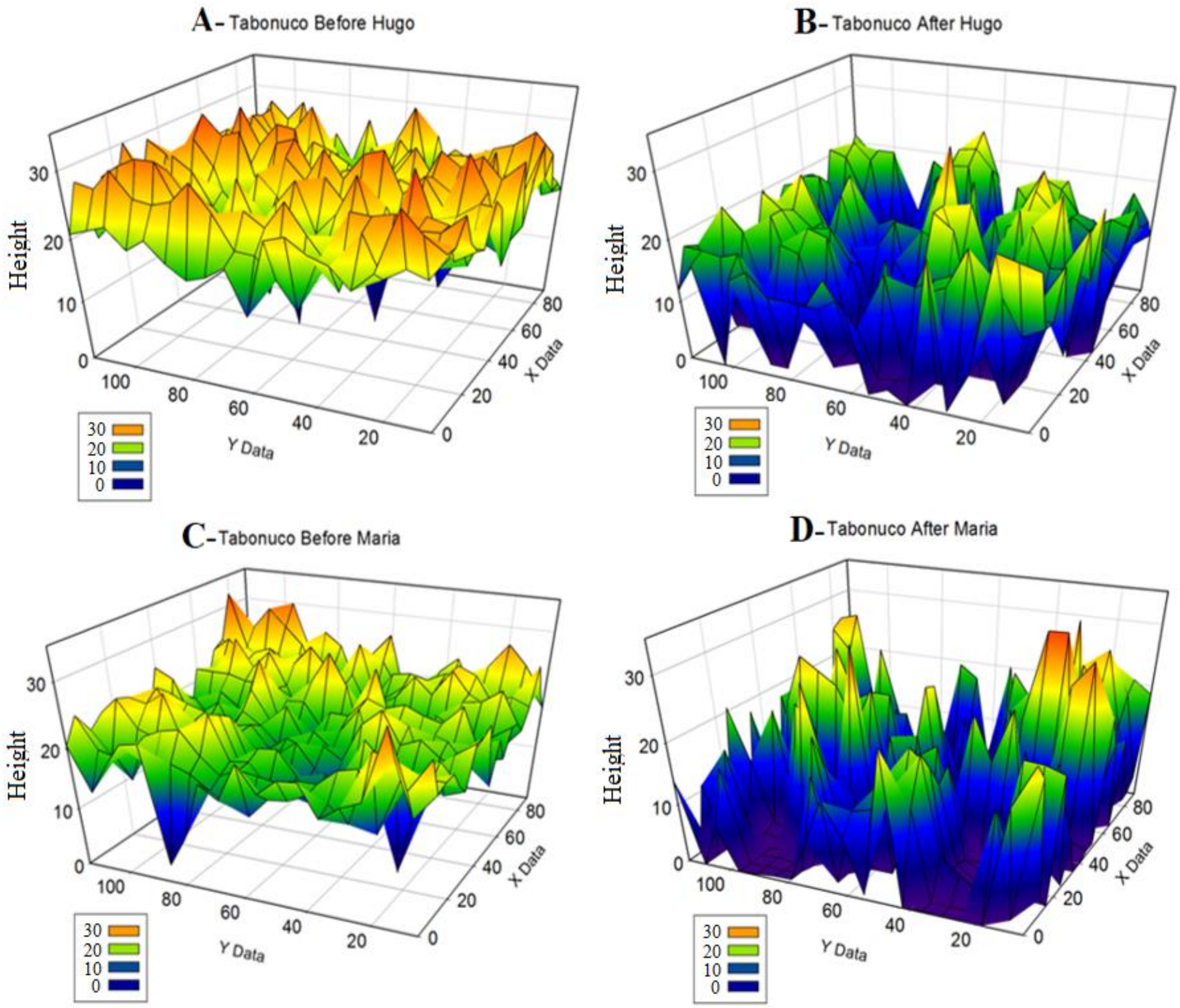

Figure 2.9. Triangulated irregular network depicting the mean maximum canopy height of Tabonuco forest in Puerto Rico, before and after Hurricanes Hugo, and María. Data are measured at 475 points in a 1.08 ha plot.

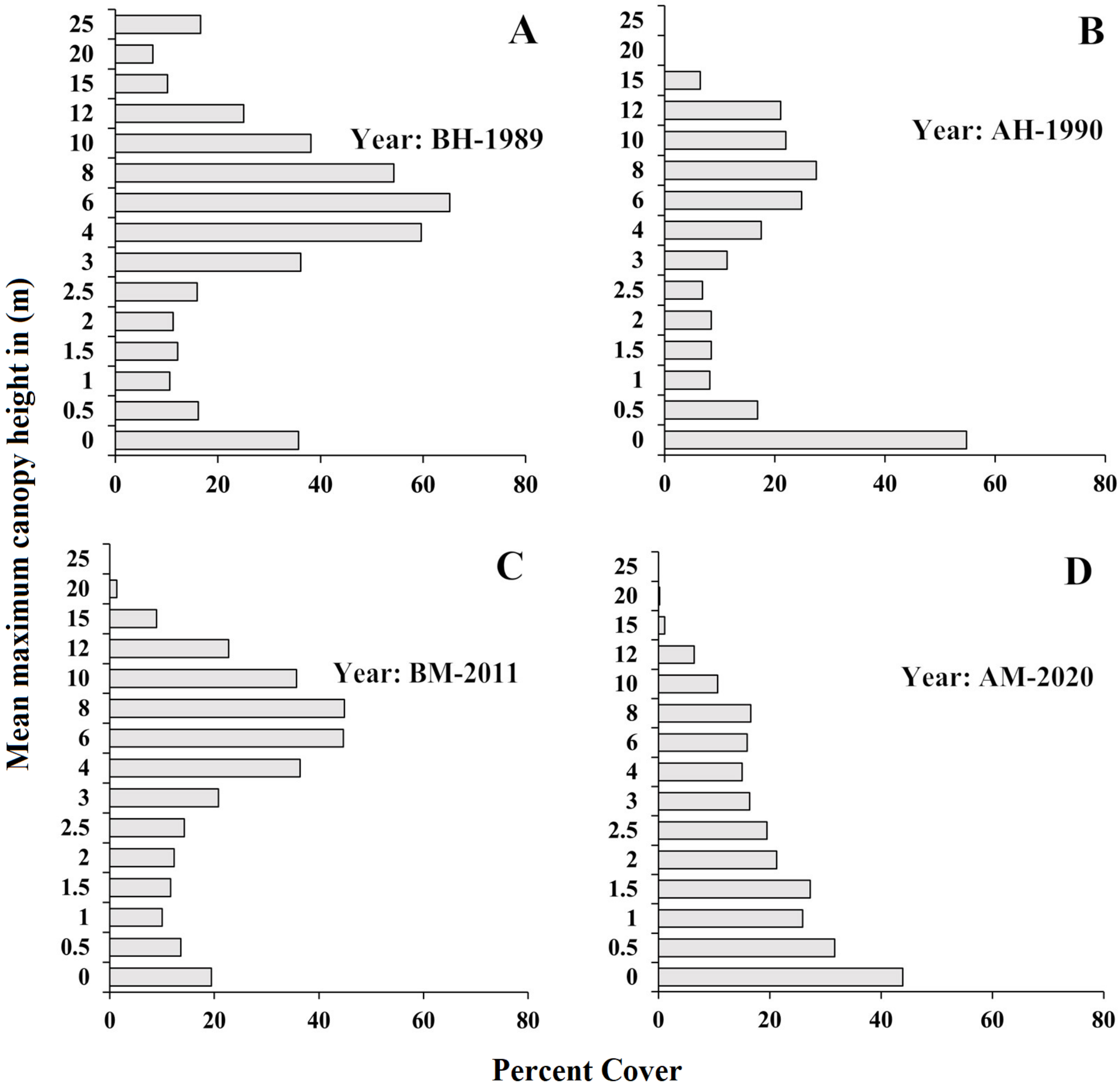

Figure 2.10. Vegetation height profiles in Colorado (750 m elevation) forest plots in the Luquillo Experimental Forest, Puerto Rico (BH = Before Hurricane Hugo, AH = After Hurricane Hugo, BM = Before Hurricane Maria, AM = After Hurricane Maria). Horizontal scale shows total points with cover as percent of total number of grid points in each plot. Vertical scale is graduated and shows the upper limit of each height interval. Data are from measurements at 451 points in a 1 ha plot.

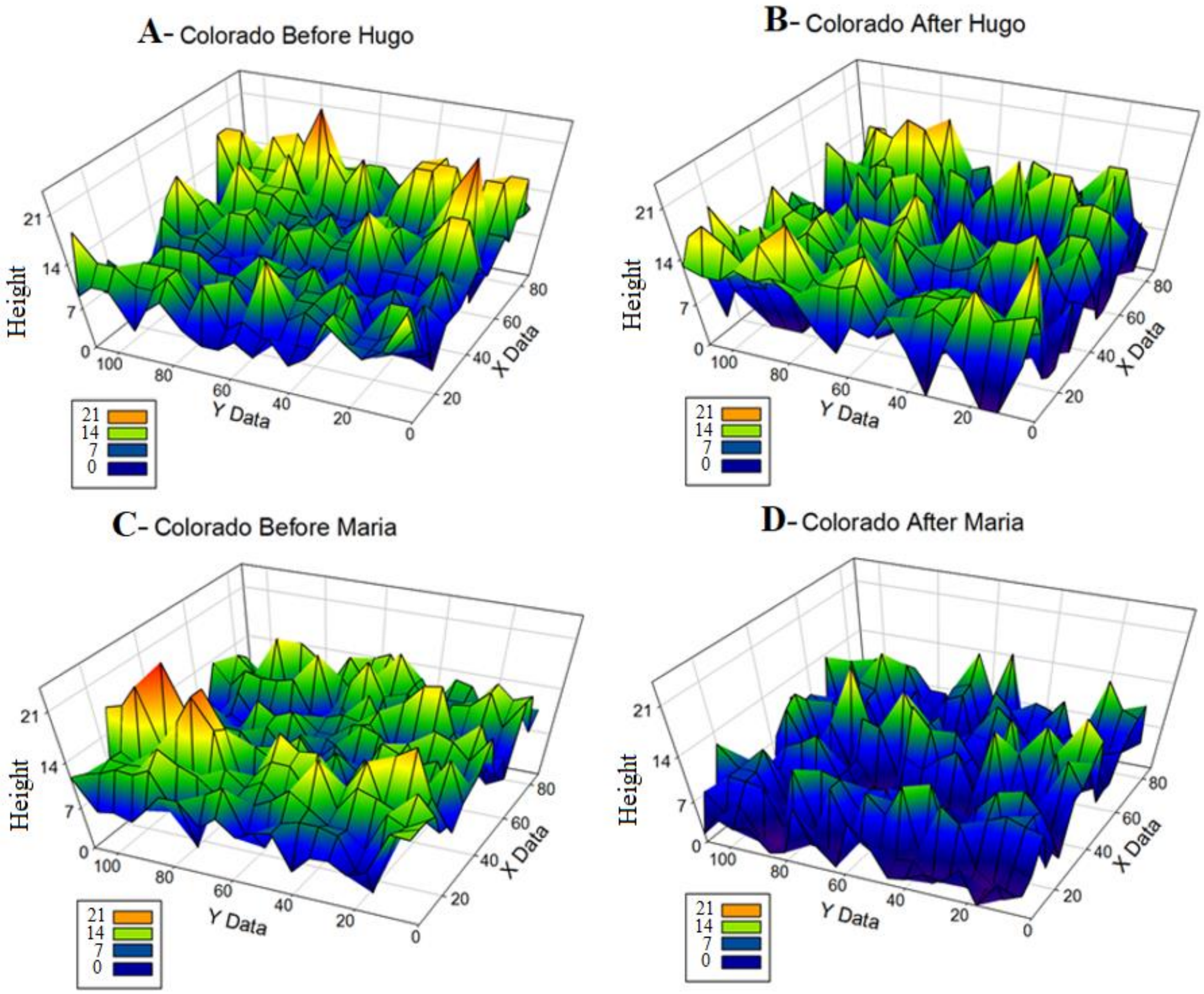

Figure 2.11. Triangulated irregular network depicting the mean maximum canopy height of Colorado forest in Puerto Rico, before and after Hurricanes Hugo, and María. Data are measurements at 451 points in a 1ha plot.

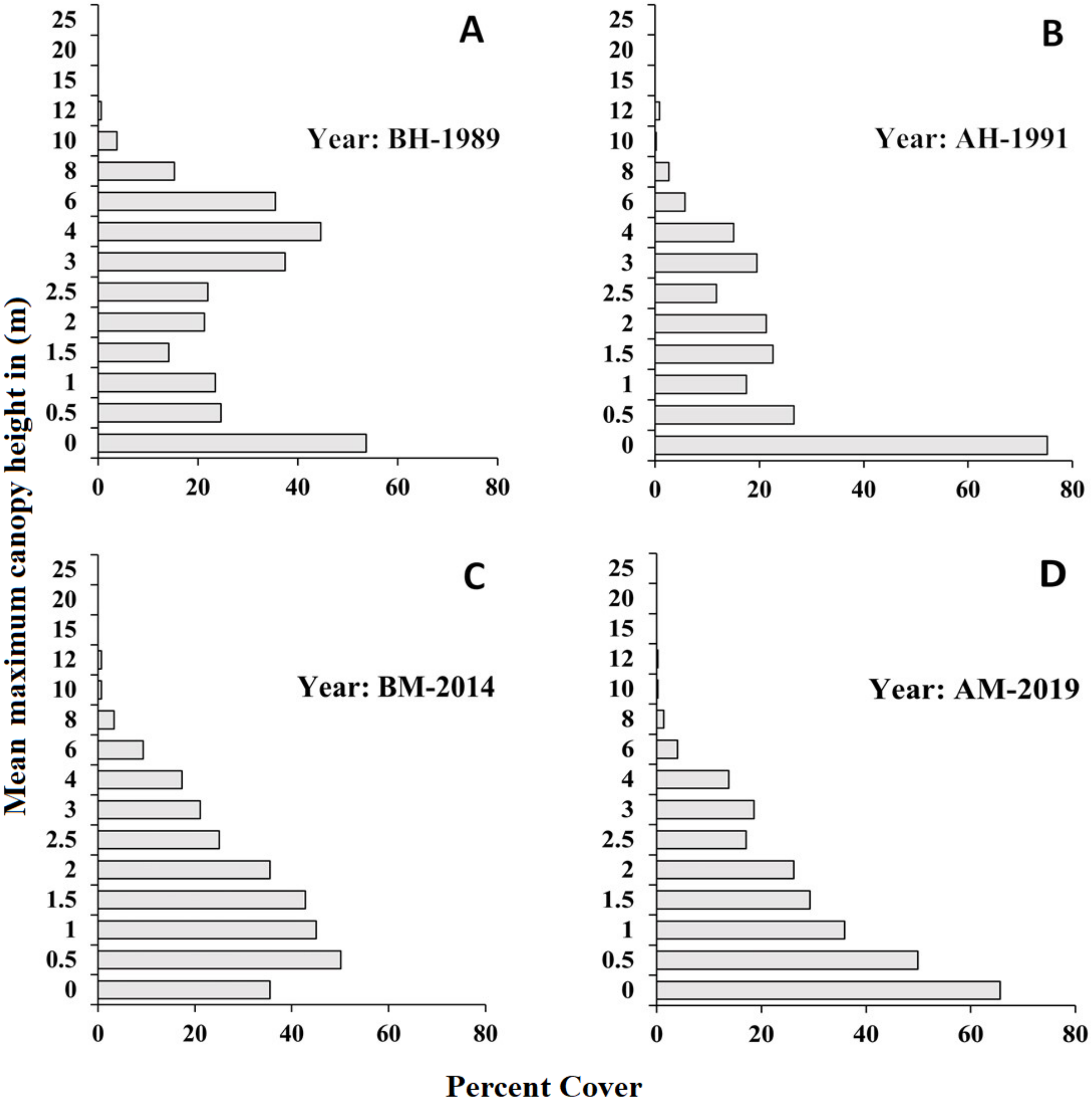

Figure 2.12. Vegetation height profiles in Dwarf (1000 m elevation) forest plots in the Luquillo Experimental Forest, Puerto Rico (BH = Before Hurricane Hugo, AH = After Hurricane Hugo, BM = Before Hurricane Maria, AM = After Hurricane Maria). Horizontal scale shows total points with cover as percent of total number of grid points in each plot. Vertical scale is graduated and shows the upper limit of each height interval. Data are from measurements at 451 points in a 1 ha plot.

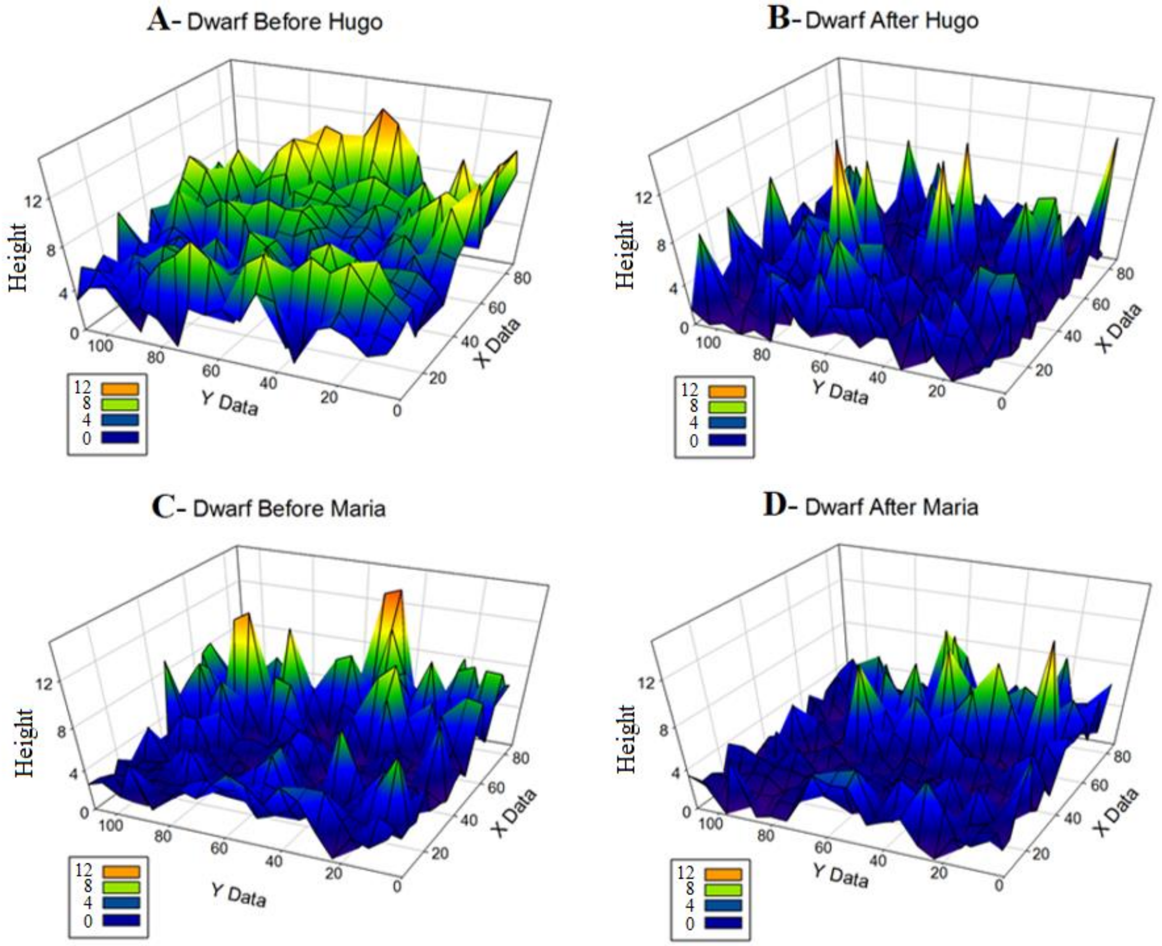

Figure 2.13. Triangulated irregular network depicting the mean maximum canopy height of Dwarf forest in Puerto Rico, before and after Hurricanes Hugo, and María. Data are measurements at 451 points in a 1ha plot.

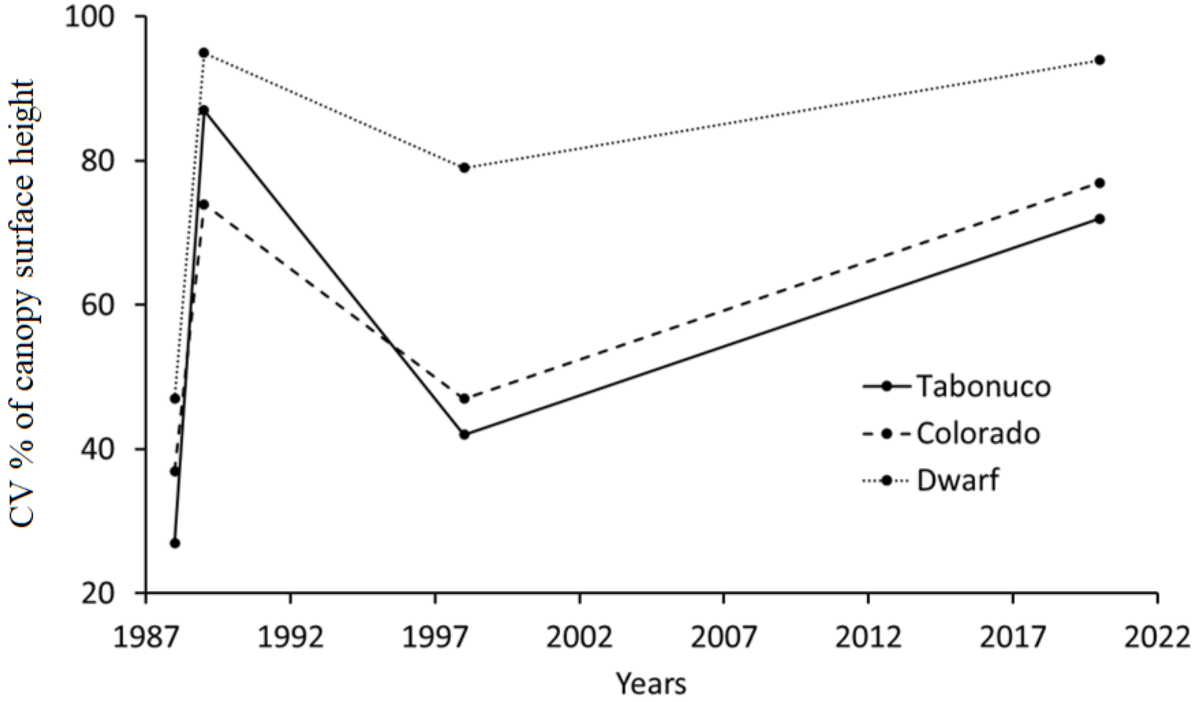

Figure 2.14. coefficient of variation (CV) of canopy surface height in Tabonuco, Colorado, and Dwarf forest plots at LEF, Puerto Rico, in relation to major hurricanes. Hurricanes decrease the mean canopy height and increase CV of canopy height, while recovery does the opposite.

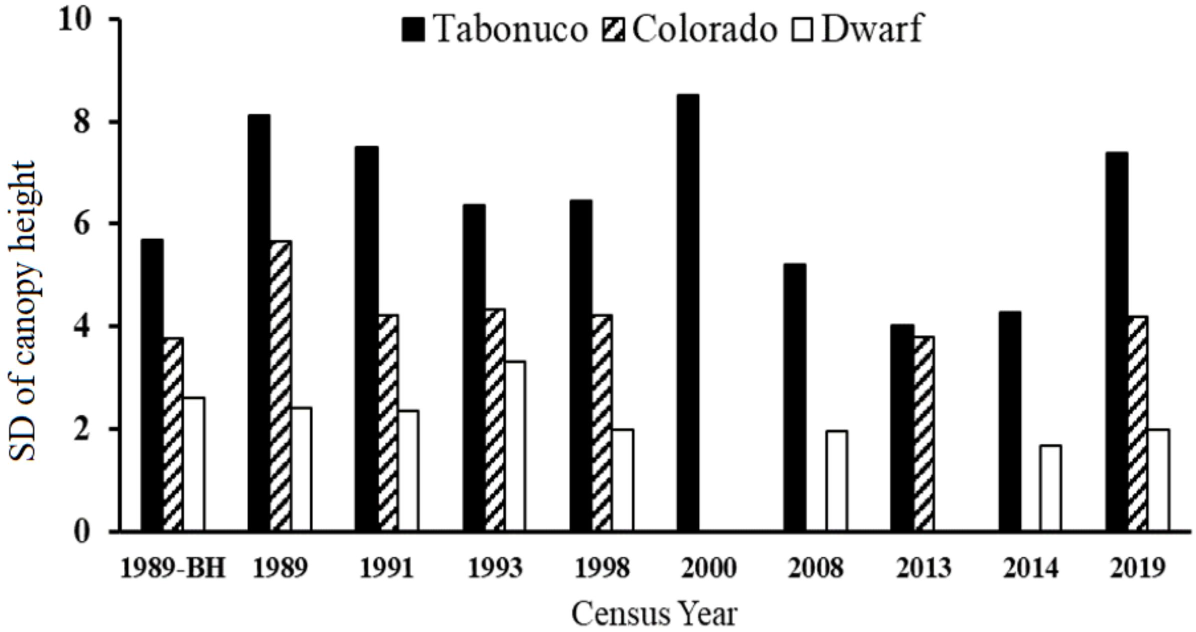

Figure 2.15. Distribution of standard deviation (SD) of forest canopy height showing variations in canopy surface. Data for Colorado forest in 2000, 2008, 2014 and for Dwarf forest in 2000 are not available.

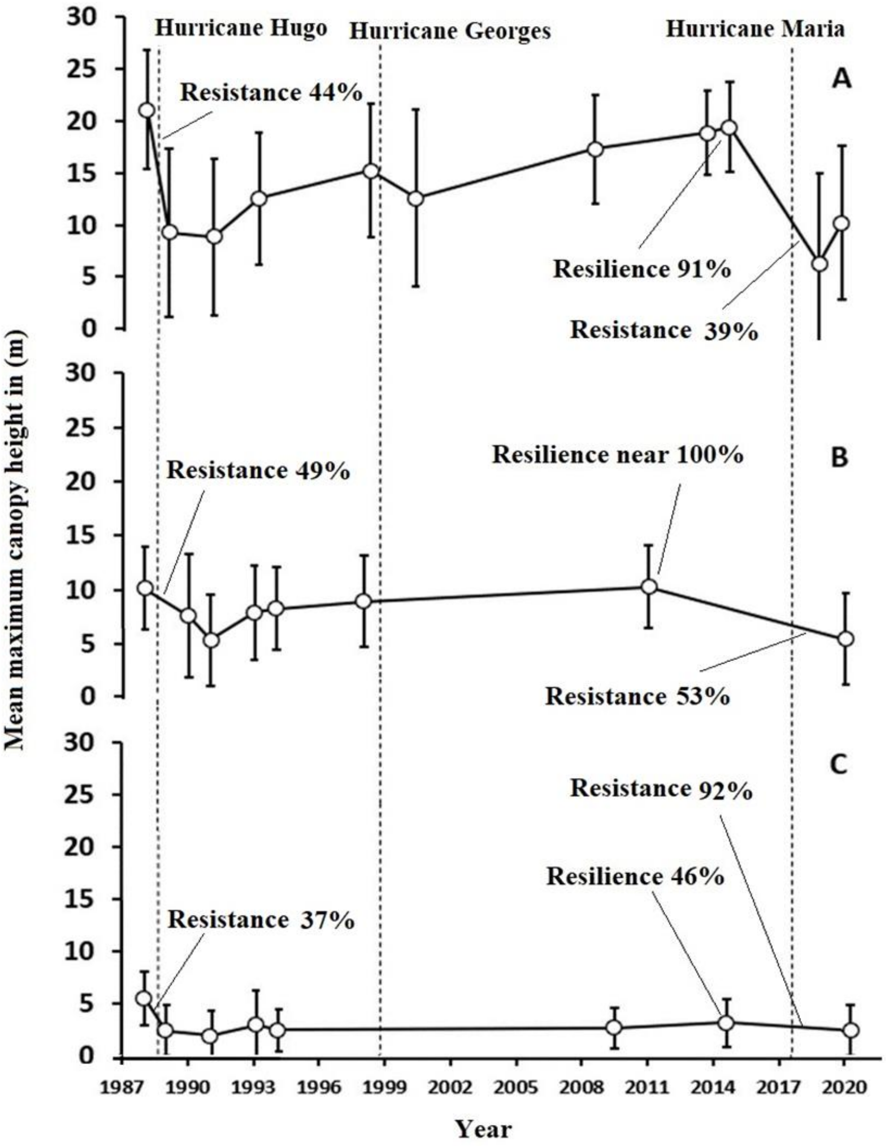

Figure 2.16. Resistance and resilience of the Luquillo Experimental Forest to Hurricane Hugo and Maria. The bars represent standard deviation of height of upper surface of forest canopy from 1989 to 2020, in Puerto Rico. A= Tabonuco forest, at 360 m asl; B= Colorado forest at 700 m asl.; and C= Dwarf forest, at 1000m asl. Hurricane events are indicated in the relevant intervals between measurements. NB.: Resistance is computed right after the passage of the hurricane while resilience after a certain regrowth before any other major hurricane.

CHAPTER 3

POST-HURRICANE UNDERSTORY RESPONSE OF TWO PIONEER SPECIES IN A TROPICAL RAINFOREST IN PUERTO RICO

Abstract

Hurricanes play important role in community dynamics in tropical forests by killing or removing organisms from the community while facilitating the establishment of others. In the Tabonuco forest, I investigated the understory response of two pioneer species to canopy opening after the passage of Hurricane Maria. I made two censuses. The first was in June 2019, two years after the hurricane while the second was in December 2021. I counted cell by cell *Cecropia schreberiana* and *Heliconia caribaea* present in our grid system. I correlated the abundance of these two species to the maximum canopy height per cell. The results indicated that there was strong correlation between canopy opening and the upcoming of these pioneer species. In 2019, I recorded 2030 ha^{-1} of *Cecropia*. One year and six months later, the *Cecropia* density had diminished by 66%, when I registered just 715 ha^{-1}. The lost was mostly observed in the 1 to 10 cm DBH category (Fig. 3.4). As for the *Heliconia*, I recorded 1123 ha^{-1} in 2019 and 647 ha^{-1} in 2021. The density had decreased by 42 %. In other words, recruitment of Cecropia and *Heliconia* was decreasing as canopy was closing, for the data indicated an increase of 27% of canopy from 2017 to 2019. Despite the significant diminution of the *Cecropia* and *Heliconia* population, I believe some of them will survive specifically the *Cecropia.*

Key words: Hurricanes, pioneer species, *Cecropia schreberiana*, *Heliconia caribaea* canopy height, tropical forest

3.1 INTRODUCTION

Disturbance is a major factor affecting forest development. It is defined as a relatively discrete event in time that causes abrupt changes in ecosystem, community, or population structure and that changes resource availability, substrate availability, or the physical environment (Emery 2010). It plays important roles in succession of plant communities because it kills or removes organisms from the community (Krohne 2000). It causes changes in the physical environment (e.g., increased temperature, soil moisture, light) that affect the biota. The amount of light reaching the forest floor is among the most dramatic changes produced by hurricanes in tropical forest (Fernandez and Fetcher 1991). In the Luquillo Experimental Forest, 10 months after the passage of Hurricane Hugo in 1989 the median of the total daily PPFD received along the transect of 32 m was between 7.7-10.8 mol m^{-2} range which is between the amount of PPFD received by a large gap > 400 m^2 and a clearing (Fernandez and Fetcher 1991). Because disturbance creates gaps in forest canopies, it affects germination of seeds and growth rates and survival of plants (Brokaw 1985a, Denslow 1987), due primarily to modifications in the quality and quantity of light (Welden et al. 1991). More intense sunlight reaches the plants in gaps for longer periods than plants in the forest understory (Brandani et al. 1988, Lieberman et al. 1989).

In 1989 Hurricane Hugo, the fourth largest of the six hurricanes to affect the island of Puerto Rico since 1899 (Scatena and Larsen, 1991), struck the Luquillo Experimental Forest in Puerto Rico and removed leaves from the canopy and snapped trees, causing a more than tenfold increase in light intensity on the forest floor (Krohne 2000). Alterations of the forest floor commonly lead to appearance of pioneer species in this tropical forest. For instance, Guzman-Grajales and Walker (1991) cited by Walker (1991) found graminoids increased in the understory in areas of severe disturbance for 2-8 mo after the hurricane, nevertheless within 1 yr., the graminoids were substituted by fast-growing, early successional species such as *Cecropia schreberiana* L. ex. *C. peltata*.

Ecologists describe pioneer species as the first colonists of sites affected by a disturbance (Dalling 2008). Depending on disturbance severity or sources, pioneers can be either primary or secondary. Primary pioneer species usually take place after extreme disturbances, such as landslides and volcanic eruptions, creating new habitats by covering bare substrate, soil while secondary pioneer species colonize sites where the severity of disturbance is insufficient to remove all the existing vegetation (Dalling 2008). Secondary pioneer species or secondary succession usually occurs after disturbances such as fire, flooding, windstorms, and human activities.

In September 2017, Hurricane Maria struck the island of Puerto Rico as a category 4 storm with sustained winds up to 250 Km hr^{-1} and precipitation of 500 mm. Since the passage of Hurricane San Felipe II in 1928, Hurricane Maria has been the most powerful hurricane to make direct landfall, and it killed twice as many trees as did Hurricane Hugo in 1989 (Uriarte et al. 2019). In Chapter 2 of this dissertation, I assessed the effect of the hurricanes on the Luquillo Experimental Forest where canopy height has been measured. Massive changes occurred in the forest canopy, but how does this affect plant regeneration? Therefore, I used a 1.08 ha plot in Tabonuco forest in the Luquillo Experimental Forest, in Puerto Rico to investigate the outcome of forest canopy changes on *Cecropia schreberiana* and *Heliconia caribaea*. These two species were selected because of their abundance, and they are model organisms in this case to use to illustrate pioneer response to the hurricane. Our general purpose was to investigate how the understory and tree recruitment responded to the canopy openness. I measured canopy height in 2019 and 2021, after Hurricane Maria, and I hypothesize that initial conditions, that is, canopy height in 2019, when colonization was beginning, will be more strongly correlated with abundance in 2019 than canopy height in 2021. I expect that because the canopy grows back and shades the understory, reducing plant recruitment.

Cecropia schreberiana, known as "guarumo" or “guarumo macho” is a dioecious plant that may reach a height of 20 meters and a diameter of 60 centimeters in the LEF (Brokaw 1998). Its size decreases with elevation (Weaver1986). The leaves of mature trees are simple, alternate (but clustered), 30-75 cm broad, and have seven to eleven large lobes extending from a stout petiole (Fig. 3.1A). The silvery undersides of the leaves make them visible from a distance on windy days. The branches are few and sturdy, supporting a sparse, spreading canopy. The bark is smooth and gray in hue; younger branches have triangular leaf scars. The tree's wood is fragile, weak, and lightweight (Brokaw 1998). Stilt roots extend to the ground from around one meter up the trunk.

Cecropia schreberiana can be found in the LEF as young trees in newly disturbed regions, as trees of all ages on stable borders like roadside ditches and stream banks, and as mature trees in older forests (Silander 1979). It can be found in nearly every type of forest in the LEF (Weaver 1994) but is most prevalent at mid-elevations in the Tabonuco forest (Briscoe and

Wadsworth 1970), moderately abundant in Colorado and palm forests (Weaver 1986), absent from the Dwarf forest except along roads and as a rare colonizer in other human disturbances there (Zimmerman et al. 1995).

Heliconia caribaea, known as “wild plantain,” is a perennial, large, erect herb capable of vegetative reproduction (Berry and Kress 1991). It is the only native species of the genus *Heliconia* in Puerto Rico, and it is found all across the island. It has a pseudostem and manages to grow up to 4.3 m tall (Fig. 3.1B), including the enormous, erect, leathery, dark green leaves (Meléndez-Ackerman et al. 2003). It occupies forest habitats that range from full sun to 40% shade (Berry and Kress 1991). At the Luquillo Experimental Forest (LEF) in Puerto Rico, *H. caribaea* appears to prefer open sites in secondary growth both within the forest and at the forest edge (Richardson and Hull 2000). Erect shoots are composed of a stem (made up by an axis covered by overlapping sheathing leaf petioles (hence technically a pseudostem) and leaves. When mature, the pseudo stem (made up by an axis coveredby overlapping sheathing leaf petioles) is terminated by an erect, bright yellow inflorescence that lasts 1–3 month (Meléndez-Ackerman et al. 2003). *H. caribaea* appears to favor open areas in secondary growth at the LEF in Puerto Rico, both within the forest and at the forest edge (Richardson and Hull 2000), although there is little quantitative information on the dynamics of this species' colonization. Given its habitat type and apparent distribution across the forest, *H. caribaea* should act as a pioneer species in response to hurricane-related forest disturbances (Meléndez-Ackerman et al. 2003).

Meléndez-Ackerman et al. (2003) in their research after Hurricane Georges explored how large disturbances may affect population dynamics of *H. caribaea* by analyzing how resilient adult individuals of this species were after a hurricane. They also studied the relationship between canopy openings and *Heliconia* seedling colonization. They found that seedlings were more abundant than adults or juveniles within areas with low canopy densities than within areas with high canopy densities. Our work will complement Meléndez-Ackerman et al. study by using a greater sample size (1.08 ha) and a longer time frame, 3.5 years.

3.2 METHODS

3.2.1 Study area

The study area is in the Tabonuco forest, in old-growth forest near the El Verde Field Station (EVFS; 18°20’ north, 65°49′ west), a principal research site of the Luquillo Long-Term Ecological Research Program (LTER). The elevation is 340 - 485 m a.s.l., and the terrain is steep and rocky (24% average slope, 25% area covered by boulders: Soil Survey Staff 1995). Soils at EVFS are Oxisols and Ultisols (Soil Survey Staff 1995, Shiels et al. 2010). Soils at EVFS area are mainly Zarzal clay series, which are deep Oxisols and Ultisols that originated from volcaniclastic parent material (Soil Survey Staff 1995). A large fraction of the forest to the north of our study site was clear-cut, according to a 1936 air photograph, and small patches of coffee (*Coffea arabica* L.) were also grown around EVFS (Shiels et al. 2010). The annual rainfall averages 3500 mm (Shiels et al. 2010), and monthly precipitation is variable, but May to December are usually the rainiest months and January to April are typically drier (Zimmerman et al., 2007***)***. Tabonuco forest is a *subropical wet forest* in the Holdridge System (Ewel and Whitmore 1973). The most common tree species at the site are *Dacryodes excelsa* (Burseraceae;

commonly named Tabonuco), the palm *Prestoea acuminata* var. *montana* (Arecaceae), *Sloanea berteroana* (Elaeocarpaceae), and *Manilkara bidentata* (Sapotaceae; Shiels et al. 2015).

Study site

Our study took place in a 1.08 ha (90 x 120 m) plot, gridded every 5 m to create 475 grid points (including perimeter points), that was established in 1989 (Brokaw and Grear 1991). I measured the maximum canopy height directly above each grid point, by sighting an imaginary line along a 3-m pole, held vertically, and measuring with a range finder the distance along the line from ground level to the highest point of contact with branch or foliage. I measured these canopy heights in 2019 and 2021, two and four years after Hurricane Maria, respectively.

In June 2019, one year and nine months after the passage of Hurricane Maria, I counted *Cecropia schreberiana* and *Heliconia caribaea* cell by cell within our gridded system. I counted all *C. schreberiana* ≥ 1 cm DBH present in our plot. I measured the stem diameter of *Cecropia schreberiana* using a diameter tape for trees greater than 10 cm DBH and a digital caliper for seedlings and saplings between 1-10 cm DBH. For *H. caribaea,* I counted clumps. I defined a clump as every 5 or more stems grouped together in one spot. I used a distance of 25 cm to separate close clumps. I used clumps instead of single stems because the *Heliconia caribaea* was extremely dense. Single stems were not counted. In December 2021, I made another census of *Cecropia schreberiana* and *Heliconia caribaea* in the grid system following the same protocol from 2019. As for *Heliconia,* in addition to the clumps, I also recorded the number of *Heliconia caribaea* that bore fruits or flowers and counted individual plants of all size.

3.2.2 Data analysis

For the analysis, I used the 475 grid points to create 432 cells of 5 x 5 m (Fig. 3.2). Using the maximum canopy height (MCH) for the four points for each cell, I calculated the average canopy height for each cell. I made a regression analysis by plotting MCH versus the densities of *Heliconia* and *Cecropia* to see the effects of canopy height on *C. schreberiana* and *H. caribaea.* I also made a second analysis to see if the neighboring trees and/or branches would have had an influence on the light reaching the cells, consequently influenced plant recruitments. I enlarged the MCH 15 x 15 m by combining 8 cells of 5x5 m around a focal cell. The focal cell is a 5x5 m cell within 8 other 5x5 m cells. To compute MCH for that focal cell, I took the average the canopy height of the focal with the other 8 adjacent cells. For this analysis I also removed the cells on the edge of 1.08 ha plot, because they have adjacent cells on only three sides. Then, I correlated plant densities within the focal cells with obtained MCH. Finally, I made a third analysis to make sure that overhead light is a good measure of what is important for *Heliconia* and *Cecropia* as I did in the first analysis. I only used *Heliconia* and *Cecropia* in the focal cell as proceeded in the second analysis. This time, instead of using canopy height of 8 adjacent cells to compute the average MCH, I averaged the canopy height of the focal cell and canopy height above 12 adjacent canopy points (16 points in total). Then, I regressed plant densities and MCH. For the regression analysis, I used Poisson because I was measuring number trees and or woody plants on a unit area of 1.08 ha.

3.3 RESULTS

Hurricane Maria significantly struck the tabonuco forest as the MCH greatly reduced from 19.1 m to 7.4 m (Fig. 3.3). Two years later, in 2019, the last measurement indicated a 27% of forest canopy recovery. The MCH increased from 7.4 m to 10.2 m. The change in the forest canopy influenced the survival of *Cecropia* and *Heliconia.*

Two years after the hurricane, in 2019, I recorded 2030 ha^{-1} of *Cecropia*. One year and six months later, the *Cecropia* density had reduced by 66%, when I registered just 715 ha^{-1}. Most of those lost were 1 to 10 cm DBH (Fig. 3.4). The loss of *Cecropia* in this category shows how recruitment was slowing with the canopy closure. The *Cecropia* density in 2019 was significantly correlated to the canopy height, meaning that their presence was significantly higher where the canopy was shorter (Fig. 3.5A and 3.5B, *P* = 0.001 for 2019 and 2021).

Heliconia followed the same trend with *Cecropia*. I recorded 1123 ha^{-1} in 2019 and 647 ha^{-1} in 2021. The density had decreased by 42 %. Like the *Cecropia*, the *Heliconia* density was significantly correlated to canopy height. The density was lower where the canopy was higher. (Fig. 3.5C and 3.5D; *P* = 0.001 for 2019 and 2021). Significant change was also observed in the number of *Heliconia* inflorescences. In 2019, I censused 8181 flowers and fruits while in 2021 I found just 3307, a 60% decrease (Fig. 3.5E and 3.5F).

The preliminary results revealed that there was a strong relationship between *C. schreberiana* and *H. caribaea* when I used a 5x5 m grid for the MCH. I made a second a second correlation test where I enlarged the cell 15x15 m for canopy and correlated *Cecropia* and *Heliconia* within the 5 x 5 m cell. I also found significant correlation (Fig. 3.6 A and B for *Cecropia* and 3.7 A and B for *Heliconia*; $P = 0.001$). In the last correlation test, I correlated the *Cecropia* and *Heliconia* density within the 5x5 m focal cell with the average canopy height above that cell and the 12 adjacent canopy points (16 points in total). Significant correlation between *Cecropia*, *Heliconia* and MCH was also found (Fig. 3.6 C and D for *Cecropia* and 3.7 C and D for *Heliconia* $P = 0.001$).

3.4 DISCUSSION

In the Tabonuco forest plot Hurricane Maria substantially reduced the percent cover in the main upper canopy (see chapter 2, Brokaw and Grear 1991). This created large gaps in the Tabonuco forest. As a result, two years after the hurricane, two pioneer species *Cecropia schreberiana* and *Heliconia caribaea* appeared abundantly in the forest floor. *The Cecropia schreberiana* abundance was significantly correlated to the mean maximum canopy height. It was predicted because *Cecropia schreberiana* requires patchy space and episodic time to thrive (Brokaw 1998). The best time they show up is usually after disturbance caused specially by hurricanes (Brokaw 1998). Bell 1970 (cited by Brokaw 1998) has revealed that *Cecropia schreberiana* seeds germinate when the forest canopy is opened by disturbance. Its germination success is positively correlated to light and temperature and negatively linked with litter and saturated soil.

Nevertheless, in 2021, 3.5 years after the hurricane, the results indicated that the

Cecropia population decreased by 66 %, most of them were in the category of plant that are less or equal 10 cm DBH. This diminution may be primarily explained by canopy closure. It might also be explained by background mortality. Only a tiny fraction generally reached maturity. Most of the germinated seeds after canopy opening are quickly followed by massive seedling death (Brokaw 1998). In his study of *Cecropia* survivorship, Silander (1979), found that 99.7 % of the seedlings die within a year, even in open areas. Another factor contributing to the *Cecropia* population diminution is interspecific competition. The canopy closure prevented them from finding enough sunlight to develop as a result they died. While there was a 66% diminution in the stem that belong to 1 – 10 cm DBH category, there was a 6% increase in the category that are greater or equal to 10 cm DBH. Perhaps, at this stage, since they are tall enough, they were able to survive intraspecific competitions. The 6% increase may be explained by recruitment from the lower category.

Like the *Cecropia schreberiana, Heliconia caribaea* was very abundant two years after Hurricane Maria struck the forest. Light availability is probably the main reason explaining their abundance. In tropical lowland rain forest, light is a strong limiting factor for the establishment and growth for plants on the forest floor (Dossa et al. 2013). The forest floor is only reached by about 2% of the photosynthetically active radiation (Chazdon and Fetcher 1984), preventing development of plants in the lowest height classes, 0, 0.5, 1, 1.5 to 2 m (Fig. 3.8). Hurricane Maria strongly changed the canopy cover in the Tabonuco forest (see chapter 2) which increased light and temperature on the forest floor. Consequently, the microenvironment altered to favor the germination of pioneer species (Meléndez-Ackerman et al. 2003). However, 3.5 years after the hurricane, the *Heliconia* density decreased by 42%. Like the *Cecropia,* the main reason explaining the *Heliconia* density declination is the intraspecific competition for light as the canopy started to close as our results indicated that the *Heliconia* density was higher where the canopy was more open. Similar results on *Heliconia* in the Luquillo were found by Meléndez-Ackerman et al. (2003) that seedlings were more abundant than adults or juveniles within areas with low canopy densities than within areas with high canopy densities. Another possible explanation of the *Heliconia* density decline is age. They reached maturity as most of them terminated by an erect, bright yellow inflorescence which may last 1 to 3 mo (Meléndez-Ackerman et al. 2003). After dying, the fruits fell on the ground perhaps to increase the seedbank.

In the second and third analysis, I expanded the area of MCH 15x15 m to correlate it with the plant results for each 5 x 5 focal cell in an attempt to improve the correlation. I found no significant difference with the first analysis where I correlated the *Cecropia* and *Heliconia* in the 5x5 m cell with MCH. That indicates that light directly overhead is a good measure of what is important for *Heliconia* and *Cecropia*.

3.5 CONCLUSION

Hurricane created-gaps in forest canopies are ideal conditions for rapid plant reproduction and growth (Muscolo et al. 2014). Gap radically changes light, temperature, soil moisture, and available nutrients to create an environment which will favor some species while preventing others from thriving (Muscolo et al. 2014). Canopy opening increases air temperature close to the ground, due to the increase in direct radiation, to increase soil temperature which will cause the mortality of young tree seedlings when the topsoil temperature is >50° C (Muscolo et al. 2014). Many rainforest trees depend on gaps at some stage of their life cycle (Denslow 2013). Whitmore (1974) found that out of 12 important big tree species at Kolombangara, Solomon Islands, the germination and/or growth of eight are enhanced by the presence of a gap. Our study has confirmed once again that plant regenerations are closely linked to canopy disturbance or forest gaps. However, their success is limited due to environmental and biotic factors.

In this chapter, I have shown how post-hurricane changes in canopy are correlated with the population dynamics of two indicator pioneer species in the LEF. How do changes in canopy height and cover, and post-hurricane population dynamics affect carbon storage? In the next chapter, I will show how canopy trimming and plant recruitment influence above ground carbon.

Literature Cited

Bell, C.R. 1970. Seed distribution and germination experiment. Pages DI77-D182 m H. T. Odum and R.F. Pigeon (eds.), A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico. National Technical Information Service, Springfield, VA.

Berry, F.W. and J. Kress. 1991. Heliconia: an identification guide. Smithsonian Institution Press. Washington. 344 pp.

Brandani, A., G. S. Hartshorn, and G. H. Orians. 1988. Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. *Journal of Tropical Ecology* 4: 99-119.

Briscoe, C.B. and F.H. Wadsworth. 1970. Stand structure and yield in the Tabonuco forest of Puerto Rico. Pages B79-B89 in H. T. Odum and R. F. Pigeon (eds.), A tropical rain forest:

A study of irradiation and ecology at El Verde, Puerto Rico. National Technical Information Service, Springfield, VA.

Brokaw, N.V.L. 1998. *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. *The Botanical Review*, 64(2): 91-120.

Brokaw, N.V.L. 1985a. Treefalls, regrowth, and community structure in tropical forests. Pages 53-71 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Dalling, J.W. 2008. Encyclopedia of Ecology || Pioneer Species. 2779-2782. doi:10.1016/b978-008045405-4.00534-6.

Denslow, J.S. 2013. Gap partitioning among tropical rainforest trees. *Biotropica* 12(2): 47-55.

Denslow, J. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18: 431-451.

Emery, S.M. 2010. Succession: A Closer Look | Learn Scienceat Scitable.

Fernández D.S. and N. Fetcher. 1991. Changes in light availability following Hurricane Hugo in a Subtropical Montane Forest in Puerto Rico. *Biotropica* 23(4a):393 399

Guzmán-Grajales, S. M., and L.R. Walker. 1991. Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23: 407-413.

Krohne, D.T. *General Ecology*. Second edition ed., 511 Forest Lodge Road, Pacific Grove,CA 93950 USA, Brooks/Cole/Thomson Learning, 2000.

Lieberman, M., D. Lieberman, and R. Peralta. 1989. Forests are not just Swiss cheese: canopy stereo geometry of non-gaps in tropical forests. Ecology 70:550-552.

Meléndez-Ackerman, E., C. Calisto-Pérez, M. Morales-Vargas, and J. Fumero-Cabán. 2003. Post-Hurricane recovery of a herbaceous understorey plant in a tropical rain forest in Puerto Rico. Journal of Topical Ecology, 19(6), 677–84.

Muscolo, A., S. Bagnato, M. Sidari, and R. Mercurio. 2014. A review of the roles of forest canopy gaps. *Journal of Forestry Research* 25(4), 725-736. https://doi.org/10.1007/s11676-014-0521-7

Richardson, B.A., G.A. Hull. 2000. Insect colonization sequences in bracts of *Heliconia caribaea* in Puerto Rico. Ecological Entomology 25:460–466.

Scatena, F.N., and M.C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropic*a 23: 364-372.

Shiels, A.B., J.K. Zimmerman, D.C. García-Montiel, I. Jonckheere, J. Holm, D. Horton, and N.V. Brokaw. 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *Journal of Ecology* 98:659-673.

Shiels, A.B., G. Gonzalez, D. J. Lodge, M. R. Willing, and J. K.Zimmerman. 2015. Cascading effects of canopy opening and debris deposition from a large-scale hurricane experiment in a tropical rain forest. *Bioscience* 65: 871-81.

Silander, S.R. and A.E. Lugo. 1990. Cecropia peltata L.: Yagrurno hembra, trumpet tree. Pages 244-249 in Silvies of North America. Vol. 2: Hardwoods. Agricultural Handbook 654, U.S. Department of Agriculture, Washington, DC.

Silander, S. R. 1979. A study of the ecological life history of Cecropia peltata L., an early secondary successional species in the rain forest of Puerto Rico. M.S. Thesis, University of Tennessee, Knoxville.

Soil Survey Staff. 1995. Order 1 soil surveys of Luquillo Long-Term Ecological Research Grid, Puerto Rico. United States Department of Agriculture, Natural Resource Conservation Service.

Uriarte, M., J. Thompson, and J.K. Zimmerman. 2019. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. *Nature Communications*, 10(1), 1362-. https://doi.org/10.1038/s41467-019-09319-2

Weaver, P.L. 1994. Baño de Oro Natural Area Luquillo Mountains, Puerto Rico. general technical report SO-I 11. U.S.D.A. Forest Service, Southern Forest Experiment Station, New Orleans.

Walker, L.R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23:379-385.

Weaver, P. L. 1986. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science* 22: 53-70.

Welden, C.W., S.W. Hewtt, S.P. Hubbell, and R.B. Foster. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, 72(1): 35-50

Whitmore, T.C. 1974. Change with time and the role of cyclones in tropical rain forests on Kolombangara, Solomon Islands. *Journal of Ecology* 63 (2): 723-24.

Zimmerman, J.K., T. M. Aide, M. Rosario, M. Serrano and L. Herrera. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology Management*. 77: 65-76.

Figure 3.1. Photographs of plant recruitment at El Verde after Hurricane Maria near the Tabonuco plot. A is Cecropia schreberiana *and B is* Heliconia caribaea *(Photos taken by Nicholas Brokaw).*

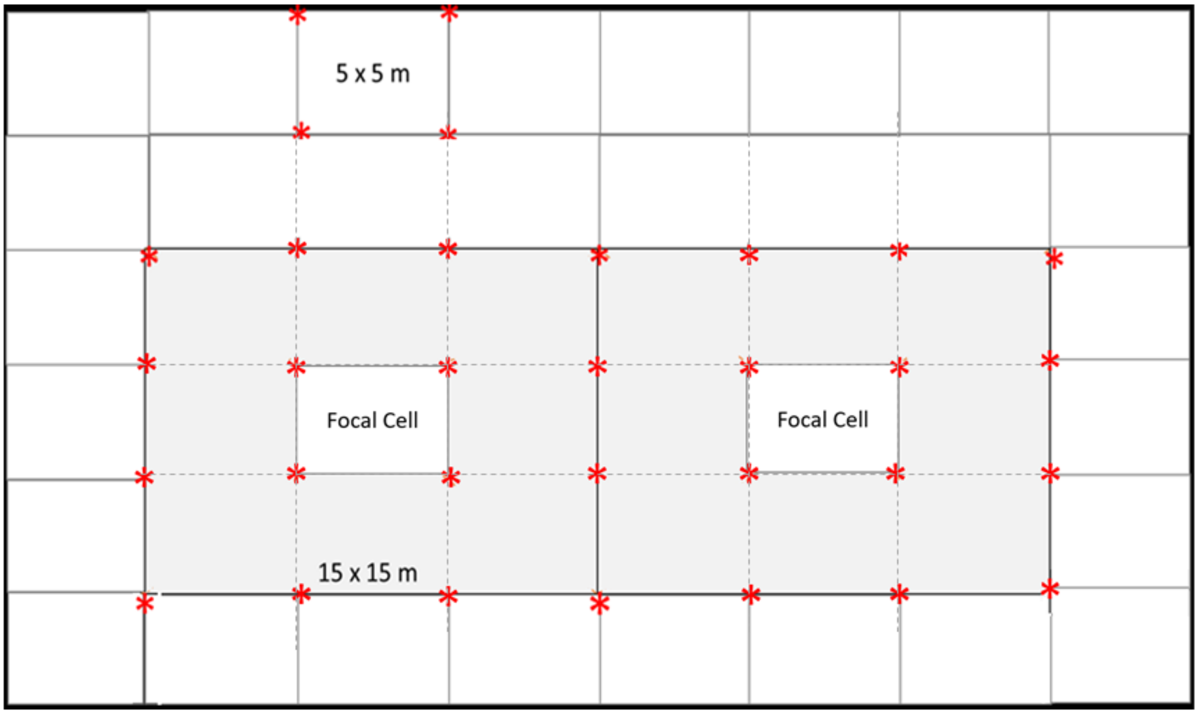

Figure 3.2. The grid points used to collect data on Cecropia and Heliconia. Two different size cells were used, the 5 x 5 m and the 15 x 15 m. Nine 5 x 5 m cells were combined to create 15 x 15 focal cell. I averaged the maximum canopy height of these nine cells and summed all Cecropia *and* Heliconia *within the focal cell. Each red asterisk represents a point of enlarged cell*

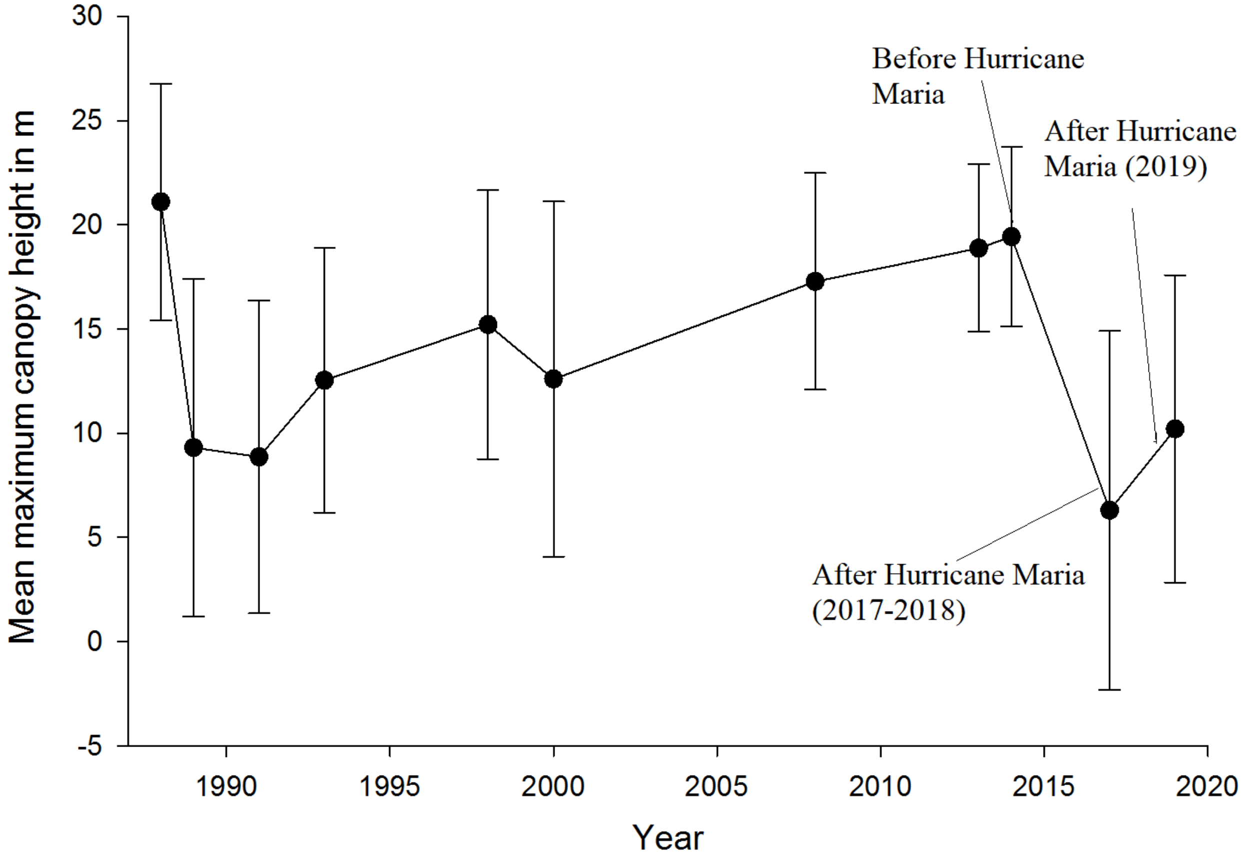

Figure 3.3. Average *height of upper surface of forest canopy from 1989 to 2020, in Puerto Rico in the Tabonuco forest, at 360 m asl. The last measurement before Hurricane Maria was from 2013 to 2014. After Hurricane maria, 2 other measurements were taken. The first was from 2017 to 2018 and the second was in 2019.*

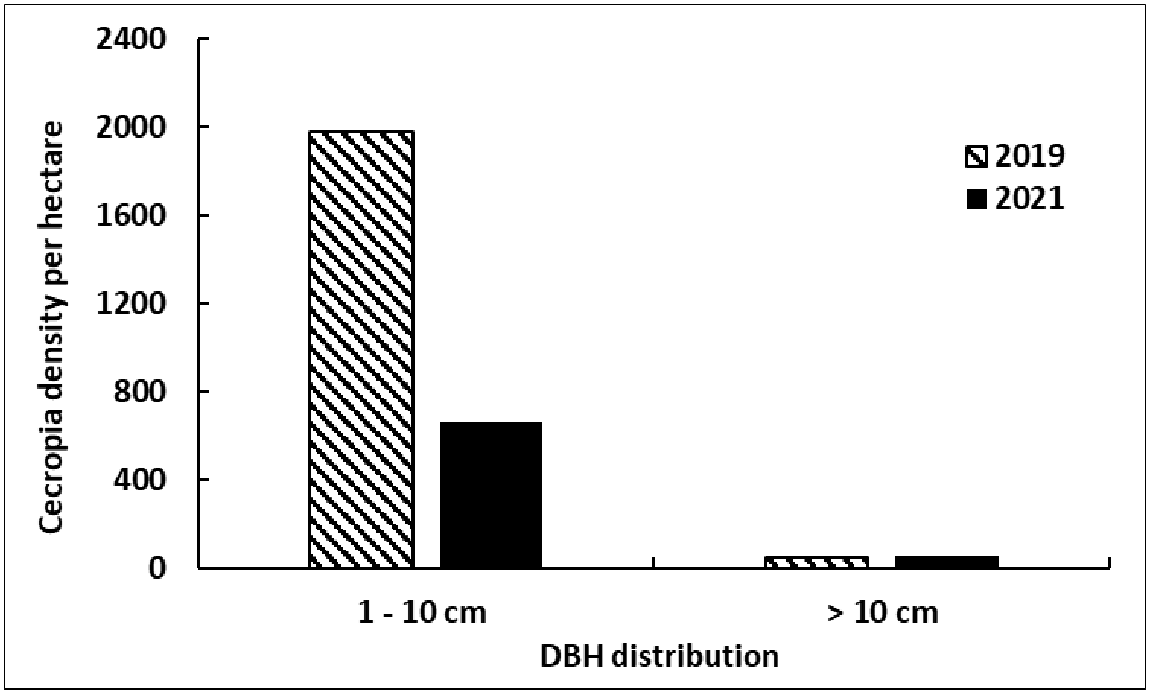

Figure 3.4. Stem size-class distribution of Cecropia schreberiana *within 2019 and 2021 censuses.*

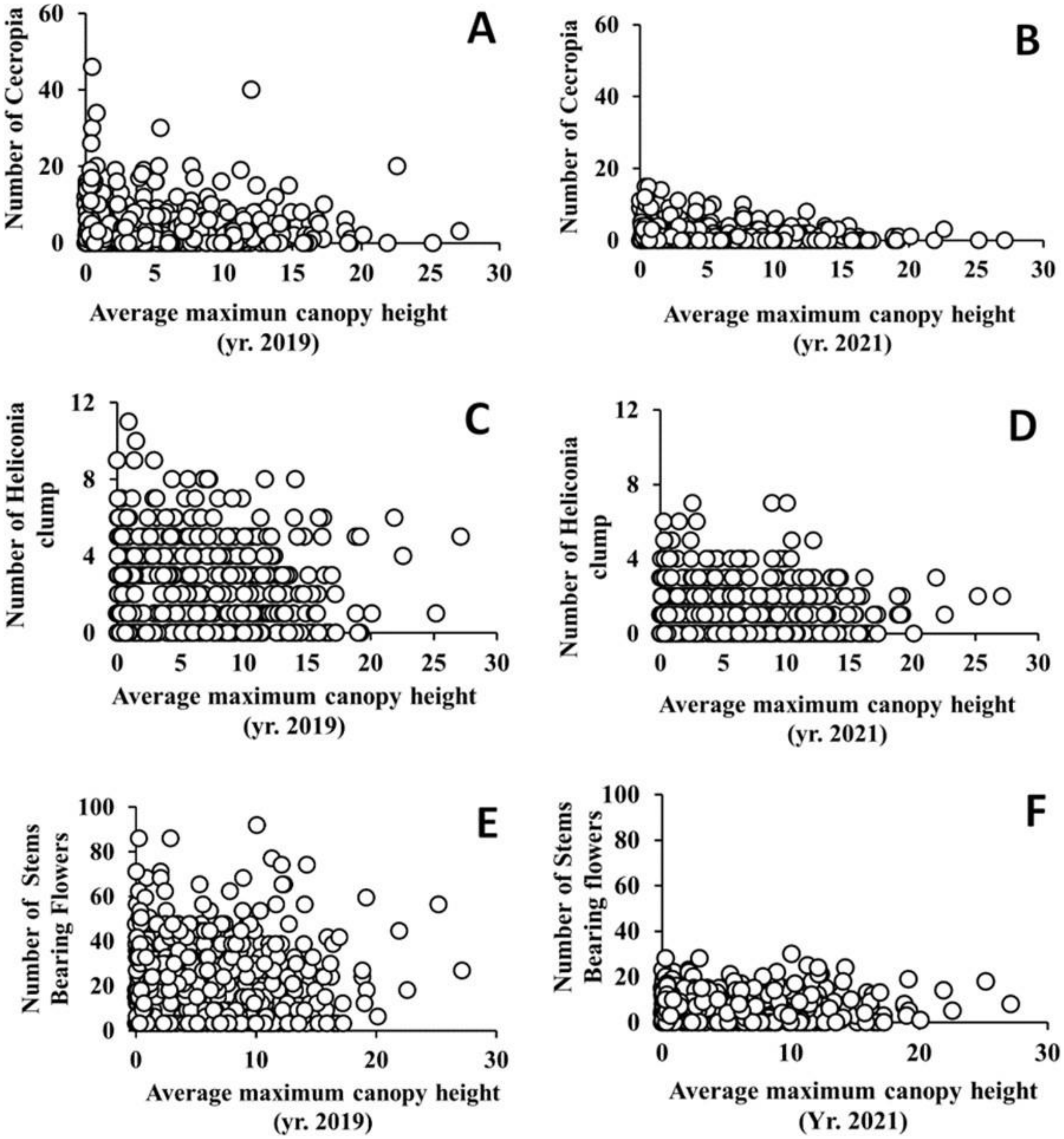

Figure 3.5. Three years and half of understory response of C. Schreberiana *and* H. Caribaea *to forest canopy openness. These two species show high density after Hurricane Maria where mean canopy heightis low. Data for mean canopy height are measurements at 475 points in a 1.08 ha plot. Plant data are from censuses in 5 x 5 m subplots in the 1.08 ha plot.*

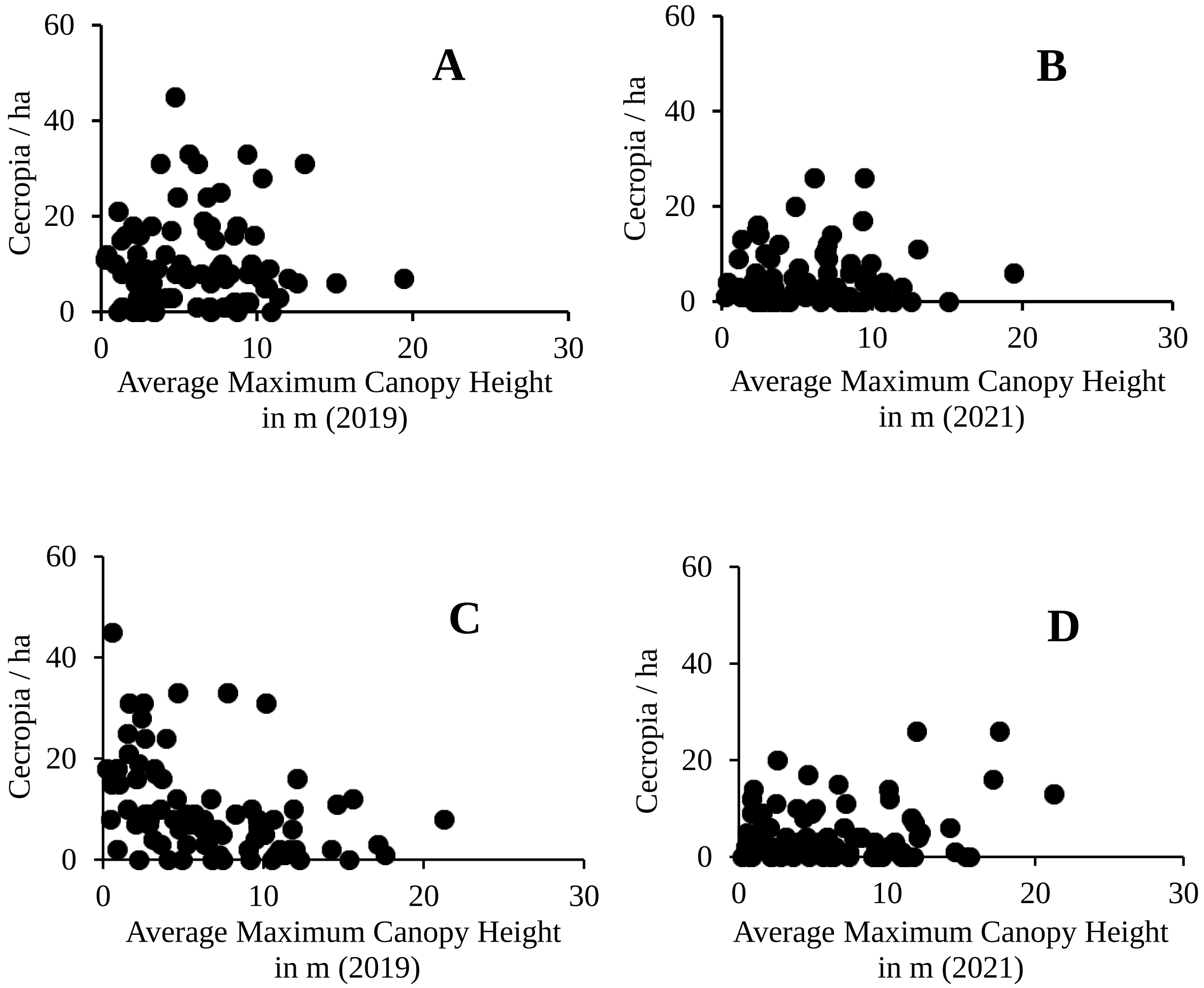

Figure 3.6. Three years and half of understory response of C. Schreberiana *to forest canopy openness. This species shows high density after Hurricane Maria where mean canopy height is low. Plant data are from censuses in 5x5 m subplots at 475 points in a 1.08 ha plot. Data for canopy height in A and B are measurements of average 4 points above the focal cell and 9 neighboring adjacent cells (32 points) in the 1.08 ha plot while C and D are average canopy based on the four points above each 5x5 m focal cell and the 12 adjacent canopy points (16 total).*

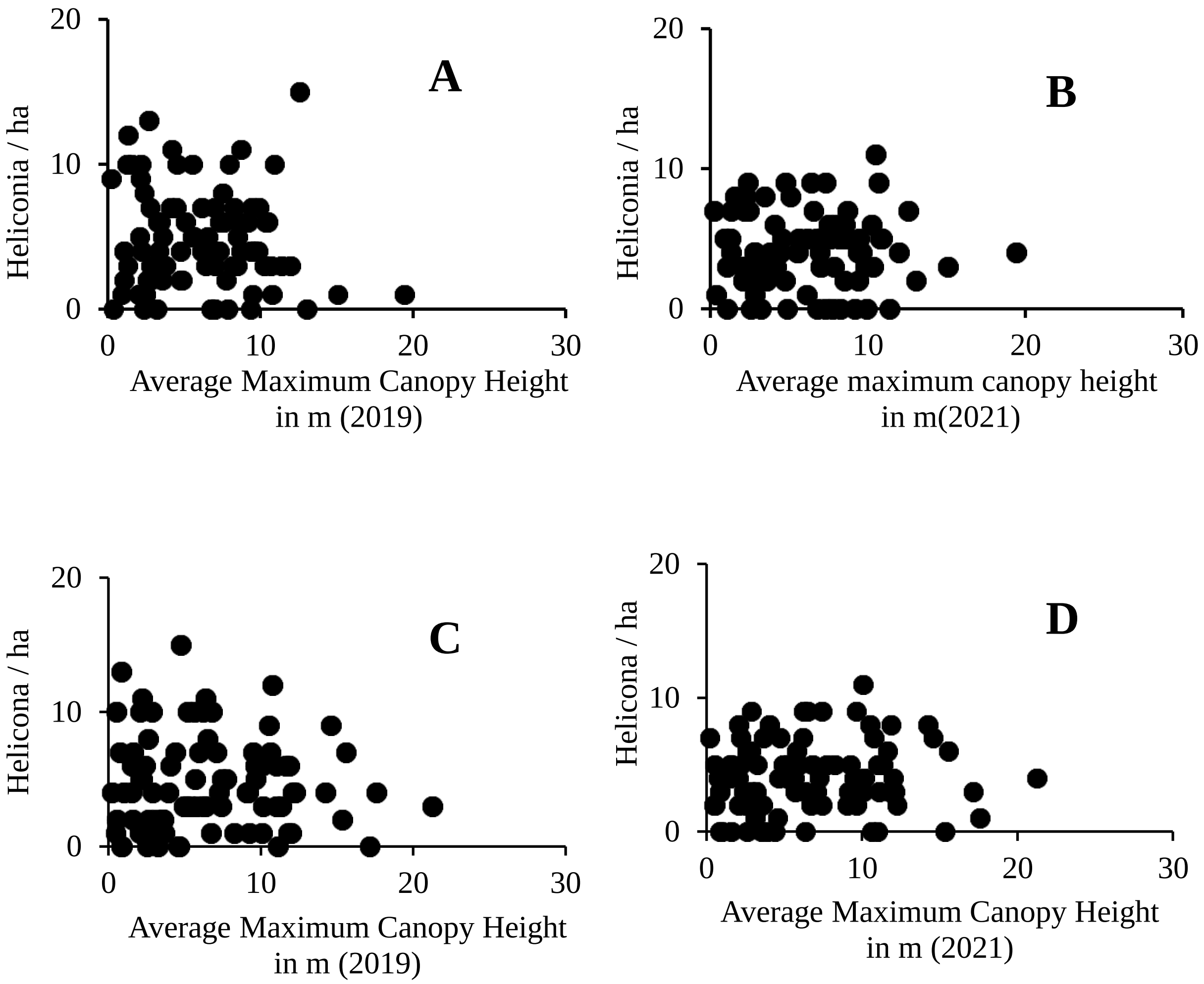

Figure 3.7. Three years and half of understory response of H. Caribaea *to forest canopy openness. This species shows high density after Hurricane Maria where mean canopy height is low. Plant data are from censuses in 5x5 m subplots at 475 points in a 1.08 ha plot. Data for canopy height in A and B are measurements of average 4 points above the focal cell and 9 neighboring adjacent cells (36 points) in the 1.08 ha plot while C and D are average canopy based on the four points above each 5x5 m focal cell and the 12 adjacent canopy points (16 total).*

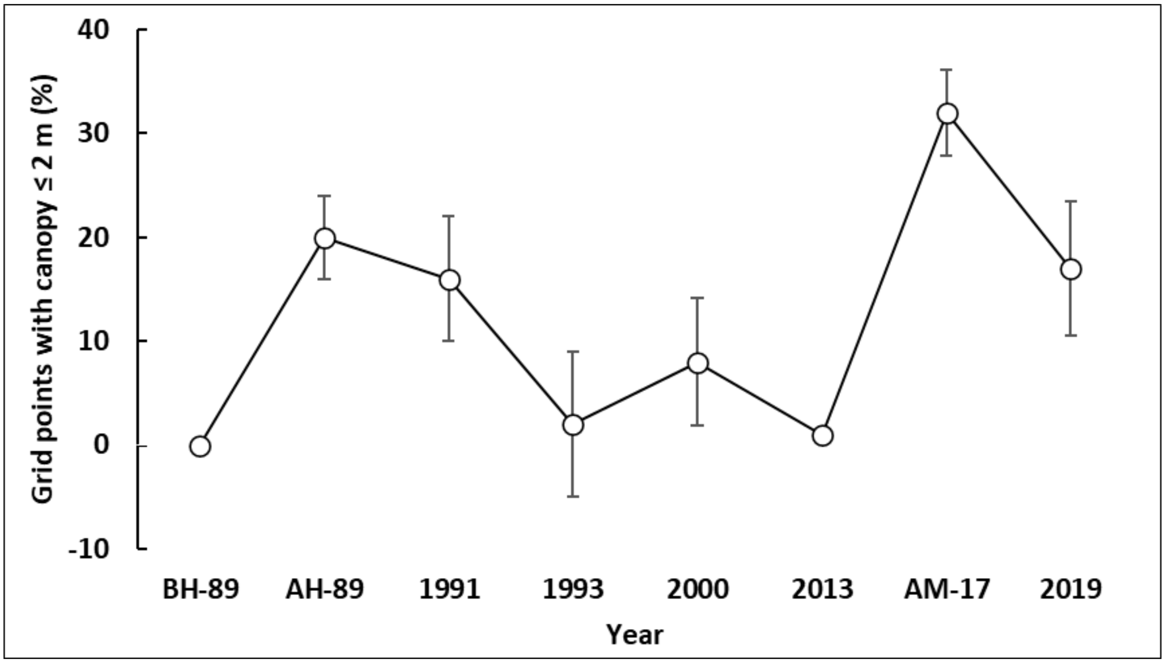

Figure 3.8. Distribution of grid points categories of 0 to 2 cm from before Hurricane Hugo to after Hurricane Maria.

CHAPTER 4

ABOVEGROUND CARBON RESPONSES TO EXPERIMENTAL AND NATURAL HURRICANE IMPACTS IN A TROPICAL WET FOREST IN PUERTO RICO

Hervé Chevalier[1*], Nicholas Brokaw[1], Sheila E. Ward[2], Jess K. Zimmerman[1], Aaron B. Shiels[3], John Bithorn[1], and Samuel Matta Carmona[1]

[1]Department of Environmental Science, University of Puerto Rico-Río Piedras, P.O. Box 70337, Río Piedras, PR 00936-8377

[2]Urbanización Villa Nevárez, 1057 Calle 8, San Juan, Puerto Rico 00927

[3]USDA APHIS, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521 USA

*Corresponding author: hercheve@yahoo.fr

The data used in this research are already published, with those publications and datasets properly cited in this submission. Datasets and Data availability information:

The Canopy Trimming Experiment tree dataset (from which sapling abundances and sizes are derived) is archived and available through EDI at the following link:(Zimmerman 2020b) https://doi.org/10.6073/pasta/a78ae17d741ace1db304491f7ec5b73f

Abstract

Climate change and disturbance make it difficult to project long-term patterns of carbon sequestration in tropical forests, but large ecosystem experiments in these forests can inform predictions. The Canopy Trimming Experiment (CTE) manipulates two key components of hurricane disturbance, canopy openness and detritus deposition, in a tropical forest in Puerto Rico. I documented how the CTE and a real hurricane affected tree recruitment, biomass, and aboveground carbon storage over 15 years. In the CTE treatments I trimmed branches, but I did not fell trees. I expected that during the 14-year period after canopy trimming, regrowth of branches and stems and stem recruitment stimulated by increased light and trimmed debris would help restore biomass and carbon loss due to trimming. Compared to control plots, in the trimmed plots recruitment of palms and dicot trees increased markedly after trimming, and stem diameters of standing trees increased. Data showed that recruitment of small trees adds little to aboveground carbon, compared to the amount in large trees. Nevertheless, this response restored pre-treatment biomass and carbon in the experimental period. In particular, the experimental additions of trimmed debris on the forest floor seemed to stimulate increase in aboveground carbon. Toward the end of the experimental period Hurricane Maria (Category 4 hurricane) trimmed and felled large trees but reduced aboveground carbon less in the plots (including untrimmed plots) than experimental trimming had. Thus, it appears that the amount of regrowth recorded after experimental trimming could also restore aboveground carbon in the forest after a severe hurricane in the same time span. However, Hurricane Maria, unlike the trimming treatments, felled large trees, and it is not certain that over the long term, and with predicted,

more frequent severe hurricanes, that the continued loss of large trees would not eventually result in less aboveground carbon stored in this forest.

Key words: aboveground carbon; biomass; hurricanes; Puerto Rico; subtropical wet forest

4.1 INTRODUCTION

Tropical forests have a strong influence on the global carbon cycle. Tropical forests contain about 553 Pg of carbon, which accounts for 40% of the total carbon in the terrestrial biosphere, with 58% in tropical forest vegetation, 41% in its soil, and 1% in its litter (Soepadmo 1993). Moreover, nearly 20% of the CO_2 currently produced globally by industrial emissions and land conversion is absorbed by tropical forests (Lewis et al. 2009, Viswanath 2019). However, it is uncertain if tropical forests will continue to be carbon sinks or shift to net carbon sources (Clark 2004, Cavaleri et al. 2015), making understanding of their carbon flux and aboveground storage imperative.

Major climatic events affect tropical forest carbon sequestration (Newbery and Lingenfelter 2004, Feeley et al. 2011). For instance, large cyclonic storms (hurricanes, typhoons, cyclones) can quickly modify the structure and dynamics of an ecosystem (Lin et al. 2011, Navarro-Martínez et al. 2012). Hurricane disturbances increase rates of mortality, recruitment, and growth of trees and, consequently, can alter the composition, structure, biomass, and carbon storage of forests (Harmon et al. 1991, Navarro-Martínez et al. 2012, Zimmerman et al. 2014).

Hurricanes have two main impacts on forests. They create forest gaps in which light reaches the forest floor, and they drop debris that decomposes on the forest floor. Thus, hurricanes provide light and nutrients that can promote post-hurricane plant recruitment and growth (Chazdón 1984). This growth restores biomass and stores aboveground carbon (Seedre 2014). Estimation of aboveground carbon is a fundamental to studies of carbon storage, since it is a major compartment in the global carbon balance (Seedre 2014).

In the Luquillo Experimental Forest (LEF) of Puerto Rico, we are conducting a large-scale field experiment, the Canopy Trimming Experiment (CTE), in which canopy is trimmed and resulting debris is manipulated in order to simulate and compare the two main direct effects of hurricanes—increased light in gaps and debris deposition on the forest floor—on post-hurricane forest regrowth (Shiels and González 2014). Because the CTE includes measurements of tree density and size over 15 yr, both before and after the experimental treatments, I can use the experiment to understand the potential effects of hurricane disturbance on biomass and aboveground carbon (Shiels et al. 2015). Moreover, Hurricane Maria in 2017 also affected the CTE experimental plots.

Therefore, I used the CTE to address the following questions. Firstly, do recruitment and growth after trimming in the CTE compensate for aboveground carbon losses due to trimming, in the 15 years of the study, and secondarily: 1) which effect—canopy removal versus debris deposition—had more impact on carbon storage, and 2) how does a real hurricane affect aboveground carbon? Our hypothesis was that regrowth would compensate for carbon loss due to experimental trimming in the period of the study. If this is not true it implies that a predicted increase in frequency of intense hurricanes (Knutson et al. 2010) could eventually reduce aboveground carbon in forests subjected to strong cyclonic storms.

4.2 METHODS

4.2.1 Study site

The study site was in the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico (coterminous with El Yunque National Forest), near El Verde Field Station (EVFS; 18°20’ north, 65°49′ west), a research site of the Luquillo Long-Term Ecological Research Program (Fig.4.1). The elevation is 340-485 m a.s.l., and the terrain is steep and rocky (24% average slope, 25% area covered by boulders; Soil Survey Staff 1995). The soils at EVFS are Oxisols and Ultisols (Soil Survey Staff 1995). The study site showed > 80% forest cover in a 1936 aerial photograph (Shiels et al. 2010). The annual rainfall averages 3500 mm (Shiels et al. 2010). The study site is in “Tabonuco forest” which is a *subtropical wet forest* in the Holdridge System (Ewel and Whitmore 1973). The most common large trees at the site are *Dacryodes excelsa* (Burseraceae; commonly named “Tabonuco”), *Prestoea acuminata* var. *montana* (Arecaceae), *Sloanea berteroana* (Elaeocarpaceae), and *Manilkara bidentata* (Sapotaceae) (Shiels et al. 2015).

As of 1989 the LEF had experienced major hurricanes on average every 50–60 years, including Hurricane Hugo in 1989 (based on records 1769-1989, Scatena and Larsen 1991). But by 2017 it had experienced three severe hurricanes in 28 years (Hugo in 1989, category 5; Georges in 1998, category 3; Maria in 2017, category 4).

4.2.2 Experimental design and treatments

The CTE is a 2 x 2 factorial randomized block design established in Tabonuco forest sites of similar age and land-use history. Three blocks (A, B, C) were established in the Tabonuco forest (within approximately 50 ha). Each of the three blocks had four 30 x 30 m treatment plots (each 0.09 ha; 12 plots in total; Fig. 4.1). Plot size was chosen to reflect the apparent patch size of impacts to forest canopies observed in the LEF following Hurricane Hugo (Brokaw and Grear 1991, Zimmerman et al. 2010, 2014). The 30 x 30 m plots within blocks were located at least 20 m distant from the edge of adjacent plots.

Each 30 m x 30 m plot had a 20 m x 20 m interior plot measurement area, leaving a 5-meter margin around each plot to minimize edge effects. A 1.5-year monitoring period began in 2003, before applying treatments. Each of the four plots within a block was randomly assigned one of four types of treatment: 1) *Trim, debris not removed*, 2) *Trim, debris removed*, 3) *No trim, debris added*, and 4) *Control* (no trim, no manipulation of debris, Fig.4.2). Thus, each block had one of each treatment. Arborists applied these treatments during November 2004 to June 2005 for TRIM 1.

I defined the area trimmed as the vertical projection of the boundaries of the 30 m x 30 m plot. All non-palm trees ≥ 15 cm diameter at 1.3 m height (DBH) inside the 30 m x 30 m area had their branches < 10 cm diameter trimmed (cut off). For non-palm trees between 10 and 15 cm DBH, each tree was trimmed starting at 3 m height and continuing up the stem. For all palm trees ≥ 3 m height, fronds were trimmed at the connection with the main stem; however, the apical meristem was preserved. Vegetation below 3 m height was not trimmed, except that I did trim palm fronds below 3 m. In *Trim debris moved* and *Trim debris not removed* plots, there was an average increase of about 16% in canopy openness (Shiels et al. 2010, Shiels and González 2014, Zimmerman et al. 2014).

The debris resulting from the trimming was sorted into three types: wood (branches ≥ 1.5 cm diameter), leaves and twigs (branches < 1.5 cm diameter and all non-palm foliar material), and palm fronds. To establish wet mass, the debris was weighed immediately after trimming; then samples of debris were weighed and dried at 45°C until constant mass was achieved, to establish wet/dry mass ratios. Then, within each block, all detritus of each of the three types was spread evenly on *Trim, debris not removed* and *No trim, debris added* plots. On average 11,157±362 kg (mean ±SE) of wet mass detritus (6,530 ±186 kg dry mass) was cut on each of the six *Trim* plots.

I made TRIM 2 in 2014, with just one manipulative treatment: *Trim, debris not removed.* Thus in 2014 I did not remove debris from any plots nor add debris to any plots. The same trimming protocol was used for *Trim, debris not removed* plots in 2014 as in 2004. On average 9,379 ±179 kg (mean ±SE) of wet mass detritus (3,995 ±170 kg dry mass) was trimmed.

4.2.3 Plant measurements

Pre-treatment measurements were taken in March 2003 and October 2004. In all manipulative and *Control* treatments in all blocks, I measured the diameter at breast height (DBH, H = 130 cm) of all woody plants ≥ 1 cm DBH, including trees, shrubs and lianas (hereafter termed “stems”). After TRIM 1, measurements were made in September 2007, October 2008, November 2009, February 2011, February 2012, and February 2014. Following TRIM 2, in October 2014, measurements were taken in October 2014, October 2015, and October 2016. Measurements were also taken in December 2017, after the passage of Hurricane Maria, and in November 2018.

I followed the Center for Tropical Forest Science protocol (Condit 1998) for measuring stems. To minimize sampling error between subsequent measurements, I marked points of measurement with lumber crayons. Vernier calipers were used to measure stems with DBH < 5 cm. Diameter tapes were used to measure stems with diameters ≥ 5 cm DBH.

4.2.4 Aboveground carbon calculations

Our study focused on live aboveground carbon. I did not consider belowground carbon nor litter in our analysis. To measure the effect of canopy trimming on the aboveground carbon dynamics, I estimated aboveground biomass and converted biomass to carbon. I used biomass equations previously used in the forests of the LEF. I separately estimated biomass of palms and non-palm trees. For palms, I used: $Y = ax + b$, where Y is aboveground biomass, x is height in m, and a and b are estimated parameters of the fitted models (Frangi and Lugo 1985). For non-palm trees, I used two equations: 1) for trees < 5 cm DBH, $Y = 0.3210D^{1.3925}$ and 2) for trees > 5 cm DBH, $Y = 4.7306-2.8566D+0.5832D^2$, where Y is estimated biomass and D is the diameter at breast height in cm (Weaver and Gillespie 2017. I then multiplied the aboveground biomass by 0.47 to obtain aboveground carbon (Macías et al. 2017). Our statistical analyses were made in R, SigmaPlot, and Excel. I made a general linear model to determine which hurricane effect—canopy removal versus debris deposition—had more impact on carbon storage.

Preliminary analysis showed that using DBH to estimate biomass loss and gain in the *Trim* treatments was not adequate. This is because trees were not felled (thus not greatly changing biomass), and because DBH does not take into account the biomass of branches that were trimmed nor branches that regrew on the trimmed trees. Therefore, I used the following method to estimate biomass loss and gain in *Trim, debris not removed* (the only treatment for which this calculation was possible). As described above I weighed trimmed material to estimate biomass loss after both TRIM 1 and after TRIM 2. Most important, I used the same guidelines (branches <10 cm diameter trimmed, etc.) to perform both trims. So, whatever I trimmed at TRIM 2 was what had regrown since TRIM 1. Thus, the weight trimmed at TRIM 1 is biomass loss, and the weight trimmed at TRIM 2 is biomass gained between treatments (plus gains or losses estimated from DBH).

4.3 RESULTS

Our dataset contained a cumulative total of 24,678 individual stems of 83 species (Supplementary table 4.1) for the whole study period. Among these 24,678 stems, 7,545 were in *Trim, debris not removed*; 8,490 were in *Trim, debris removed*; and 3,688 were in *No trim, debris added*; and 4,955 were in *Control.*

4.3.1 Stem recruitment and dynamics

The total number of stems ≥ 1.0 cm DBH in all plots was decreasing before any treatments (Fig. 4.3), perhaps due to natural thinning after previous hurricanes. But after TRIM 1 in 2004, stem number increased respectively by 65% and 151% of pre-trim values in *Trim,* *debris removed* and *Trim, debris not removed*, where there were significantly more stems than in *No trim, debris added* and *Control* (*P < 0.05). However, the increase was transitory; by 2009, the number of stems in both *Trim* plots had fallen (Fig. 4.3), to reach 26% in *Trim, debris removed* and 15% *Trim, debris not removed* of peak values by 2014. It increased again by 114% of lowest value in *Trim, debris not removed* after TRIM 2 (not applied to *Trim, debris removed*) in 2016.

It was mainly the number of small stems that increased in the *Trim* treatments (Fig. 4.4). These stems peaked in 2007-2008, then declined until increasing again after TRIM 2 in *Trim, debris not removed*. The decline of stems < 5 cm DBH was mostly due to mortality, not to growth into larger diameter classes (Fig. 4.5). There were only slight changes in stems < 10 cm DBH in *No trim, debris added* and *Control*, until after Hurricane Maria, when small stems increased in all three manipulative treatments and *Control* (Fig. 4.5)

4.3.2 Aboveground carbon dynamics

Aboveground carbon, as determined from stem DBH, was increasing in all manipulative treatments and *Control* before any treatments (Fig. 4.6), perhaps due to recovery after previous hurricanes. Between trims it increased in *Trim, debris not removed, No trim, debris added,* and *Control*; it decreased in *Trim, debris removed* 3 years after TRIM 1. It increased fastest in *No trim, debris added*. After 2014 aboveground carbon leveled off, then declined. After Hurricane Maria aboveground carbon declined in all treatments and *Control* (Fig. 4.6). From 2016 to 2018 (before to after Hurricane Maria) aboveground carbon decreased in *Trim, debris not removed* by

4,689 kg/ha, in *Trim, debris removed* by 4,949 kg/ha, in *No trim, debris added* plot decreased by 7,800 kg/ha, and in *Control* by 10,068 kg/ha.

In *No Trim, debris added*, debris deposition had a significant effect (***$P < 0.001$) during the experimental period, 2004-2017 (Fig. 4.6). It also has a significant effect in *Trim, debris not removed* (**$P < 0.01$) in this period. By contrast, in *Trim, debris removed* there was a significant increase of aboveground carbon only in 2007 (**$P < 0.01$).

The many small DBH stems recruited during the experiment in all treatments and *Control* contributed little to aboveground carbon, whereas the many fewer large DBH stems contributed greatly and disproportionately more (Fig. 4.7). For instance, 17,215 trees with diameters ranging from 1 to 10 cm accounted for more than 73% of all stems but contributed only 3.27% of aboveground biomass, while 221 trees with diameters greater or equal to 50 cm accounted for 0.94% of stems contributed to 35% of aboveground biomass.

Based on trimmed material removed, the average aboveground carbon loss at TRIM 1 in *Trim, debris not removed* was 11,157 kg, and the average loss at TRIM 2 was 9,379 kg, using the same trim protocol as for TRIM 1. Therefore *Trim, debris not removed* had gained 9,379 kg due to stem recruitment and regrowth of branches < 10 cm diameter and leaves between 2004 and 2014. It had also gained 3,117 kg due to recruitment and DBH increment between 2004 and 2014. Adding these together I get 1,339 kg, which is the total increment after the TRIM 1 loss. This exceeds the loss due to TRIM 1. Thus, in *Trim, debris not removed* aboveground carbon gained via recruitment, regrowth of branches and leaves, and diameter increment, all together, did compensate for its loss at TRIM 1. Hurricane Maria removed 4,684 kg ha^{-1}, 4,949 kg ha^{-1}, 7,800 kg ha^{-1}, and 10,068 kg ha^{-1} respectively from *Trim, debris not removed*, *Trim, debris removed, No trim, debris added,* and *Control*. These amounts for *Trim, debris not removed*, and *Trim, debris removed* are less than was removed at TRIM 1 in the two trim treatments.

4.4 DISCUSSION

This paper describes stem number and aboveground carbon dynamics through 15 years of pre- and post-treatments designed to simulate hurricane impacts, and it describes the effects of a true hurricane. Our results showed an increase of more than 60% in stem density (compared to post-trim density) 3 years after TRIM 1 in the two *Trim* treatments. However, this increase was transitory; after 3 years stem density dropped, as found by Shiels et al. (2010) and Zimmerman et al. (2014). In both *Trim* treatments, recruitment of saplings after TRIM 1 (2004) seemed to end in 2007, and recruitment after the TRIM 2 (2014) seemed to end in 2017. It appears that canopy opening offered opportunity for seedlings and saplings to establish. Then as the forest canopy closed, the light available declined rapidly at the forest floor (Shiels et al. 2010, Shiels and González 2014), and recruitment diminished. In 2017 Hurricane Maria disturbed the canopy in all plots and induced stem recruitment.

This plant recruitment had little effect on the dynamics of aboveground carbon, because recruited stems were small and mostly short-lived. Similarly, in their study of above-ground biomass accumulation after hurricanes in Nicaragua Mascaro et al. (2005) found that trees ranging from 3.2–10 cm in DBH made up more than 89% of all stems but accounted for only

2.5% of aboveground biomass, while seven trees > 70 cm DBH made up 1.4% of stems but accounted for 45% of aboveground biomass. Other studies in Nepal (Gautam and Mandal (2016), in Ethiopia (Yohannes and Teshome (2015), and in Tanzania (Mwakisunga and Majule (2012) all report that large diameter trees account for the bulk of aboveground carbon in forests (Lutz et al. 2018).

In *No trim, debris added* aboveground carbon increased by 4% in 2007 and 9% in 2014, while in *Trim, debris removed* there was a 2% increase by 2007 then a decrease of 5% in 2014, before the second trim. Thus, adding debris seems to have increased aboveground biomass. In earlier analyses, debris added to *No Trim, debris added* appeared to increase basal area increment (Shiels et al. (2010). This increase was attributed to a fertilization effect, the benefits of soil moisture increase, or other unmeasured effects of decomposing debris on tree growth (Zimmerman et al. 2014). Consequently, from CTE results I conclude that adding debris as a hurricane effect had a greater effect than trimming the canopy on aboveground carbon. Debris deposition also influences belowground carbon. In a previous study in the CTE, Gutiérrez and Silver (2018) found that belowground carbon significantly increased in *No trim, debris added*. They also argued that canopy opening as a treatment alone did not significantly affect carbon.

Over the first 14 yr of the experiment (2003-2017), before Hurricane Maria, net aboveground carbon increased in all treatments including the control, except in *Trim, debris removed*, despite experimental trimming that had removed 11,157 kg of biomass in TRIM 1. This recovery of aboveground carbon demonstrates a degree of forest resilience to biomass and aboveground carbon loss. Thus, results from the CTE confirm our expectation that during the period after experimental canopy trimming (but no experimental tree felling), stem recruitment, regrowth of branches, and stem growth would substantially restore biomass and carbon loss. Then, toward the end of the experimental period, Hurricane Maria both trimmed and felled trees, and aboveground carbon decreased from 65,005 to 60,320 kg/ha in the *Trim, debris not removed* treatment and 53,607 to 43,539 kg/ha in *Control* plots. This reduced aboveground carbon less in the plots (especially untrimmed plots) than experimental trimming had. Thus, it appears that the amount of regrowth recorded after experimental trimming would also restore aboveground carbon in the forest after a severe hurricane in the same time span.

However, Hurricane Maria, unlike the trimming treatments, felled large trees. Hurricanes affect large trees more than small trees (Everham and Brokaw 1996), and Caribbean hurricanes are projected to be more intense due to atmospheric warming (Knutson et al. 2010). Over the long term, a continued loss of large trees could eventually result in less aboveground carbon stored in this Puerto Rican Forest and in other hurricane-affected tropical forests.

4.5 ACKNOWLEDGEMENTS

Jess K. Zimmerman, Aaron B. Shiels, and Nicholas Brokaw developed the CTE plan; Shiels directed the field work; Samuel C. Matta and John Bithorn worked on the trims and collected routine field data over the 15 years of the project; Hervé Chevalier performed the data analysis; Chevalier, Brokaw, Sheila E. Ward, Shiels, and Zimmerman wrote the manuscript. I thank the volunteers and staff who performed the physically demanding task of canopy detritus collection and redistribution; the team of professional arborists from Econet S.A, headed by William González, for their trimming expertise; and J. Aaron Hogan for sharing data and valuable editing. Funding for this research was provided by cooperative grants from the US National Science Foundation (NSF), the University of Puerto Rico, and the International Institute of Tropical Forestry USDA Forest Service, supporting the Luquillo LTER program (NSF grants DEB-0218039 and DEB-0620910).

4.6 LITERATURE CITED

Aide, T.M., M.A. Clark, D. Redo, M. Bonilla-Moheno et al. 2013. Deforestation and reforestation of Latin America and the Caribbean (2001-2010). *Biotropica* 45:262-271.

Brokaw, N.V., E.M. Everham III. 1996. Forest Damage and Recovery from Catastrophic Wind. *The Botanical Review* 62:113–85.

Brokaw, N.V., and J.S. Grear. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica* 23:386-392.

Cavaleri, A.M., S.C. Reed, W.K. Smith, and T.E. Wood. 2015. Urgent need for warming experiments in tropical forests. *Global Change Biology* 21: 2111-2121. https://doi.org/10.1111/gcb.12860.

Cházdon, R.L. and N. Fetcher. 1984. Photosynthetic light environments in a lowland rain forest in Costa Rica. *Journal of Ecology* 72:553-564.

Condit, R. 1998. Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. Springer-Verlag, Berlin.

Ewel, J. J., and J. L Whitmore.1973. Ecological life zones of Puerto Rico and US Virgin Islands. United States Forest Service Research Paper. ITF-18. Institute of tropical forestry, Rio Piedras, Puerto Rico.

Feeley, K.J., S.J. Davies, R. Perez, S.P. Hubbell, and R.B. Foster. 2011. Directional changes in the species composition of a tropical forest. *Ecology* 92:871-82.

Frangi, J.L., and A.E. Lugo. 1985. Ecosystem dynamics of a subtropical floodplain forest. *Ecological Monographs* 55:351-369. https://www.jstor.org/stable/1942582?seq=1.

Gautam, T.P., and T.N. Mandal. 2016. Effect of disturbance on biomass , production and carbon dynamics in moist tropical forest of Eastern Nepal. *Forest Ecosystems* 3:11. https://doi.org/10.1186/s40663-016-0070-y.

Harmon, M.E., D.F. Whigham, J. Sextone, and I. Olmstead. 1991. Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. *Biotropica* 27:305-316.

Karnosky, D.F. 2003. Impacts of elevated atmospheric CO_2 on forest trees and forest ecosystems : knowledge gaps. *Environment International* 29:161-169.

Knutson, Thomas R, J.L. Mcbride, J. Chan, K. Emanuel, G.Holland, C.Landsea, I. Held, J.P. Kossin, A.K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. *Nature Geoscience* 1–7. https://doi.org/10.1038/ngeo779.

Lewis S.L., G. Lopez-Gonzalez, B. Sonké et al. 2009. Increasing carbon storage in intact African Tropical Forests. *Nature* 457(7232):1003-6

Lin, T., S.P. Hamburg, K. Lin, L. Wang, C. Chang, Y. Hsia, M.A. Vadeboncoeur, C.M.M. Mcmullen, and C. Liu. 2011. Typhoon disturbance and forest dynamics: lessons from a northwest pacific subtropical forest. *Ecosystems*, 127-43. https://doi.org/10.1007/s10021-010-9399-1.

Lodge, D.J., F.N. Scatena, C.E. Asbury, and M.J. Sánchez. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. *Biotropica* 23:364-372.

Lutz, J.A., T.J. Furniss, D.J. Johnson, S.J. Davies, D. Allen, A. Alonso, K.J. Anderson-Teixeira, et al. 2018. Global importance of large-diameter trees. *Global Ecology Biogeography* 1-16. https://doi.org/10.1111/geb.12747.

Macías, C.A.S., J.C.A. Orihuela, and S.I. Abad. 2017. Estimation of aboveground live biomass and carbon stocks in different plant formations and in the soil of dry forests of the Ecuadorian Coast. *Food and Energy Security* 6:e115

Mascaro, J., I. Perfecto, O. Barros, D.H. Boucher, I. Granzow de la Cerda, J. Ruiz, and J. Vandermeer. 2005. Aboveground biomass accumulation in a tropical wet forest in Nicaragua following a catastrophic hurricane disturbance. *Biotropica* 37:600-608.

Mwakisunga B., Majule A.E. 2012. The Influence of Altitude and Management on Carbon Stock Quantities in RungI Forest, Southern Highland of Tanzania. *Open Journal of Ecology* 2:214-221.

Navarro-Martínez, A., R. Durán-García, and M. Méndez-González. 2012. The impact of the Hurricane Dean on the structure and arboreal composition of a managed forest in Quintana Roo, Mexico. *Madera y Bosques* 18:57-76.

Newbery, D.M., and M. Lingenfelter. 2004. Resistance of a lowland rain forest to increasing drought intensity in Sabah, Borneo. *Journal of Tropical Ecology* 20:613-624.

Plotkin, B.A., D. Foster, J. Carson, and A. Magill. 2013. Survivors, not invaders, control forest development following simulated hurricane. *Ecology* 94:414-423.

Scatena, F.N., M.C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica* 23:317-323.

Seedre, M. 2014. Disturbance effects on boreal forest ecosystem carbon dynamics. Dissertation. Estonian University of Life Sciences, Friedrich Reinhold Kreutzwaldi 1a, 51014 Tartu, Estonia.

Shiels, A.B., G. González, D.J. Lodge, M.R. Willing, and J.K. Zimmerman. 2015. Cascading effects of canopy opening and debris deposition from a large-scale hurricane experiment in a tropical rain forest. *BioScience* 65: 871-81.

Shiels, A.B., and G. González. 2014. Understanding the key mechanisms to tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects. *Forest Ecology Management* [this issue].

Shiels, A.B., J.K. Zimmerman, D.C. Garcia-Montiel, I. Jonckheere, J. Holm, D. Horton, and N.V. Brokaw. 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *Journal of Ecology* 98:659-673.

Soepadmo, E. 1993. Tropical rain forests as carbon sinks. *Chemosphere* 27:1025-1039.

Soil Survey Staff. 1995. Order 1 soil surveys of Luquillo Long-Term Ecological Research Grid, Puerto Rico. United States Department of Agriculture, Natural Resource Conservation Service.

Souza, A.F, and S.J. Longhi. 2019. Disturbance history mediates climate change effects on subtropical forest biomass and dynamics. *Ecology and Evolution* 9:7184-7199.

Viswanath, S., and S. Sandeep. 2019. Carbon dynamics in tropical forest ecosystems. Pages 1-16 in Institute of Wood Science and Technology, editors. 14th National Sylviculture Conference. Forest and sustainability: securing a common future. Indian Consul of Forestry Research and Education, Dehradun. 18th Cross, Malleswaram, Bengaluru-560003, Karnataka, India.

Weaver, P.L., and A.J.R. Gillespie. 2017. Tree biomass equations for the forests of the Luquillo Mountains, Puerto Rico. *The Commonwealth Forestry Review* 71:35-39.

Yohannes, H., and T. Soromessa. 2015. Carbon stock analysis along forest disturbance gradient in Gedo Forest : implications of managing forest for climate change mitigation. *Journal of Ecosystem and Ecography* 5:3.

Zhao, H., Z. Li, G. Zhou, Z. Qiu, and Z. Wu. 2020. Aboveground biomass allometric models for evergreen broad-leaved forest damaged by a serious ice storm in southern China. *Forests* 11:320

Zimmerman, J.K., J.A. Hogan, A.B. Shiels, J.E. Bithorn, S. Matta Carmona, and N.V. Brokaw. 2014. Seven-year responses of trees to experimental hurricane effects in a tropical rainforest, Puerto Rico. *Forest Ecology and Management* 332:64-74.

Zimmerman, J.K., L.S. Comita, M. Uriarte, N.V. Brokaw, and J. Thompson. 2010. Patch dynamics and community metastability of a tropical forest: compound effects of natural disturbance and human Land use. *Landscape Ecology* 25:1099-1111.

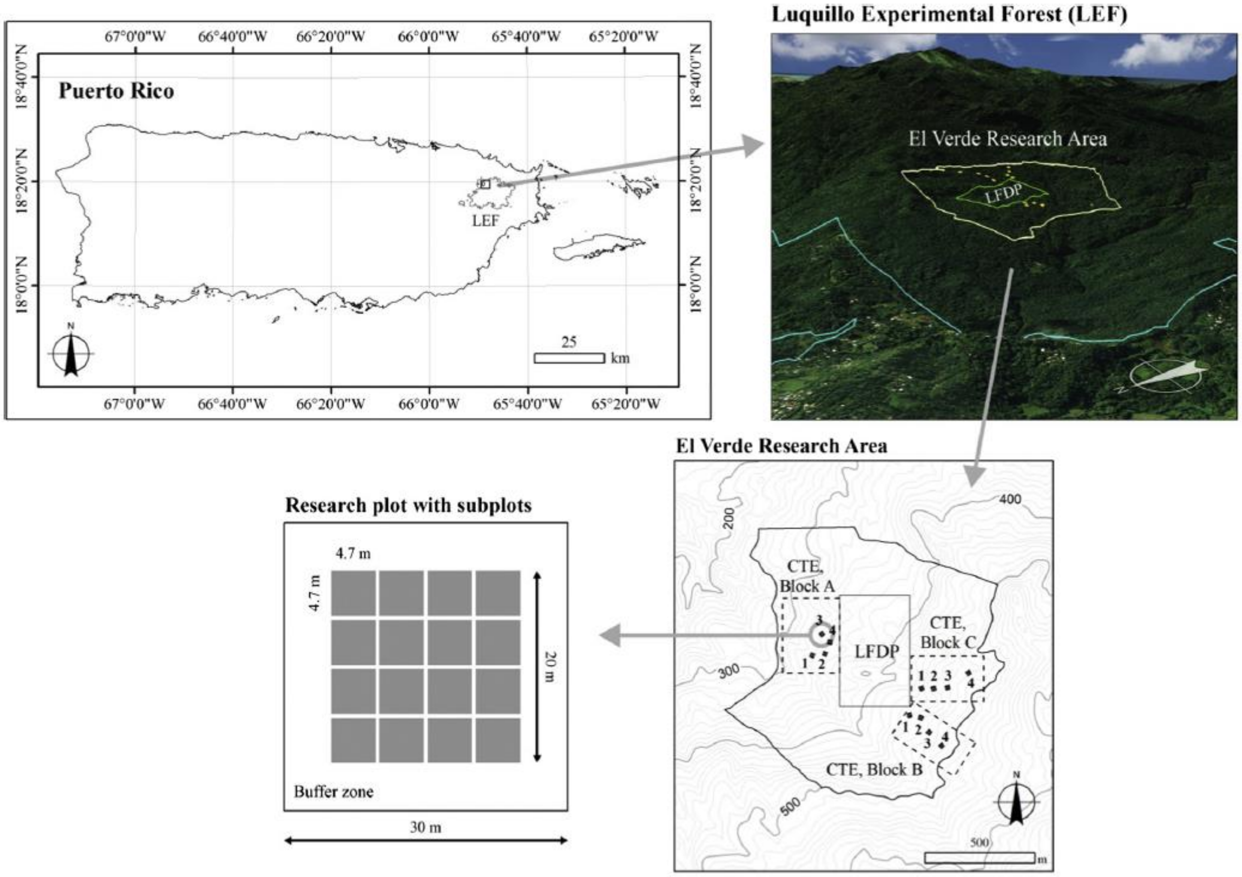

Figure 4.1 Location of the Canopy Trimming Experiment (CTE) in El Verde research area within the Luquillo Experimental Forest (LEF), northeastern Puerto Rico. CTE blocks are adjacent to the Luquillo Forest Dynamic Plots (LFDP), and inferred area covered by each block (broken lines) is 40,000 m^2*. Treatment plots (square plots, numbered 1 - 4 within each block) are each 30 x 30 m. Within each plot, a 5 m buffer area surrounds a 20 x 20 m core measurement area where 16 subplots (quadrats, each 4.7 x 4.7 m) are separated by trails (white lines) to minimize observer impacts. Figure from Aaron B. Shiels and Grizelle González (2014).*

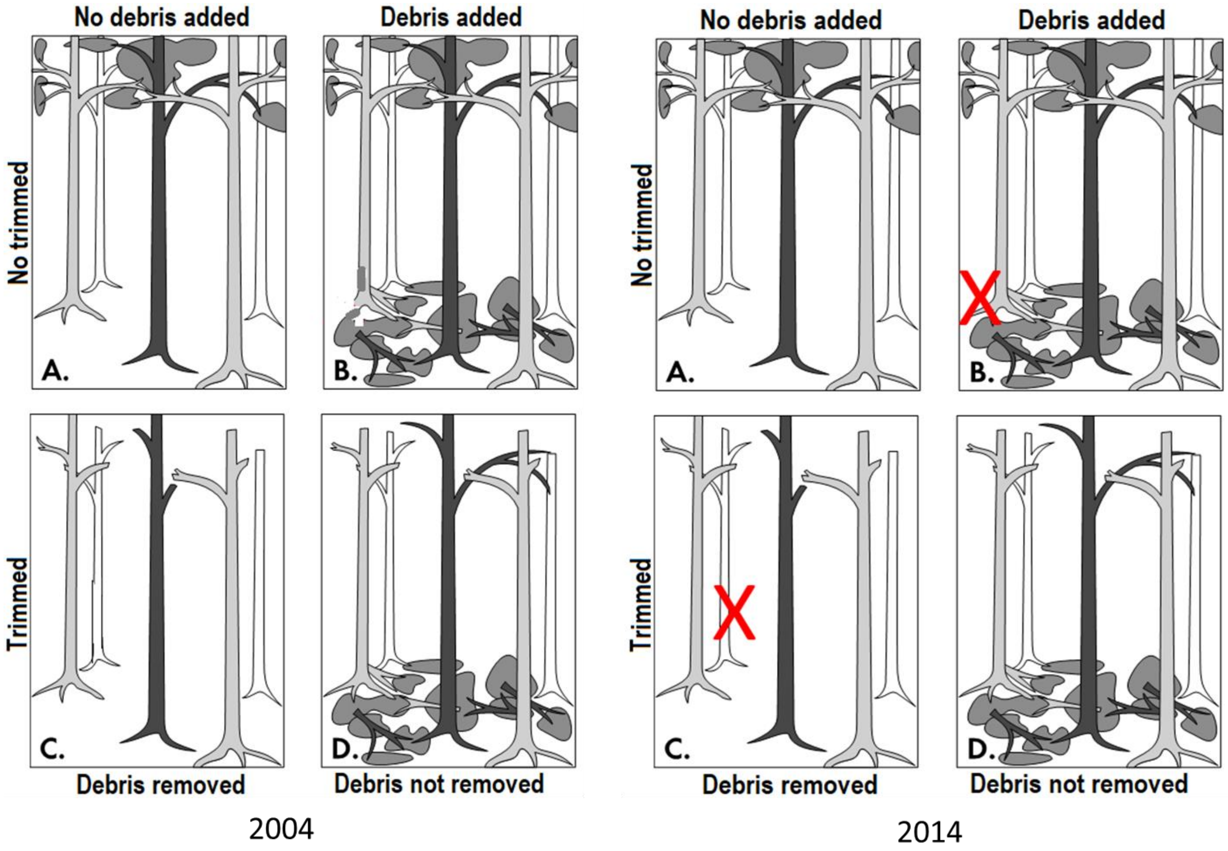

Figure 4.2. Canopy trimming experiment diagrams. In 2004, I had four treatments (No Trim, No debris added (control); No Trim, Debris added, Trim, Debris removed, Trim, Debris not removed) but in 2014 I only applied 2 treatments (No Trim, No Debris added and Trim, Debris not removed).

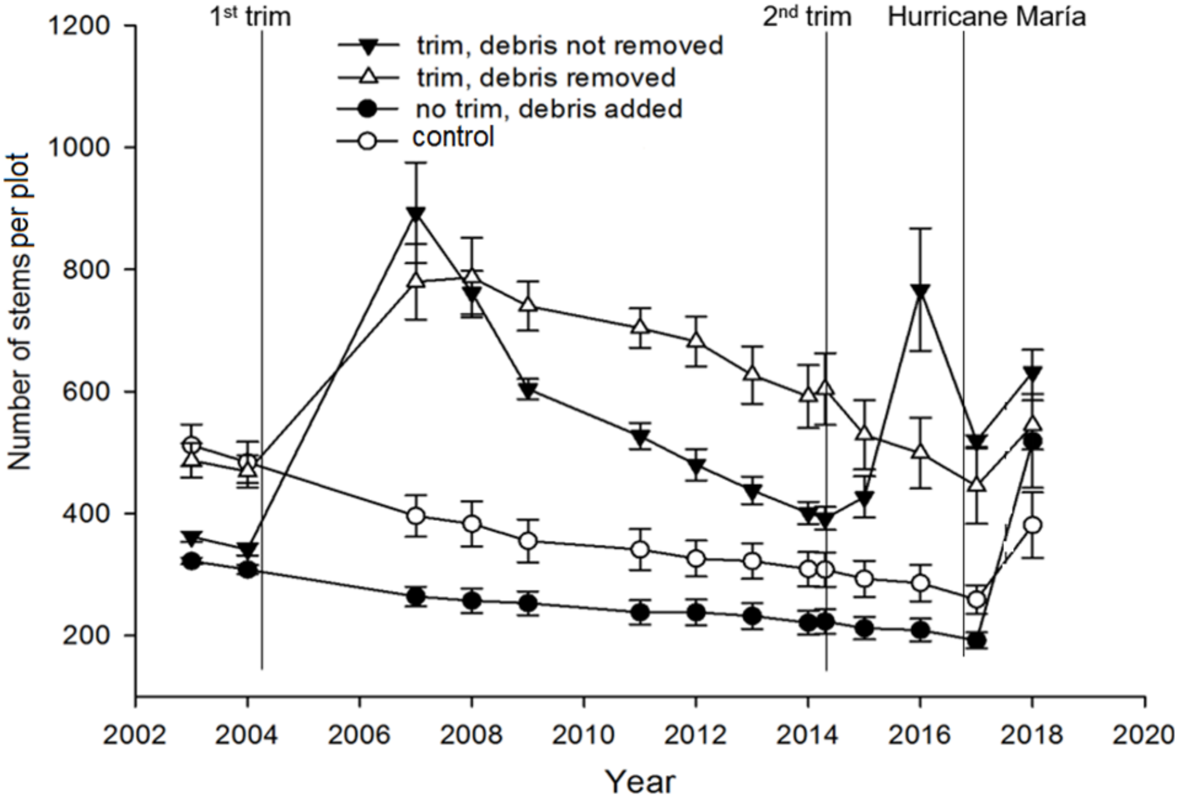

Figure 4.3. Stem (≥ 1cm DBH) recruitment dynamics over time. The three vertical bars indicate the dates of TRIM 1, TRIM 2, and Hurricane Maria. The error bars are standard deviations. The two error bars in 2014 indicate the two censuses for that year (February and October, respectively). The number of stems is the mean and standard deviation among three replicates of each treatment. TRIM 2 was performed only for Trim, debris not removed.

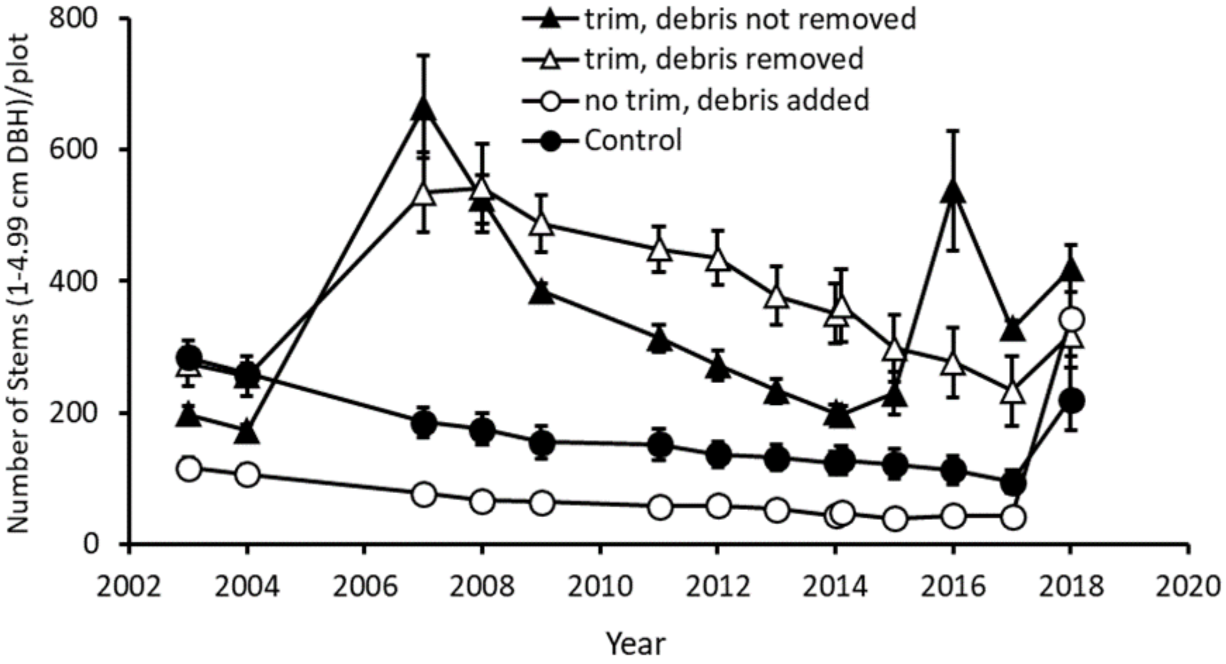

Figure 4.4. Number of stems ranging from 1 to 4.99 cm DBH within the treatments.

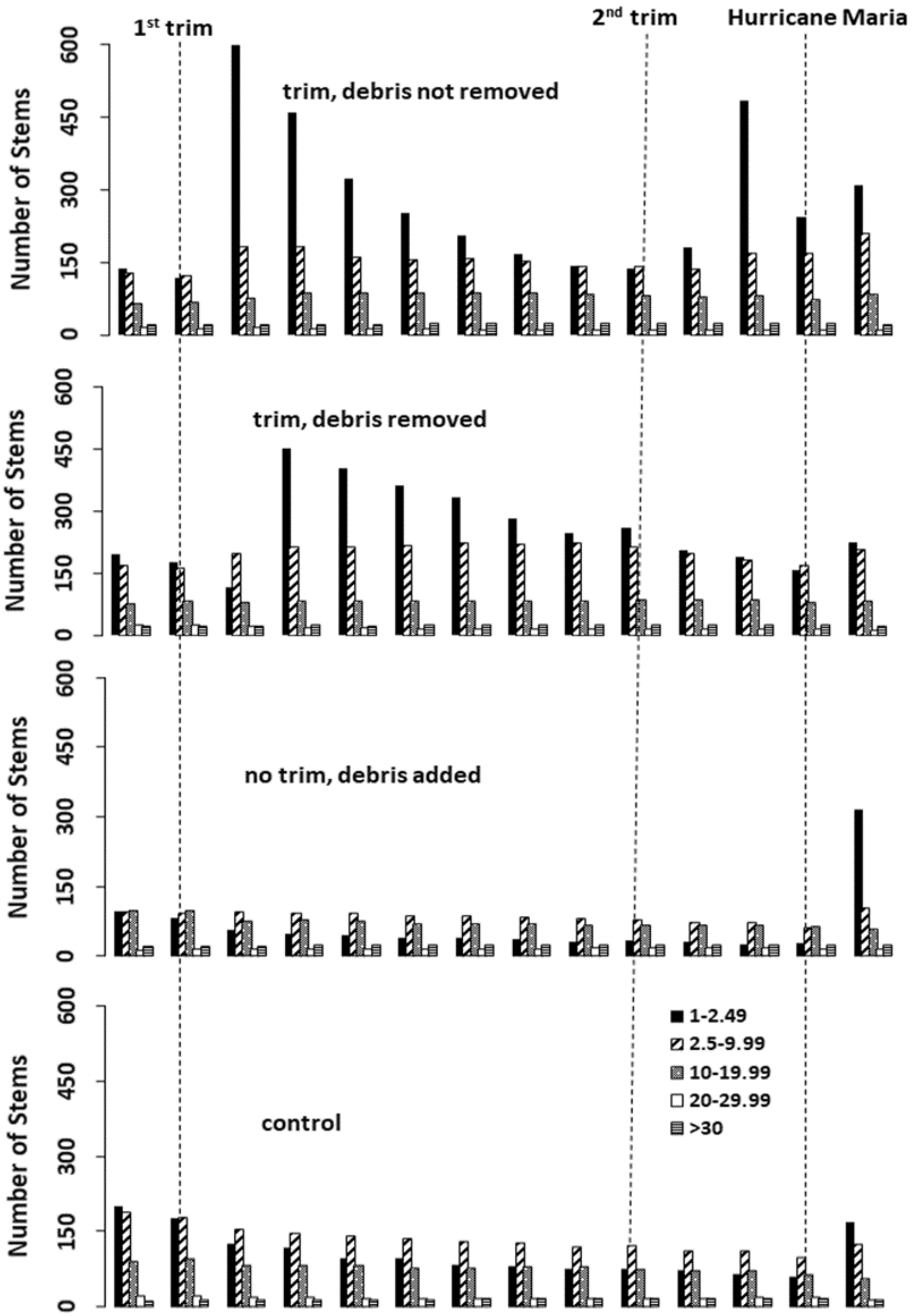

Figure 4.5. Diameter-class distributions of stems ≥ 1 cm DBH at each census date (2014a and 2014b) indicate the two censuses in 2014. TRIM 2 was performed only for Trim, debris not removed.

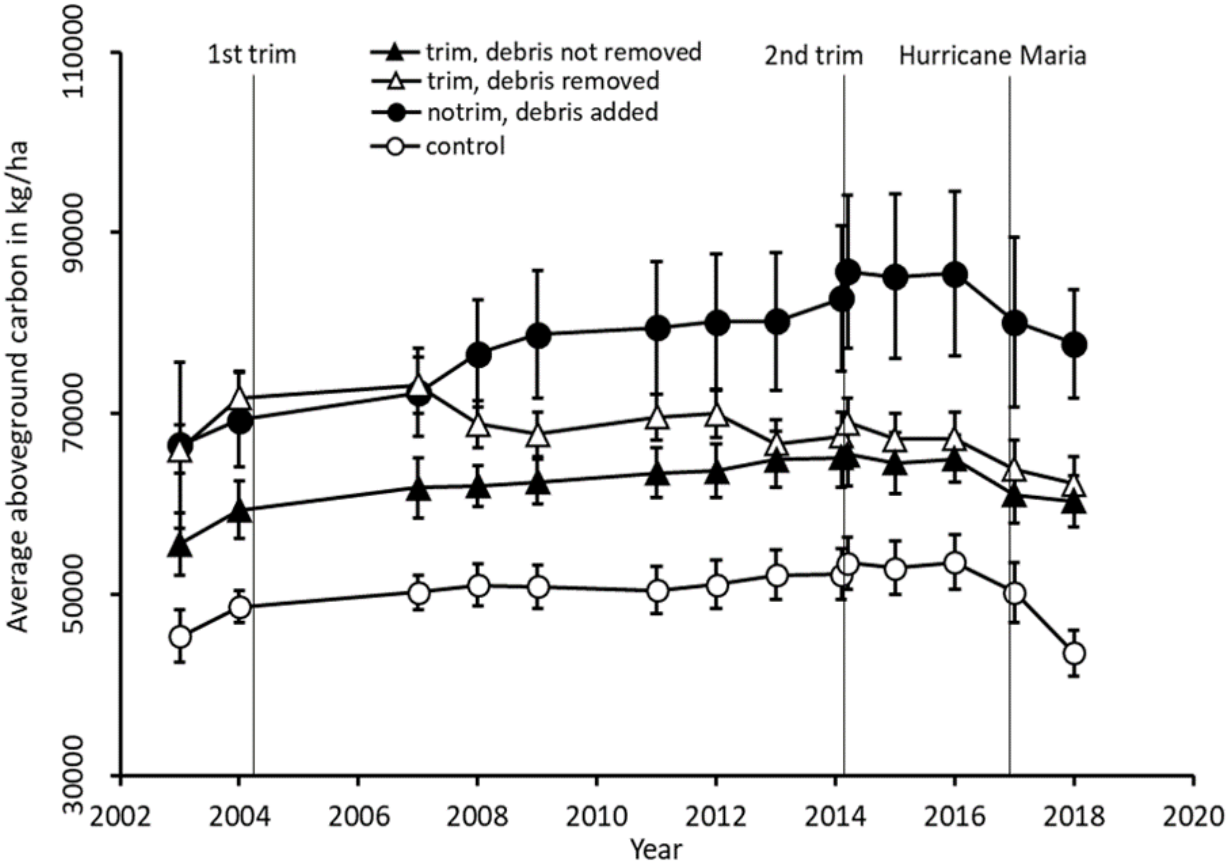

Figure 4.6. Aboveground carbon changes over time. The three vertical bars indicate the dates of TRIM 1, TRIM 2, and Hurricane Maria. The two error bars in 2014 indicate the two censuses for that year (February and October, respectively). The aboveground carbon is the mean and standard deviation among three replicates of each treatment. TRIM 2 was performed only for Trim, debris not removed.

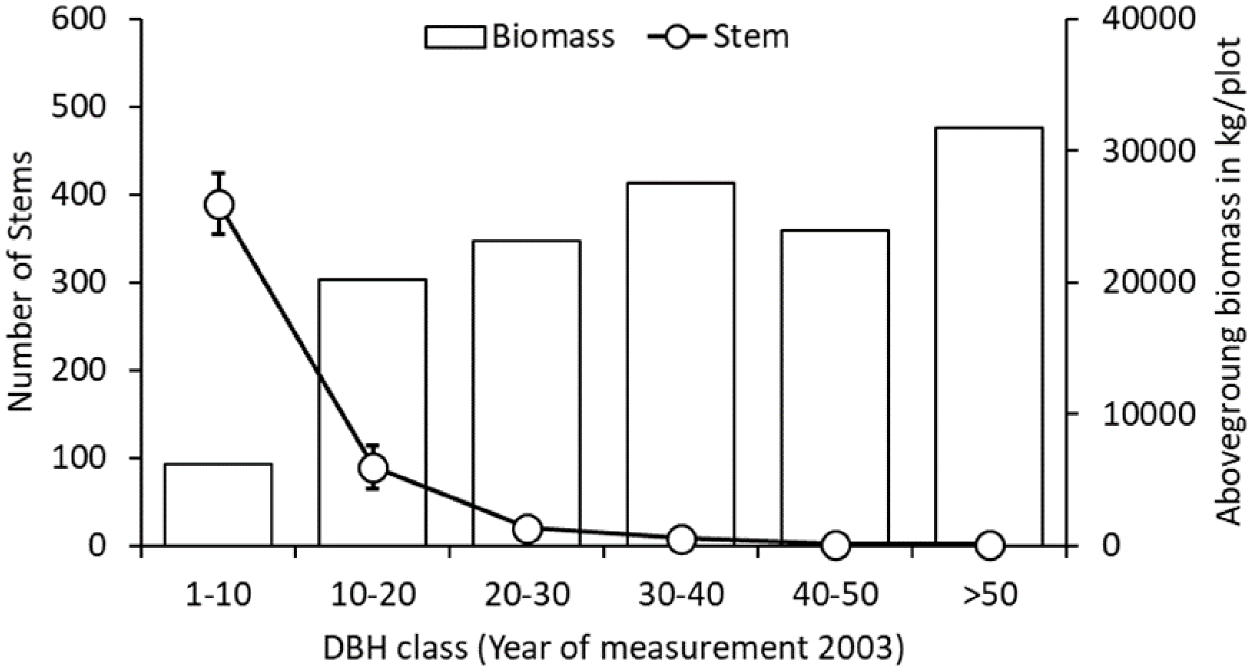

Figure 4.7. Relationship between stem size and aboveground biomass in Control (no manipulation) in 2003. The error bars are standard deviations.

Supplementary Table 4.1

Species used in the analysis. TNI= total number of individuals. TCS= total carbon stock. TCS is the sum of carbon produces by the TNI of a species for the whole study period.

Code	Scientific Name	Family	TNI	TCS
ALCFLO	*Alchorneopsis floribunda*	Euphorbiaceae	112	14385.3
ALCLAT	*Alchornea latifolia*	Fabaceae	61	742.5
ANTOBT	*Stenostomum obtusifolium*	Rubiaceae	13	219.4
ARDGLA	*Ardisia glauciflora*	Myrsinaceae	68	80.4
BUCTET	*Buchenavia tetraphylla*	Combretaceae	178	141746.2
BYRSPI	*Byrsonima spicata*	Malpighiaceae	38	39.4
BYRWAD	*Byrsonima wadsworthii*	Malpighiaceae	31	1108.6
CALCAL	*Calophyllum antillanum*	Calophyllaceae	28	12.0
CALSQU	*Henriettea squamulosum*	Melastomataceae	17	1191.8
CASARB	*Casearia arborea*	Salicaceae	968	9945.1
CASSYL	*Casearia sylvestris*	Salicaceae	160	737.2
CECSCH	*Cecropia schreberiana*	Urticaceae	1892	7834.8

CESMAC	*Cestrum laurifolium*	Solanaceae	2	0.7
CHIDOM	*Chionanthus domingensis*	Oleaceae	38	6233.4
CHOVEN	*Chione venosa*	Rubiaceae	12	2.8
CLIERO	*Clibadium erosum*	Asteraceae	20	4.8
COCDIV	*Coccoloba diversifolia*	Polygonaceae	4	1.2
COCPYR	*Coccoloba pyrifolia*	Polygonaceae	14	69.5
COFARA	*Coffea arabica*	Rubiaceae	19	6.0
CORBOR	*Cordia borinquensis*	Boraginaceae	460	1797.2
CORSUL	*Cordia sulcata*	Boraginaceae	56	5045.0
CROPOE	*Croton poecilanthus*	Euphorbiaceae	21	531.8
CSSGUI	*Cassipourea guianensis*	Rhizophoraceae	129	406.4
CYRRAC	*Cyrilla racemiflora*	Cyrillaceae	44	49100.2
DACEXC	*Dacryodes excelsa*	Burseraceae	1754	359426.7
DAPPHI	*Daphnopsis philippiana*	Thymelaeaceae	10	4.1
DITMYR	*Ditta myricoides*	Euphorbiaceae	2	8.0
DRYALB	*Drypetes alba*	Putranjavaceae	1	0.33
DRYGLA	*Drypetes glauca*	Putranjavaceae	114	2759.7

EUGDOM	*Eugenia domingensis*	Myrtaceae	13	4.3
EUGSTA	*Eugenia stahlii*	Myrtaceae	293	1522.0
FAROCC	*Faramea occidentalis*	Rubiaceae	37	18.4
FICAME	*Ficus americana*	Moraceae	2	0.3
FICCIT	*Ficus citrifolia*	Moraceae	6	1.0
GONSPI	*Gonzalagunia hirsuta*	Rubiaceae	4	1.7
GUAGLA	*Guarea glabra*	Meliaceae	121	233.3
GUAGUI	*Guarea guidonia*	Meliaceae	33	773.9
GUEVAL	*Guettarda valenzuelana*	Rubiaceae	16	50.8
GUTCAR	*Guatteria caribaea*	Annonaceae	245	1909.4
HIRRUG	*Hirtella rugosa*	Chrysobalanaceae	948	6534.9
HOMRAC	*Homalium racemosum*	Salicaceae	243	104009.6
ILESID	*Ilex sideroxyloides*	Aquifoliaceae	49	101.7
INGLAU	*Inga laurina*	Fabaceae	179	5509.9
INGVER	*Inga vera*	Fabaceae	26	818.8
IXOFER	*Ixora ferrea*	Rubiaceae	160	843.4
LAEPRO	*Laetia procera*	Salicaceae	82	2723.2

LONLAT	*Lonchocarpus heptaphyllus*	Fabaceae	13	6.9
MANBID	*Manilkara bidentata*	Sapotaceae	1460	209894.2
MATDOM	*Matayba domingensis*	Sapindaceae	216	26533.9
MELHER	*Meliosma herbertii*	Sabiaceae	107	1055.3
MICIMP	*Miconia impetiolaris*	Melastomataceae	12	6.4
MICMIR	*Miconia mirabilis*	Melastomataceae	8	3.3
MICPRA	*Miconia prasina*	Melastomataceae	578	675.9
MICRAC	*Miconia racemosa*	Melastomataceae	81	17.6
MICTET	*Miconia tetrandra*	Melastomataceae	103	1194.8
MIRGAR	*Micropholis garciniifolia*	Sapotaceae	185	37749.1
MYRDEF	*Myrcia deflexa*	Myrtaceae	138	253.4
MYRLEP	*Myrcia amazonica*	Myrtaceae	386	782.1
MYRSPL	*Myrcia splendens*	Myrtaceae	23	10.6
OCOLEU	*Ocotea leucoxylon*	Lauraceae	200	77.8
OCOMOS	*Ocotea moschata*	Lauraceae	13	5513.2
OCOSIN	*Nectandra turbacensis*	Lauraceae	15	1116.3
OCOSPA	*Ocotea spathulata*	Lauraceae	8	5.1

ORMKRU	*Ormosia krugii*	Fabaceae	19	320.9
PALRIP	*Palicourea croceoides*	Rubiaceae	626	221.5
PHYRIV	*Phytolacca rivinoides*	Phytolaccaceae	13	2.5
PREMON	*Prestoea acuminata*	Arecaceae	3337	32396.4
PSYBER	*Psychotria berteroana*	Rubiaceae	2307	987.9
PSYBRA	*Psychotria brachiata*	Rubiaceae	88	22.8
RHEPOR	*Garcinia portoricensis*	Clusiaceae	933	1923.9
ROYBOR	*Roystonea borinquena*	Arecaceae	14	5600.3
SAMSPI	*Samyda spinulosa*	Salicaceae	33	15.1
SAPLAU	*Sapium laurocerasus*	Euphorbiaceae	10	1925.9
SCHMOR	*Schefflera morototoni*	Araliaceae	596	4987.9
SIMAMA	*Simarouba tulae*	Simaroubaceae	21	9.0
SLOBER	*Sloanea berteroana*	Elaeocarpaceae	3741	42092.5
SOLTOR	*Solanum torvum*	Solanaceae	3	0.9
SWIMAC	*Swietenia macrophylla*	Meliaceae	2	0.8
TABHET	*Tabebuia heterophylla*	Bignoniaceae	191	6076.3
TETBAL	*Tetragastris balsamifera*	Burseraceae	384	3886.4

TREMIC	*Trema micrantha*	Cannabaceae	32	30.5
TRIPAL	*Trichilia pallida*	Meliaceae	49	129.6
ZANMAR	*Zanthoxylum martinicense*	Rutaceae	1	0.2

CHAPTER 5

GENERAL CONCLUSION

The objectives of this research were to assess the effects of hurricanes on tropical rainforest, using El Yunque National Forest of Puerto Rico as example. I correlated this generalized goal with the following specific objectives: 1) measure the forest canopy change through time and on the elevation gradient, 2) measure the effect of the canopy opening on the understory using two pioneer species, 3) measure the hurricane disturbance effects on aboveground carbon through time in a simulation plot. Stronger storms in the future due to climate change will affect forest structure by snapping down or uprooting big trees, defoliating them, or by just killing them immediately or weeks later. The loss of big trees allows more sunlight to reach the forest floor and consequently facilitate the upcoming of small wood plants that can possibly compensate the loss of carbon from dead big trees (see Fig. 1.1).

I began this dissertation by summarizing the importance of tropical forest structure and how they are being affected by hurricane disturbances. In chapter 2, I presented the forest profile and showed how the canopy has changed overtime on the elevation gradient from Hurricane Hugo to Hurricane Maria. I made triangulated irregular networks to show evolution in the canopy surface before and after any major hurricanes. I also showed forest resistance and resilience within the three study plots. Tabonuco forest seems to be more resilient compared to the other plots. After each major disturbance, the forest height drops more than the other plots. However, the Dwarf forest looks more resistant but less resilient to hurricane disturbances. It failed to return or nearly return to its initial state before Hurricane Hugo. Its failure to return to its initial condition makes us believe that it may change permanently.

In chapter 3, I showed how the canopy opening due to hurricane disturbances influences the understory. I used *Cecropia Schreberiana* and *Heliconia caribaea* as two pioneer species in my analysis. In 2019, two years after Hurricane Maria struck the forest, *Cecropia Schreberiana* and *Heliconia caribaea* were very abundant. In 2021, four years later, more than 60% of *Cecropia Schreberiana* and *Heliconia caribaea* died due to canopy closure and perhaps by intercompetition. In the case of *Heliconia caribaea*, senescence may be the other factor explaining their reduction.

In chapter 4, I present results related to aboveground biomass from human-made and natural hurricanes. I analyze data from the Canopy Trimming Experiment and data collected 1 year after Hurricane Maria to show how aboveground carbon changes over time. I found that over the first 14 yr of the experiment (2003-2017), before Hurricane Maria, net aboveground carbon increased in all treatments including the control, except in *Trim, debris removed*, despite experimental trimming that had removed 11,157 kg of biomass in TRIM 1. I deeply believe that this recovery of aboveground carbon demonstrates a degree of forest resilience to biomass and aboveground carbon loss. Thus, results from the CTE confirm our expectation that during the period after experimental canopy trimming (but no experimental tree felling), stem recruitment, regrowth of branches, and stem growth would substantially restore biomass and carbon loss. Then, toward the end of the experimental period, Hurricane Maria both trimmed and felled trees, and aboveground carbon decreased from 65,005 to 60,320 kg/ha in the *Trim, debris not removed* treatment and 53,607 to 43,539 kg/ha in *Control* plots. This reduced aboveground carbon less in the plots (especially untrimmed plots) than experimental trimming had. Thus, it appears that the amount of regrowth recorded after experimental trimming would also restore aboveground carbon in the forest after a severe hurricane in the same time span.

In the tropics, hurricanes have a highly variable impact on forest, ranging from moderate damage to severe damage. The gaps resulted from these damages in the forest canopies affect the germination of seeds and the growth rates and survival of plants and then the storage of carbon. Forest structure, plant dynamics, and carbon storage will greatly depend on intensity and frequency of disturbance. Climate change is predicted to intensify and increase storms frequency. Our 31-year study period in El Yunque National Forest, Puerto Rico, has shown that this forest is resistant and resilient. Despite the frequent disturbances, the forest tends to grow back to nearly reach the stage before being struck by hurricanes in terms of plant recruitment, canopy height, and carbon storage. However, the results also indicated that Dwarf forest, which is the highest plot in the elevational gradient was less resilient than the other plots. This suggests that stronger hurricanes and elevational differences in resistance and resilience will result in long-term differential impacts on forests at different elevations in the Luquillo Experimental Forest.