THESIS

HURRICANE DISTURBANCE AND VEGETATION DYNAMICS IN THE CORDILLERA CENTRAL, DOMINICAN REPUBLIC

Submitted by

Benjamin Gannon

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Spring 2012

Master's Committee:

Advisor: Patrick Martin

Michael Lefsky
Robin Reich

ABSTRACT

HURRICANE DISTURBANCE AND VEGETATION DYNAMICS IN THE CORDILLERA CENTRAL, DOMINICAN REPUBLIC

Hurricanes are intense, frequent disturbances in the Caribbean basin, often regarded as important agents in structuring ecological patterns and processes. The topography and vegetation of tropical montane forest landscapes interact with the forces of hurricanes to create complex patterns of disturbance. In this study, remote sensing and field inventory of forests were used to reconstruct wind and rain disturbance from Hurricane Georges in the Cordillera Central, Dominican Republic. Spatial patterns of hurricane disturbance and the relationship of disturbance with the topography, the physical forces of the hurricane, and the biota of the landscape were analyzed using geographic information systems. The effects of hurricanes on forests were addressed by comparing structure and composition across forest types and levels of hurricane severity.

Hurricane disturbance was distributed over a small portion of the study area; only 11.3% of the landscape was disturbed by wind and 4.3% was disturbed by rain. Disturbance from wind was concentrated at high elevations to the south of the site's major topographic divide. Pine forest was disproportionately affected both in terms of area disturbed and the severity of effects on forests. The proportion of live undamaged basal area was reduced by 7.1% in cloud forest, 32.0% in mixed pine, and 60.5% in pine forest compared to undisturbed control plots. Whereas effects were most severe in pine forest, pine forest composition was unchanged because of the overriding influence of climate. Cloud forest composition saw minor changes with increasing importance of several early-successional species. In mixed pine forest, areas disturbed by the hurricane saw *Pinus occidentalis* Swartz decrease in importance, but the low magnitude of this change suggests it may take several hurricanes to convert these communities to cloud forest.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Patrick Martin, for encouraging me to take on a project that was considerable in scope and allowed me the freedom to develop my own ideas. I would like to thank my minor committee members, Michael Lefsky and Robin Reich, for providing valuable critique of my work and for advice on technical matters of remote sensing and spatial modeling.

I would also like to thank Patrick Martin and the CSU Horticulture and Landscape Architecture Department for helping me through the technicalities of travelling abroad for this research.

I would like to thank all those who helped on field work for this project. Working in Dominican cloud forest is not easy. Thank you to Matt Warman, Justin McDuffie, Becky Fahey, and Ruth Sherman. I would also like to thank our Dominican host, Dr. Radhames Lora, for his support and gracious accommodations.

This material is based upon work supported by the National Science Foundation under Grant No. 0921925.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1

Chapter 2

LIST OF TABLES

Chapter 1

Chapter 2

LIST OF ABBREVIATIONS

cat	-	Saffir-Simpson Hurricane Category
CC	-	Cordillera Central
CIR	-	Color Infrared
CIR OM	-	Color Infrared Orthomosaic
CVA	-	Change Vector Analysis
DBH	-	Diameter at Breast Height
Deg	-	Degree
DN	-	Digital Number
DOS	-	Dark Object Subtraction
DR	-	Dominican Republic
E	-	East
Fpar	-	Fraction of Photosynthetically Active Radiation
GIS	-	Geographic Information System
LAI	-	Leaf Area Index
N	-	North
NDII	-	Normalized Difference Infrared Index
NDMI	-	Normalized Difference Moisture Index
NDVI	-	Normalized Difference Vegetation Index
NP	-	Number of Patches
OM	-	Color Infrared Orthomosaic
PCA	-	Principal Components Analysis
PCC	-	Post Classification Comparison

PLAND	-	Percentage of Landscape
PTDIST	-	Percentage of Total Disturbed
RGB	-	Red Green Blue
S	-	South
SD	-	Standard Deviation
TA	-	Total Area
TCB	-	Tasseled Cap Brightness
TCG	-	Tasseled Cap Greenness
TCW	-	Tasseled Cap Wetness
TMF	-	Tropical Montane Forest
UID	-	Univariate Image Differencing
VI	-	Vegetation Index
W	-	West

CHAPTER 1

Quantifying and Analyzing the Distribution of Disturbance from Hurricane Georges in the Cordillera Central, Dominican Republic

1. Introduction

Disturbance regimes play a central role in the dynamics of forested landscapes, and a thorough understanding requires an appreciation of the causes and consequences of the spatial heterogeneity inherent in disturbance impacts (Sousa 1984, White and Pickett 1985). At landscape-scales, even catastrophic disturbances tend to result in gradients of damage and mortality in vegetation communities. In particular, the spatial distribution, extent and severity of a disturbance are key factors in its effects on the dynamics of landscapes. Distribution includes the spatial patterns of disturbance and its relationship to geography, topography, environmental and community gradients (White and Pickett 1985). Understanding the spatial distribution of a disturbance also includes an emphasis on the number, size, and shape of disturbed patches whose properties can affect the magnitude of change in conditions within patches, the species composition within patches, and the mode of recovery (Runkle 1985).

Hurricanes (also tropical cyclones and typhoons) are notably large and catastrophic agents of disturbance, capable of impacting vast areas of forested landscapes. Yet despite their massive scale and intensity, impacts are inherently patchy because the physical forces of the hurricane interact with the abiotic and biotic features of affected landscapes (Foster and Boose 1992, Boose *et al.* 1994, Everham and Brokaw 1996). Hurricanes also have variable wind fields, resulting in gradients of wind speed and direction over the landscape (Boose *et al.* 1994, Ramsey III *et al.* 2001, Doyle *et al.* 2009). The topography of the landscape determines patterns of exposure to wind (Bellingham 1991, Boose *et al.* 1994) while soils and geomorphology affect windthrow susceptibility (Everham and Brokaw 1996) and landslide distribution (Scatena and Larsen 1991). Biotic attributes of landscapes also contribute to the patterns of hurricane impacts, especially tree species' characteristics, such as size (Walker 1991) and wood density (Zimmerman *et al.* 1994), and stand attributes, such as species composition (Zimmerman *et al.* 1994), diversity (Tanner and Bellingham 2006), and structure (Brokaw and Grear 1991).

Tropical montane forests (TMFs) in the Caribbean offer a model system to study hurricanes impacts on forest dynamics. Hurricanes are especially frequent and intense in the Caribbean basin and substantial areas of TMF have been protected. Caribbean TMFs support a variety of forest types that are generally zoned along broad gradients of elevation and climate with stand-scale patterns driven by physiography (Tanner 1977, Ewel and Whitmore 1973, Sherman *et al.* 2005, Martin *et al.* 2011) and disturbance (Zimmerman *et al.* 1995, Martin and Fahey 2006, Sherman *et al.* 2008). Hurricanes impacts have been studied in Nicaragua following Hurricane Joan in 1998 (Boucher *et al.* 1990), in Puerto Rico following Hugo (Brokaw and Grear 1991, Boose *et al.* 1994), and in Jamaica following Hurricane Gilbert (Tanner and Bellingham 2006). Detailed descriptions and analyses of hurricane disturbances at landscape scales, however, are lacking for the TMFs of the Caribbean. The exception is Boose *et al.* (1994), who used aerial photography to map the severity of wind damage across the Luquillo Experimental Forest (LEF) in Puerto Rico following Hurricane Hugo (1989). Based on a model of topographic exposure to hurricane winds, Boose *et al.* (1994) found good agreement between actual and predicted patterns of hurricane disturbance at the scale of the LEF. Work in Puerto Rico (Brokaw and Grear 1991) and Jamaica (Bellingham 1991), however, suggests that topographic effects may not be consistent at small scales. Specifically, Brokaw and Grear (1991) found no difference in the canopy height reduction of cloud forest in the LEF on slopes with contrasting exposure to Hurricane Hugo, while in Jamaica after Hurricane Gilbert in 1988, Bellingham (1991) found significant differences in canopy damage (e.g. percent stem breakage, percent crown defoliation, and total crown loss) between forest on windward slopes, ridge crests, and leeward slopes, but no significant differences in mortality between exposed and unexposed forests. The importance of topography can also change from storm to storm for the same forest as reported by Ostertag *et al.* (2005) for portions of the LEF hit by both Hurricane Hugo (1989) and Hurricane Georges (1998). These findings raise questions about the consistency of topographic exposure as a predictor of hurricane impacts, the scale at which topography is important, and its importance relative to other abiotic and biotic variables.

Hurricane impacts are not limited to wind damage. Coastal areas are prone to storm surge (e.g. from Hurricane Katrina in the US Gulf Coast; Wang and Xu 2009) and inland areas can be subject to intense flooding associated with storm rains. The steep mountains of the Caribbean are prone to hurricane-induced landslides, especially when combined with heavy hurricane rains (Guariguata 1990, Scatena and Larsen 1991), and its deeply dissected topography rapidly channels precipitation into streams resulting in pronounced erosion and scouring. The impacts of stream scouring and landslides are quantitatively and qualitatively different than wind, and result in fundamentally different forest recovery patterns (Walker 1994, Walker *et al.* 1996, Lugo 2008). Despite these importance differences, most hurricane studies have focused exclusively on the impacts of wind or water. Integrated assessment of wind and rain impacts in the Caribbean has only been completed at small scales (e.g. Scatena and Lugo 1995).

Despite the abundance of hurricane-related ecological research in the Caribbean Basin, little work has been done to describe the spatial and temporal components of the hurricane regime at landscape scales. Specifically, there is a dearth of information on the area disturbed by individual hurricanes and realistic return intervals for the impacted landscapes, making estimates of higher order descriptors, especially rotation periods, inadequate. Basic descriptions of the disturbance regime like area disturbed and return intervals are needed to fully integrate the extensive work describing hurricane effects (Brokaw and Walker 1991, Tanner *et al.* 1991) and recovery (Zimmerman *et al.* 1996) at the landscape scale.

The spatial and temporal components of hurricane regimes are commonly described in terms of frequency or return intervals (e.g. Walker *et al.* 1991, Tanner *et al.* 1991). Detailed information on hurricane size is often lacking for historical hurricanes so generic estimates of hurricane radii are used to approximate the scope of hurricane influence. The 75 nm (138.9 km) radius commonly used for this purpose has its origin in NOAA risk analysis (Neumann 1987) and is generally larger than the true radius of hurricane-force winds. Hurricane frequencies and return intervals are often calculated from the number of hurricanes to strike an island over a given period of time, which may work well to describe the hurricane regime of a small island (e.g. Nassau, Bahamas), but some landmasses in the Greater Antilles, namely Hispaniola and Cuba are large enough that hurricanes which strike the island do not necessary expose all or even most of the landmass to hurricane forces. Furthermore, hurricanes lose power as they travel over land and significant topography while making landfall (e.g. Hurricane Georges and Hispaniola; see Gerts *et al.* 1999), so island interiors and mountains may experience lesser forces.

A different approach is to model the meteorology of individual storms (e.g. Boose *et al.* 2004 for Puerto Rico), but such work requires detailed information on hurricane size and wind speeds that are usually unavailable or difficult to obtain. Published weather reports are usually collected from sites such as airports and cities near the coast so there is often a lack of weather data for the interior regions of large islands. This approach is too time consuming to apply to large areas and may not yield improved results if calibration data is lacking or of questionable accuracy.

Remote sensing analyses of recent hurricanes (Ramsey III *et al.* 1997, Lee *et al.* 2008, Staben and Evans 2008, Bianchette *et al.* 2009, Wang and Xu 2009, Wang and Xu 2010, Wang *et al.* 2010) have demonstrated the potential for using satellite-borne spectral sensor data for describing the distribution and severity of hurricane disturbance on forested landscapes. Remote sensing has been underutilized in the tropics in a large part because of the challenges presented by frequent cloud cover, but recent advances in compositing techniques (Helmer and Ruefenacht 2005) make it possible to utilize more of the available data. Remote sensing provides a more complete and continuous view of the landscape over broader spatial extents than field-based assessment. Geographic information systems (GIS) then can be used to ask questions about how remotely sensed hurricane disturbance measures relate to the abiotic and biotic components of TMF landscapes.

In the Dominican Republic, the Cordillera Central mountain range is home to the Caribbean's largest area of protected TMF, and it is frequently impacted by hurricanes including Hurricanes David (1979) and Georges (1998). The Cordillera Central supports a diverse mosaic of forest types (Sherman *et al.* 2005), including a discrete and striking ecotone between cloud forest and monodominant pine forest with pronounced differences in structure, diversity, and species adaptations to disturbance (Martin *et al.* 2007). Yet, little is known about the impacts of hurricane disturbance on the TMFs of this region. A field-based vegetation study of the area (Sherman *et al.* 2005) pointed to species-specific responses to wind and led to hypotheses of how hurricane wind disturbance may influence the region's landscape dynamics (Martin *et al.* 2011).

If there is a unifying theme of hurricane research in the Caribbean it is that hurricanes and their effects on forests are highly variable. Scaling stand-level studies, which are the basis of our understanding in the region, up to the landscape is inherently problematic, hindering realistic predictions of how hurricanes influence forested landscapes as repeat disturbances. Re-measurement of previously established plots provides important information on the mechanisms of change, but these plots may not capture severely disturbed portions of the landscape. For example, tree mortality from Hurricane Hugo at the El Verde site in Puerto Rico was only 7%, suggesting little hurricane-associated changes in forest composition, but elsewhere on the landscape, the Bisley field site experienced an estimated 50% mortality (Walker 1991), illustrating the strong patch-dependency of hurricane influences on forest dynamics. Hurricane Georges, which passed nearby the study site as only a category 1 hurricane, disturbed portions of the landscape, sufficiently in those areas to change forest dynamics (Sherman *et al.* 2005).

Remote sensing can provide continuous measures of hurricane effects over entire landscapes, allowing us to then test the controls on the spatial distribution of hurricane effects. From work in Puerto Rico (Boose *et al.* 1994) it has been established that topographic exposure plays a role in the spatial distribution of hurricane wind damage, but that other factors also influence patterns at smaller scales (Bellingham 1991, Brokaw and Grear 1991). We expect that the highly contrasting forest structures, species composition, and diversity of the adjacent cloud and pine forests in the Cordillera Central will influence the spatial patterns of hurricane wind effects. Cloud forest and its response to hurricane wind disturbance is relatively unstudied, but Brokaw and Grear (1991) found reductions in the percent cover in upper canopy height levels months after Hurricane Hugo and Weaver (1999) found that cloud forest stem density was 21% lower 5 years after Hugo. While there are few generalizations about the immediate impacts of hurricanes on pines versus broadleaves, the findings of Boucher *et al.* 1990 suggest severe wind damage to pines is more lethal, with 58% mortality in stands of *Pinus caribaea* compared on only 13% for broadleaf forest after Hurricane Joan (1988) in Nicaragua. Pine forest should be more strongly affected by the hurricane because it lacks adaptations (e.g. sprouting) allowing current canopy trees to recover from severe damage. Cloud forest is far more species rich than pine forest (Sherman *et al.* 2005) and species differences in resistance and resilience to wind combined with local variation in cloud forest species composition may create patchier damage in cloud forest than pine forest.

In this study, these issues were addressed with an examination of the landscape-level impacts of Hurricane Georges on the TMFs of the Cordillera Central, DR. The distribution and severity of disturbance impacts from Hurricane Georges were described with a combination of remote sensing and field sampling, with attention to the separate forces of wind and rain. Field sampling was stratified by wind disturbance severity and forest type to validate the remote sensing results and to quantify the direct effects of wind damage on TMFs. Logistic regression was used to explore the relative influence of abiotic and biotic landscape factors in determining the distribution and severity of hurricane disturbance. Landscape metrics were used to describe the size component of the disturbance distribution.

2. Methods

2.1. The Study Area

The Cordillera Central mountain range is located in the center of Hispaniola. Our study area encompassed c. 330 km^2 within two national parks (Parques Armando Bermúdez and Carmen Ramírez), ranging in elevation from 1100 m to over 3000 m, and spanning the windward (north-eastern) and leeward (south-western) slopes of the central massif. Annual precipitation on the windward slopes averages about 1800 mm. The Cordillera Central exhibits a significant rainshadow, with markedly lower rainfall on leeward slopes. The topography is rugged, with steep and sharply dissected slopes.

Forest vegetation across the study area has been classified into five major associations: 1) low-elevation secondary riparian forests, 2) low-to-mid-elevation evergreen broadleaf forests, 3) mixed broadleaf–pine forests, 4) high-elevation cloud forests, and 5) open and closed monodominant and monospecific pine forests at the highest elevations and on the leeward slopes described in detail in Sherman *et al.* (2005) and in Table 2-1.

Table 2-1: summary of forest type characteristics taken from the permanent plot data of Sherman *et al.* 2005. Numbers in column 1 refer to numbers in text above. Stand structural information is reported for all stems ≥ 10.0 cm DBH. Species richness is reported as the total number of species encountered in all plots of that forest type.

Summary of Forest Type Characteristics	Elevation (m)	Mean Stem Density (stems/ha)	Mean Basal Area (m^2/ha)	Mean Canopy Height (m)	Species Richness (# of species)
1) Secondary Riparian	1100-1350	577	21.7	26.3	45
2) Broadleaf	1140-1580	650	28.2	22.8	92
3) Pine-Broadleaf	1120-2220	753	29.3	21.0	65
4) Cloud	1560-2230	939	26.4	15.6	80
5) Pine	1460-3030	560	21.3	18.7	41

Hurricane winds, landslides and fires are frequent in the study area. However, no hurricane has hit the area since Hurricane Georges, enabling a post-event reconstruction of ground-level damage. Without hurricanes, high winds are very rare at the site due to the distance from the coast and the “damming” of trade winds by the large size of the Cordillera Central (PH Martin, personal observation). The fire regime is mixed, with frequent surface fires and occasional crown fires; the site mean point fire return interval averages 31.5 years and exhibits significant elevational variation, with the longest fire interval at mid-elevations on the windward slope and the shortest on the leeward slopes (Martin and Fahey 2006).

2.2. Hurricane Georges

The last major storm to affect the Cordillera Central was Hurricane Georges in 1998. While convention is to describe hurricanes by their maximum intensity, this ignores the dynamic nature of hurricane weather, and may poorly describe the intensity of a storm at places in space and time other than the peak. The physical forces of weather provide the context for interpreting hurricane disturbance effects across storms and sites (Lugo 2008) and for this reason, some pertinent details about Hurricane George will be discussed.

Hurricane Georges obtained its maximum intensity on 09.20.1998 while over the Atlantic as a Saffir-Simpson category (cat) 4 hurricane. The storm traveled through the Caribbean, passing over Puerto Rico, Hispaniola, and Cuba, before turning north towards the US Gulf Coast (see Figure 2-1). As it moved across the island of Puerto Rico, Georges weakened to a cat 2 hurricane. Georges made landfall with the Dominican Republic on 09.22.1998 as a cat 3 hurricane. As Georges passed over the mountains of Hispaniola it weakened to a cat 2 and then to a cat 1 hurricane. The center of Hurricane Georges passed just 15 km south of the study site.

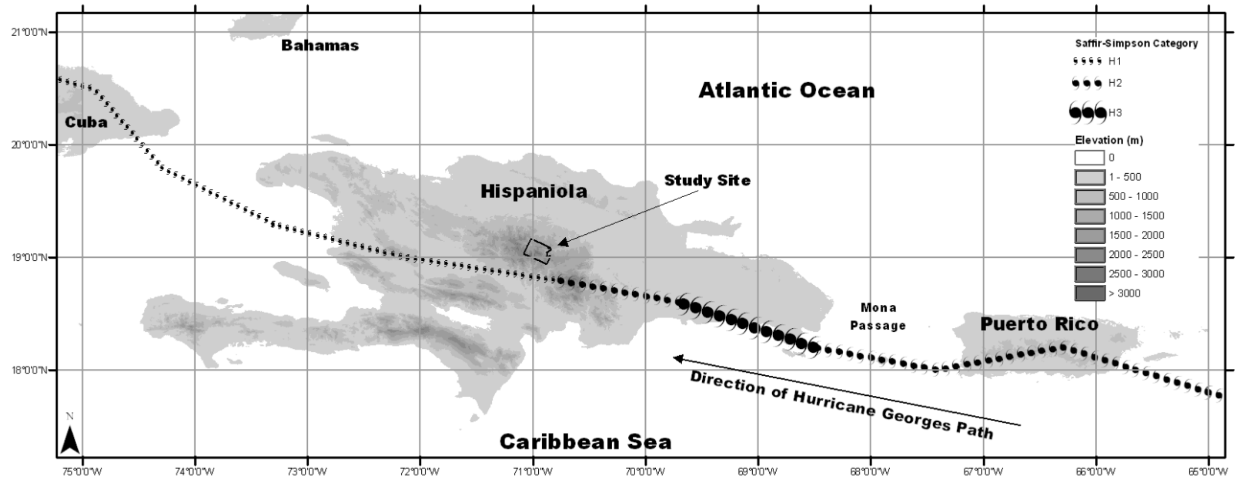

Figure 2-1: Track of Hurricane Georges (NOAA 2009) in relation to the study site.

The structure of Hurricane Georges' wind field was affected by the Cordillera Central. Convective changes within the hurricane eye were observed as the hurricane interacted with the topography causing it to quickly weaken from a cat 3 hurricane to a cat 1 hurricane (Geerts *et al.* 1999). The rapid weakening of the hurricane was accompanied by changes in hurricane morphology. The hurricane eye was well defined as Georges made landfall with Hispaniola (see Figure 2-2 Panel A), but as the hurricane travelled over the Cordillera Central the structure of the eye broke down (see Figure 2-2 Panels B and C). These land and topography-induced changes likely resulted in weakened eye wall, where highest wind speeds are usually observed, and a more chaotic wind field.

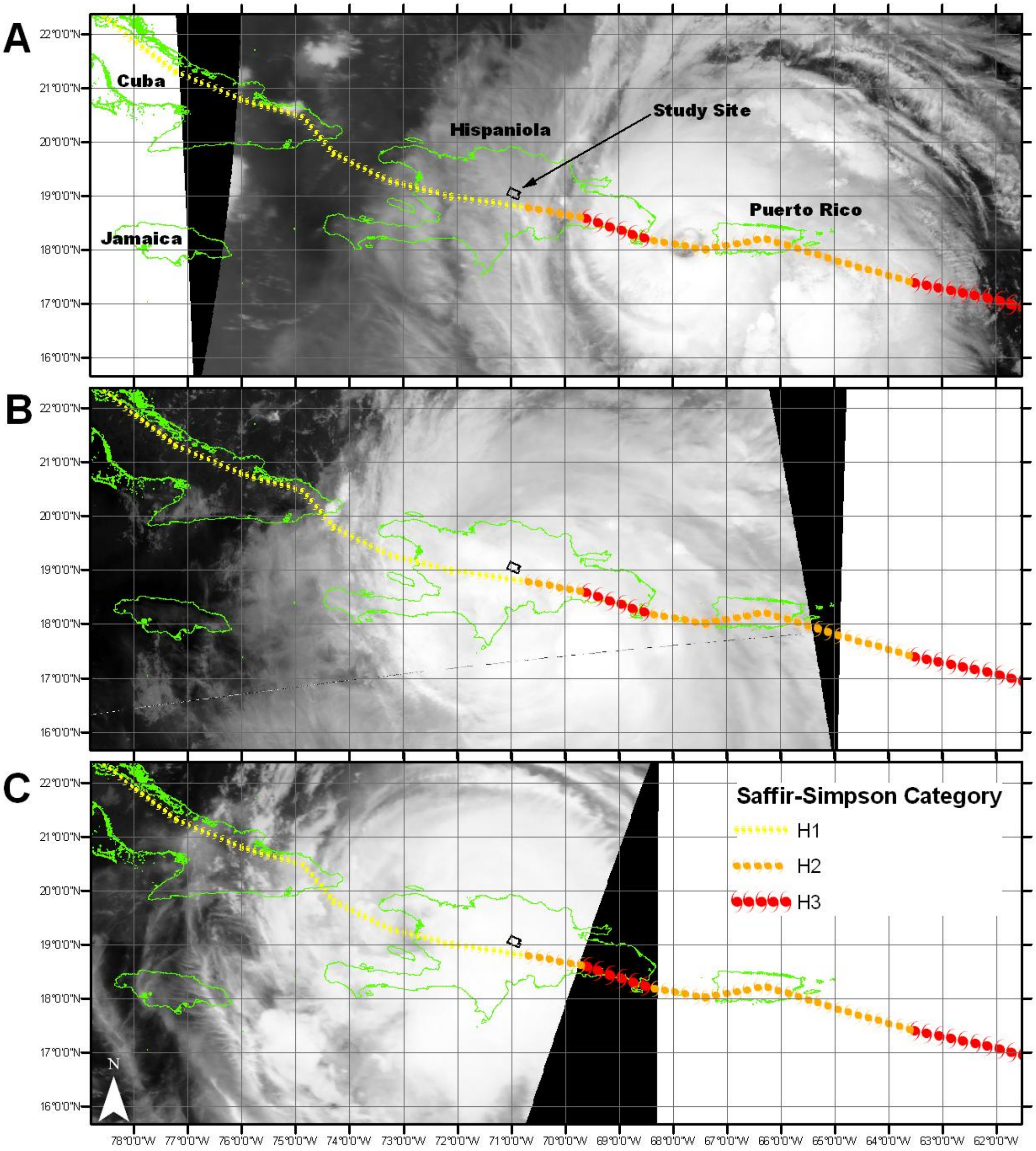

Figure 2-2: Hurricane Georges passing shown in AVHRR channel 5 during a) 09.22.1998 07:00 UTC, b) 09.22.1998 23:00 UTC, and c) 09.23.1998 08:30 UTC

There are no published records of Hurricane Georges rainfall for the site, but satellite estimates suggest that up to 991 mm of precipitation fell over parts of Hispaniola during 24 hrs (Guiney 1999) creating flash floods and landslides. Extreme flooding in the Tablones and Guanos Rivers washed out roads and bridges in the communities downstream of the study area (PH Martin, personal observation).

2.3. Hurricane Regime

A simple improvement in storm frequency and area calculations can be made by assigning hurricanes more accurate buffer distances and by recording hurricane strikes for smaller units of space. If hurricane occurrence varies within the study area (as it should for any large landscape) then considering every hurricane that touches just part of the landscape a “strike” for the entire landscape will overestimate the hurricane frequency as a function of area. Hurricane strikes can be recorded for small units of area (i.e. a pixel) to better express the variability in hurricane frequency within a larger area (i.e. composed of multiple pixels). The hurricane frequency for a discrete area can then be expressed as the mean frequency for all enclosed pixels. This way if a hurricane only affects 1/3 of the landscape it will only contribute 0.33 to the frequency calculation at the scale of the entire landscape.

Extended best track datasets were acquired from the Cooperative Institute for Research in the Atmosphere at Colorado State University (http://www.cira.colostate.edu/) which include hurricane wind field radii for four quadrants (NE, SE, SW, NW) from the periods 1851-1987 (based on climatologies; see Knaff *et al.* 2007) and 1988-2009 (based on observations; see Demuth *et al.* 2006) for wind speeds of 34, 50, and 64 kt. The wind radii correspond to the 6 hr track points of the HURDAT best track dataset which was acquired from NOAA in polyline shapefile form (including Atlantic Basin hurricanes 1851-2009; NOAA 2009). The extended best track datasets contain many missing values, so the analysis was limited to storm points of hurricane intensity with at least one non-zero 64 kt wind speed radii. The 64 kt wind speed radii were used because 64 kt corresponds to the lower wind speed threshold of a hurricane. The radius of the hurricane at a given point was considered the average of all non-zero 64 kt wind speed radii. In total there were 14,062 6 hr track points meeting the criteria for inclusion.

Hurricane radius varied by storm intensity (ANOVA, p-value = 0) with significant differences between Saffir-Simpson category 1 (mean radius = 40.4 nm), category 2 (51.5 nm), and category 3-5 (59.3 nm) hurricanes. The HURDAT best track polylines were buffered by the mean radii of each Saffir-

Simpson category. Buffer polygons from the same storm were merged to their neighbors to prevent double counting area affected by the same storm. A series of GIS procedures were used to calculate the frequency of hurricane strikes (overlap of buffer and grid cell), and strikes by category, for each 90 by 90 m pixel within a grid encompassing the Greater Antilles (approx. 17.5 to 23.5° N and 64.5 to 85.5° W). Hurricane frequency was then calculated for the site as the mean hurricane frequency of all enclosed pixels divided by the time interval. To illustrate how this method compares to standard object-based strike calculations both methods were used to calculate return intervals for 1) the Greater Antilles, 2) Hispaniola, and 3) the study site.

2.4. Remote Sensing

Several remotely sensed data products were utilized in this study (see Table 2-2). Spectral data from Landsat 5 (USGS 2011) was utilized for land cover classification, classification of landslides and stream scouring, and for change detection analysis of Hurricane Georges. ASTER Global Digital Elevation Model (DEM) data (ERSDAC 2011) was used for land cover classification and to derive terrain variables used in land cover classification and spatial analyses. Color infrared (CIR) aerial photography (GPS Aerial Services, Inc. 1999) was used for initial assessment of change detection results and for collection of training data for land cover classification and for classification of landslides and stream scouring.

Table 2-2: Remotely sensed data products utilized in this study.

Item	Collection Date	Source	Resolution or Scale	Spectral Properties	Notes
Landsat 5 TM Pre-Georges Scene	09.02.1998	USGS 2011	30m	3 Vis, 2 NIR, 1 MIR	Path 8 Row 47, 2% cloud cover, Quality 9, L1T correction
Landsat 5 TM Post-Georges Scene	05.16.1999	USGS 2011	30m	3 Vis, 2 NIR, 1 MIR	Path 8 Row 47, 50% cloud cover, Quality 9, L1T correction
Landsat 5 TM Post-Georges Scene	06.01.1999	USGS 2011	30m	3 Vis, 2 NIR, 1 MIR	Path 8 Row 47, 25% cloud cover, Quality 9, L1T correction
Landsat 5 TM Post-Georges Scene	07.19.1999	USGS 2011	30m	3 Vis, 2 NIR, 1 MIR	Path 8 Row 47, 10% cloud cover, Quality 9, L1T correction
Color Infrared Aerial Photos	02-03.1999	GPS Aerial Services, Inc. 1999	1:24,000	2 Vis, 1 NIR	Orthorectified and mosaiced
ASTER GDEM	multidate	ERSDAC 2011	30m	Elevation	Resampled and coregistered with Landsat

2.4.1. Aerial Photography

High resolutions scans of the 1999 color infrared (CIR) aerial photographs (Table 2-2) were orthorectified and mosaiced using ERDAS Imagine 2010 (ERDAS 2010). Orthorectification was performed using the AutoSync workstation with a 30m resolution DEM (ERSDAC 2011) and a pan-sharpened Global Land Survey orthorectified Landsat 7 ETM+ image from 2000 (USGS and NASA 2010) for geographic reference. A direct linear transform geometric model was used for all geometric transformations. Ground control points were manually generated until model root mean square errors were less than 20 m. Mosaicing was performed using the Mosaic Pro workstation. Images were selected for the mosaic and seamlines were generated to maximize near-nadir coverage.

2.4.2. Land Cover Classification

A land cover classification map was created for the site by classifying spectral and terrain data derived from the Landsat 5 TM pre-hurricane scene and the ASTER GDEM. Land cover classes follow the plant associations of Sherman *et al.* 2005 except that the Pine and Pine-Broadleaf associations were combined into a single Pine class (see Appendix I). Training (n=350) and testing (n=173) data points came from the permanent plots of Sherman *et al.* 2005 (n=140), pine and cloud forest field plots of this study (n=75), and photointerpreted points (n=308) from the color infrared orthomosaic (CIR OM).

The raster predictor variables used in the analysis (see Appendix I) were selected with the goal of balancing accuracy with model parsimony. The Landsat 5 TM pre-hurricane data was transformed into principal components using bands 1-5 and 7 to reduce correlation among predictor variables and to separate topographic shadowing effects (which fell into PCA Band 1). The ASTER GDEM and derived terrain variables were coregistered with the Landsat data.

Land cover was modeled using Random Forests (Breiman 2001) which leverages the power of many decision trees. An optimization procedure was used to pick the number of trees, number of variables sampled at each split, method of sampling (with or without replacement), and the minimum size of terminal nodes used in the model. The model was optimized with 300 trees, a variable pool of 3 for each split, sampled without replacement, and with a minimum terminal node size of 4. Accuracy assessment was performed with the independent testing data.

2.4.3. Change Detection

2.4.3.1. Imagery Acquisition

Landsat TM imagery (Path 8 Row 47) one year prior and one year after Hurricane Georges, was examined for suitability for change detection analysis on the basis of cloud cover, image quality, and proximity to the hurricane event. The 09.02.1998 pre-hurricane reference image (Table 2-2, Appendix II Figure II-1) was selected for its close temporal proximity to the event, optimal quality, and lack of cloud cover. The three post-hurricane images were collected on 05.16.1999, 06.01.1999, and 07.19.1999 (Table 2-2, Appendix II Figure II-1). The Landsat scenes were available with L1T correction (USGS 2011). Visual inspection of the images confirmed adequate spatial alignment.

2.4.3.2. Atmospheric Correction

The spectral bands of the Landsat scenes were radiometrically corrected using simple dark object subtraction (DOS) per Song *et al.* 2001 to reduce atmospheric effects. The subtraction values were determined on a per-band basis by identifying the lowest digital number (DN) with at least 1000 pixels in the scene (Appendix II Table II-1).

2.4.3.3. Compositing the Post-Hurricane Image

No post-hurricane image had complete cloud-free coverage of the study site (see Appendix III Figure III-1). Three compositing methods were assessed for constructing a post-hurricane composite image with more complete cloud-free coverage, including 1) atmospheric correction using dark object subtraction, 2) linear correction, and 3) histogram matching (Image Match as described in Helmer and Ruefenacht 2005).

The post-hurricane images ranged in cloud cover from 2.3 to 34.8% and in shadowed area from 1.7 to 8.0% (Appendix III Table III-1). For compositing, the 07.19.1999 date was chosen as the base image because it had the lowest percentage of cloud cover. For details on processing steps see Appendix III. The resulting three post-hurricane image composites were assessed visually to choose a single post-hurricane composite for use in further analyses. The atmospheric and linear correction methods resulted in overly bright and overly dark gap fills that did not preserve relative band brightness levels. The histogram matching method resulted in the most spectrally consistent composite. The histogram matching composite was used in all subsequent analyses.

2.4.3.4. Vegetation Indices

A variety of remotely sensed data sources and methods have been used in previous studies to describe hurricane damage. Two recent studies (Wang and Xu 2010, Wang *et al.* 2010) specifically address which common vegetation indices (VIs) and change detection methods are best for quantifying hurricane disturbance to forests. Wang and Xu (2010) found that tasseled cap wetness (TCW; Crist *et al.* 1986) was the most accurate VI for classifying disturbed forests while Wang *et al.* (2010) found that the normalized difference infrared index (NDII) was most sensitive to hurricane forest disturbance. TCW and NDII are highly correlated (Jin and Sader 2005) because they both contrast the mid-infrared, which changes with forest mortality (Collins and Woodcock 1996), with the visible and/or near-infrared. In addition to measuring vegetative wetness, NDII and TCW are also affected by forest structure. For example, TCW is more highly correlated with stand structural attributes in temperate Douglas-fir/western hemlock than tasseled cap brightness or tasseled cap greenness (Cohen and Spies 1992) and NDII is more highly correlated with tropical broadleaf forest structure than the normalized difference vegetation index (Freitas *et al.* 2005). Sensitivity to structural change is likely what makes NDII and TCW more effective at detecting partial forest disturbances than greenness indices. NDII has been used to detect disturbance in temperate broadleaf and coniferous forests with similar accuracies (Jin and Sader 2005) and has been used to detect forest cover change in tropical broadleaf forests (Hayes and Cohen 2007).

In Caribbean forests, tree mortality following hurricane events is rarely recorded, but in general appears to be low, in the range of 3-13% (Tanner *et al.* 1991). If representative, this relatively small reduction in tree density may not be detected by greenness indices. Furthermore, tree species in Jamaica and Puerto Rico are highly resilient to defoliation, branch, and canopy damage from hurricanes due to resprouting adaptations (Bellingham *et al.* 1994, Zimmerman *et al.* 1994). Defoliation should drastically alter the greenness of forests, but this change is relatively short-lived. Given the high similarity in forest composition in Dominican montane forests and other Caribbean islands, broadleaf tree species at the site should have similar resprouting abilities. As the change detection interval for this study was approximately 10 months long, many trees likely recovered from minor branch and canopy damage, although not from severe stem damage. Changes in forest structure should be better described by changes in wetness indices (TCW and NDII) than greenness indices (TCG and NDVI).

Atmospherically corrected pre- and post-hurricane image digital numbers (DNs) were converted to reflectance values using the Landsat calibration tool in ENVI 4.8 (ITT VIS, Inc. 2011). NDVI and NDII were calculated from reflectance values per equations in Table 2-3. For Landsat 5 TM data, only coefficients developed for DNs were available (Crist *et al.* 1986). TCG and TCW were calculated from the radiometrically corrected DN data per equations in Table 2-3.

Table 2-3: Vegetation indices used in the change detection analysis. ' Calculated from radiometrically corrected reflectance values * Calculated from radiometrically correction DN values

Index	**Equation**	**Citation**
NDVI'	$\mathrm{NDVI} = \frac{NIR-red}{NIR+red}$	Rouse *et al.* 1973
NDII, NDMI'	$\mathrm{NDII} = \frac{NIR-SWIR}{NIR+SWIR}$	Hardisky *et al.* 1983
TCG*	TCG = B1(-0.2728) + B2(-0.2174) + B3(-0.5508) + B4(0.7221) + B5(0.0733) + B7(-0.1648)	Crist *et al.* 1986
TCW*	TCW = B1(0.1446) + B2(0.1761) + B3(0.3322) + B4(0.3396) + B5(-0.6210) + B7(-0.4186)	Crist *et al.* 1986

2.4.3.5. Change Detection Algorithm

While other methods are available which may be highly accurate (Wang and Xu 2010), given that little *a priori* information was available for interpreting change detection results, simple image subtraction was chosen for its ease of interpretation and lack of user inputs. All change images were produced by subtracting the pre-hurricane VI images from the post-hurricane composite VI images.

2.4.3.6. Initial Assessment and Classification of Change Detection Results

NDII change detection best captured changes in forest structure (see Methods for details) and was used in all subsequent analyses. A goal of this study was to describe damage severe enough to affect forest dynamics. The NDII change detection results were classified based on standard deviations (SDs), with change being negative values > 1 SD away from 0 (see Table 2-4). The resulting damage classes cover a wide range of variation in NDII change.

Table 2-4: Classification scheme used for change detection.

Bins from Statistical Distribution	NDII Change Values	Disturbance Classes	Disturbance Severity Classes
Max to – 1 SD	Max to -0.07	No damage	No damage
-1 to -2 SD	-0.07 to -0.14	Damage	Low damage
-2 to -3 SD	-0.14 to -0.21	Damage	Moderate damage
-3 SD to Min	-0.21 to Min	Damage	High damage

The ability of the NDII change detection to correctly classify hurricane disturbance (any decrease in NDII > 0.07; see Table 2-4) was assessed using the 1999 CIR OM as reference. Disturbed forest in the 1999 CIR OM was defined as having at least 25% of the forest canopy dead or damaged. Damage in the 1999 CIR OM was visually interpreted as cyan to green hues resulting from lower reflectance in the near infrared and a higher soil fraction, also changes in texture from reduction of canopy cover, and in some cases downed trees, providing direct evidence of windthrow. Points were randomly generated within forested areas classified as disturbed (n=75) and undisturbed (n=75) for both cloud forest and pine forest for a total of 300 test points. Disturbance was interpreted within the area of the Landsat pixel containing each randomly generated point. Classification accuracy was compared between pine forest and cloud forest using the overall accuracies, the errors of omission rates, and the errors of commission rates.

2.4.4. Scouring and Landslide Classification

Stream scouring and landslides were mapped through a hybrid approach of change detection and spectral classification using the post-hurricane Landsat composite. Scoured streams and landslides were distinguishable as bright features in the post-hurricane composite. Scouring and landslides also reduce NDVI and TCG values because they completely denude affected areas of vegetation. Random

Forests (Breiman 2001) were used to classify stream scouring and landslides from predictor variables including the spectral bands of the post-hurricane composite, derived indices (see Appendix IV), and NDVI and TCG change detection values. Training (n=515) and testing (n=258) data points (see 0) came from the vegetated training and testing points (described previously) and from interpretation of the CIR OM and post-hurricane Landsat composite for stream scouring and landslides.

The same optimization and accuracy assessment methods as described for land cover classification were used for the stream scouring and landslide classification. The Random Forests model was optimized with 100 trees, a variable pool of 4 for each split, sampled with replacement, and with a minimum terminal node size of 5.

2.4.5. Composite Classified Disturbance Map

A final classified disturbance map was made by combining the classified change detection results with the scouring and landslide classification. The scouring and landslide class was given priority for the composite as many of these features were also detected by the NDII change detection.

2.5. Hurricane Effects on Forests

2.5.1. Field Sampling Design

The effects from Hurricane Georges' winds on high elevation forests were quantified with 100 vegetation plots (Figure 2-3). The sampling was implemented to both quantify hurricane wind effects on forests and to validate the change detection results. Plots were located using a stratified random design based on forest type (cloud forest, mixed pine forest, and pine forest, per Sherman *et al.* 2005) and disturbance severity (high, moderate, low, and no disturbance) in elevations above 1800 m. Given the resolution of the change detection, the accuracy of GPS, and the patchy nature of hurricane wind disturbance, only continuous patches of disturbance at least 90 m (or three pixels) wide were used to avoid sampling along the boundaries of a disturbance severity class. Furthermore, since exposure to wind is a key factor in hurricane damage, plots were relocated when the random coordinates fell in areas which spanned different wind exposures, such as across a ridgeline or drainage bottom. No areas of moderate or high severity cloud forest or mixed pine forest damage were large enough to meet the sampling requirements. Cloud forest and mixed pine forest damage severity classes were therefore combined into single damage classes for field sampling. The distribution of sampling plots is presented in Table 2-5.

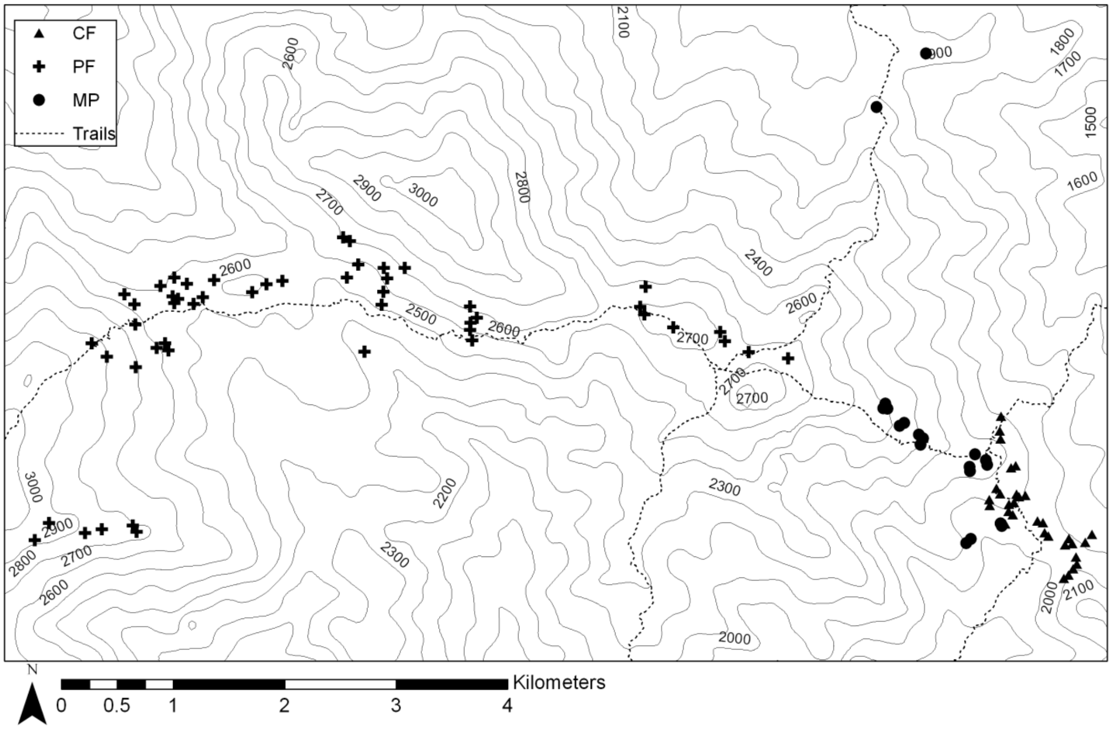

Figure 2-3: Location of vegetation plots. Elevation is in meters. CF = cloud forest, PF = pine forest, and MP = mixed pine.

Table 2-5: The distribution of hurricane plots across forest ecosystems and disturbance categories.

Forest Type	Disturbance Class	n
Cloud Forest	Disturbed	20
	Undisturbed	11
Mixed Pine	Disturbed	13
	Undisturbed	6
Pine Forest	High Severity	20
	Moderate Severity	7
	Low Severity	8
	Undisturbed	15
Total		100

Vegetation plots were rectangular in shape. Given the wide range of structures, a variable plot size was used: 10 × 20 m for cloud forest, 15 × 30 m for pine forest, and 10 × 20 m or 15 × 30 m for mixed pine forest depending on the density of vegetation in the plot. All plots were oriented with the long axis parallel to the average aspect. Aspect was measured with a sighting compass; slope was measured with a clinometer. Coordinates and elevations of plot centers were collected using a Garmin GPS Map 60CS to a horizontal accuracy of 5 m.

2.5.2. Damage Quantification and Vegetation Sampling

All live and dead stems ≥ 4 cm diameter at breast height (DBH) were tallied and measured for DBH. All live stems were identified to species or to genus in the case of a few morphologically similar species. Efforts were made to identify dead stems, but species was only recorded when characteristics necessary for identification were present (e.g. distinctive bark or live root collar sprouts).

Disturbance was categorized for live and dead trees to quantify changes in forest structure. Live trees were classified as follows: 1) undamaged, 2) crown damaged, or 3) tipped. Crown damage was classified as light crown damage (< 20% crown loss), moderate crown damage (20-50% crown loss), or high crown damage (> 50% crown loss). Stems tilting 40° or more from vertical were classified as tipped, the angle from horizontal was estimated, and the direction of tip was measured with a compass.

Dead trees were classified as 1) standing dead, 2) tipped, 3) downed dead, 4) uprooted, or 5) snapped. If the stem was vertical without any evidence of traumatic break it was categorized as standing dead. Tipped was again defined as tilt ≥ 40° from vertical. Downed dead was used to describe prostrate steams without evidence of how they died. Uprooted was used to describe tipped or prostrate stems with displaced roots. Snapped describes trees with a traumatic break to the main stem. The directions of all tipped, downed dead, and uprooted stems were taken with a compass. The heights of snaps were recorded.

Understory structure and composition was inventoried in a 2-m-wide strip oriented lengthwise down the center of the plot. Stems were tallied by species for all stems originating within the strip and by three size classes: seedlings 0.2-1.3 m in height, saplings 0-2 cm DBH, and saplings 2-4 cm DBH.

A large fire burned through much of site's monospecific pine forest and parts of the high-elevation monodominant pine forest in 2005 (Sherman *et al.* 2008). For detailed collection protocols for fire affected stands see Appendix V.

2.5.3. Analysis

Differences in live, damaged, and dead basal were interpreted as the effects of Hurricane George. Differences were tested for groups of forest type and disturbance (disturbed versus undisturbed) using two-way ANOVA. For pine forest, disturbance severity differences were tested using one-way ANOVA. Greater proportions of damaged and dead basal area in the disturbed versus undisturbed groups would indicate that the change detection captured broad variation in disturbance severity.

2.6. Disturbance Distribution

2.6.1. Landscape Metrics

The mapped hurricane disturbance types and severities of this study can be considered relatively homogeneous patches of the landscape. The spatial patterns of wind and rain disturbance were analyzed using class metrics for area and core area from FRAGSTATS 3.3 (McGarigal *et al.* 2002). Patches were defined as continuous areas of the same disturbance type and/or severity. Landscape metrics were computed for three different landscapes: 1) the total study site, 2) cloud forest, and 3) pine forest. The classes analyzed are those from the composite damage maps: 1) wind damage (all wind damage and wind damage broken down by severity) and 2) stream scouring and landslide damage.

2.6.2. Topographic Exposure

The program EXPOS (Boose *et al.* 1994) was used to model topographic exposure to wind for all wind directions in 10° increments starting from 0°. The EXPOS output is a binary map classifying each pixel of the landscape as either exposed or protected from wind of a given direction. The ASTER GDEM was used for the terrain surface. A 6 deg inflection angle was assumed. The association between disturbance and predicted wind exposure was measured using Cole’s Coefficient (Cole 1949, Boose *et al.* 1994) using all pixels in the study area. Associations were measured for all wind disturbance, the three severity levels of wind disturbance, and stream scouring and landslide disturbance.

2.6.3. Disturbance Drivers

Analyses of wind and water damage were conducted using the composite classified change detection results and coregistered raster data representing physical aspects of the hurricane, topography, land cover, and hydrology (see Table 2-6). Distance from the track of Hurricane Georges was calculated as the shortest Euclidean distance from each pixel to the hurricane track. Topographic exposure to hurricane winds was represented by a composite of the EXPOS rasters found to have high association with wind disturbance. An exposure index was also calculated as the sum of all 36 wind direction EXPOS outputs. The exposure index is a measure of landscape exposure independent of wind direction. Terrain variables were derived from the ASTER GDEM including elevation, slope, and aspect (decomposed into indices of northness and eastness). Landforms were classified from the ASTER GDEM using terrain position index (Majka *et al.* 2007) into valley bottoms, flat-gentle slopes, steep slopes, and ridgetops. Land cover variables included the land cover classification from this study, and pre-hurricane NDVI and TCW. NDVI is well correlated with total biomass while TCW is related to stand structural attributes (Cohen and Spies 1992). Hydrology variables were derived from the ASTER GDEM including flow accumulation, upstream flow length, curvature, profile curvature, and plan curvature using hydrology tools in ArcGIS 9.3.

Logistic regression was used to model the associations between hurricane disturbance (disturbed or undisturbed) and physical aspects of the hurricane, topography, land cover, and hydrology (Table 2-6) using the glm function in R (R Development Core Team 2011). Separate models were constructed for wind and water using a 10% random sample (n = 36,646) of the entire landscape. Odds ratios were calculated for each variable using the logistic model coefficient. Reduced models were also built to explore the effects of highly correlated variables.

Table 2-6: Variables used in wind and rain models. * = used in model.

Variable	Data Type	Wind	Rain
Elevation	continuous	*	*
Slope	continuous	*	*
Eastness	continuous	*	*
Northness	continuous	*	*
Terrain Position	categorical	*	*
Exposure	Binary	*	
Distance to Track	continuous	*	
Divide	Binary	*	
Land Cover	categorical	*	*
NDVI	continuous	*	*
TCW	continuous	*	*
Flow Accumulation	continuous		*
Flow Length Up	continuous		*
Curvature	continuous		*
Plan Curvature	continuous		*
Profile Curvature	continuous		*

3. Results

3.1. Remote Sensing

3.1.1. Land Cover Classification

The land cover classification is shown in Figure 3-1. The overall classification accuracy was 89.6% and the confusion matrix is reported in Appendix I Table I-3. The majority of the study site (69.4%) was pine forest followed by cloud forest (17.0%) and broadleaf forest (12.1%). Agriculture (0.8%), secondary riparian forest (0.6%), and grassland (0.2%) cover types accounted for only a small percentage of the study site.

Visual inspection of the model results confirms the high overall accuracy of the model. A particular objective was to accurately discriminate between the pine and cloud forest cover types. Producer's and user's accuracies for these cover types were all greater than 80% and visually there is high correspondence between the modeled pine-cloud forest boundary and the actual ecotone (see Appendix I Figure I-1). The most important predictor variables based on both mean decrease in accuracy and GINI were elevation, PCA band 2, and PCA band 3.

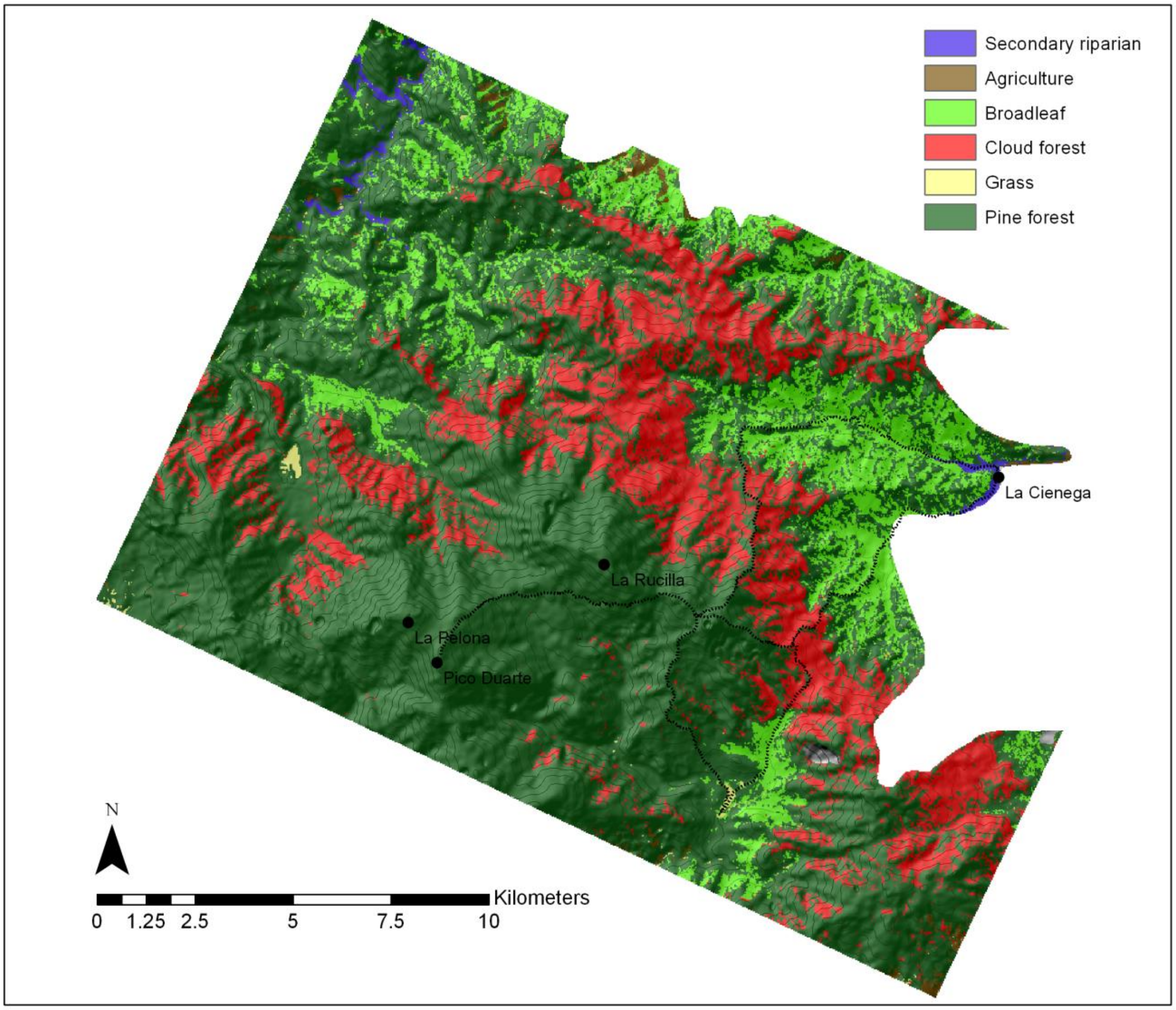

Figure 3-1: Land cover classification of the study site with hillshade and 100 m contour line background. The dotted black line represents the trail system.

3.1.2. Hurricane Regime

As expected there was considerable variability in the spatial patterns of hurricane strikes at the scale of individual islands (Figure 3-2). The larger landmasses of Cuba and Hispaniola have some areas with very few hurricane strikes since 1851 and some areas with many strikes. The eastern portion of Cuba was the most frequently impacted portion of the Greater Antilles. Two areas of low hurricane activity were the northern half of Hispaniola and the northern part of eastern Cuba. Both of these dead spots are on the leeward side of mountain ranges for hurricanes that cross the Caribbean along the typical path from southeast to northwest.

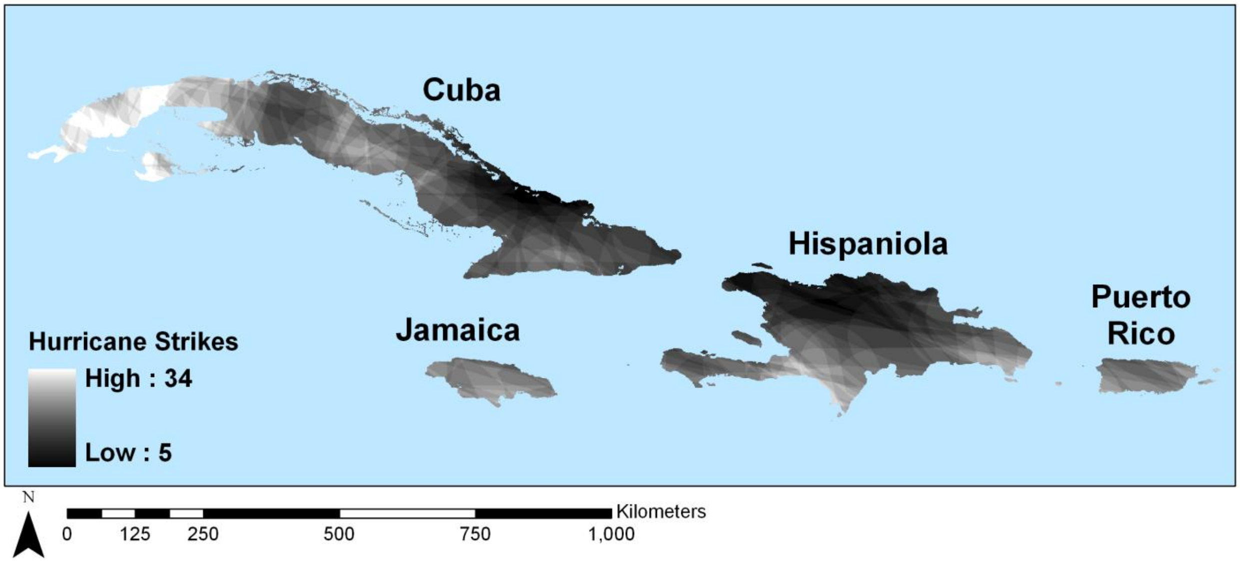

Figure 3-2: Map of hurricane strikes in the period 1851-2009 for the Greater Antilles based on buffer radii of 40.4 nm for category 1, 51.5 nm for category 2, and 59.3 nm for category 3-5 hurricanes. Hurricane tracks from HURDAT (NOAA 2009).

Return intervals using the method described here yield more conservative measures (fewer strikes and longer return intervals) as long as some hurricanes affect only part of the landscape. The category-specific buffer distances derived from 64 kt wind radii were all significantly less than 75 nm and should provide a more accurate estimate of the area impacted by true hurricane-force winds.

During the period of analysis (1851-2009) the Greater Antilles were struck by 182 hurricanes (1.2 strikes/yr), but the most that any one pixel within the Greater Antilles was struck was 34 times (0.2 strikes/yr; Table 3-1). Averaging the strikes of all pixels within the Greater Antilles yields a mean of 15.7 strikes, or 0.1 strikes/yr, or a return interval of 10.0 yrs. The interpretation is that although a hurricane hits part of the Greater Antilles every 0.9 yrs, the average pixel is only struck every 10.0 yrs. Shrinking the extent of the study landscape reduces the number of strikes recorded and increases the return intervals using either method. The average return interval increases from 10.0 yrs for the Greater Antilles, to 11.3 yrs for Hispaniola, to 14.4 yrs for the study site. Hispaniola and the mountains of the

Cordillera Central in particular are less frequently impacted by hurricanes than the Greater Antilles average. Puerto Rico and Jamaica have shorter mean return intervals than Hispaniola, of 8.9 and 8.5 yrs respectively.

Table 3-1: Hurricane strikes and return intervals at three different extents using the standard 75 nm strike method with the target areas as polygon features and using the category-specific buffer distances and averaged for all pixels (90 x 90 m) within the target areas.

Return Interval Comparison	**75 nm strike method**		**Category-specific buffer normalized by area**			
Antilles	**Strikes**	**Return Interval**	**Min Strikes**	**Mean Strikes**	**Max Strikes**	**Return Interval**
All Hurricanes	182	0.9	5	15.7	34	10.0
Category 1	137	1.2	1	8.6	17	18.4
Category 2	90	1.8	0	5.3	15	29.8
Category 3	66	2.4	1	4.4	13	35.8
Category 4	31	5.1	0	2.2	7	70.3
Category 5	5	31.6	0	0.3	3	556.6
Hispaniola						
All Hurricanes	69	2.3	5	13.9	25	11.3
Category 1	49	3.2	1	7.9	17	19.9
Category 2	28	5.6	0	3.6	10	44.4
Category 3	20	7.9	1	3.6	7	43.6
Category 4	9	17.6	0	2.2	4	71.3
Category 5	2	79.0	0	0.5	1	327.4
Study Site						
All Hurricanes	27	5.9	9	11.0	13	14.4
Category 1	22	7.2	5	7.5	10	21.0
Category 2	5	31.6	3	3.7	4	42.6
Category 3	7	22.6	2	2.1	3	75.9
Category 4	3	52.7	2	2.0	2	79.0
Category 5	1	158.0	1	1.0	1	158.0

3.1.3. Change Detection

3.1.3.1. Vegetation Indices

The accuracy and sensitivity of NDVI, TCG, NDII, and TCW were assessed in terms of spatial consistency between the change detection and damage visible in the CIR OM, the distributions of pre- and post-vegetation indices (VIs), and the distributions of VI differences.

The broad spatial distributions of negative change detection values (interpreted as disturbance) were relatively consistent across the four VIs (Appendix VI Figures VI-1, VI-2, VI-3, and VI-4). The linear patterns of scoured streams were picked up by all four VIs, though contrast was highest for these features in NDVI and TCG. Large patches of windthrown pine forest are present in the south-central portion of the study site (see Figure 3-3). The change detection using TCG shows little contrast in these areas suggesting that TCG is not very sensitive to windthrow. Change detection using NDVI, NDII, and TCW all detected the large windthrow patches.

The shape of VI distributions changed from pre- to post-hurricane (Appendix VI Figures VI-1, VI-2, VI-3, and VI-4), except for TCG. The post-hurricane distributions of NDVI, NDII, and TCW are all shifted to the left with long left tails. These changes suggest no-to-low severity disturbance for much of the landscape and high severity disturbance for the minority of the landscape. NDII had the most pronounced shift in distribution from pre- to post-hurricane and had the most contrast in cloud forest. The NDII change detection results were used in all subsequent analyses.

3.1.3.2. Initial Assessment and Classification of Change Detection Results

The NDII change detection was then classified (Appendix VII Figure VII-1) based on standard deviations as outlined in Table 2-4. Based on this classification scheme, 13.9% of the landscape was disturbed. Areas classified as high disturbance closely matched the spatial distribution of large windthrown pine areas based on visually evident windthrown trees in the aerial photos (see Figure 3-3). NDII change detection also picked up much of the stream scouring and landslides which appear as interconnected linear features (Appendix VII Figure VII-1).

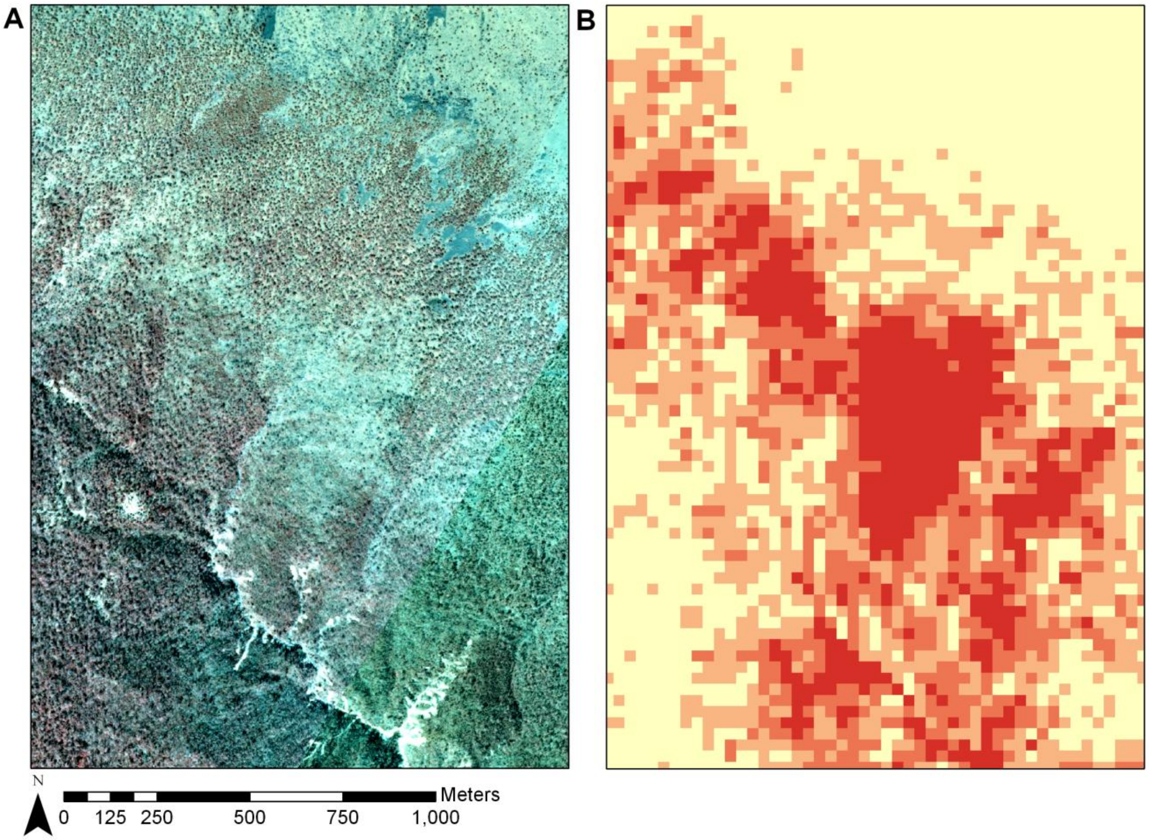

Figure 3-3: Comparison of pine forest windthrow in a) CIR OM (lighter areas) and b) the NDII change detection.

The NDII change detection had an overall classification accuracy (as assessed from the photo interpreted testing points) of 81.7% and an overall kappa statistic of 0.633, which are similar to values reported by Wang and Xu (2010) for change detection of Hurricane Katrina damage using tasseled cap wetness. NDII change detection in this study had similar classification accuracies for both cloud forest (79.3%) and pine forest (84.0%). Errors of omission were slightly higher for cloud forest (20.0%) than for pine forest (13.3%), but errors of commission were very similar between cloud forest (21.3%) and pine forest (18.7%).

3.1.3.3. Scouring and Landslide Classification

Only 4.3% of the total landscape was classified as stream scouring or landslide disturbance (Appendix IV Figure IV-1, Table IV-3). Overall accuracy of the classification was 95.3%. The confusion matrix is reported in Appendix IV Table IV-4. The most important variables were change in NDVI, PCA band 3, and NDVI. The modeled stream scouring and landslides closely match the site's stream network and captured many of the noticeable landslides in the CIR OM.

3.1.3.4. Composite Classified Damage Map

The classified NDII change detection was combined with the scouring and landslide classification to produce a single product (Figure 3-4), separating wind disturbance from rain disturbance. The NDII change detection picked up much, but not all of the scour/landslide class as change. Precedence was given to the scouring and landslide classification when combining the two products.

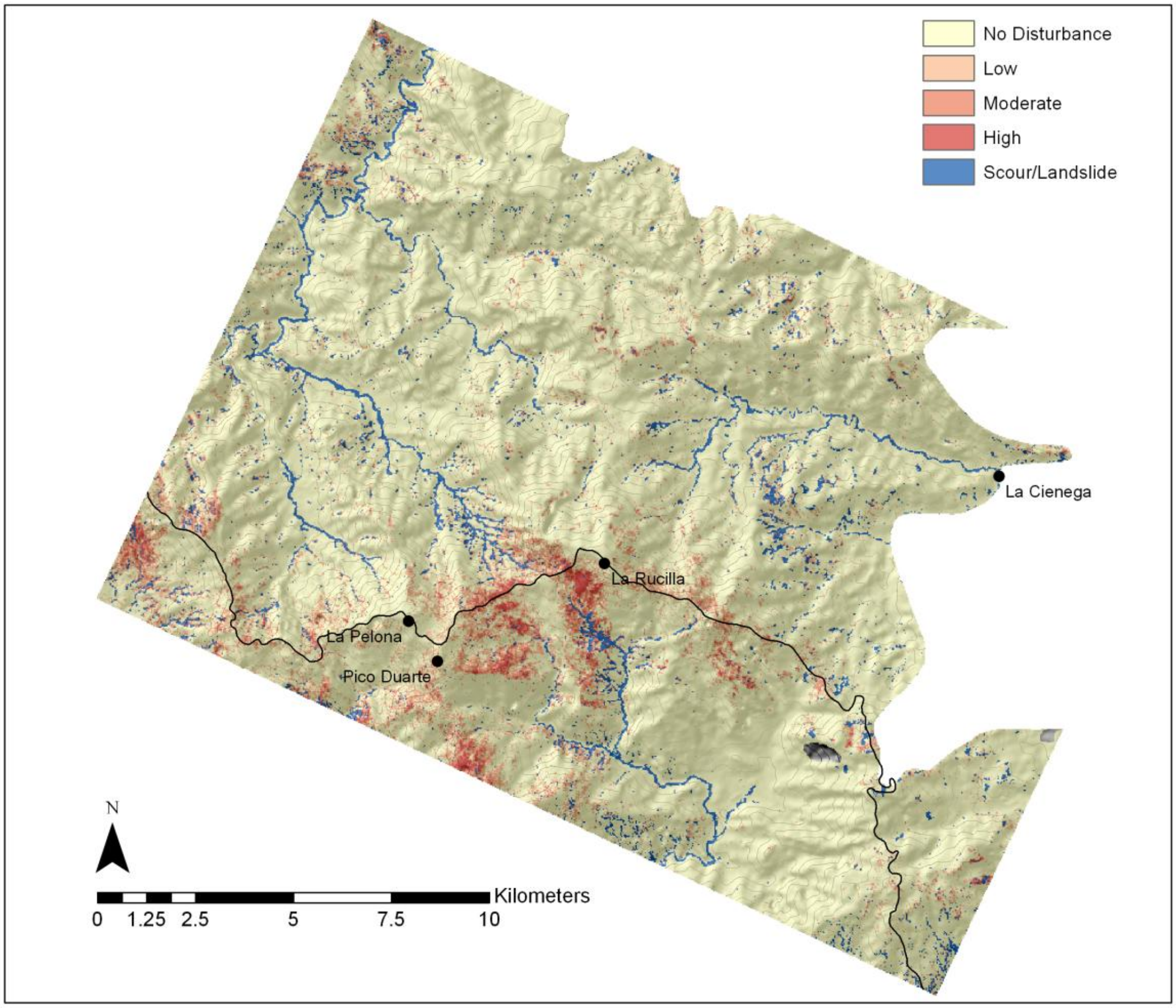

Figure 3-4: Composite disturbance map with wind and water disturbance from stream scouring and landslides over a hillshade and 100 m contour backdrop. The solid black line represents the major divide of the site.

Combining the two data sources resulted in a reduction in the percent of the study site classified as wind disturbed (13.9% to 11.3%), as there was overlap between wind and scour/landslide classes. Most wind disturbance was low severity (8.7% of the total landscape), followed by moderate (2.0%), and then high severity (0.6%). Disturbance from water seems to be distributed throughout the study site mainly around stream channels but also as small linear features (i.e. landslides) in steep terrain.

Wind disturbance appears non-random in its distribution, especially in the highest elevation pine forest. There are notably large patches of high severity wind disturbance just south of the divide near the center of the study area. Two more large patches of high disturbance lie due south of the major disturbance zone and at the west corner of the study area. There also appears to be a zone of scattered low to moderate severity wind disturbance extending from Pico La Rusilla to the east, along and slightly to the north of the divide. North of the divide, wind disturbance is more scattered in small patches with little moderate and high severity disturbance.

3.2. Hurricane Effects on Forests

Patterns of wind disturbance were strongly associated with forest type. Due to differences in the total basal area (BA) between forest types and disturbance categories, proportions of BA were used to assess wind disturbance effects (Figure 3-5). Hurricane Georges significantly increased the proportion of dead BA in the disturbed plots (two-way ANOVA; proportion dead BA ~ forest type + disturbance, forest type p-value = 0.83, disturbance p-value = 1.53e-08), but post-hoc comparisons show that the effect was only significant for pine forest (t-test, p-value = 1.26e-14) and cloud forest (p-value = 0.03), but not mixed pine (p-value = 0.46). For all forest types the proportion of live undamaged basal area was lower in the disturbed plots and the proportion of dead basal area was higher. In all but cloud forest, the proportion of live damaged basal area was also higher in the disturbed plots. The effect of the hurricane was strongest on pine forest. The disturbed pine forest plots had 60.5% less live undamaged basal area than the undisturbed plots, compared to differences of 32.0% for mixed pine and 7.1% for cloud forest.

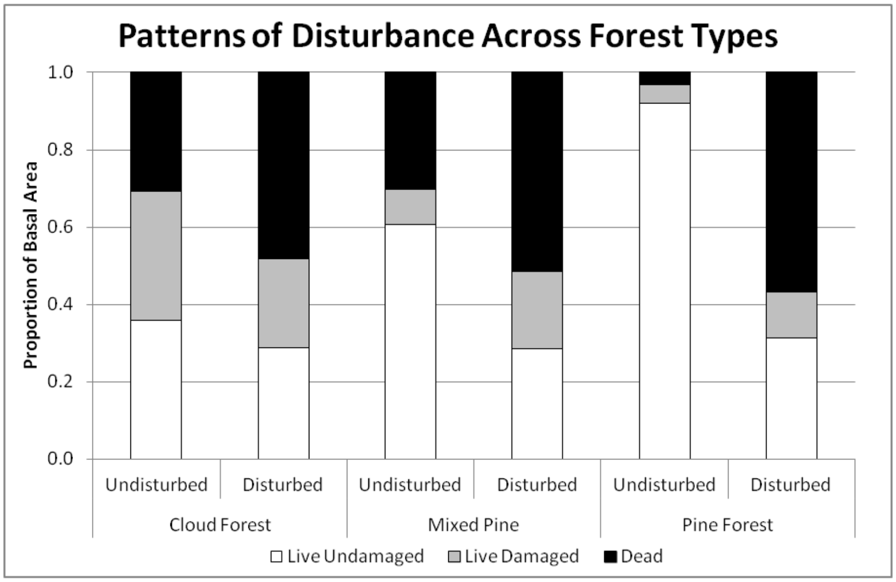

Figure 3-5: Hurricane wind effects across forest types and disturbance categories.

Field sampling in pine forest was stratified across 4 levels of wind disturbance severity. The proportion of undamaged live basal area decreased from low to high severity wind disturbance (one-way ANOVA; proportion dead BA ~ disturbance level, p-value = 2.20e-16, Figure 3-6). The change detection severity categories captured the broad range in hurricane effects. The high severity plots had 70.0% less live undamaged basal area than the undisturbed plots. Almost all of this decrease was due to mortality. In the low and moderate severity pine forest a larger proportion of the total basal area was live but damaged.

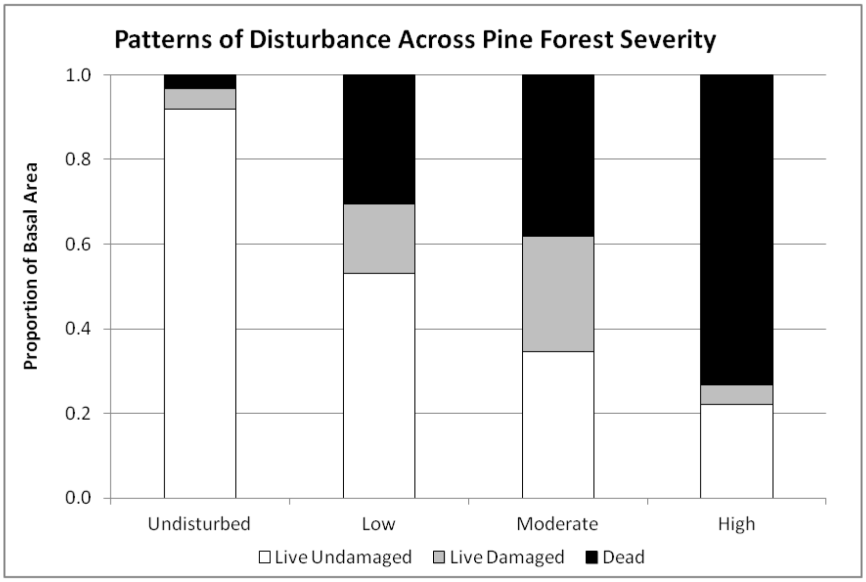

Figure 3-6: Patterns of wind effects across levels of disturbance severity in pine forest.

Disturbance indicators varied across forest types and disturbance categories (**Table 3-2**). Uprooting was the primary cause of mortality in pine forest, accounting for 35.5% of basal area for all disturbed pine forest, increasing from 0.7% in undisturbed plots to 46.7% in the high severity plots. Uprooting was rare in cloud forest; only 1.1% of the disturbed cloud forest basal area was uprooted. Uprooting accounted for 11.1% of basal area in the disturbed mixed pine plots compared to only 3.7% in the undisturbed plots. In cloud forest there was 13.1% more downed dead basal area in the disturbed plots. Downed dead trees could be the result of delayed mortality from hurricane-related injuries, but the exact cause of death is unknown. Snapped stems were common in all three forest types, but were found in nearly equal proportions in the disturbed and undisturbed cloud forest. Snapped stems were slightly more common in the disturbed than undisturbed mixed pine plots. Snapped stems increased with wind disturbance severity from 2.6 to 23.4% of total basal area.

Table 3-2: Summary of lethal and non-lethal disturbance indicators by forest type and either disturbance or disturbance severity.

Field Categories		Disturbance Indicators (Proportion of Basal Area)								
		Lethal Disturbance Indicators					Non-lethal Disturbance Indicators			
							Crown Damage			
Forest Type	Disturbance Category	Uprooted	Snapped	Tipped	Standing Dead	Downed Dead	Low	Moderate	High	Tipped
Cloud Forest	Disturbed	0.01	0.15	0.06	0.08	0.17	0.04	0.03	0.06	0.10
	Undisturbed	0.00	0.17	0.02	0.07	0.04	0.08	0.10	0.05	0.11
Mixed Pine	Disturbed	0.11	0.21	0.02	0.09	0.08	0.11	0.06	0.01	0.02
	Undisturbed	0.04	0.17	0.01	0.06	0.02	0.06	0.02	0.00	0.01
Pine Forest	Disturbed	0.35	0.20	0.00	0.01	0.01	0.05	0.06	0.01	0.00
	High	0.47	0.23	0.01	0.01	0.01	0.02	0.02	0.00	0.00
	Moderate	0.23	0.15	0.00	0.00	0.00	0.13	0.11	0.04	0.00
	Low	0.17	0.13	0.00	0.00	0.00	0.06	0.10	0.00	0.00
	Undisturbed	0.01	0.03	0.00	0.00	0.00	0.04	0.01	0.00	0.00

Consistent across all three forest types, stems of larger size were damaged more frequently than stems of smaller size (Figure 3-7). Pine forest had the highest number of large trees. Dead stems larger than 20 cm DBH made up only 6.1% of cloud forest and 6.5% of mixed pine compared to 18.9% of pine forest. Large trees account for most of the basal area, so it should come as no surprise that most the dead basal area was in the larger size classes. Stems larger than 20 cm in DBH made up 68.7% of cloud forest, 82.0% of mixed pine, and 97.1% of pine forest dead basal area.

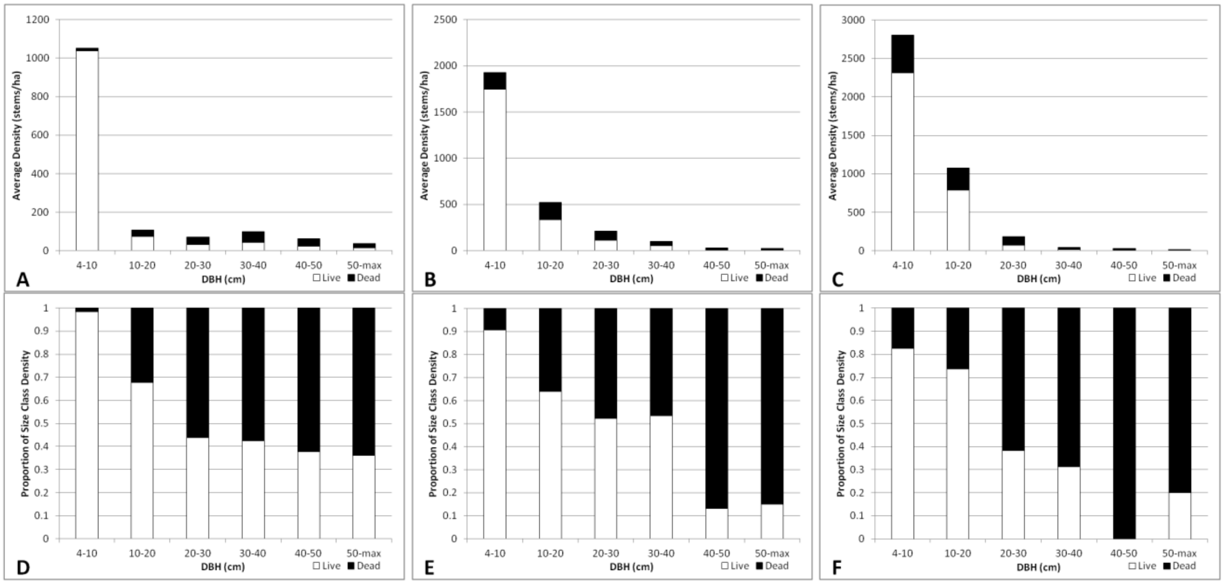

Figure 3-7: Stem size distribution of live and dead stems for disturbed a) pine forest, b) mixed pine, and c) cloud forest. Proportion of live and dead stems for disturbed d) pine forest, e) mixed pine, and f) cloud forest.

3.3. Disturbance Distribution

3.3.1. Landscape Metrics

The spatial patterns of disturbance varied by disturbance type, disturbance severity, and forest type (**Table 3-3**). At the scale of the total landscape wind accounted for more disturbance (PLAND = 11.2%) than rain (4.3%) and there were more than twice as many patches of wind disturbance (NP = 3704) than rain disturbance (1430). Wind disturbed patches were slightly larger (A_MEAN) and were more variable in size (A_SD) than rain patches. Rain disturbed patches were more linear than wind disturbed patches because drainage networks magnify the power of rain. Wind disturbance also had greater than six times more core area (TCA) than rain disturbance and had a greater number of disjunct core areas (NDCA).

Table 3-3: Landscape metrics presented for disturbance at three extents (total landscape, cloud forest, and pine forest). All area measurements are presented in ha. CA = class (total) area, PLAND = percentage of landscape, NP = number of patches, PD = patch density (patches/100 ha), A_MEAN = mean patch size, A_MAX = maximum patch size, A_SD = standard deviation of patch size, TCA = total core area, CPLAND = core area percentage of landscape, and NDCA = number of disjunct core areas. For further description of landscape metrics see McGarigal et al. (2002)

Total Landscape	**CA**	**PLAND**	**NP**	**PD**	**A_MEAN**	**A_MAX**	**A_SD**	**TCA**	**CPLAND**	**NDCA**
Scour/Landslide	1430	4.3	3060	9.3	0.47	69.3	2.7	124.1	0.4	468
Wind	3704	11.2	7332	22.2	0.51	543.0	9.4	758.6	2.3	686
Low	2856	8.7	8127	24.6	0.35	25.1	2.3	109.3	0.3	563
Moderate	651	2.0	2461	7.5	0.26	6.1	0.9	13.6	0.0	95
High	197	0.6	629	1.9	0.31	18.0	1.2	29.8	0.1	39
Cloud Forest										
Scour/Landslide	242	4.3	784	14.0	0.31	11.7	0.9	13.2	0.2	56
Wind	439	7.8	2035	36.3	0.22	7.9	0.4	10.4	0.2	41
Low	379	6.8	2025	36.1	0.19	2.5	0.3	2.7	0.0	19
Moderate	53	0.9	396	7.1	0.13	1.4	0.1	0.0	0.0	0
High	7	0.1	64	1.1	0.10	0.3	0.0	0.0	0.0	0
Pine Forest										
Scour/Landslide	969	4.2	2691	11.8	0.36	58.6	1.8	52.2	0.2	247
Wind	3045	13.3	5379	23.5	0.57	542.9	10.9	711.5	3.1	584
Low	2277	9.9	5995	26.2	0.38	25.1	2.7	97.0	0.4	492
Moderate	580	2.5	2033	8.9	0.29	6.1	1.0	12.9	0.1	91
High	188	0.8	565	2.5	0.33	18.0	1.3	29.7	0.1	38

The patch level metrics for wind disturbance change depending on the disturbance severity of focus. The total area (CA), percentage of landscape (PLAND), number of patches (NP), and patch density (PD) all declined from low to high severity wind disturbance. Interestingly, the mean patch area (A_MEAN) did not decline with increasing wind severity; the mean patch size of high severity disturbance was larger (0.31 ha) than the mean patch size of moderate severity disturbance (0.26 ha). The maximum patch size (A_MAX) and the total core area (TCA) were also larger for high severity than moderate severity wind disturbance. This suggests that although high severity disturbance is rare, it is clustered in larger patches.

There are interesting differences in the class level metrics for the cloud forest and pine forest landscapes (**Table 3-3**). A greater percentage of pine forest was wind disturbed (PLAND = 13.3%) than cloud forest (7.8%), but the patch density (PD) was higher for cloud forest (PD = 36.3 patches/100 ha) than pine forest (23.5 patches/100 ha). This means that wind disturbance in cloud forest is distributed in many small patches. There was proportionately more pine forest in the higher severity wind disturbance classes than cloud forest. The mean patch area (A_MEAN) of wind disturbed pine forest (0.57 ha) was more than twice as large as cloud forest (0.22 ha) and the same is true for each of the wind disturbance severity classes. Pine forest also contained almost 70 times more total core area (TCA) than cloud forest and there was no core area for cloud forest in the moderate and high severity disturbance severity classes.

Measures of mean patch area were highly skewed by numerous small patches consisting of only 1 or 2 Landsat pixels, so to highlight differences in larger patches, further analyses focused on the wind disturbed patches of pine forest bigger than the biggest disturbed patch of cloud forest. Very large patches of pine forest account for a large portion of the total landscape wind disturbance (Table 3-4). There are 30 patches (NP) of wind disturbed pine forest (0.4% of all patches) larger than the largest cloud forest patch, accounting for 38.1% of total disturbed area (PTDIST). Much of the total wind disturbed area in the low, moderate, and high disturbance classes was in large pine forest patches. This trend is strongest for high severity wind disturbance; these large patches of pine forest account for 62.0% of the total high severity disturbance area. The spatial distribution of the plots described in Table 3-4 is illustrated in Figure 3-8. These large wind-disturbed pine forest patches are concentrated to the south of the divide primarily in elevations above 1800 m.

Table 3-4: Patches of disturbed pine forest larger than the largest patches of cloud forest. NP = number of patches, TA = total area, PLAND = percentage of landscape, and PTDIST = percentage of total disturbed

Pine Forest	**NP**	**TA**	**PLAND**	**PTDIST**
Wind	30	1410	4.28	38.1
Low Damage	96	532	1.61	18.6
Moderate Damage	46	109	0.33	16.8
High Damage	98	122	0.37	62.0

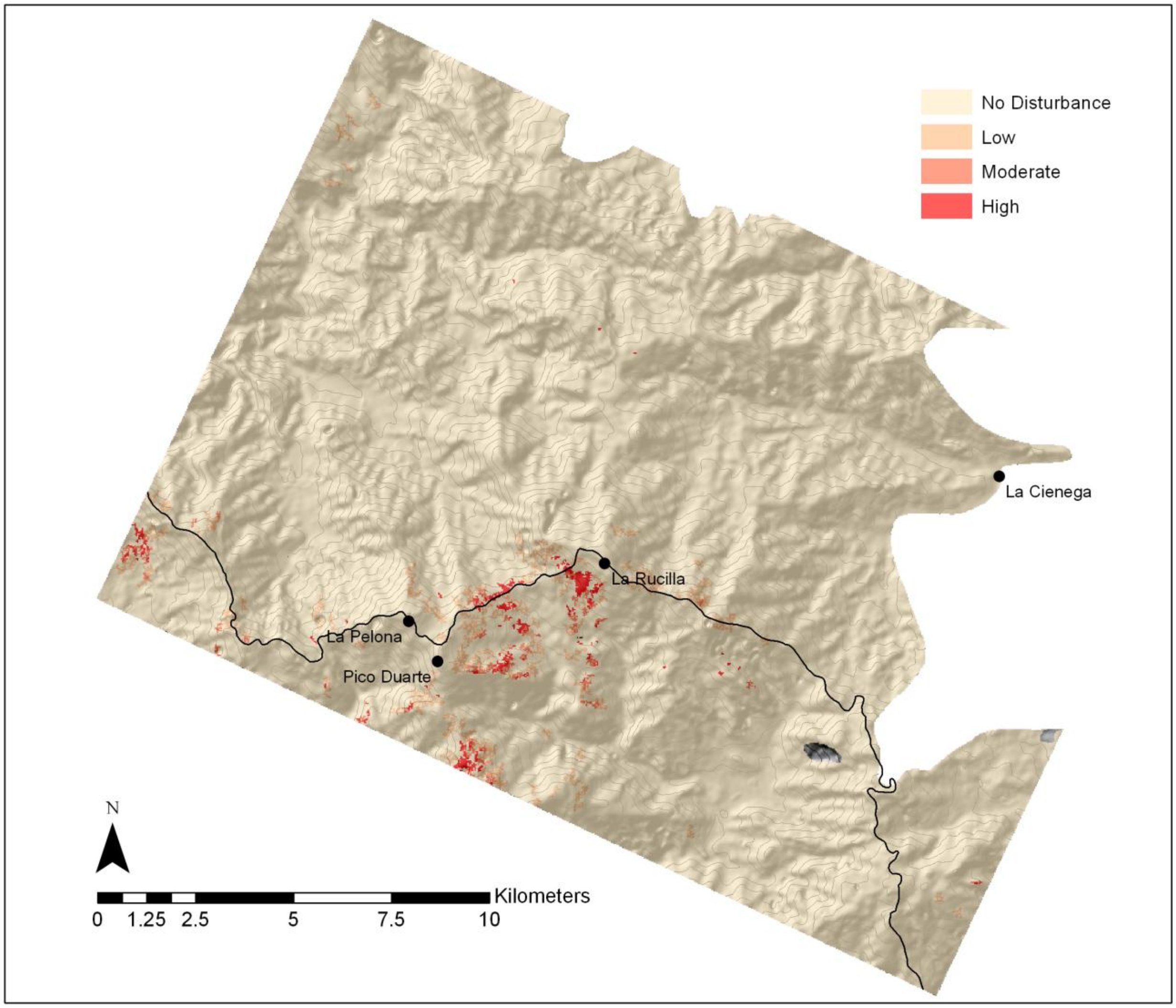

Figure 3-8: Wind disturbed pine forest patches larger than the largest disturbed cloud forest patches by disturbance severity class over hillshade and 100 m contour background. The solid black line represents the major divide of the site.

3.3.2. Topographic Exposure

Topography can drive patterns of hurricane disturbance through its influence on exposure to wind. The EXPOS model (Boose *et al.* 1994) provides a binary prediction of landscape exposure to wind of a specified direction. Strong association between predicted exposure to a given wind direction and patterns of wind disturbance may indicate the dominant wind direction. Associations between wind disturbance and predicted wind exposures are presented in Figure 3-9. Association values vary by wind direction. For all wind damage (Panel A, Figure 3-9), low damage (Panel B), and moderate damage (Panel

C) the association is strongest for predicted exposure to 140° wind. Spatially there is good agreement between predicted exposure to 140° wind and observed patterns of wind disturbance (Figure 3-10) and 140° is close to the expected wind direction from Hurricane Georges given its path (Figure 2-1). Associations are similarly strong for wind directions + or – 20° of the 140° peak. The associations between stream scouring/landslide disturbance and predicted exposure to wind were negative for all wind directions confirming that different forces drive patterns of rain disturbance.

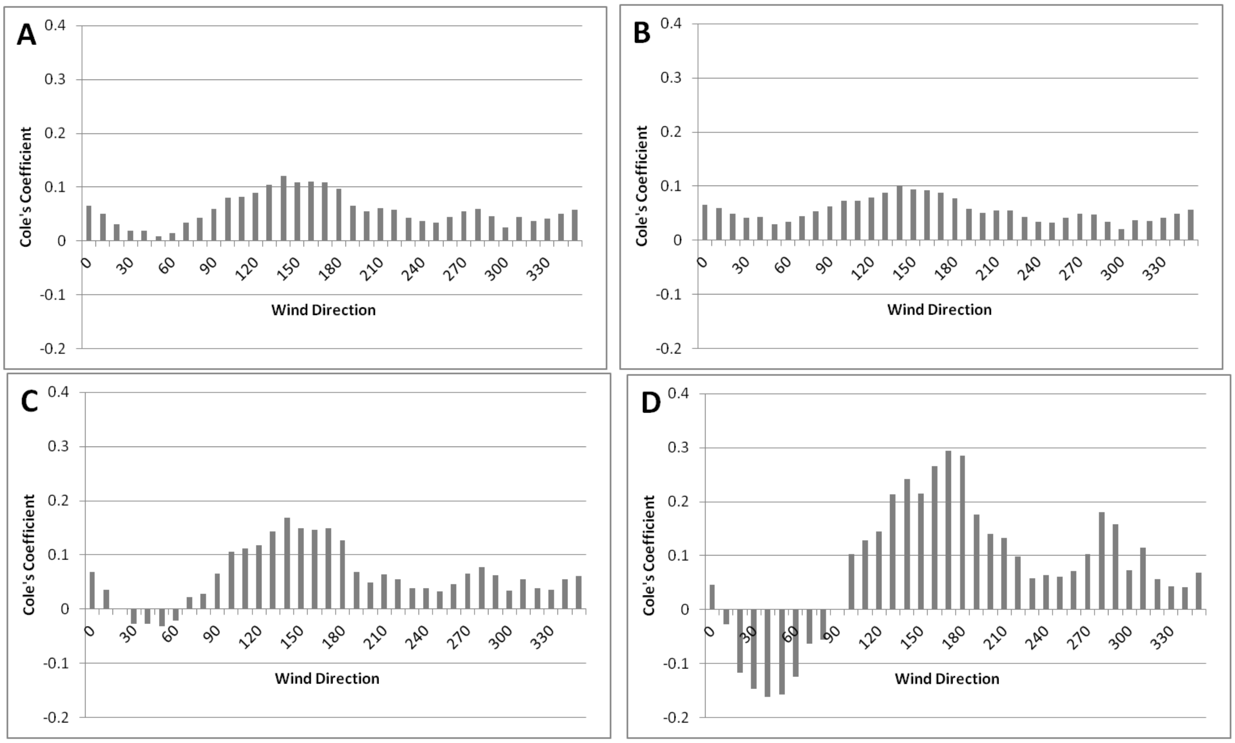

Figure 3-9: Cole's coefficients of association between wind disturbance and predicted exposure by wind direction for a) all wind damage and for b) low, c) moderate, and d) high severity damage.

Across disturbance severities, from low to high, the strength of the association became stronger. High damage was most strongly associated with the predicted exposure to 170° wind (Panel D Figure 3-9, Figure 3-11). Strong association with this different wind direction may correspond to a short duration of gusty wind capable of uprooting and snapping stems.

Disturbance associations with wind directions from 20 to 60° were consistently weak and sometimes negative. Inflow winds to the right of Hurricane Georges' path were likely weakened or blocked by the divide of the Cordillera Central which runs through the center of the study site from southeast to northwest.

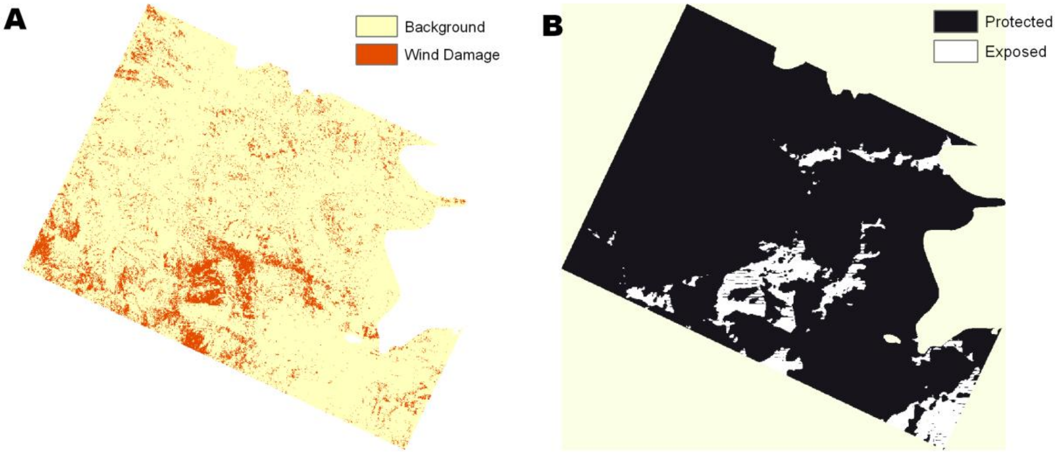

Figure 3-10: Spatial distribution of a) wind disturbance and b) predicted exposure to 140 deg winds.

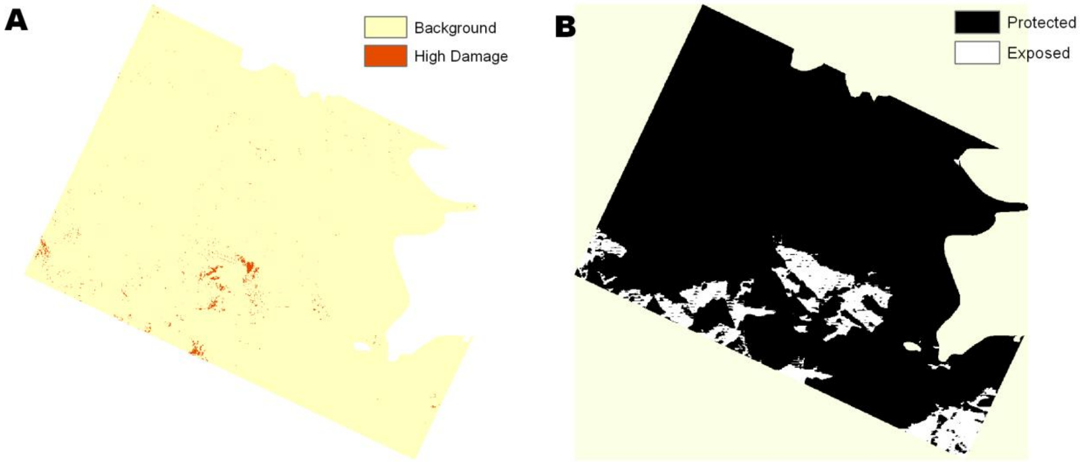

Figure 3-11: Spatial distribution of a) high severity wind disturbance and b) predicted exposure to 170 deg winds.

3.3.3. Disturbance Drivers

Topographic exposure is only one of many factors that influence landscape disturbance patterns. The relationship between disturbance and physical aspects of the hurricane, topography, land cover, and hydrology was explored in two ways: first the proportion of area disturbed along gradients of single disturbance drivers are presented and then multivariate models (logistic regression) are used to integrate these drivers into a single analysis framework.

3.3.3.1. Wind

There are strong patterns between wind disturbance and factors related to the physical aspects of Hurricane Georges. Over 18% of the area south of the divide was damaged by wind, versus only 8.4% north of the divide (Figure 3-12, Panel A). The area south of the divide is only 27.4% of the landscape area, but it contains 45.6% of all wind disturbance, and 56.7% of the moderate severity and 71.5% of the high severity disturbance. Wind intensity varies by distance from the hurricane. The strongest winds are in the hurricane eyewall, some distance from the center of the hurricane. Wind speeds decline rapidly as distance increases outside the eyewall. The proportion of area disturbed is higher for parts of the landscape within 30 km of the track (Figure 3-12, Panel B). The relationship between disturbance and distance from the hurricane is non-linear with the peak proportion of area disturbed in the 20-30 km instead of the closest distance range. Wind disturbance has a strong positive relationship with exposure index (Figure 3-12, Panel C). The portion of the landscape in the 20-30 km distance range contains the highest elevation in the landscape, which has higher predicted exposure to wind.

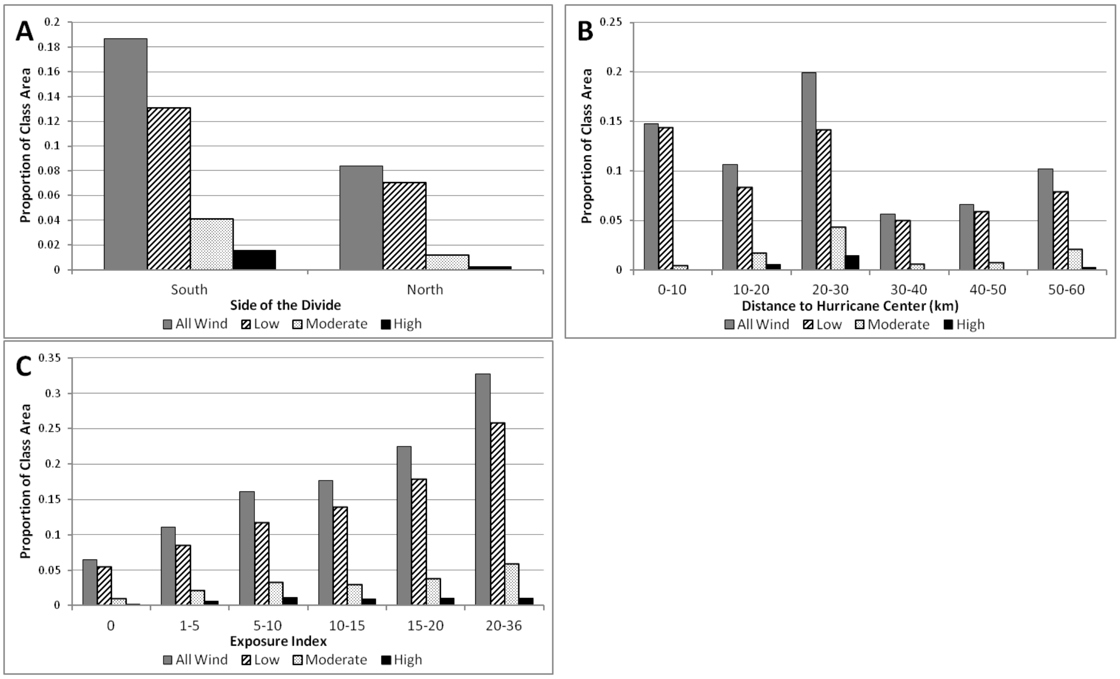

Figure 3-12: The distribution of wind disturbance relative to physical aspects of Hurricane Georges' wind as represented by a) side of the divide, b) distance to the hurricane, and c) topographic exposure index.

Some topographic factors seem to influence disturbance distribution (Figure 3-13). The proportion of area disturbed was much greater above 2000 m with a peak in the 2500-3000 m range (Figure 3-13, Panel A). Hurricane wind speeds do not differ much within the vertical profile of the hurricane, so there is no physical reason why elevation would drive disturbance other than through its control on exposure. There is little difference in the proportion of area disturbed by aspect (Figure 3-13, Panel B) or by slope (Figure 3-13, Panel C) except for slopes steeper than 50°. Terrain position (Figure 3-13, Panel D) does not appear to be a major driver of disturbance. There is a slightly higher proportion of area disturbed on ridgetops than canyon bottoms or flat-gentle slopes. Possibly the classification of these terrain positions does not match the scale at which topographic position influences disturbance.

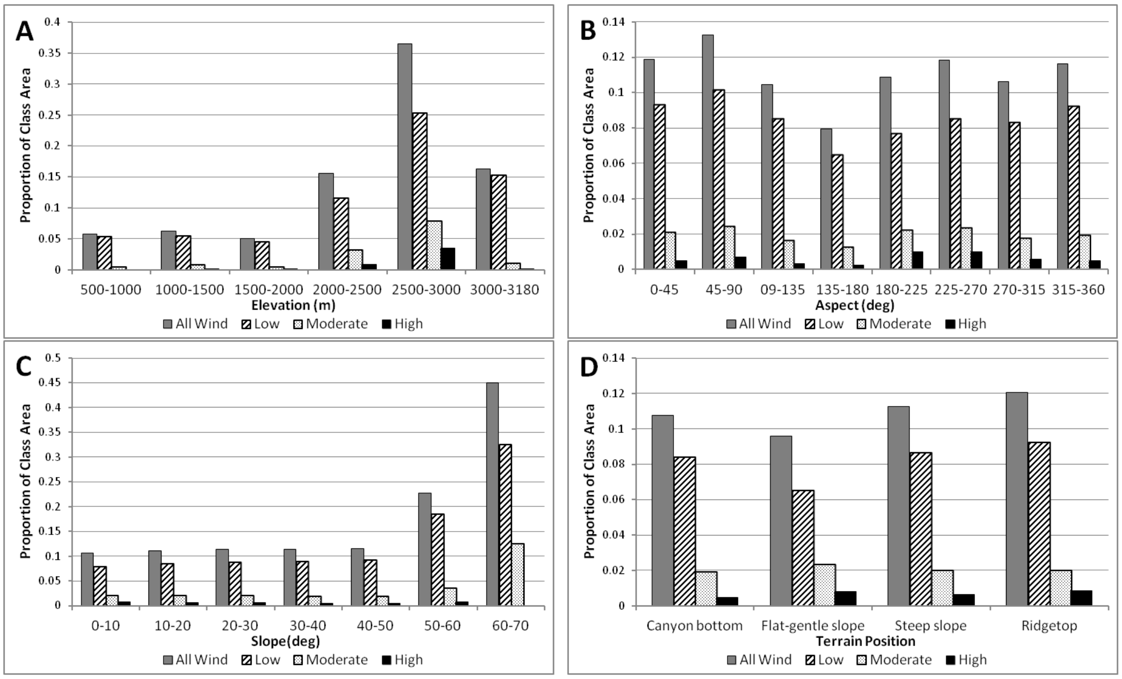

Figure 3-13: The distribution of wind disturbance relative to topography: a) elevation, b) aspect, c) slope, and d) terrain position.

There were differences between land cover types in the proportion of area disturbed by wind (Figure 3-14). The grass and agriculture cover types had the lowest proportion of area disturbed. Forested land cover types had proportionately more area damaged. Pine forest had the highest proportion of area disturbed by wind and the highest proportion disturbed in the low, moderate, and high severity classes. Higher proportion of wind disturbance in pine forest and cloud forest is in part due to the position of these land cover types within the landscape. Cloud forest and pine forest are higher in elevation than broadleaf and secondary riparian forests and wind affected a greater proportion of the high elevation landscape.

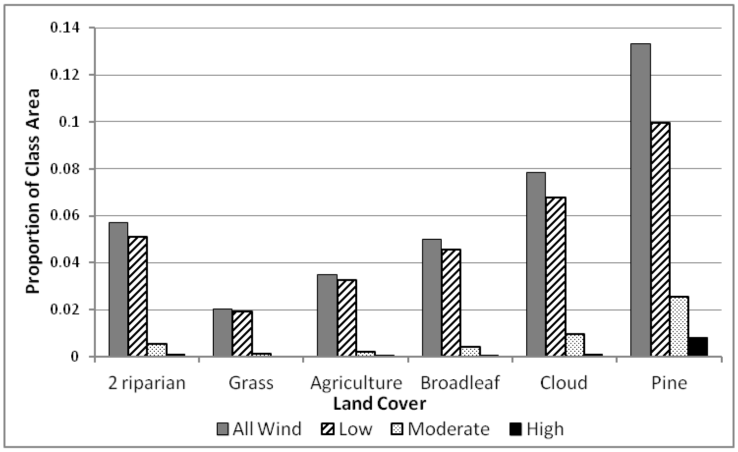

Figure 3-14: Proportions wind disturbed by land cover types.

3.3.3.2. Wind Extent Model

All variables (Table 3-5) were significant for the wind extent model at the α = 0.05 level (Table 3-5: and Wald test for overall significance of categorical variables). Odds ratios > 1 indicates higher than 50% probability of occurrence, while those < 1 indicate lower than 50% probability of occurrence. If the 95% confidence interval for the odds ratio does not overlap 1, then there is a significant influence on the odds of disturbance, with values greater than 1 indicating the factor increases odds of disturbance and the values less than 1 indicating the factor decreases the odds of disturbance. Odds of wind disturbance increase with elevation, decrease with slope, and are higher for east- and north-facing aspects. Contrary to Figure 3-13, Panel D, the model suggests terrain position does influence wind disturbance odds. Ridgetops were the least likely landform to be disturbed by wind.

Table 3-5: Logistic regression model of wind disturbance extent. * = significant at the 0.001 level.**

Logistic Regression Model of Wind Extent				
		Wald Confidence Limits		
Variable	Odds Ratio	2.5%	97.5%	Sig
Intercept	0.104	0.035	0.306	***
Elevation (m)	1.003	1.002	1.003	***
Slope (°)	0.988	0.983	0.992	***
Eastness	1.154	1.092	1.220	***
Northness	1.670	1.566	1.781	***
Terrain Position 2 vs 1	1.021	0.765	1.349	
Terrain Position 3 vs 1	0.724	0.655	0.801	***
Terrain Position 4 vs 1	0.588	0.519	0.665	***
Exposure 2 vs 1	1.597	1.435	1.778	***
Distance to Track (km)	1.000	1.000	1.000	***
Divide 2 vs 1	2.012	1.808	2.240	***
Land Cover 2 vs 1	1.012	0.442	2.281	
Land Cover 3 vs 1	0.289	0.169	0.535	***
Land Cover 4 vs 1	0.209	0.122	0.386	***
Land Cover 5 vs 1	0.522	0.116	1.695	
Land Cover 6 vs 1	0.369	0.217	0.678	***
NDVI	0.015	0.007	0.033	***
TCW	1.138	1.124	1.152	***

The physical aspects of the hurricane also had a significant influence on wind disturbance extent. Hurricane exposure was approximated in the model by the union of EXPOS predictions for wind directions from 120 to 180 deg. These wind directions all had association values much higher (> 1 SD) than the mean for all wind directions and also corresponded to the expected wind directions from a hurricane passing to the south. Pixels within the area of predicted exposure were 1.6 times more likely to be disturbed by wind than those that weren't. There was a small positive effect from distance from the hurricane, which may be due to the high proportion of wind disturbance at the highest elevations which are of intermediate distance from the hurricane track. Alternatively, this pattern could result if the eyewall of the hurricane, which was probably weak at the time of passing (Gerts *et al.* 1999), intersected with the site. The divide had a strong affect on wind disturbance odds. Areas south of the divide were more than twice as likely to be disturbed as those north of the divide.

The full model suggests that cloud forest had the lowest odds of disturbance of any land cover type. Odds for pine forest was also low, but significantly higher than cloud forest (Wald test on coefficients, p-value = 0). Since land cover is highly correlated with topographic variables, a reduced model was built without elevation, slope, aspect, or terrain position. Land cover was significant in the reduced model (Wald test on coefficients, p-value = 1.6e-11) and pine forest showed the highest odds of wind disturbance (Odds Ratio = 1.364). NDVI decreased wind disturbance odds, while TCW increased odds. Our interpretation is that denser stands have decreased odds of disturbance (higher NDVI) and more mature stands with greater structural complexity (higher TCW) have increased odds of disturbance.

3.3.3.3. Water

The relative importance of wind and water disturbance varied by land cover (Figure 3-15, Panel A) and by terrain position (Figure 3-15, Panel B). The secondary riparian and grass land cover types had high proportions of water disturbance. Secondary riparian forest and grass cover types are closely associated with stream channels and valleys making them more susceptible to stream scouring, as canyon bottoms and flat-gentle slopes have more water disturbance than steep slopes and ridgetops (Figure 3-15, Panel B). The relative importance of water disturbance (proportion of area disturbed) was also higher in cloud forest whereas the relative importance of wind disturbance was higher in pine forest.

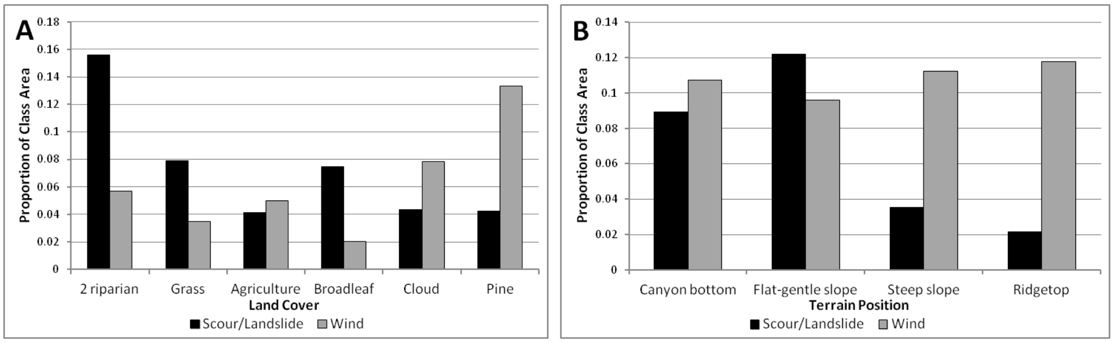

Figure 3-15: The proportion of area disturbed by wind or water by a) land cover and b) terrain position.

The distribution of water disturbance shows strong patterns with hydrology variables (Figure 3-16). Proportion of area disturbed is highest at very low and very high slopes (Figure 3-16, Panel A). There are trends of increasing water disturbance for increasing flow accumulation (Figure 3-16, Panel B), increasing upstream flow length (Figure 3-16, Panel C), and decreasing curvature (Figure 3-16, Panel D). This means that water damage was more common on terrain that funnels water from larger catchments and over longer runs.

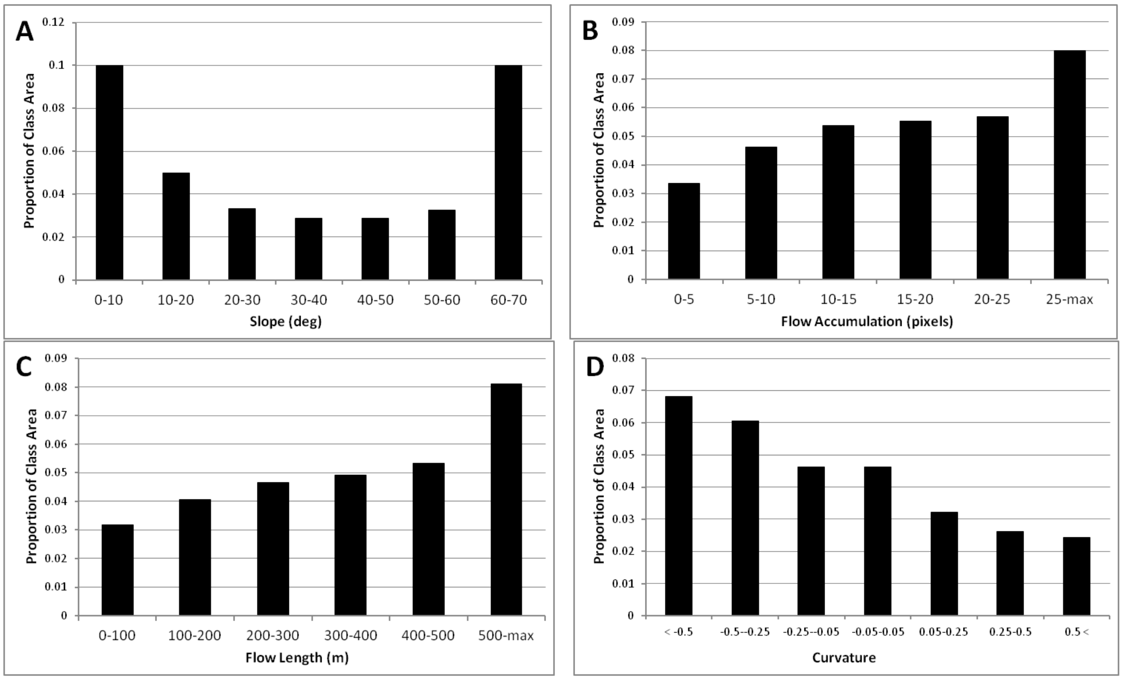

Figure 3-16: The proportion of area disturbed by water across gradients in hydrology factors: a) slope, b) flow accumulation, c) flow length, and d) curvature.

3.3.3.4. Water Extent Model

All variables (Table 3-6) were significant for the water extent model at the 0.01 level (Table 3-6: and Wald test for overall significance of categorical variables). Odds of rain disturbance decrease with elevation, decrease with slope, and are higher for west- and north-facing aspects. Terrain position and land cover significantly affected the model. Canyons had the highest odds of disturbance from rain. Similarly, secondary riparian forests that line the stream channels at lower elevations were the land cover type with the highest odds of disturbance.

Table 3-6: Logistic regression model of rain disturbance extent. ** = significant at the 0.01 level. * = significant at the 0.001 level.**

Logistic Regression Model of Rain Extent				
		Wald Confidence Limits		
Variable	**Odds Ratio**	**2.5%**	**97.5%**	**Sig**
Intercept	0.966	0.624	1.471	
Elevation (m)	0.999	0.999	0.999	***
Slope (°)	0.965	0.959	0.972	***
Eastness	0.943	0.873	1.019	
Northness	1.767	1.630	1.917	***
Terrain Position 2 vs 1	0.864	0.649	1.141	
Terrain Position 3 vs 1	0.444	0.383	0.516	***
Terrain Position 4 vs 1	0.265	0.203	0.345	***
Land Cover 2 vs 1	0.776	0.412	1.412	
Land Cover 3 vs 1	0.384	0.260	0.577	***
Land Cover 4 vs 1	0.756	0.507	1.146	
Land Cover 5 vs 1	0.670	0.283	1.448	
Land Cover 6 vs 1	0.852	0.585	1.264	
Flow Accumulation	1.000	1.000	1.000	**
Flow Length Up	1.000	1.000	1.000	***
Curvature	0.423	0.300	0.606	***
Plan Curvature	3.343	2.239	4.958	***
Profile Curvature	0.523	0.352	0.784	**

Hydrology variables were all significant in the full model. Flow accumulation and flow length had very little effect on the odds of rain disturbance in the full model in contrast to the strong patterns seen in Figure 3-16. The effects of flow accumulation and flow length probably saturate beyond certain thresholds; that is the marginal effect of one more cell of accumulation at 1,000 is not as strong as the marginal effect of one more cell at 5. Areas that channelize flow are more likely to be disturbed by rain than those that don’t as suggested by the odds ratios of curvature, plan curvature, and profile curvature.

4. Discussion

4.1. Remote Sensing

The change detection captured the major spatial patterns (Figure 3-4) of disturbance over a broad range of disturbance severities (Figure 3-5). The categorization of the initial NDII change detection results was necessary to simplify the image data for interpretation in the field and to analyze the spatial patterns of disturbances as patches. The classes were defined by broad intervals of NDII change because little *a priori* information was available for developing classes before the field sampling. Field data collected in this study validated the change detection results, but also confirmed that disturbance effects were highly variable both within and between forest types.

NDII was chosen as the final measure of hurricane wind disturbance in this study based on initial agreement with windthrow visible in the CIR OM and because it showed greater contrast for cloud forest compared to change detection based on greenness indices. Two previous papers have directly assessed the ability of vegetation indices and change detection algorithms to detect hurricane disturbance to forests (Wang *et al.* 2010, Wang and Xu 2010). Neither of these works specifically addressed how vegetation indices relate to hurricane disturbed forest. Wang and Xu (2010) only describe forest as disturbed or undisturbed while Wang *et al.* (2010) used the proportion of basal area damaged in four tree-level damage categories from 18 plots to validate their disturbance measure. NDII change in this study was most strongly related to the proportion of dead BA. Much of the reduction in BA was from mortality of trees in the larger size classes. Loss of large trees should reduce shadowed area in the stand, which is probably the functional link between wetness indices and stand structure (Crist *et al.* 1986).

4.2. Wind Disturbance

Wind disturbance affected 11.3% of the total landscape area, compared to only 4.3% affected by rain. The definition of wind disturbance used in this study was rather conservative (> 1 SD from the NDII change detection mean). One reason for this was out of practicality given that twelve years passed between Hurricane Georges and the field work for this study. It was also a goal to capture disturbance severe-enough to affect forest dynamics. The 3-13% mortality rates (Tanner 1991) reported for other hurricane-disturbed Caribbean forests may not have captured the most severely disturbed parts of those landscapes. While the majority of our study site was undisturbed (84.4%), the small proportion that was disturbed by wind had 18-70% more dead BA. Of the three forest types examined in this field portion of this study, cloud forest was least affected by the hurricane both in terms of proportion of area disturbed and in terms of reduction in BA. The 18% reduction in live cloud forest BA is similar to mortality (21% by density) reported by Weaver (1999) for cloud forest in Luquillo. The effect of Hurricane Georges on the proportion of dead BA in pine forest was greater than that of cloud forest, ranging from 27.2% in low to 70.0% in high severity disturbance. Walker (1991) concluded that the effects of Hurricane Hugo would not appreciably change the forest composition of his plots near the El Verde field site in Luquillo. While much of the Cordillera Central landscape shares this prognosis, stand-scale dynamics will be highly influenced by Hurricane Georges in areas of high severity disturbance.

The stand-level effects of wind disturbance were highly variable. While the major trend was for damaged plots to have higher proportions of dead and damaged stems, the mode of death or damage that caused that pattern differed between forest types and damage severities, with much variability within groups. Much of the pine forest mortality was from causes of death clearly attributable to the hurricane, including uprooted (61.4%) and snapped stems (35.1%). The average canopy height of pine forest sampled in this study was 23.4 m compared to only 6.2 m for cloud forest. Based on tree height alone, *Pinus occidentalis* should be the most susceptible species to windthrow. There are other factors including tree rooting architecture and wood density (Zimmerman *et al.* 1994) that could make pines more susceptible to windthrow, although size determinant selection is consistent with the measured changes in forest structure (Figure 3-7), which showed proportionately more dead stems in the larger size classes regardless of forest type.

Crown architecture, stand structure, and non-tree life-forms were also probably important drivers of wind disturbance in the Cordillera Central. Cloud forest is dense and it is common for most tree crowns to be in physical contact with their neighbors, while pine forest stem density averaged 60% less than cloud forest. There is also a far higher abundance of vines in cloud forest (Martin *et al.* 2007) that may add structural support by weaving together the canopy. Pine stands are much more open and vines are rare making the individual stems more exposed to wind. There were also differences in stand structure within forest types captured by the field sampling. The average total basal area (all live and dead) of disturbed cloud forest was only 46.3 m^2/ha compared to 72.1 m^2/ha in undisturbed cloud forest. Such a striking difference suggests that cloud forest with less BA was more susceptible to wind disturbance. Hurricane David passed through the Cordillera Central as a category 5 hurricane in 1979 along a track very similar to Georges. It is possible that these forests of low pre-Hurricane Georges BA were previously disturbed by David and had not fully recovered. In pine forest the opposite may be true, whereas stands with more BA were more susceptible to wind disturbance. Wind affected stands averaged a total (live and dead) BA of 38.8 m^2/ha, 14.8 m^2/ha more than undisturbed pine forest. In pine forest, higher BA means bigger trees and lower density, both of which increase susceptibility to wind. NDVI and TCW correlate well with live biomass and stand structural attributes. The significance of pre-hurricane NDVI and TCW in the full model of wind extent also supports the influence of stand structure on wind disturbance susceptibility.

4.2.1. Spatial Patterns of Wind Disturbance

One of the most drastic differences between cloud forest and pine forest was in the size and configuration of wind disturbed area. Patches of wind disturbed cloud forest averaged half the size of wind disturbed pine forest. Wind disturbed areas of pine forest also had greater than seven times more core area (> 30 m from an edge) than cloud forest. Cloud forest also had no core area in the moderate and high severity disturbance classes. There were also many disturbed patches of pine forest that were larger than any disturbed cloud forest patches. These large pine forest patches accounted for a disproportionately large amount of the total wind disturbed area. This size disparity is important for several reasons. The smaller patches of disturbed cloud forest could relate to underlying biotic or abiotic patterns in the landscape. Cloud forest has much higher species richness, especially in the canopy, compared to pine forest and tropical montane forests are known for having high landscape-scale species richness (Williams-Linera 2002). Patchy arrangements of species that differ in their susceptibilities to wind damage can result in patchy patterns of wind disturbance. The topography is more dissected in the cloud forest zone at spatial scales smaller than that captured by the 30 m ASTER GDEM (BM Gannon, personal observation). A rougher topography could also create patchier wind disturbance through its effect on wind exposure.

The size of the disturbed patches may also influence ecological processes. Large areas of reduced canopy coverage can change the microclimate of stands more than small gaps created by isolated treefalls. Reduction of upper canopy layers can provide more light to the understory (Brokaw and Grear 1991) potentially making conditions better for pioneer species establishment and growth. Increasing light levels may be detrimental to other species, especially for individuals that were growing in very low light conditions (Wadsworth and Englerth 1959, Guzmán-Grajales and Walker 1991). Bird communities of the Caribbean are also sensitive to the size, arrangement and severity of forest disturbances (Waide 1991). The large patches of wind disturbed pine have increased surface fuel loads and reduced canopy fuels, which may affect fire spread or severity.

4.2.2. Cloud Forest and Pine Forest

The comparatively diffuse impact of wind damage on cloud forest tree species (e.g. Bellingham *et al.* 1992, Bellingham *et al.* 1994) and the twelve year interval since the hurricane passed through the site made interpreting on the ground how Hurricane Georges impacted cloud forest challenging. The most common form of dead BA in cloud forest was the downed dead category – i.e. trees dead on the ground without any sign of uprooting. It is possible that these trees sustained injuries during the hurricane that resulted in delayed mortality. Only 1% of the reduction in the proportion of live BA was from uprooting. The second most common form of death in cloud forest was snapped stems. The key measure is the average reduction in the proportion of live basal area between disturbed (69.3%) and undisturbed (51.7%) cloud forest (Figure 3-4). Georges had an important impact on mortality rates in cloud forest despite the resiliency of cloud forest species to wind damage and the potentially diluting effect of Hurricane David. In contrast, the cause of live-damaged BA in cloud forest may not relate to Hurricane Georges given that there was more of it in the undisturbed cloud forest. Sprouting has been pointed to (Bellingham *et al.* 1994, Zimmerman *et al.* 1994) as the primary resilience mechanism in tropical montane forests and it has important implications for our understanding of how hurricanes influence succession in forests. If most damaged trees sprout new stems, hurricanes will have little influence on forest dynamics, as the same trees will maintain their dominance of the canopy. No work has addressed sprouting in the Dominican cloud forest, but Weaver (1986) suggests that sprouting would be a major mechanism of recovery of cloud forest in Puerto Rico. It was impossible to reliably distinguish sprouting twelve years after Georges, but it probably made cloud forest more resilient to wind disturbance than pine forest.

Uprooting was the primary agent of change in pine forest; it ranged from 17% of the total basal area in low severity disturbance to 47% in high severity disturbance. Snapping was the second most important damage type, accounting for 13-23% of the total BA from low to high severity disturbance. Uprooting and snapping of pines, results in near 100% mortality because *Pinus occidentalis* does not have adventitious buds. Uprooting may also be more lethal in pine forest because root masses are exposed to drying conditions due to the open structure of pine forest. Uprooted trees in the cool damp understory of cloud forest may live long enough to re-establish roots and re-direct growth. The life history traits of *Pinus occidentalis* make it less resilient to hurricane disturbance than most cloud forest species.

The majority of monodominant pine forest is on the leeward side of the divide. Precipitation and cloud cover is insufficient on the southwest side of the divide to support cloud forest. We don't expect much of the disturbed leeward pine forest to change in composition because its climate points towards continued pine dominance. In contrast, the mixed pine forest occurs on the windward side of the divide where climate can support cloud forest. Wind disturbance was rare on this side of the divide because of Hurricane George's path, but this mixed pine zone is of interest because disturbance to canopy trees could reduce pine dominance, favoring cloud forest species in the understory (Martin *et al.* 2007, Martin *et al.* 2011). Mixed pine was similar to cloud forest in the amount of dead and damaged basal area. Eleven percent of the BA in these plots was dead from uprooting and 21% was from snapped stems, most of which were pines. The limited spatial extent of disturbance in the mixed pine zone suggests that Hurricane Georges did not affect vegetation zonation, but the plot data reaffirms the potential for hurricane wind disturbance to reduce pine canopy dominance.

4.2.3. Landscape-scale drivers of wind disturbance patterns

At the largest scale, disturbance was distributed over the landscape in association with the physical forces of wind and water, but there was significant local variability in disturbance severity.

Variables related to topography and hurricane meteorology were all significant in the full model of wind extent. Significance should be interpreted with caution given the large sample size (n = 36,646) used to construct the model, which was needed in order gain sufficient samples within disturbed portions of the landscape (which were by far the minority). In particular, the predicted exposure to hurricane winds, the distance from the hurricane, and the position of the divide explain why most damage was concentrated in high elevation pine forest in the south half of the site. Interpreting the patterns of wind disturbance in relation to individual factors (Figure 3-12 through Figure 3-14), however, was complicated by covariance.

The representation of hurricane wind used in this study was very rough. By the time Hurricane Georges was over the Cordillera Central it lacked a clear central eyewall and became asymmetrical (Gerts *et al.* 1999) making it difficult to model wind speeds or directions with models like HURRECON (Boose *et al.* 1994). The hurricane passed close by to the south of the study site placing the most intense winds to the right of the hurricane track approximately at the study site. The peak association between wind disturbance and exposure was with a wind direction of 140 deg (Figure 3-9) which fits with the hurricane's passage from southeast to northwest. In this case the association of wind disturbance with predicted exposure meshes with our knowledge of the hurricane meteorology, but it would be far preferred to use measures of wind direction and intensity to validate wind models. Modeling hurricane wind fields with HURRECON may be an exercise in futility given the assumptions of the model and how much the Cordillera Central violates those assumptions. HURRECON ignores the influence of topography on wind fields, which played a major role in the meteorology of Hurricane Georges (Gerts *et al.* 1999).

The maximum association between predicted exposure (from EXPOS; Boose *et al.* 1994) and wind disturbance measured in this study was 0.12. Association values were stronger (max of 0.29) for the high severity wind disturbance. These association values are generally lower than reported by Boose *et al.* (1994) for the Luquillo landscape. Lower association values in this study are probably explained by two factors: one being the conservative threshold for wind disturbance, which made disturbance a rather rare event on the landscape and another being the lack of wind disturbance in the northern half of the study area, where it was predicted by EXPOS, but did not occur (probably because of the divide).

Variables related to vegetation, including land cover, NDVI, and TCW were also significant in the full and reduced models. In either model pine forest had significantly higher odds of disturbance than cloud forest, but this difference was greater when elevation was removed from the model. As discussed above, pine forest should be more prone to wind disturbance due to a combination of species' susceptibilities to disturbance, tree heights, and stand structure. Little was known about the pre-hurricane structural variability within forest types for the site. NDVI and TCW were included in the logistic regression model to represent some of this variability. The decreasing odds of wind disturbance with increasing NDVI is probably functionally related to stand density and total biomass. The increasing odds of wind disturbance with increasing TCW is likely related to the presence of taller trees in more structurally mature stands.

4.3. Rain Disturbance

Wind disturbed more of the landscape than rain, but areas disturbed by rain underwent drastic physical and biotic changes. In this study 4.3% of the total area was disturbed by rain, which is high relative to the 0.14% of the Luquillo Experimental Forest affected by Hugo-related landslides (Scatena and Larsen 1991). The amount of rain that fell over the Cordillera Central during Hurricane Georges was approximately three times greater than rainfall from Hugo in Luquillo (~991 versus 339mm; Scatena and Larsen 1991) possibly explaining the greater area disturbed. There was also no attempt in this study to differentiate between stream scouring and landslides, which could be separated using thresholds of slope, as Larsen and Torres-Sánchez (1998) found that slopes greater than 12 deg were more likely to slide in Puerto Rico.

Landslides effectively clear the biota from the path, initiating primary succession. No quantitative work was done for this study to describe landslide effects as they have been well documented in other areas (Walker 1994, Walker *et al.* 1996) and our personal observations (PH Martin and BM Gannon) fit these patterns. Landslides in the Cordillera Central are quickly colonized by ferns, vines, and the shrub (*Rubus eggersii* Rydb.). Fern thickets are believed to retard woody plant succession; Slocum *et al.* (2004) found that removal of fern thickets increased colonization of sites by woody species in TMFs of the Dominican Republic. Disturbance effects are more severe on landslides and recovery from early stages can be slow and possibly slowed further by development of alternate stable ecosystems. Ferns and vines can spread into a landslide scar without having to establish from seed giving them a head start on woody plants.

4.3.1. Spatial Patterns of Rain Disturbance

The spatial patterns of rain disturbance were different from wind disturbance, mainly in measures reflective of patch shape (**Table 3-3**). The average patch size of rain disturbance was nearly as large as wind disturbance, but rain disturbance had a lower max patch area. There was less core area in rain disturbance, but this core area was distributed in many small disjunct areas compared to wind disturbance.

4.3.2. Landscape-scale Drivers of Rain Disturbance

Separating out the forces of wind and rain is important for landscape studies utilizing remote sensing, versus a targeted collection of one disturbance's effects (e.g. Boose *et al.* 1994). When modeling the association of disturbance with ecological landscape factors, including both wind and rain disturbance in one model may lead to poor or confusing results. Remote sensing analyses of forest disturbance from Tropical Cyclone Monica in Australia (Staben and Evans 2008) and Hurricane Katrina in the US Gulf Coast (Wang and Xu 2009) found that water-related disturbances were significant in their landscapes.

Hydrology variables including flow accumulation, flow length, and curvature explained most rain disturbance in the Cordillera Central. Curvature had the largest effect on the odds ratio in the model of rain disturbance affects. Flow accumulation and flow length are probably only important below certain thresholds. There are some parts of the landscape which may be susceptible to both wind disturbance and landslides, but stream scouring is associated with forest types and topography least likely to be disturbed by wind. Secondary riparian forest had the highest odds of rain disturbance. Our model would likely benefit from modeling stream scouring and landslides separately. In the final rain disturbance model, slope decreased the odds of disturbance, which is counter to our understanding of landslides, which are more common on steeper slopes.

5. Conclusions

The effects of Hurricane Georges, both from wind and rain, varied across the landscape due to the meteorology of the hurricane, the physical structure of the landscape, and the characteristics of contrasting forest types. Hurricane Georges disturbed a greater proportion of pine forest than cloud forest, the disturbed patches of pine forest were larger than disturbed patches of cloud forest, and the damage to pine forest resulted in greater mortality. Pine forest resiliency to hurricane winds is low, because *Pinus occidentalis* is prone to uprooting and snapping, and it lacks the ability to sprout – an adaptation that may account for the lower magnitude of change in cloud forest. Patches of wind disturbed cloud forest averaged half the size of pine forest patches and cloud forest had very few large patches and low core area. The patchier nature of wind disturbance in cloud forest could be the result of spatial patterns of forest composition.

The drivers of wind and rain disturbance differed. Variables relating to wind exposure and hurricane structure were significant in predicting wind disturbance extent while, hydrology variables were important for predicting rain disturbance extent. The divide of the Cordillera Central was a disruptive feature to hurricane winds and probably shielded much of the landscape from intense wind. Topography and land cover were significant in both wind and rain disturbance models. The variability in abiotic and biotic features of the landscape modify the exposure and intensity of hurricane forces contributing to the patchy distribution of hurricane effects on forests.

CHAPTER 2

Hurricanes and Forest Dynamics in the Cordillera Central, Dominican Republic

1. Introduction

Hurricanes are one of nature's most intense disturbances, with sustained wind speeds of 119 km/hr or greater, and are of a massive scale, spanning tens of kilometers in diameter. In the Caribbean basin, hurricanes occur regularly, and consequently the immediate impacts of hurricanes on tropical montane forests and the short-term responses of forests to disturbance have been extensively studied (see reviews in Brokaw and Walker 1991, Tanner *et al.* 1991, Zimmerman *et al.* 1996), most recently in Jamaica following Hurricane Gilbert in 1988 (e.g., Bellingham 1991, Bellingham *et al.* 1992, Bellingham *et al.* 1994) and in Puerto Rico following hurricanes Hugo in 1989 and Georges in 1998 (e.g., Brokaw and Grear 1991, Walker 1991, Lugo and Waide 1993, Zimmerman *et al.* 1994, Ostertag *et al.* 2005).

Despite the abundance of hurricane research In the Caribbean, there have been relatively few studies of forest dynamics encompassing periods longer than 5 years post-disturbance, and most have been limited to analysis of a small number of long-term datasets in Puerto Rico (e.g., Crow 1980, Weaver 2002) and Jamaica (Tanner and Bellingham 2006). In Puerto Rico, records at the Luquillo Experimental Forest (LEF) provide a 50+ year perspective on tabonuco forest dynamics (Crow 1980, Weaver 2002) characterized by cycles of disturbance and recovery, in which the early post-hurricane periods show increases in stem density among smaller size classes along with increased richness through addition of rare species. Tanner and Bellingham (2006) found increasing abundance of light demanding species post-Hurricane Gilbert in some, but not all of the Jamaican forest types, increasing the diversity of the most severely impacted forests. These long term studies generally support a model of forest dynamics in which competitive dominants are reduced in abundance by hurricanes, providing niche opportunities for early successional species (Doyle 1980).

Apart from the limited analyses of these long-term datasets, there has been much discussion of hurricane dynamics in Caribbean forests, extrapolating from the immediate impacts from, and short-term responses to recent hurricanes. Hurricanes Gilbert, Joan, and Hugo provided opportunities to describe the direct effects of hurricanes on Caribbean forests (Brokaw and Walker 1991, Tanner *et al.* 1991), which previously lacked quantitative rigor (one exception being Lugo *et al.* 1983). The main effects of these hurricanes on forest canopies were severe defoliation, stem breakage, and uprooting, but surprisingly mortality was low, in the range of 3-13% (Tanner *et al.* 1991). In addition, many observations (Walker 1991, Yih *et al.* 1991, Bellingham *et al.* 1994, Zimmerman *et al.* 1994) established the importance of direct regeneration via sprouting as a mode of forest recovery. Low mortality and high rates of direct regeneration in the Luquillo Mountains of Puerto Rico (Frangi and Lugo 1991, Walker 1991) and the Blue Mountains of Jamaica (Bellingham *et al.* 1992) following Hurricanes Hugo and Gilbert suggest that hurricanes do not always create significant canopy turnover.

Interspecific differences in resistance and resilience of current canopy occupants to hurricane disturbance, as well as the response of seed and advanced regeneration to an altered forest environment form the basis for directional change in forest composition. Investigation of species-specific damage from Hurricane Hugo in the LEF found that hurricanes can reinforce dominance of later-successional species, as Hugo selected against pioneer species in the pre-hurricane canopy with low wood density (Zimmerman *et al.* 1994). Resiliency can also vary widely between species, the most notable contrast being made between pines and broadleaves, where broadleaves are generally more resilient due to sprouting abilities (Boucher *et al.* 1990, Yih *et al.* 1991). Hurricanes alter forest structure by thinning upper canopy layers, increasing light levels in the understory (Brokaw and Grear 1991), and transferring litter to the forest floor (Guzmán-Grajales and Walker 1991), all of which influence seedling establishment and growth. Regeneration of early successional species was observed in hurricane disturbed forest in Puerto Rico (Frangi and Lugo 1991, Walker 1991) and Jamaica (Tanner and Bellingham 2006) and may be further accelerated by forest floor turnover via uprooting because early successional species establishing from seed benefit from reduced litter (Guzmán-Grajales and Walker 1991), while surviving advanced regeneration (You and Petty 1991) experienced high post-hurricane growth rates due to increased light and nutrient availability. Longer periods of analysis are needed to measure the influence of understory response on canopy composition.

The efforts at documenting immediate impacts and responses may seem short sighted, but they are incredibly important for establishing the mechanisms of forest dynamics. Wind effects on forest can be highly variable, resulting from characteristics of species, stands, and storms (Everham and Brokaw 1996). Furthermore, hurricane disturbance is spatially complex in the tropical montane forests of the Caribbean because of the sheltering effect of the topography (Bellingham 1991, Boose *et al.* 1994). The type, severity, and spatial patterns of hurricane damage may influence the mode of recovery and therefore successional trajectories (Runkle 1985). For example, Walker's (1991) study plot had only 7% mortality but elsewhere in the LEF mortality was estimated at 50%; study of the most disturbed portions of the landscape may yield different conclusions about the effect of hurricanes on forest dynamics. In fact, the weak link in the long-term records from Puerto Rico (Crow 1980, Weaver 2002) is that they lack information on the type, severity, and spatial patterns of hurricane damage (particularly from Hurricane San Cipriano) making it difficult to mechanistically link observed forest dynamics to a particular form of hurricane disturbance.

On September 22, 1998 Hurricane Georges made landfall with the Dominican Republic as a Saffir-Simpson category 3 hurricane with wind speeds of 194 km/hr. Over the next 21 hours it passed over Hispaniola on a northwestward path taking it over the Cordillera Central, with the center tracking just south of Parques Armando Bermúdez and Carmen Ramírez, only 15 km away from the permanent plots described in Sherman *et al.* (2005) and Martin *et al.* (2007). The forest types of the Cordillera Central (Sherman *et al.* 2005) provide interesting contrasts in many of the factors that control resistance and resilience to wind disturbance (Everham and Brokaw 1996). A discrete ecotone serves as the boundary between cloud forest at mid-elevations and the higher elevation pine-dominated ecosystems (Martin *et al.* 2007). The Dominican cloud forest has low stature, high density, and relatively high species richness (Sherman *et al.* 2005). In contrast, pine forest is much taller, has lower density, and the overstory is dominated by one species, *Pinus occidentalis* Swartz.

Observations elsewhere in the Caribbean suggest that pine forests may be more severely affected by hurricanes than other forest types (Boucher *et al.* 1990, Bellingham *et al.* 1992). Whether pines are more prone to windthrow or stem damage, they usually lack sprouting adaptations that make cloud forest tree species of the region resilient to wind disturbance (e.g. Bellingham *et al.* 1994). There is relatively little information on hurricane effects in cloud forest (Brokaw and Grear 1991, Weaver 1986, Weaver 1999). However, Hurricane Hugo reduced the dwarf forest density in the LEF by 21% (Weaver 1999) which is higher than mortality reported by Walker (1991) for the tabonuco forest, suggesting there is potential for hurricanes to alter the dynamics of cloud forest. The impacts of Hurricane Georges on pine forest were expected to be greater followed by slower recovery than cloud forest.

In this study forest structure and composition was measured with attention to indicators of wind disturbance, across levels of disturbance severity from Hurricane Georges and three forest types in the highest elevations of the Cordillera Central. The abundance of disturbance indicators were compared between forest types and between levels of disturbance severity to describe how Hurricane Georges changed forest structure. Comparisons were also made between forests either disturbed or undisturbed by the hurricane to describe the impacts of Hurricane Georges on forest dynamics 12 years after the storm.

2. Methods

For details on the site and physical aspects of Hurricane Georges, see Methods, Chapter 1.

The effects of wind from Hurricane Georges on high elevation forests were quantified with 100 vegetation plots (Figure 2-1). Plots were located using a stratified random design based on forest type (cloud forest, mixed pine forest, and pine forest, per Sherman *et al.* 2005) and disturbance severity (high, moderate, low, and no disturbance) in elevations above 1800 m. Disturbance severity was determined by means of Landsat change detection in the normalized difference infrared index (NDII) (for details see Methods, Chapter 1), and classified into low, moderate and high severity disturbance categories. Given the resolution of the NDII change detection, the accuracy of GPS, and the patchy nature of hurricane wind disturbance, only continuous patches of disturbance at least 90 m (or three pixels) wide were used to avoid sampling along the boundaries of a disturbance severity class. Furthermore, since exposure to wind is a key factor in hurricane damage, plots were relocated when the random coordinates fell in areas which spanned different wind exposures, such as across a ridgeline or drainage bottom. In cloud forest and mixed pine forest there were no areas of moderate or high severity damage large enough to meet the sampling requirements. Cloud forest and mixed pine forest damage severity classes were therefore combined into binary (disturbed or undisturbed) classes for field sampling. The distribution of sampling plots is presented in Table 2-1.

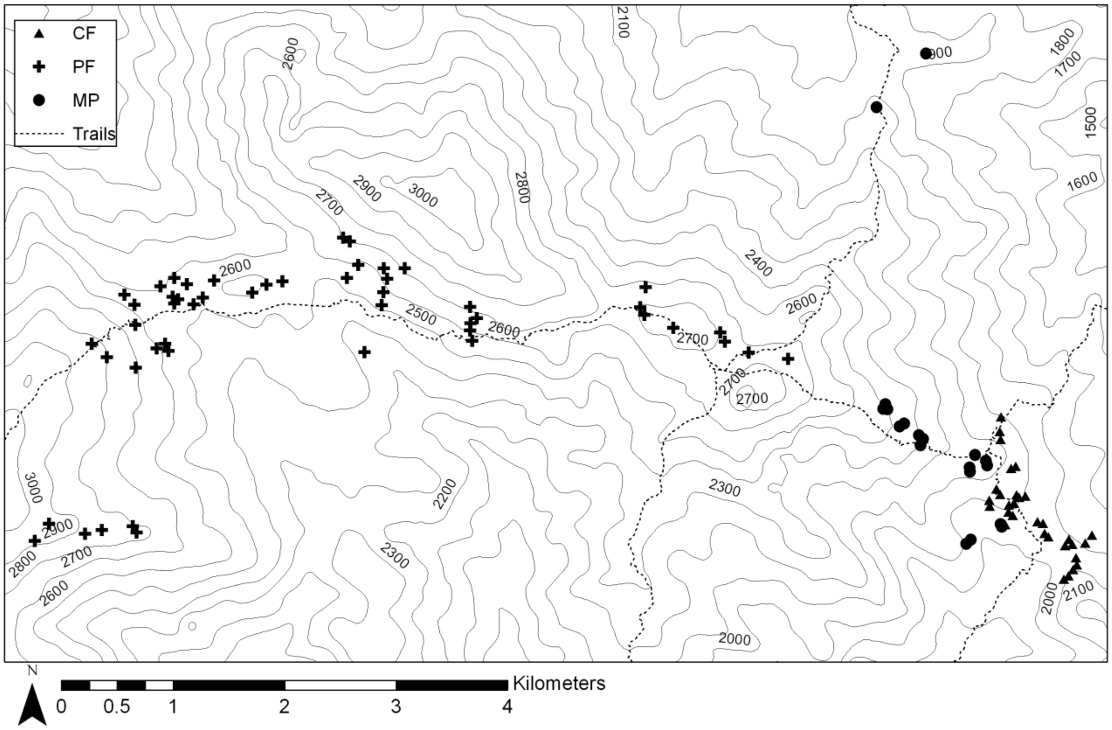

Figure 2-1: Location of vegetation plots. Elevation is in meters for 100 m contours. CF = cloud forest, PF = pine forest, and MP = mixed pine.

Table 2-1: The distribution of hurricane plots across forest ecosystems and disturbance categories.

Forest Type	Disturbance Class	N
Cloud Forest	Disturbed	20
	Undisturbed	11
Mixed Pine	Disturbed	13
	Undisturbed	6
Pine Forest	High Severity	20
	Moderate Severity	7
	Low Severity	8
	Undisturbed	15
Total		100

Vegetation plots were rectangular in shape. Given the wide range of structures, a variable plot size was used: 10 × 20 m for cloud forest, 15 × 30 m for pine forest, and 10 × 20 m or 15 × 30 m for mixed pine forest depending on the density of vegetation in the plot. All plots were oriented with the long axis parallel to the average aspect. Aspect was measured with a sighting compass; slope was measured with a clinometer. Coordinates and elevations of plot centers were collected using a Garmin GPS Map 60CS to a horizontal accuracy of 5 m.

2.1. Damage Classification and Vegetation Sampling

All live and dead stems ≥ 4 cm diameter at breast height (DBH) were tallied and measured for DBH. All live stems were identified to species or to genus in the case of a few morphologically similar species. Efforts were made to identify dead stems, but species was only recorded when characteristics necessary for identification were present (e.g. distinctive bark or live root collar sprouts).

Disturbance was categorized for live and dead trees to quantify changes in forest structure. Live trees were classified as follows: 1) undamaged, 2) crown damaged, or 3) tipped. Crown damage was classified as light crown damage (< 20% crown loss), moderate crown damage (20-50% crown loss), or high crown damage (> 50% crown loss). Often crown loss included obvious signs of broken branches, but for trees with small crowns and slender branches (i.e. most cloud forest trees) these secondary features were not always present. Stems tilting 40° or more from vertical were classified as tipped, the angle from horizontal was estimated, and the direction of tip was measured with a compass.

Dead trees were classified as 1) standing dead, 2) tipped, 3) downed dead, 4) uprooted, or 5) snapped. If the stem was vertical without any evidence of traumatic break it was categorized as standing dead. Tipped was again defined as tilt ≥ 40° from vertical. Downed dead was used to describe prostrate steams without evidence of how they died. Uprooted was used to describe tipped or prostrate stems with displaced roots. Snapped describes trees with a traumatic break to the main stem. The directions of all tipped, downed dead, and uprooted stems were taken with a compass. The heights of snaps were recorded.

Understory structure and composition was inventoried in a 2-m-wide strip oriented lengthwise down the center of the plot. Stems were tallied by species and size-class (seedlings, stems < 1.3 m in height; saplings, stems < 4 cm DBH and ≥ 1.3m in height) into 2 diameter classes: 0-2 cm and 2-4 cm DBH for all stems originating within the strip.

The percent cover of thicket-forming shrubs (*Rubus eggersii*), ferns, and vines were visually estimated for each plot. Vine cover includes both vine mats on the forest floor and in the canopy.

A large fire burned through much of site's monospecific pine forest and parts of the high-elevation monodominant pine forest in 2005 (Sherman *et al.* 2008). For detailed collection protocols for fire affected stands see Appendix V.

2.1.1. Summary and Analysis of Disturbance Effects across Forest Types

Hurricane effects were compared across forest types and disturbance categories in terms of the proportion of basal area live, damaged, and dead, and by specific disturbance indicators. Ferns, vines, and the shrub *Rubus eggersii* are associated with small openings in the Cordillera Central (PH Martin, personal observation) and may be a sign of disturbance. The percent cover of these non-tree structures were compared between disturbed and undisturbed plots using one-sided t-tests.

2.1.2. Size-related trends

Size can influence tree susceptibility to certain damages (e.g. uprooting or snapping; Walker 1991) through the mechanics of the tree-wind interaction and through exposure relative to other trees in the stand. Trees were binned into six size classes based on diameter: 4-10, 10-20, 20-30, 30-40, 40-50, and > 50 cm. Density and the proportion of density for live and dead stems were compared across these size classes. The proportion of basal area in each size class was also used to assess size-related influence on the probability of damage.

2.1.3. Species susceptibilities to Disturbance

For live trees with non-lethal damages the proportion of the species basal area affected by each disturbance was used to compare relative effects between species. For dead stems there were very few instances where broadleaf remains were identifiable to species so most dead stems were binned into the following taxonomic groups: broadleaf, *Cyathea* species, and *Pinus occidentalis*. These groups were used to compare the proportion of lethal damages.

2.2. Composition

Composition of disturbed and undisturbed plots was compared within forest types to assess the effect of Hurricane Georges on the current (2010) live vegetation. Overstory composition was described in terms of relative importance (relative importance = (relative dominance + relative density)/2) and understory composition was described in terms of relative density.

3. Results

3.1. Hurricane Effects

Hurricane effects were strongly related to forest type (Figure 3-1). The proportion of dead basal area was greater in disturbed plots (two-way ANOVA; proportion dead BA ~ forest type + disturbance, forest type p-value = 0.83, disturbance p-value = 1.53e-08), and there was a greater proportion of damaged basal area in the disturbed plots of mixed pine and pine forest, but not cloud forest. The proportion of live basal area in the disturbed plots decreased by 17.6%, 21.4%, and 53.6% compared to the undisturbed plots of cloud forest, mixed pine, and pine forest, respectively. The proportion of undamaged live basal area similarly decreased by 8.6%, 31.8%, and 60.5% for cloud forest, mixed pine, and pine forest.

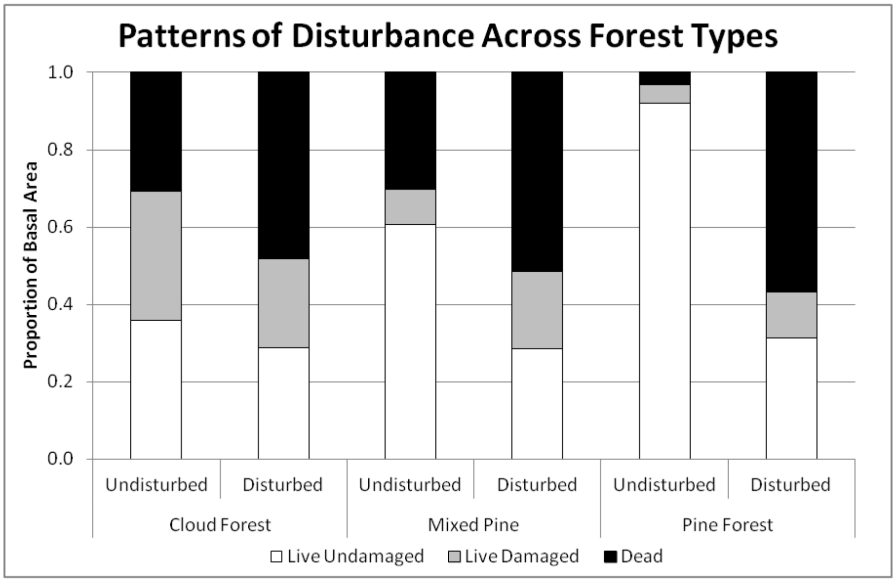

Figure 3-1: Hurricane effects across forest types and disturbance levels. Damaged includes tipped live or crown damaged stems.

Cloud forest and mixed pine had more dead or damaged basal area in the undisturbed controls compared to pine forest. The Dominican cloud forest tends to have more standing dead stems than pine forest (Sherman *et al.* 2005). This could be because fires are generally excluded from cloud forest (Martin *et al.* 2007) whereas they play an important role in reducing woody biomass in pine forest (Martin and Fahey 2006). Unexpectedly, the undisturbed cloud forest had a higher proportion of live disturbed basal area (Figure 3-1). Given the 12-year time period since the hurricane, it is probable that some of the observed damage, especially in cloud forest, was not directly related to Hurricane Georges.

The pronounced effect of Hurricane Georges on pine forests (Figure 3-1) is a direct reflection of the markedly higher occurrence of the moderate and high severity disturbance categories in pine forest. Indeed, there were no areas of moderate and high severity disturbance categories in the mixed pine and cloud forest large enough to sample, given our minimum size requirement. The patterns of damage and mortality in pine forest were strongly related to disturbance severity (Figure 3-2). The proportions of live basal area and live undamaged basal area decreased from undisturbed to high severity pine plots. The low and moderate severity disturbance classes had more live damaged basal area than either the undisturbed or high severity disturbance categories.

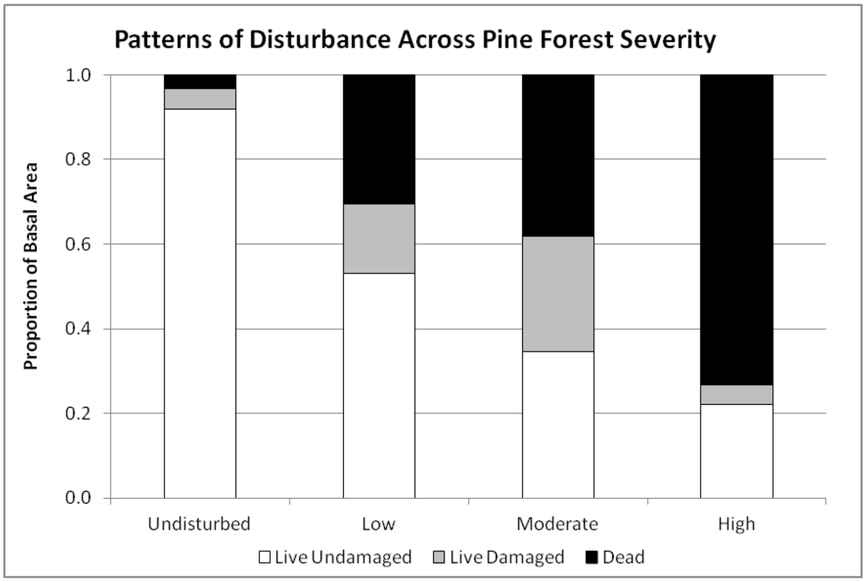

Figure 3-2: Hurricane effects on pine forest across the range of disturbance severities.

3.1.1. Disturbance Indicators

3.1.1.1. Disturbance Indicators by Forest Types

Disturbance indicators varied between forest types (Figure 3-3) and point to the cause of mortality or the specific type of damage. Uprooted stems made up a large proportion of damaged basal area (Figure 3-3), but as a form of lethal wind damage, it was the least important in cloud forest and the most important in pine forest. Snapped stems were common across all forest types, accounting for between 15.0 and 21.4% of disturbed forest basal area. There is a clear increase in snapped stems between undisturbed and disturbed pine forest (Figure 3-3). While measures of snapped basal area are similarly high in disturbed cloud forest and mixed pine, the undisturbed plots have almost as much (mixed pine) or slightly more (cloud forest). Cloud forest had the highest proportion of live and dead tipped basal area. It is possible that either the shorter stature of cloud forest trees or their rooting architecture makes them resistant to complete uprooting. Cloud forest and mixed pine had more standing dead and downed dead basal area than pine forest; standing dead and downed dead trees are not clearly related to wind disturbance as are uprooted, snapped, and tipped trees.

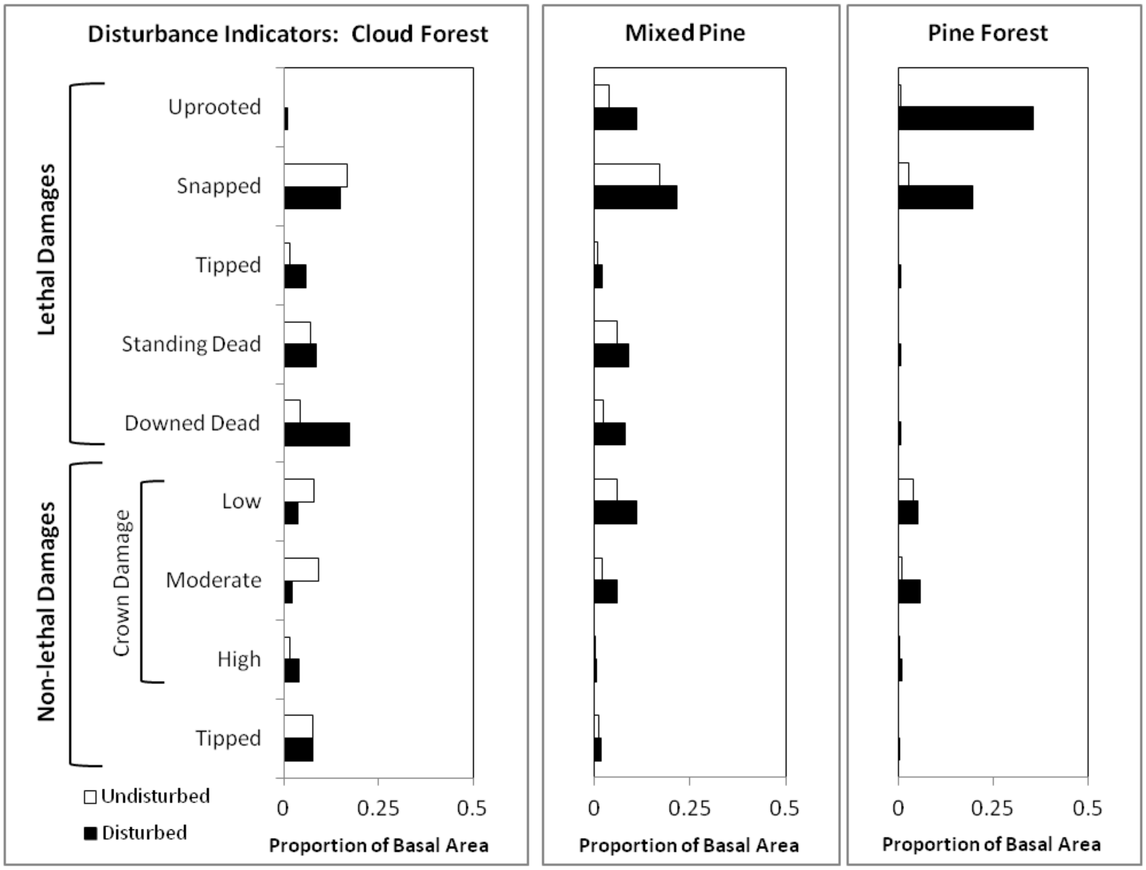

Figure 3-3: Disturbance indicators by forest and disturbance type. Uprooted includes trees > 40° out of vertical with exposed root masses. Snapped refers to dead crown-less stems with clear evidence of abrupt trauma. Tipped refers to any stem > 40° out of vertical but without exposed roots. Standing dead includes upright dead stems with branches (i.e. not snapped). Downed dead stems include prostrate stems unconnected to roots. Crown damage: low (<20% loss), moderate (20-50% loss), and high (>50% loss).

Non-lethal crown damage was almost twice as common in undisturbed (18.9%) versus disturbed cloud forest (10.0%); only high severity crown damage was more abundant in disturbed cloud forest. Crown damage was more abundant in disturbed mixed pine and pine forest compared to undisturbed controls; disturbed mixed pine had 17.7% crown damaged basal area compared to only 8.1% in the undisturbed plots. Crown damaged basal area was lowest in the pine forest type; but the disturbed plots (11.6%) still had greater than the amount in undisturbed plots (4.8%). Live tipped basal area was most abundant in cloud forest, but again it did not differ between disturbed and undisturbed plots.

3.1.1.2. Disturbance Indicators by Species

Species differed in their susceptibility and/or response to Hurricane Georges (Figure 3-4 and Figure 3-5). Across the top ten most abundant species, there was much variability in the total proportion of live damaged basal area and the type of damages. Tree ferns (*Cyathea* spp.) were rarely crown damaged and/or were successful at recovering because of their unique morphology. *Podocarpus aristulatus* had proportionately more crown damage than any other species. It appears that the older *P. aristulatus* at the site may have weathered several disturbances and despite losing most branches, continue to persist (BM Gannon, personal observation). Other species with high proportions of crown damage include *Tabebuia vinosa, Brunellia comocladifolia*, and *Lyonia alainii. Brunellia comocladifolia* is a pioneer species with decurrent branching habit, so it is not surprising that it was prone to crown damage. Damage to *L. alainii* may be due, at least in part, to their position; many individuals of this species were found as lone trees within small fern-dominated gaps (BM Gannon, personal observation). Without the protection of neighboring trees *L. alainii* may be more exposed to damaging winds.

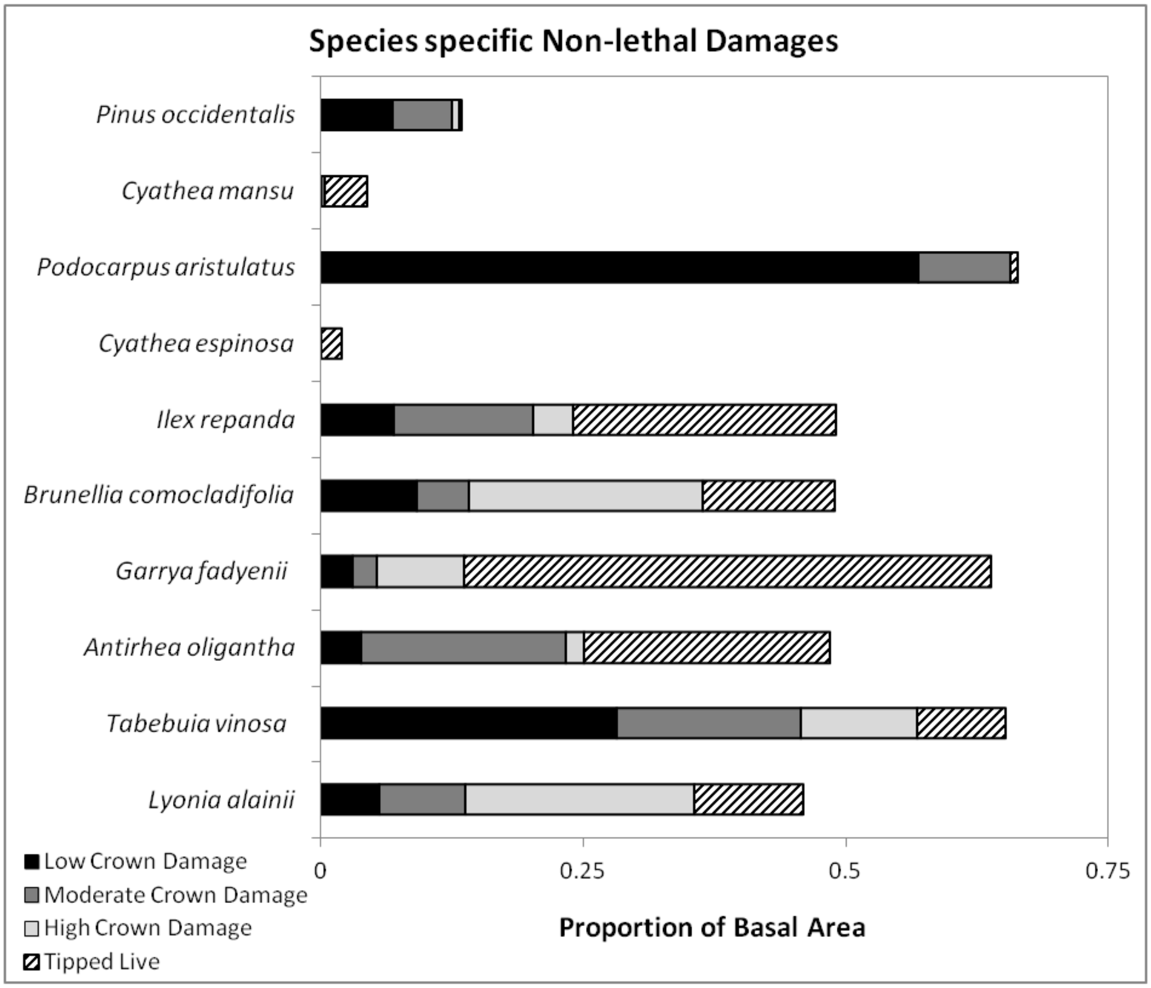

Figure 3-4: Proportion of the top ten species by basal area affected by non-lethal disturbance indicators. Crown damage: low (<20% loss), moderate (20-50% loss), and high (>50% loss). Tipped live refers to any stem > 40° out of vertical but without exposed roots.

The proportion of tipped basal area varied by species and is likely a more reliable indicator of wind disturbance than crown damage. *Garrya fadyenii* had the highest proportion of tipped live basal area. Either this species is especially prone to tipping or is incredibly tolerant of the conditions it faces once tipped. The distribution of *G. fadyenii* is associated with wind disturbance throughout the Cordillera Central (Sherman *et al.* 2005). *Antirhea oligantha* and *Ilex repanda* also had high proportions of tipped live basal area. Both species appeared to be highly capable of redirecting growth from the surviving stem back to the canopy (BM Gannon, personal observation).

Very few dead broadleaf trees were able to be identified to species, so they had to be grouped for this analysis. Across all forest types and disturbance severities, *P. occidentalis* had the highest proportion of dead basal area. It also had the highest proportion of uprooted and snapped basal area. Cloud forest tree species had the lowest proportion of dead basal area. Snapped and standing dead were the most important disturbance indicators for cloud forest species. *Cyathea mansu* had proportionately more dead basal area then *C. espinosa* and more downed dead basal area. Most of the *Cyathea* species dead basal area was snapped or standing dead.

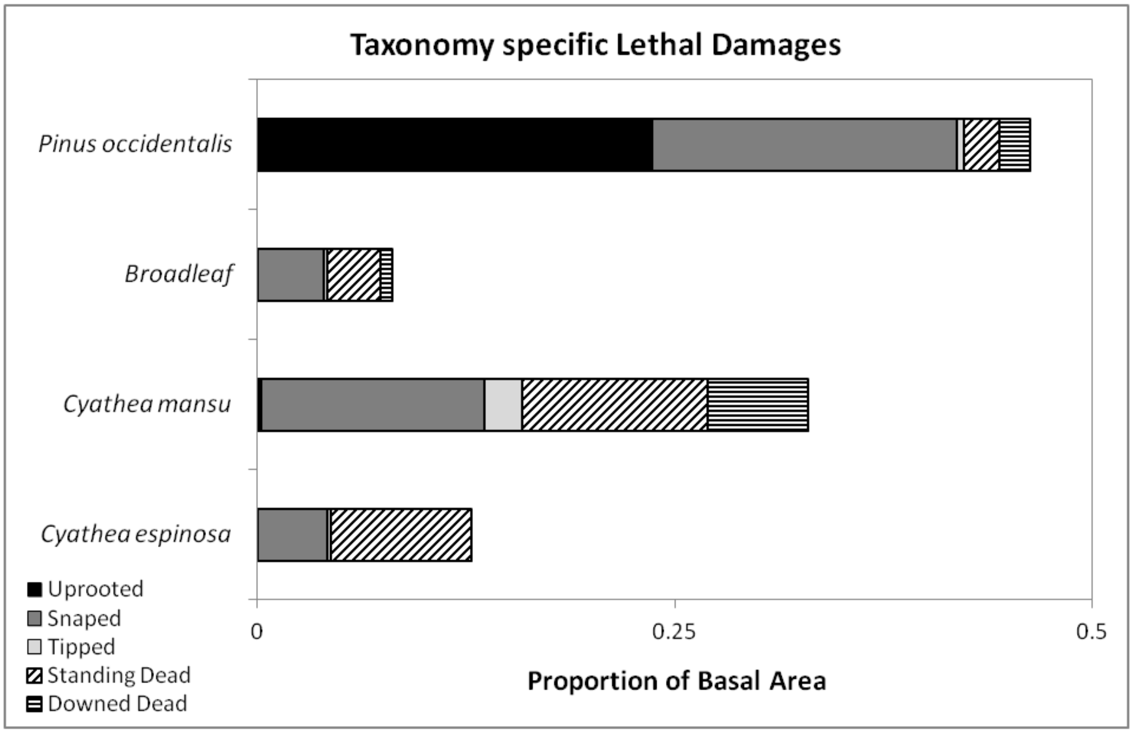

Figure 3-5: Proportion of identifiable groups killed by lethal damages. Uprooted includes trees > 40° out of vertical with exposed root masses. Snapped refers to dead crown-less stems with clear evidence of abrupt trauma. Tipped refers to any stem > 40° out of vertical but without exposed roots. Standing dead includes upright dead stems with branches (i.e. not snapped). Downed dead stems include prostrate stems unconnected to roots. Crown damage: low (<20% loss), moderate (20-50% loss), and high (>50% loss).

Pinus occidentalis occurred in all three forest types although its abundance is patchy in the cloud forest zone. The disturbed plots of every forest type had higher proportions of dead pine but disturbance indicators associated with dead pine differed between forest types (Figure 3-6). Almost all the dead pine in the disturbed pine forest plots were uprooted or snapped. A large proportion of pine in the disturbed cloud forest plots were dead, but much of the basal area was standing dead and downed dead, in addition to snapped stems.

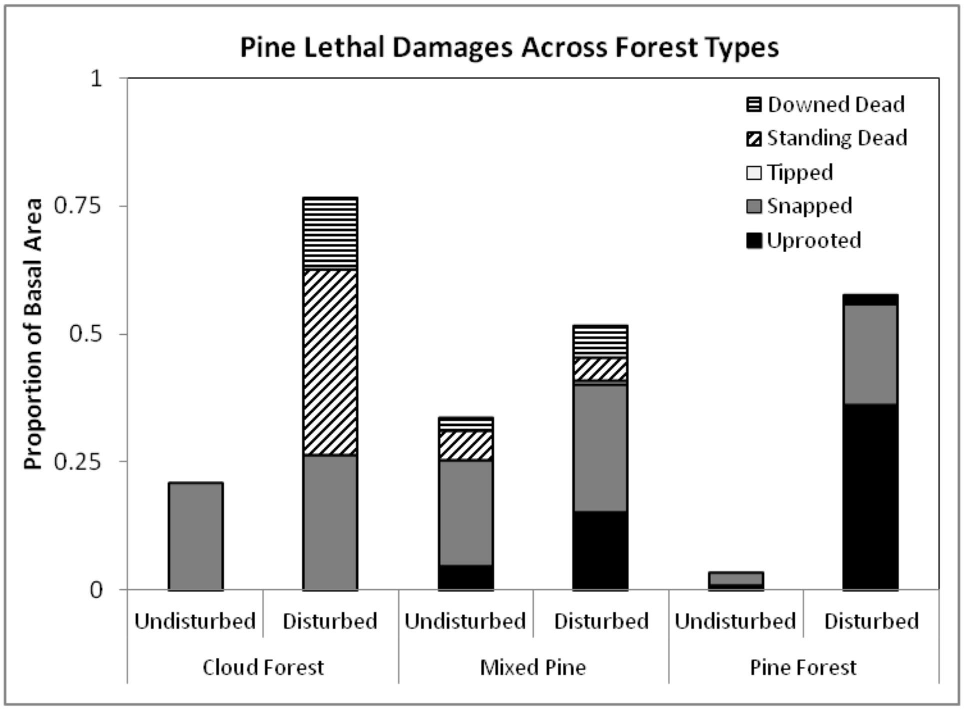

Figure 3-6: Pine disturbance indicators across forest types and disturbance groups.

3.1.1.3. Non-tree Indicators of Disturbance

Ferns were the most abundant non-tree disturbance indicators and were positively associated with disturbance in cloud forest and mixed pine (Table 3-1). *Rubus eggersii* accounted for at most 3.3% cover and was only slightly more abundant in disturbed cloud forest. Vines were most abundant in cloud forest, but had slightly lower cover in the disturbed plots (Table 3-1). Ferns were far more abundant in disturbed (37.0%) versus undisturbed (6.1%) cloud forest. Ferns were present in all forest types and disturbance categories, but the undisturbed cloud forest had the lowest fern cover. Ferns were more abundant in the disturbed mixed pine, but the increase from undisturbed mixed pine was of lower magnitude than the change observed in cloud forest.

Table 3-1: Percent cover of non-tree disturbance indicators by forest type and disturbance class.

Non-tree Indicators		**Percent Cover**		
Forest Type	**Plot Type**	***Rubus***	**Ferns**	**Vines**
Cloud Forest	Undisturbed	0.0	6.1	16.4
	Disturbed	0.6	37.0	14.5
Mixed Pine	Undisturbed	3.3	28.3	0.8
	Disturbed	2.9	36.5	2.3
Pine Forest	Undisturbed	0.0	13.7	0.0
	Disturbed	0.0	13.1	0.0

3.1.1.4. Disturbance Indicators by Tree Size

Larger diameter trees were more likely to be dead in all forest types. Figure 3-7 shows the distribution of live and dead stems by diameter size class for hurricane disturbed plots. Most of the dead stems were in the larger size classes and there was proportionately higher mortality within the larger size classes. In pine forest it appears that there may be a threshold beyond which size contributes to increased mortality; stems greater than 20 cm in DBH seem to have equal probability of death.

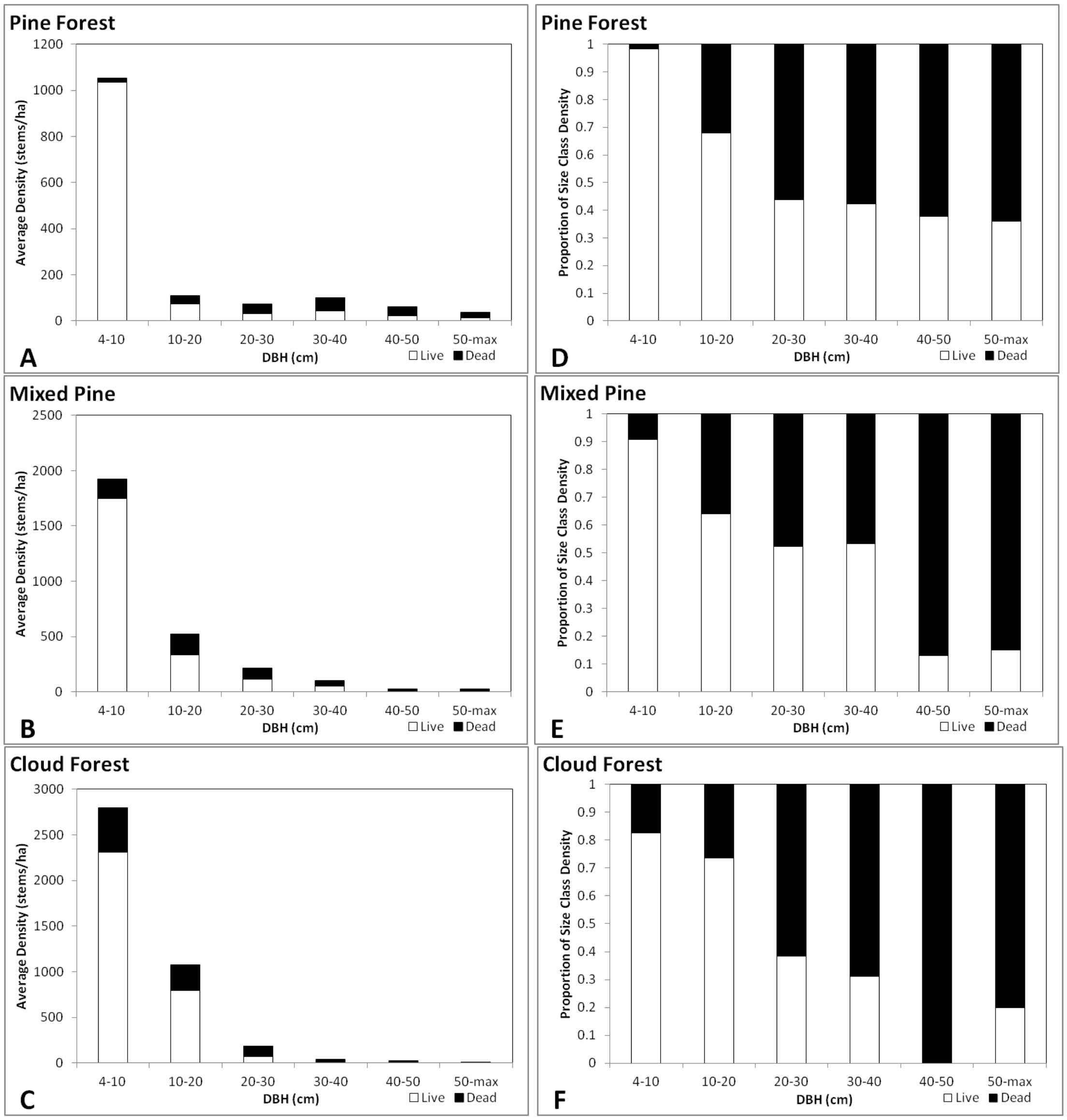

Figure 3-7: Change in forest structure highlighted by contrast of the density of live and dead stems by tree size (basal area) for disturbed plots: a-c) by average density and d-f) by proportion of density.

Across all species in all disturbed plots there were some size related trends (Figure 3-8). The proportion of uprooted basal area increased from the low to high diameter classes. Snapped stems also increased with diameter up to the 30-40 cm range and then leveled off or slightly decreased. There may also be weak trends of increasing importance for tipped and downed dead with size. The only disturbance indicator that was more common in the smaller size classes was live tipped, which was most common in cloud forest.

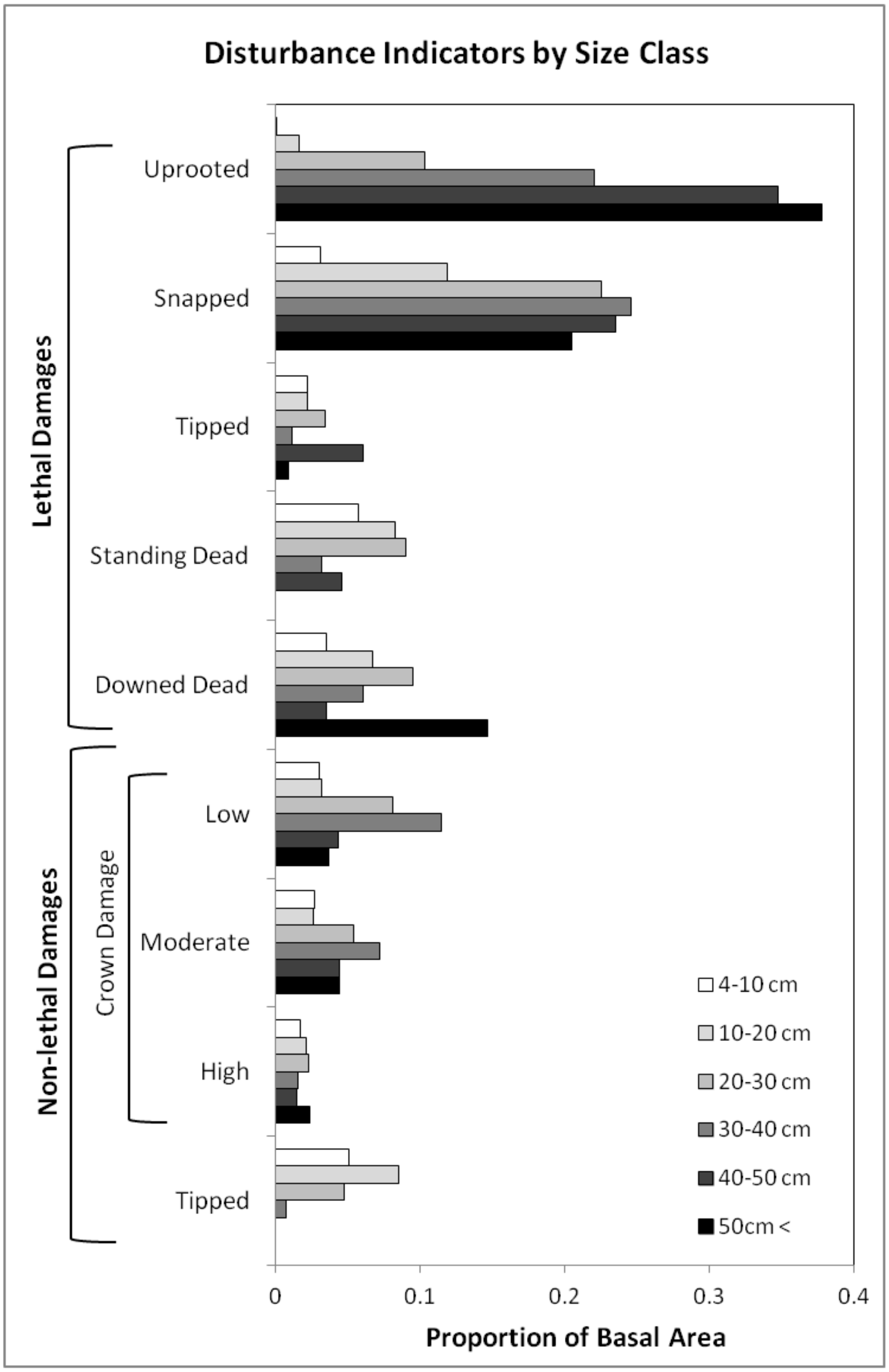

Figure 3-8: Disturbance indicators by diameter size class including all trees in all forest types.

Trends across all species may confuse size with species-specific susceptibilities to disturbance. Looking at only *P. occidentalis* from disturbed plots, there are still clear positive relationships between diameter and uprooted and snapped basal area (Figure 3-9). The increase in the proportion of snapped stems again reaches a threshold around 30-40 cm. *Pinus occidentalis* crown damage peaked at intermediate diameter. There were too few *Cyathea* species in larger diameter classes to analyze size related trends. For broadleaf species in disturbed plots there were several size related trends in the lethal damage categories. It should be noted that larger trees were rare in cloud forest; only 36 broadleaf stems (or 2.0% of all sampled stems) were larger than 30 cm DBH. There were positive size trends for uprooted, snapped, tipped, and downed dead disturbance indicators. Crown damage shows little response to size.

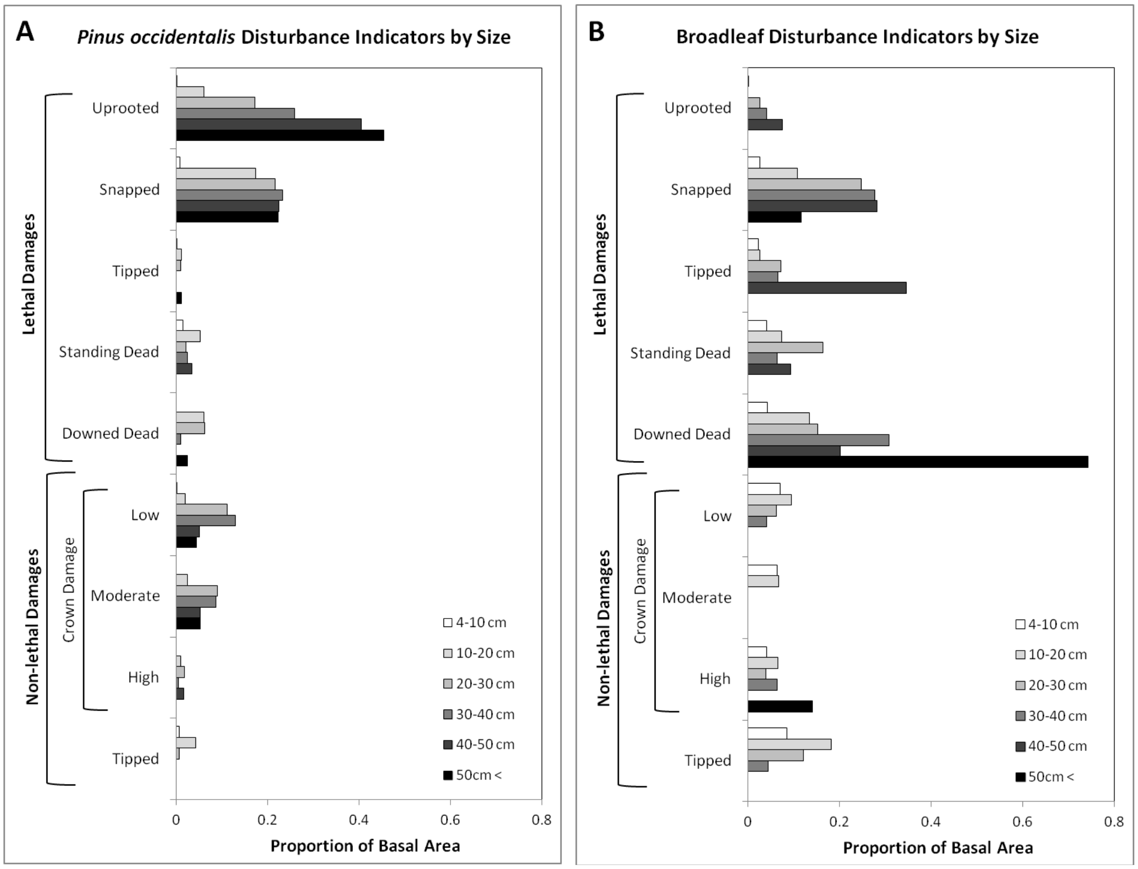

Figure 3-9: Disturbance indicators for *P. occidentalis* and all broadleaves from disturbed plots by DBH size class.

3.2. Species Composition

3.2.1. Cloud Forest

Hurricane Georges left lasting changes on the overstory and understory composition of cloud forest (Figure 3-10). Undisturbed and disturbed cloud forest both had 31 species, 24 of them shared, and 7 unique to each group, for a combined total of 38 species. The disturbed cloud forest averaged 1.3

fewer species per plot than the undisturbed cloud forest (Table 3-2). The tree fern *Cyathea mansu* was the dominant species in both disturbed and undisturbed cloud forest and it increased in importance value in the disturbed plots. The most significant changes in importance value were for *Podocarpus aristulatus* and *Brunellia comocladifolia*. *Podocarpus aristulatus* is a long-lived cloud forest dominant and it decreased in importance in the disturbed plots, moving from the 3rd to the 10th most important species. In contrast, *B. comocladifolia,* an early successional species increased in importance, from the 8th to the third most important species. There were small changes in the importance of other cloud forest dominants (Figure 3-10, Panel A). The importance value of *Garrya fadyenii* decreased by almost half but this only decreased its importance ranking by one species.

Table 3-2: Cloud forest species richness across disturbance plot types.

Species Richness					
Plot Type	**N**	**Min**	**Mean**	**Max**	**SD**
Undisturbed	11	7	11.1	16	2.6
Disturbed	20	5	9.8	15	2.8

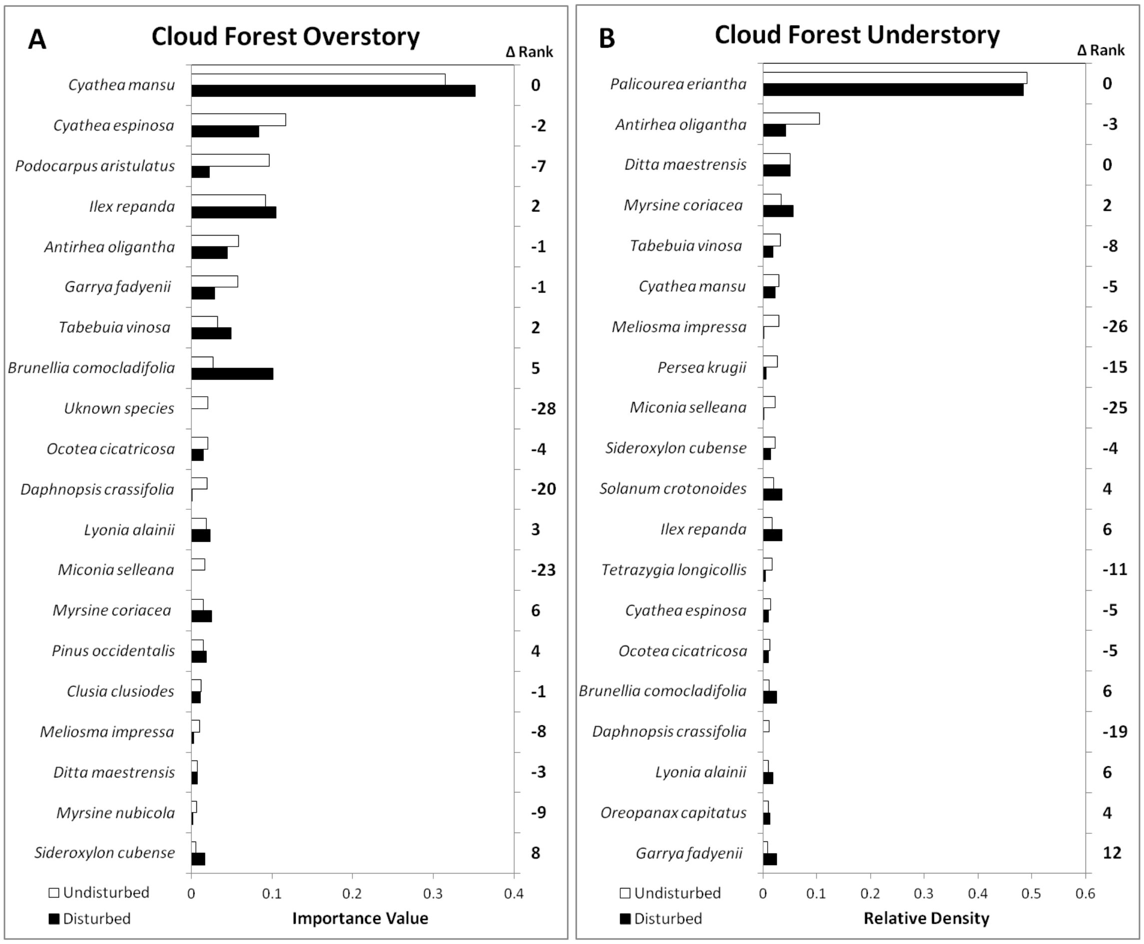

Figure 3-10: Changes in cloud forest a) overstory and b) understory composition.

The changes in cloud forest understory were less notable (Figure 3-10, Panel B). Higher understory stem density was expected in the disturbed plots given that the hurricane thinned the larger size classes. There was a small but insignificant increase in the density of all understory stems (Table 3-3, one-sided t-test p-value = 0.2563). Only the 0-2 cm diameter class increased significantly in density (one-sided t-test p-value = 0.0413).

Table 3-3: Density of understory stems across disturbance plot types.

	Average Density (stems/ha)			
Plot Type	**Seedlings**	**0-2 cm**	**2-4 cm**	**All sizes**
Undisturbed	7568	7250	1182	16000
Disturbed	6313	9588	1663	17563

Analyzing all understory stem sizes together, the shrub, *Palicourea eriantha,* dominated the cloud forest understory and there was little difference in its relative density across disturbance groups (Figure 3-10, Panel B). Ignoring *P. eriantha,* the remaining understory tree species were distributed more evenly compared to overstory species. The second most abundant species in undisturbed cloud forest, *Antirhea oligantha,* had two times lower relative dominance in the disturbed cloud forest and fell in rank from 2nd to 5th. Other species that decreased in relative density were *Tabebuia vinosa*, *Persea krugii*, and *Tetrazygia longicollis*. There were increases in the relative density of several species including *Myrsine coriacea*, *Solanum crotonoides*, *Ilex repanda*, *Brunellia comocladifolia*, and *Garrya fadyenii*.

Within the seedling and 0-2 cm size classes *P. eriantha* dominated both undisturbed and disturbed plots. In the 2-4 cm size class, *P. eriantha* was a smaller component of the assemblage and *B. comocladifolia* dominated the disturbed plots.

3.2.2. Mixed Pine

Disturbance altered mixed pine composition in the direction of reduced pine dominance of the overstory. In mixed pine there were 14 species in the undisturbed plots and 27 in the disturbed plots. All 14 species from the undisturbed plots were present in the disturbed plots. All unique species occurrences were in the disturbed plots and the highest that any ranked in importance was 10th and none were present in more than 3 of 13 plots. Sample sizes were small for mixed pine with only 6 undisturbed plots and 13 disturbed plots. It is likely that many of the rare species that make up the unique disturbed occurrences are also present in the undisturbed forest, but were not captured by the survey.

The most notable trend in overstory composition was a shift in dominance away from *Pinus occidentalis* towards cloud forest species (Figure 3-11, Panel A). The pine overstory should have afforded some wind protection to lower statured cloud forest species, but there were still small differences in importance for many of the typical cloud forest species.

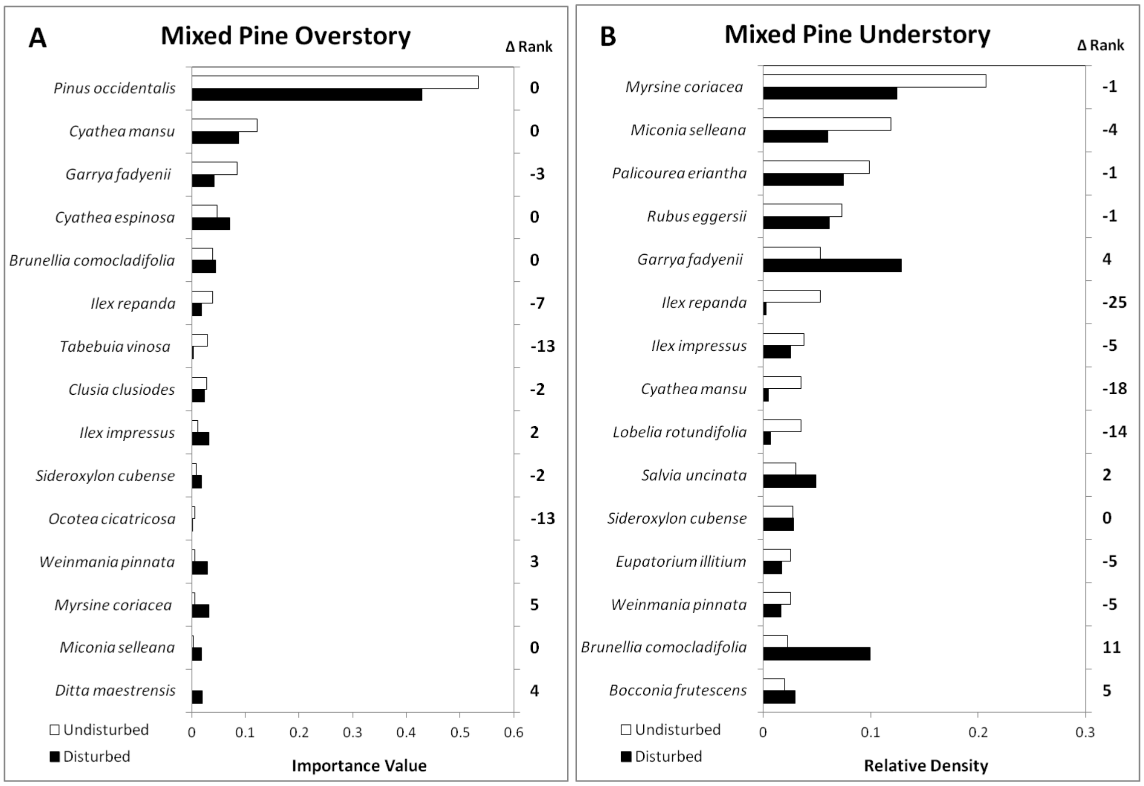

Figure 3-11: Changes in mixed pine a) overstory and b) understory composition.

In contrast to cloud forest, the mixed pine understory had much less *Palicourea eriantha*. The two most common species, *Myrsine coriacea* and *Miconia selleana* decreased in relative density in the disturbed plots. Just like cloud forest, there were large increases in the relative density of *Garrya fadyenii* and *Brunellia comocladifolia*.

3.2.3. Pine Forest

The monodominant pine forest has little potential for major change because there are no species that can compete with *Pinus occidentalis* for overstory dominance on the much drier leeward side of the range. There were only 4 overstory tree species recorded in undisturbed pine forest and only 8 species in disturbed pine forest, 4 of which were unique to disturbed plots. *Pinus occidentalis* was by far the most dominant species in both the disturbed and undisturbed plots with importance values of 0.87 and 0.90 respectively (Figure 3-12, Panel A). The next highest importance value in either disturbance class was 0.01. Species other than *P. occidentalis* were rare. The next most common species, *Garrya fadyenii*, was recorded as an overstory tree (> 4 cm DBH) in less than 20% of all pine forest plots.

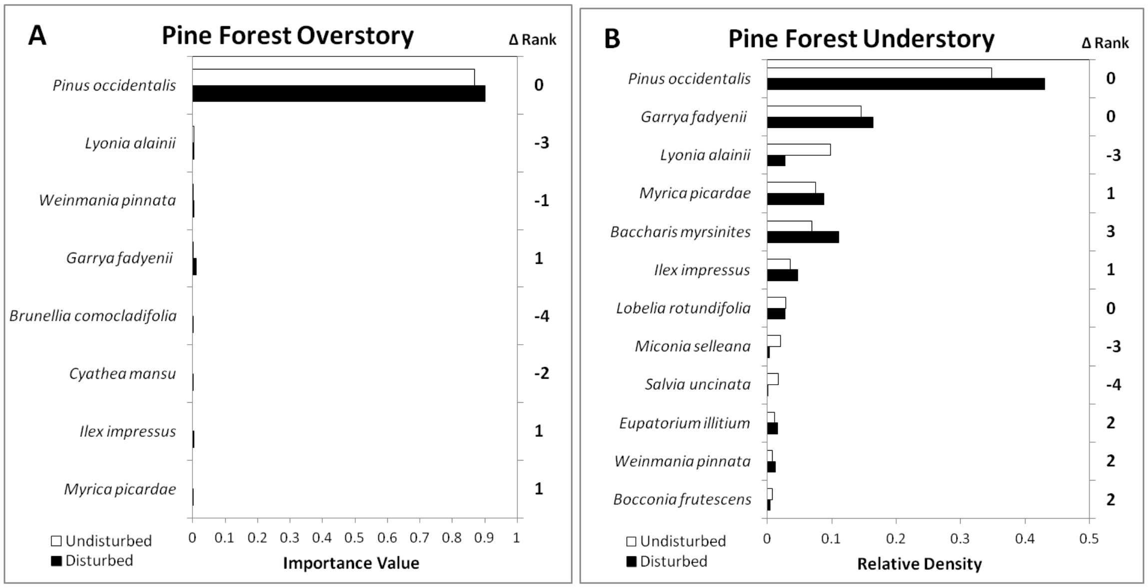

Figure 3-12: Changes in pine forest a) overstory and b) understory composition.

If anything, the hurricane strengthened pine dominance of the overstory based on the increased importance value in the disturbed plots (Figure 3-12, Panel A). The understory composition of pine forest was affected by the 2005 fire (Sherman *et al.* 2008), potentially confounding the observed understory densities. There were no major differences in understory composition across disturbance categories. *Pinus occidentalis* had the highest relative density for both groups, and actually increased in the disturbed plots. The next most abundant species, *Garrya fadyenii* sprouts from the root collar in response to fire (BM Gannon, personal observation) which may explain its high density after the recent fire.

4. Discussion

Hurricanes are but one of several disturbances (Sherman *et al.* 2005, Martin and Fahey 2006, Martin *et al.* 2007) that may leave landscape legacies (Foster *et al.* 1998) in the high elevation forests of Cordillera Central. Describing the spatial distribution (see Chapter 1) and effects of hurricanes are steps towards understanding how disturbances influence ecological patterns and processes in the landscape. Twelve years after Hurricane Georges there is still a visible imprint of the disturbance on forest structure and species composition in the Cordillera Central. Disturbance effects varied across forest types in terms of the proportional change in live and dead basal area (Figure 3-1), the specific mechanisms of change (Figure 3-3), and whether those changes were significant for community composition (Figure 3-10, Figure 3-11, and Figure 3-12).

4.1. Hurricane Effects

4.1.1. Contrasting Forest Types

Pine forest was most sensitive to hurricane disturbance in the Cordillera Central. The magnitude of decrease in the proportion of live and of live undamaged basal area was greatest for pine forest (Figure 3-1) and there was a large gradient in hurricane effects across the different pine disturbance severity levels (Figure 3-2). Our findings add to a pattern (Boucher *et al.* 1990, Bellingham *et al.* 1992) accumulating from research in the Caribbean of disproportionate hurricane effects on pine forests compared to broadleaf forests. Hurricane Georges affected cloud forest and mixed pine, but effects were less severe; cloud forest showed the lowest sensitivity to hurricane disturbance followed by mixed pine (Figure 3-1).

Crown damaged basal area may not be a good indicator of hurricane disturbance, especially for cloud forest. Unexpectedly, the proportion of live but damaged basal area was higher in the undisturbed plots than the disturbed plots. Stem density was highest in cloud forest (4295 stems/ha versus 2602 stems/ha for mixed pine and 1493 stems/ha for pine forest) so there was probably more competition for space in the canopy. What was interpreted as reduced crowns may just be suppressed growth from intense competition with neighbors. As expected, non-lethal disturbance indicators were more abundant in the disturbed plots of pine forest and mixed pine. In these more open stands, and especially with *P. occidentalis*, there were secondary signs of crown disturbance such as large broken branches, suggesting that crown damage measures in pine forest and mixed pine are more reliable.

Forest type susceptibility to hurricane wind in the Cordillera Central is probably the result of factors including stand structure, tree heights, and species-specific susceptibilities to wind.

4.1.2. Size Classes

Results of this study support that uprooting and snapping are positively related to tree size (diameter) similar to findings of Walker (1991). Canopy height ranged from 3.0 m (cloud forest minimum) to 31.5 m (pine forest maximum). This is probably a larger range in heights than what led Bellingham (1991) to conclude that size did not affect tree damage as mentioned by Brokaw and Walker (1991).

Across all species, uprooting and snapping were more common in the larger size classes (Figure 3-8) but larger size classes were dominated by *P. occidentalis*. Only 2.0% of all broadleaf stems were > 30 cm in diameter, in contrast to 38.7% for *P. occidentalis*. When looking at size trends for only *P. occidentalis* or only broadleaf species, it appears that uprooting is positively related to size, but that *P. occidentalis* is more sensitive to size effects than broadleaf species (Figure 3-9). Snapping increases with size, but levels off beyond 30 cm in DBH (Figure 3-8).

Size-related uprooting is probably more important for *P. occidentalis* because larger diameter pines are also taller and vertically oriented (BM Gannon, personal observation). Cloud forest trees are known for their squat, gnarled form (Lawton 1982) and in the Dominican cloud forest there are many large trees with horizontal or tipped stems. For pines, increasing diameter means a taller (longer) lever to be acted upon by wind, but cloud forest trees may lower statured for an equivalent diameter.

4.1.3. Species

There were some species-specific responses to wind disturbance. Non-lethal disturbances were far more common among broadleaf species than tree ferns or pines (Figure 3-4). *Cyathea* species may fare well during a hurricane if they drop their crowns early in the storm, similar to what was observed for palms and tree ferns in Puerto Rico (Brokaw and Walker 1991). *Pinus occidentalis* was uprooted more than any other species and also experienced more snapped stems (Figure 3-5). *Pinus occidentalis* uprooting is strongly related to size (Figure 3-9), but there may be other species-related traits that make it prone to uprooting, such as rooting architecture or tree habit which were not specifically addressed in this study.

Broadleaf trees fared better than pines and tree ferns in terms of the proportion of dead basal area (Figure 3-5). Most dead broadleaf trees were either snapped, standing dead, or downed dead. Disturbance measures are probably low for broadleaf species because they are resilient to wind damage (Yih *et al.* 1991, Bellingham *et al.* 1994, Zimmerman *et al.* 1994). It is possible that these measurements underestimate the direct impacts of the hurricane on cloud forest because even severely damaged stems could have grown back since the disturbance.

4.2. Composition

The composition of disturbed plots differed from their undisturbed controls. Inventory of dead stems provides a rough estimate of mortality from the hurricane, but not what species were actually killed, other than for coarse taxonomic groups (Figure 3-5). Studies that reinventory tagged pre-hurricane plots (e.g. Walker 1991) are most accurate at measuring change because they have accurate pre- and post-hurricane records allowing researchers to identify dead stems to species. For hurricane disturbance to direct change, the effects of the hurricane must be disproportionate across species, either in the overstory (short term) or the understory (long term). It is assumed that differences observed between species for non-lethal damages (Figure 3-4) and between taxonomic groups for lethal damages (Figure 3-5) would extend to interspecific mortality differences.

4.2.1. Cloud Forest

There were no drastic changes in cloud forest composition, but there were some notable changes in overstory and understory abundance. In the overstory, the top 10 species from the undisturbed cloud forest were all in the top 20 from the disturbed plots. *Brunellia comocladifolia*, an early successional species increased in importance in the overstory and in relative density in the understory of the disturbed plots similar to the post-Hurricane Gilbert forest in Jamaica (Tanner and Bellingham 2006). The late-successional species, *Podocarpus aristulatus*, decreased in abundance in the disturbed plots.

Direct regrowth should be an important part of cloud forest recovery based on similarities between cloud forest in the Cordillera Central and forests in Puerto Rico (Weaver 1986) and Jamaica (Bellingham 1994), so the overstory may not undergo much change. The hurricane did reduce the density of stems in larger size classes of cloud forest, probably allowing more light to reach the understory. Compared to undisturbed cloud forest plots, the disturbed cloud forest had higher density of stems in the smallest diameter size class (4-10 cm DBH), probably a response to increased light levels.

Palicourea eriantha dominated all understory size classes of both the undisturbed and disturbed cloud forest plots, except for the 2-4 cm size class in the disturbed plots, of which *Brunellia comocladifolia* was the species with the highest relative density.

The cloud forest understory stem density did not increase when considering all size classes, but was significantly higher for the 0-2 cm size class. *Brunellia comocladifolia* in the 2-4 cm size class could be advanced regeneration that either established or had a pulsed growth event after Hurricane Georges. In Puerto Rico, Walker (1991) suggested that patches of severe disturbance favored early successional establishment, presumably because of increased light (Brokaw and Grear 1991). Litter depth, which increases from hurricane defoliation, can select against seedlings of certain species (Guzmán-Grajales and Walker 1991) and not all species respond favorably to sudden increases in light (You and Petty 1991). While increased light levels probably had a positive influence on the density of many understory species, increased litter depth and sun-scalding may have reduced the density of others.

4.2.2. Mixed Pine

Mixed pine forest is interesting because of its species composition, environment, and position in the landscape. *Pinus occidentalis* importance decreased in the disturbed mixed pine plots and species typical of cloud forest increased in importance (Figure 3-11). The magnitude of decrease in *P. occidentalis* (-20% compared to the undisturbed importance value) was not enough to completely convert mixed pine into cloud forest. It would probably take several hurricanes of this same intensity to create the type of ecotone dynamics described in Martin *et al.* 2011. Still, it is a move towards decreasing pine dominance in line with the theory. The mixed pine plots clearly aren’t on a path towards continued pine dominance as *P. occidentalis* was not an important component of the understory (Figure 3-11, Panel B). Hurricane Georges was only a category 1 hurricane when it hit the site, but Hurricane David (1979) hit the site as a category 5 hurricane. It is probable that winds from Hurricane David were intense enough to produce more significant changes in mixed pine.

4.2.3. Pine Forest

The effects of Hurricane Georges were most severe on pine forest structure (Figure 3-1), but there were almost no effects on forest composition (Figure 3-12) especially in the overstory (Panel A).

Pinus occidentalis was by and far the most important species in the undisturbed and disturbed plots. The understory was affected by the 2005 fire, so differences may not be the direct result of Hurricane Georges, but the relative density of *P. occidentalis* was actually higher in the disturbed plots. The composition of pine forest is strictly controlled by climate and by frequent fire, particularly on the leeward side of the range (Martin and Fahey 2006). Most cloud forest species have thin bark making them poorly adapted to fire (Martin *et al.* 2007), excluding them as serious contenders in pine forest dynamics. The sensitivity of pine forest to wind disturbance should be noted by natural resource managers in the Caribbean, not just for plantations (Bellingham *et al.* 1992), but also for natural pine-dominated ecosystems at high elevations.

5. Conclusions

Hurricane Georges created patterns in forest structure and species composition that persisted 12 years after the disturbance. Differences in cloud forest understory composition suggest that the landscape legacy (Foster *et al.* 1998) of the hurricane may persist for some time. The effects of Hurricane Georges on forest structure were most severe on pine forest, moderate on mixed pine, and weak on cloud forest. Despite this trend, mixed pine and cloud forest experienced more change in composition than pine forest. The leeward side of the Cordillera Central is drier and more prone to fires, both of which favor continued dominance of *Pinus occidentalis*. Hurricane George reduced pine dominance in the mixed pine plots by disproportionately affected pine, but the effect was not strong, possibly due to the low intensity of Hurricane Georges. Cloud forest composition shifted slightly towards early successional species in the overstory and understory at the expense of at least one late successional species. The pre-hurricane difference in basal area suggests that stand structure is an important determinant of hurricane disturbance in cloud forest.

References

Ayala-Silva, T. and Twumasi, Y.A. (2004) Hurricane Georges and vegetation change in Puerto Rico using AVHRR satellite data. *International Journal of Remote Sensing*, **25(9)**, 1629-1640.

Bellingham, P.J. (1991) Landforms influence patterns of hurricane damage: evidence from Jamaican Montane Forests. *Biotropica,* **23(4a)**, 427-433.

Bellingham, P.J., Kapos, V., Varty, N., Healey, J.R., Tanner, E.V.J., Kelly, D.L., Dalling, J.W., Burns, L.S., Lee, D., and Sidrak, G. (1992) Hurricanes need not cause high mortality: the effects of Hurricane Gilbert on forests in Jamaica. *Journal of Tropical Ecology*, **8**, 217-223.

Bellingham, P.J., Tanner, E.V.J., and Healey, J.R. (1994) Sprouting of trees in Jamaican Montane Forests, after a hurricane. *Journal of Ecology*, **82(4)**, 747-758.

Bellingham, P.J. and Tanner, E.V.J. (2000) The influence of topography on tree growth, mortality, and recruitment in a tropical montane forest. *Biotropica,* **32(3)**, 378-384.

Bianchette, T.A., Liu, K.B., Lam, N.S., and Kiage, L.M. (2009) Ecological impacts of Hurricane Ivan on the Gulf Coast of Alabama: a remote sensing study. *Journal of Coastal Research*, **56**, 1622-1626.

Boose, E.R., Foster, D.R. and Fluet, M. (1994) Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs,* **64(4)**, 369-400.

Boose, E.R., Serrano, M.I., and Foster, D.R. (2004) Landscape and regional impacts of hurricanes in Puerto Rico. *Ecological Monographs,* **74(2)**, 335-352.

Boucher, D.H., Vandermeer, J.H., Yih, K. and Zamora, N. (1990) Contrasting hurricane damage in tropical rain forest and pine forest. *Ecology,* **71(5)**, 2022-2024.

Breiman, L. (2001) Random Forests. *Machine Learning,* **45(1)**, 5-32.

Brokaw, N.V.L. and Grear, J.S. (1991) Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica,* **23(4a)**, 386-392.

Brokaw, N.V.L. and Walker, L.R. (1991) Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica,* **23(4a)**, 442-447.

Canham, C.D., Thompson, J., Zimmerman, J.K., and Uriarte, M. (2010) Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica*, **42(1)**, 87-94.

Cohen, W.B. and Spies, T.A. (1992) Estimating structural attributes of Douglas-fir/Western hemlock forest stands from Landsat and SPOT imagery. *Remote Sensing of Environment*, **41**, 1-17.

Cole, L.C. (1949) The measurement of interspecific association. *Ecology*, **30(4)**, 411-424.

Collins, J.B. and Woodcock, C.E. (1996) An Assessment of Several Linear Change Detection Techniques for Mapping Forest Mortality Using Multitemporal Landsat TM Data. *Remote Sensing of Environment*, **55**, 66-77.

Crist, E.P., Laurin, R., and Cicone, R.C. (1986) Vegetation and soils information contained in transformed Thematic Mapper data. In *Proceedings of IGARSS '86 Symposium*, 1465-70.

Demuth, J., DeMaria, M., and Knaff, J.A. (2006) Improvement of advanced microwave sounder unit tropical cyclone intensity and size estimation algorithms. Journal of Applied Meteorology, 45, 1573-1581.

Denslow, J.S. (1985) Disturbance-mediated coexistence of species. In The ecology of natural disturbance and patch dynamics. Eds. S.T.A. Pickett and P.S. White. Academic Press, New York, 307-323.

Doyle, T.W. (1980) The role of disturbance in the gap dynamics of a montane rain forest: an application of a tropical forest succession model. In Forest succession: concepts and application. Eds. D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, Berlin, 56-73.

Doyle, T.W., Krauss, K.W., and Wells, C.J. (2009) Landscape analysis and pattern of hurricane impact and circulation on mangrove forests of the everglades. *WETLANDS*, **29(1)**, 44-53.

ERDAS. (2010) ERDAS IMAGINE 2010. Earth Resources Data Analysis System, Atlanta, GA.

ERSDAC. (2011) ASTER Global Digital Elevation Model. Earth Remote Sensing Data Analysis Center. Online: http://www.gdem.aster.ersdac.or.jp/.

Everham, E.M. and Brokaw, N.V.L. (1996) Forest damage and recovery from catastrophic wind. *Botanical Review*, **62(2)**, 113-185.

Ewel, J.J. and Whitmore, J.L. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA Forest Service Research Paper. ITF-18. Institute of Tropical Forestry, Rio Piedras, Puerto Rico.

Foster, D.R., Fluet, M., and Boose, E.R. (1999) Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological Applications*, **9(2)**, 555-572.

Foster, D.R., Knight, D.H., and Franklin, J.F. (1998) Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems*, **1(6)**, 497-510.

Freitas, S.R., Mello, M.C.S., and Cruz, C.B.M. (2005) Relationships between forest structure and vegetation indices in Atlantic Rainforest. *Forest Ecology and Management*, **218**, 353-362.

Geerts, B., Heymsfield, G.M., Tian, L., Halverson, J.B., Guillory, A., and Mejia, M.I. (1999) Hurricane Georges's landfall in the Dominican Republic: detailed airborne Doppler radar imagery. *Bulletin of the American Meteorological Society*, **81(5)**, 999-1018.

GPS Aerial Services, Inc. (1999) Color Infrared Aerial Photography. Anchorage, AK.

Guariguata, M.R. (1990) Landslide disturbance and forest regeneration in the Upper Luquillo Mountains of Puerto Rico. *Journal of Ecology*, **78(3)**, 814-832.

Guiney, J.L. (1999) Hurricane Georges Preliminary Report. National Hurricane Center. Online: http://www.nhc.noaa.gov/1998georges.html.

Guzmán-Grajales, S. and Walker, L.R. (1991) Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **23(4a)**, 407-413.

Hardisky, M.A., Lemas, V., and Smart, R.M. (1983) The influence of soil salinity, growth form, and leaf moisture on the spectral reflectance of Spartina alternifolia canopies. *Photogrammetric Engineering and Remote Sensing*, **49**, 77–83.

Hayes, D.J. and Cohen, W.B. (2007) Spatial, spectral and temporal patterns of tropical forest cover change as observed with multiple scales of optical satellite data. *Remote Sensing of Environment*, **106**, 1–16

Helmer, E.H. and Ruefenacht, B. (2005) Cloud-Free Satellite Image Mosaics with Regression Trees and Histogram Matching. *Photogrammetric Engineering & Remote Sensing*, **71(9)**, 1079-1089.

ITT VIS, Inc. (2011) ENVI 4.8. ITT Visual Information Solutions, White Plains, NY.

Jenness, J. (2011) DEM Surface Tools v. 2.1.292. Jenness Enterprises. Online: http://www.jennessent.com/arcgis/surface_area.htm.

Jin, S. and Sader, S.A. (2005) Comparison of time series tasseled cap wetness and the normalized difference moisture index in detecting forest disturbances. *Remote Sensing of Environment*, **94**, 364-372.

Knaff, J.A., Sampson, C.R., DeMaria, M., Marchok, T.P., Gross, J.M., and McAdie, C.J. (2007) Statistical tropical cyclone wind radii prediction using climatology and persistence, *Weather and Forecasting*, **22(4)**, 781–791.

Larsen, M.C. and Torres-Sánchez, A.J. (1998) The frequency and distribution of recent landslides in three montane tropical regions of Puerto Rico. *Geomorphology*, **24**, 309-331.

Lawton, R.O. (1982) Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation. *American Journal of Botany*, **69(8)**, 1224-1230.

Lee, M., Lin, T., Vadeboncoeur, M.A., and Hwong, J. (2008) Remote sensing assessment of forest damage in relation to the 1996 strong typhoon Herb at Lienhuachi Experimental Forest, Taiwan. *Forest Ecology and Management*, **255**, 3297-3306.

Liaw, A. and Wiener, M. (2002) Classification and Regression by randomForest. *R News*, 2(3), 18-22.

Lugo, A.E., Applefield, M., Pool, D.J. and McDonald, R.B. (1983) The impact of Hurricane David on the forests of Dominica. *Canadian Journal of Forest Research,* **13**, 201-211.

Lugo, A.E. and Waide, R.B. (1993) Catastrophic and background disturbance of tropical ecosystems at the Luquillo Experimental Forest. *Journal of Biosciences*, **18(4)**, 475-481.

Lugo, A.E. (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology*, **33**, 368-398.

Majka, D., Jenness, J., and Beier, P. (2007) CorridorDesigner: ArcGIS tools for designing and evaluating corridors. Online: http://corridordesign.org.

Martin, P.H., Sherman, R.E. and Fahey, T.J. (2004) Forty years of tropical forest recovery from agriculture: structure and floristics of secondary and old-growth riparian forests in the Dominican Republic. *Biotropica*, **36(3)**, 297-317.

Martin, P.H. and Fahey, T.J. (2006) Fire history along environmental gradients in the subtropical pine forests of the Cordillera Central, Dominican Republic. *Journal of Tropical Ecology,* **22**, 289-302.

Martin, P.H., Sherman, R.E. and Fahey, T.J. (2007) Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. *Journal of Biogeography,* **34**, 1792-1806.

Martin, P.H., Fahey, T.J., and Sherman, R.E. (2011) Vegetation zonation in Neotropical Montane Forest: environment, disturbance, and ecotones. *Biotropica*, **43(5)**, 533-543.

McGarigal, K., Cushman, S.A., Neel, M.C., and Ene, E. (2002) FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. University of Massachusetts, Amherst, MA. Online: http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Neumann, C.J. (1987) The national hurricane center risk analysis program (HURISK). National Hurricane Center. *NOAA Technical Memorandum*, NWS NHC **38**, 1-59.

NOAA (2009) IBTrACS Dataset. NOAA Satellite and Information Service. Online: http://www.ncdc.noaa.gov/oa/ibtracs/.

Ostertag, R., Silver, W.L., and Lugo, A.E. (2005) Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest. *Biotropica*, **37(1)**, 16-24.

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., and Aiello, A. (1983) Uprooting and snapping of trees: structural determinants and ecological consequences. *Canadian Journal of Forest Research*, **13**, 1011-1020.

R Development Core Team (2011) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Online: http://www.R-project.org

Ramsey III, E.W., Chappell, D.K., and Baldwin, D.G. (1997) AVHRR imagery used to identify hurricane damage in a forested wetland of Louisiana. *Photogrammetric Engineering & Remote Sensing*, **63(3)**, 293-297.

Ramsey III, E.W., Hodgson, M.E., Sapkota, S.K., and Nelson, G.A. (2001) Forest impact estimated with NOAA AVHRR and Landsat TM data related to empirical hurricane wind-field distribution. *Remote Sensing of Environment*, **77**, 279-292.

Restrepo, C., Walker, L.R., Shiels, A.B., Bussmann, R., Claessens, L., Fisch, S., Lozano, P., Negi, G., Paolini, L., Poveda, G., Ramos-Scharrón, C., Richter, M., and Velázquez, E. (2009) Landsliding and its multiscale influence on mountainscapes. *BioScience*, **59(8)**, 685-698.

Rouse, J.W., Hass, R.H., Schell, J.A., and Deering, D.W. (1973) Monitoring vegetation systems in the Great Plains with ERTS. In *Proceedings of the Third ERTS Symposium*, 309–317.

Runkle, J.R. (1985) Disturbance regimes in temperate forests. In The ecology of natural disturbance and patch dynamics. Eds. S.T.A. Pickett and P.S. White. Academic Press, New York, 17-34.

Scatena, F.N. and Larsen, M.C. (1991) Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica*, **23(4a)**, 317-323.

Scatena, F.N. and Lugo, A.E. (1995) Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. *Geomorphology*, **13**, 199-213.

Sherman, R.E., Martin, P.H. and Fahey, T.J. (2005) Vegetation-environment relationships in forest ecosystems of the Cordillera Central, Dominican Republic. *Journal of the Torrey Botanical Society,* **132**, 293-310.

Sherman, R.E., Martin, P.H., Fahey, T.J. and Degloria, S.D. (2008) Fire and vegetation dynamics in high-elevation Neotropical Montane Forests of the Dominican Republic. *Ambio,* **37**, 535-541.

Slocum, M.G., Aide, T.M., Zimmerman, J.K., and Navarro, L. (2004) Natural regeneration of subtropical montane forest after clearing fern thickets in the Dominican Republic. *Journal of Tropical Ecology*, **20**, 483-486.

Song, C., Woodcock, C.E., Seto, K.C., Lenney, M.P., and Macomber, S.A. (2001) Classification and change detection using Landsat TM data: when and how to correct atmospheric effects? *Remote Sensing of Environment*, **75**, 230-244.

Sousa, W.P. (1984) The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, **15**, 353-391.

Staben, G.W. and Evans, K.G. (2008) Estimates of tree canopy loss as a result of Cyclone Monica, in the Magela Creek catchment northern Australia. *Austral Ecology*, **33**, 562-569.

Tanner, E.V.J., Kapos, V., and Healey, J.R. (1991) Hurricane effects on forest ecosystems in the Caribbean. *Biotropica*, **23(4a)**, 513-521.

Tanner, E.V.J. and Bellingham, P.J. (2006) Less diverse forest is more resistant to hurricane disturbance: evidence from montane rain forests in Jamaica. *Journal of Ecology*, **94**, 1003-1010.

USGS and NASA. (2010) Global Land Survey 2000. USGS Center for Earth Resources Observation and Science (EROS), Sioux Falls, SD.

USGS. (2011) Earth Resources Observation and Science Center. United States Geological Survey. Online: http://glovis.usgs.gov/.

Vandermeer, J., Boucher, D., Perfecto, I., Granzow de la Cerda, I. (1996) A theory of disturbance and species diversity: evidence from Nicaragua after Hurricane Joan. *Biotropica*, **28(4a)**, 600-613.

Wadsworth, F.H. and Englerth, G.H. (1959) Effects of the 1956 hurricane on forests in Puerto Rico. Caribbean Forester, **20**, 38–51.

Waide, R.B. (1991) The Effect of Hurricane Hugo on Bird Populations in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, **23(4a)**, 475-480.

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

Walker, L.R., Lodge, D.J., Brokaw, N.V.L. and Waide, R.B. (1991) An introduction to hurricanes in the Caribbean. *Biotropica*, **23(4a)**, 313-316.

Walker, L.R. (1994) Effects of fern thickets on woodland development on landslides in Puerto Rico. *Journal of Vegetation Science*, **5**, 525-532.

Walker, L.R., Zarin, D.J., Fetcher, N., Myster, R.W., and Johnson, A.H. (1996) Ecosystem development and plant succession on landslides in the Caribbean. *Biotropica*, **28(4a)**, 566-576.

Wang, F. and Xu, Y.J. (2009) Hurricane Katrina-induced forest damage in relation to ecological factors at landscape scale. *Environmental Monitoring and Assessment*, **156**, 491-507.

Wang, F. and Xu, Y.J. (2010) Comparison of remote sensing change detection techniques for assessing hurricane damage to forests. *Environmental Monitoring and Assessment*, **162**, 311-326.

Wang, W., Qu, J.J., Hao, X., Liu, Y., and Stanturf, J.A. (2010) Post-hurricane forest damage assessment using satellite remote sensing. *Agricultural and Forest Meteorology*, **150**, 122-132.

Weaver, P.L. (1986) Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*, **22(1-2)**, 53-70.

Weaver, P.L. (1999) Impacts of Hurricane Hugo in the Dwarf Cloud Forest of Puerto Rico's Luqillo Mountains. *Caribbean Journal of Science*, **35(1-2)**, 101-111.

Weaver, P.L. (2002) A chronology of hurricane induced changes in Puerto Rico's lower montane rainforest. *Interciencia*, **27(5)**, 252-258.

White, P.S. and Pickett, S.T.A. (1985) Natural disturbance and patch dynamics: an introduction. In The ecology of natural disturbance and patch dynamics. Eds. S.T.A. Pickett and P.S. White. Academic Press, New York, 3-13.

Williams-Linera, G. (2002) Tree species richness complementarity, disturbance and fragmentation in a Mexican tropical montane cloud forest. *Biodiversity and Conservation*, **11**, 1825-1843.

Yih, K., Boucher, D.H., Vandermeer, J.H., Zamora, N. (1991) Recovery of the rain forest of Southeastern Nicaragua after destruction by Hurrican Joan. *Biotropica*, **23(2)**, 106-113.

You, C. and Petty, W. (1991) Effects of Hurricane Hugo on Manilkara bidentata, a primary tree species in the Luqillo Experimental Forest of Puerto Rico. *Biotropica*, **23(4a)**, 400-406.

Zimmerman, J.K., Everham III, E.M., Waide, R.B., Lodge, D.J., Taylor, C.M., and Brokaw, N.V.L. (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(4)**, 911-922.

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

Zimmerman, J.K., Willig, M.R., Walker, L.R., and Silver, W.L. (1996) Introduction: disturbance and Caribbean Ecosystems. *Biotropica*, **28(4a)**, 414-423.

Appendix I – Land Cover Classification

Permanent plot data of Sherman *et al.* 2005 was only used in this study if the plot had GPS coordinates and it was > 45m away from a land cover type edge (evaluated using the CIR OM). The training and testing points were not evenly distributed throughout the different land cover classes (Table I-1) because most of the site is forested, with broadleaf, cloud, and pine forest covering the majority of the landscape.

Table I-1: Training and testing data points (n) used in the land cover classification.

Cover Type	**2 riparian**	**Agriculture**	**Broadleaf**	**Cloud**	**Grass**	**Pine**
Training	12	12	40	90	12	184
Testing	6	6	22	45	6	88
Total	18	18	62	135	18	272

The final model used the seven predictor variables described in Table I-2.

Table I-2: Predictor variables used in the land cover classification.

Raster Layer	**Notes**
Elevation	From ASTER GDEM in meters
Slope	From ASTER GDEM in degrees (calculated using ArcGIS 9.3 Spatial Analyst)
Eastness	Eastness = sin([aspect x π]/180) from Zar 1999
Northness	Northness = cos([aspect x π]/180) from Zar 1999
PCA Band 2	Principal components analysis of Landsat 5 TM bands 1-5,7
PCA Band 3	Principal components analysis of Landsat 5 TM bands 1-5,7
NDVI	Normalized Difference Vegetation Index = (B4 – B3)/(B4 + B3)

The confusion matrix for the Random Forests model is presented in Table I-3. Producer's and user's accuracies were high for pine forest and cloud forests. Agriculture had the lowest producer's accuracy, but the highest user's accuracy.

Table I-3: Confusion Matrix for the land cover classification.

Predicted

Actual

	2 riparian	Broadleaf	Agriculture	Grass	Cloud	Pine	Producer's Accuracy %
2 riparian	6	0	0	0	0	0	**100.0**
Broadleaf	0	20	0	0	0	2	**90.9**
Agriculture	1	0	4	1	0	0	**66.7**
Grass	0	0	0	5	0	1	**83.3**
Cloud	0	3	0	0	36	6	**80.0**
Pine	0	1	0	0	3	84	**95.5**
User's Accuracy %	**85.7**	**83.3**	**100.0**	**83.3**	**92.3**	**90.3**	

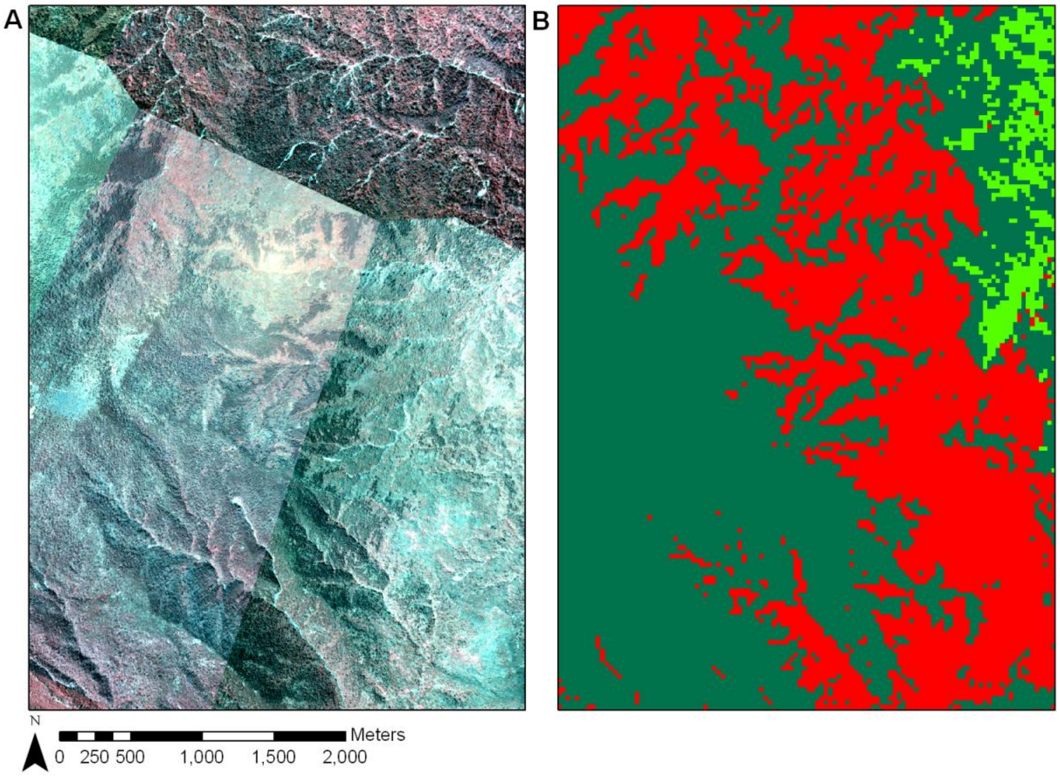

Figure I-1: Comparison of a) CIR OM and b) land cover classification. Panel b) follows the classification scheme in Figure 3-1.

Appendix II – Change Detection Supplemental Information

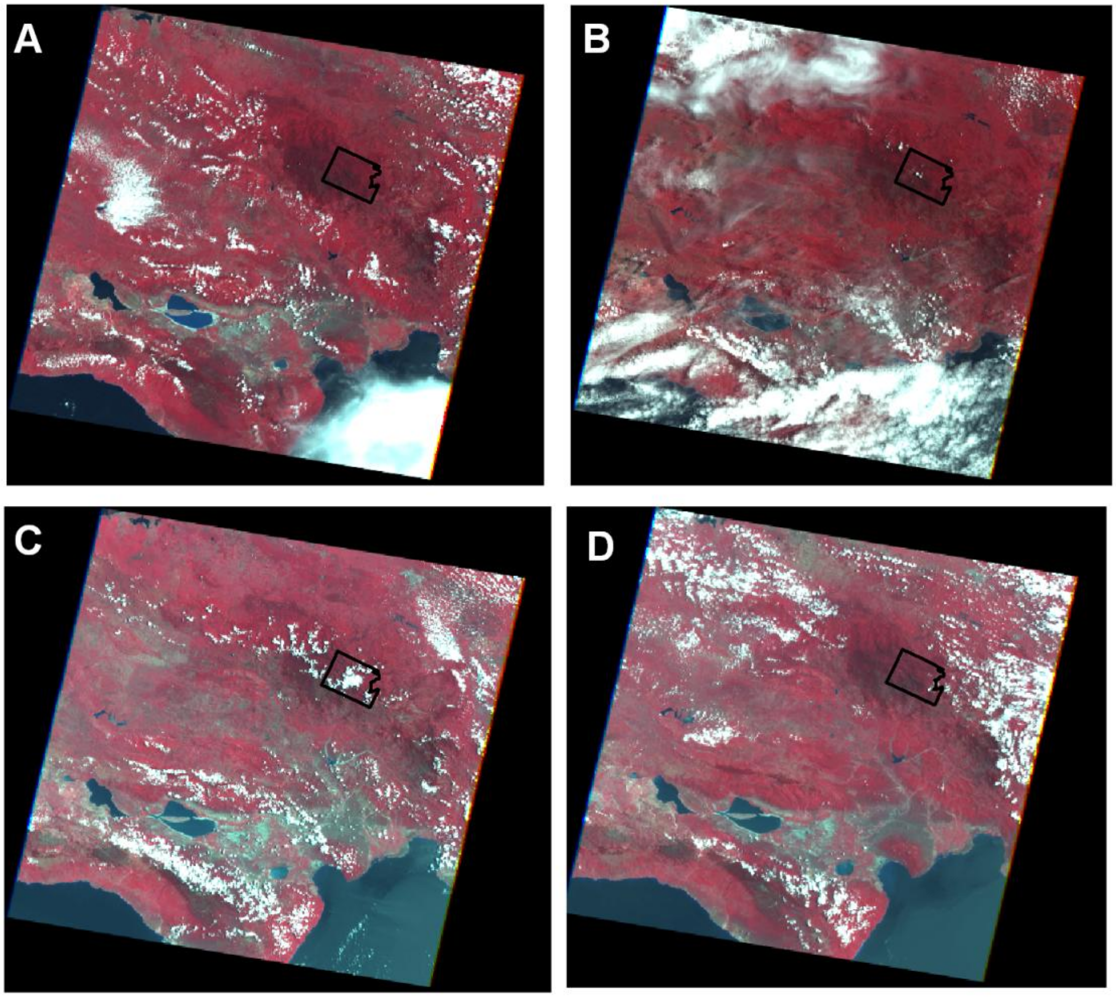

Figure II-1: CIR Landsat 5 TM images used in the analysis: a) 09.2.1998, b) 05.16.1999, c) 06.01.1999, and d) 07.19.1999. The black outline shows the extent of the study site.

Table II-1: Dark object subtraction values used in radiometric correction of atmospheric effects.

Date	**9.2.1998**	**5.16.1999**	**6.1.1999**	**7.19.1999**
Band 1	43	46	45	49
Band 2	16	17	16	20
Band 3	12	13	12	17
Band 4	9	14	13	15
Band 5	4	10	10	12
Band 7	3	5	5	6

Appendix III – Details on Compositing Methods

The image compositing was done in three steps: 1) cloud and shadow masking of base and fill images, 2) correction of fill images, and 3) gap filing of base image.

Clouds were classified using a minimum threshold on band 1 digital numbers (DNs). Shadows were classified using the minimum distance classifier in ENVI 4.8 (ITT VIS, Inc. 2011) on all seven landsat bands with training data collected from the scene to represent shaded and non-shaded vegetation. The cloud classes incorrectly included some bright features in the landscape such as landslides and scoured stream beds. The cloud rasters were manually edited to remove any non-cloud features. The shadow classes incorrectly included many areas shadowed by topography instead of by clouds. The shadow class was filtered to include only cloud shadows by selected only those shadow patches that fell within 500 m of the nearest cloud edge. The clouds and shadows were then buffered by 60 m to create a conservative boundary of cloud and shadow influence on the images and then combined into a single cloud and shadow mask for each image. The images to be masked are shown in Figure II-1 and the final cloud and shadow masks are show in Figure III-2.

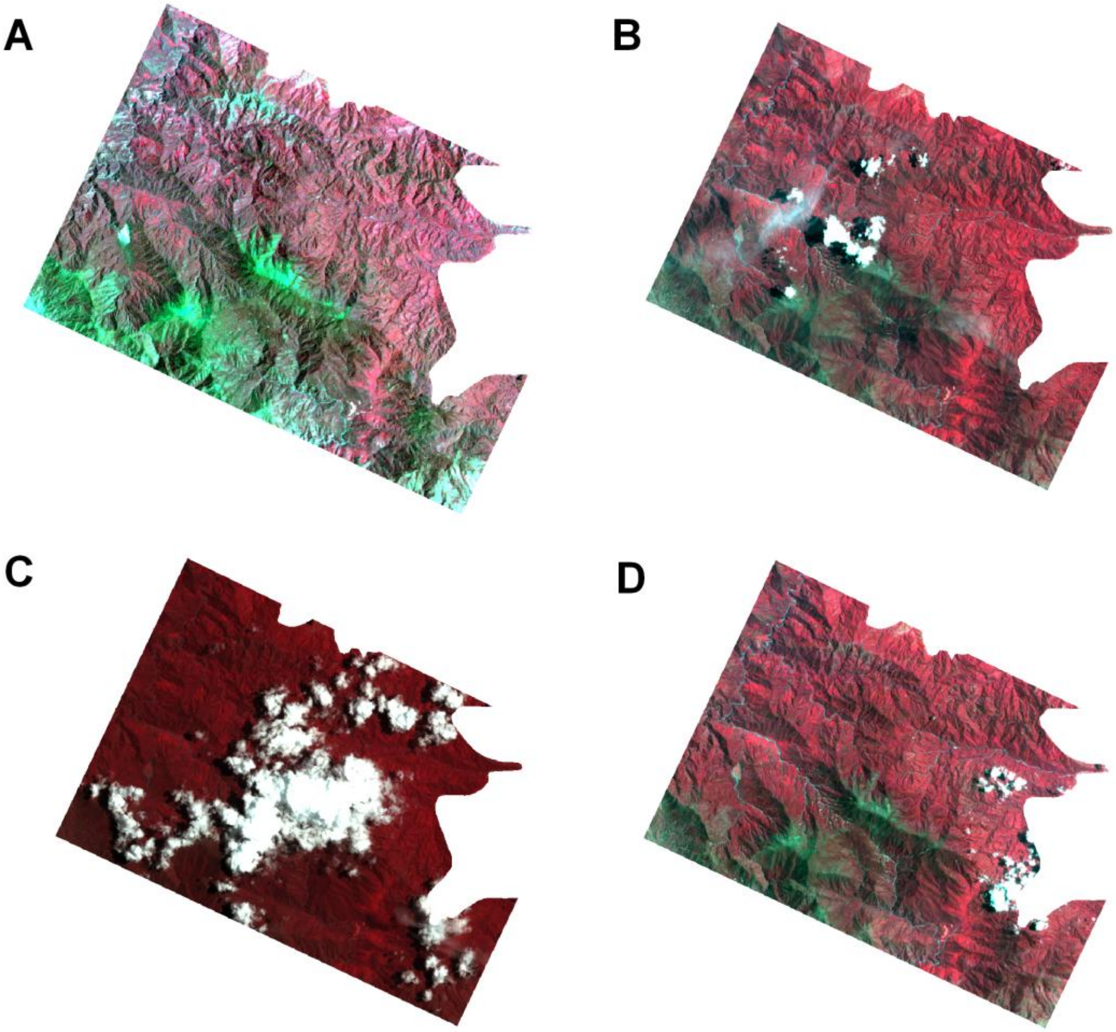

Figure III-1 CIR Landsat 5 TM images clipped to the analysis extent: a) 09.02.1998, b) 05.16.1999, c) 06.01.1999, and d) 07.19.1999 showing varying proportions of cloud cover.

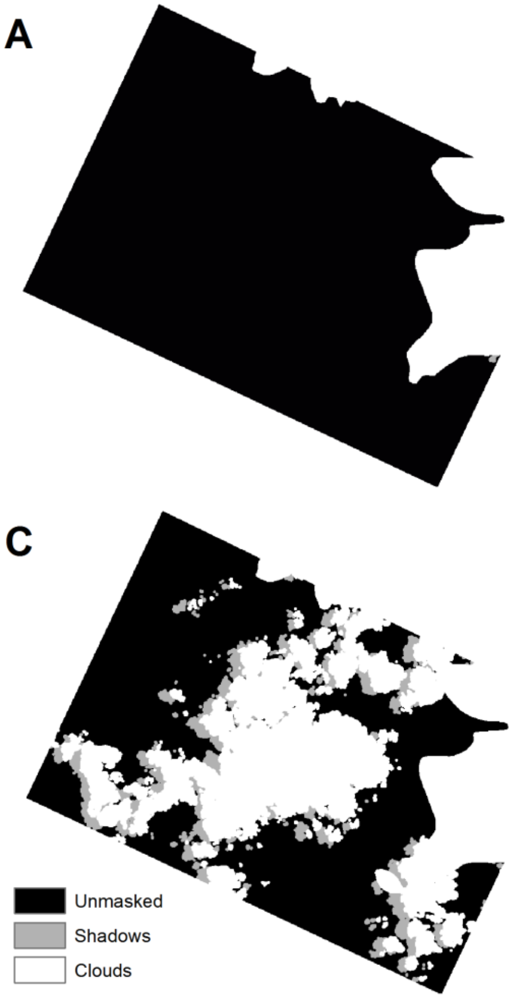

Figure III-2: Cloud and shadow masks developed for a) 09.2.1998, b) 05.16.1999, c) 06.01.1999, and d) 07.19.1999.

Table III-1: Percent of study site masked for shadows and clouds by image date.

	9.2.1998	**5.16.1999**	**6.1.1999**	**7.19.1999**
Shadow	0.04	2.41	7.99	1.65
Cloud	0.00	3.28	34.82	2.28
Total	0.04	5.69	42.81	3.93

The atmospheric correction using dark object subtraction method used the radiometrically corrected data outlined previously (Appendix II Table II-1). The linear correction and histogram matching methods corrected the 05.16.1999 and 06.01.1999 images to the 07.19.1999 base image using all pixels within the coincident cloud-free areas of image pairs.

The clouded gaps in the 07.19.1999 were filled with corrected data from the cloud-free coincident areas of first the 06.01.1999 image and then the 05.16.1999 image. This order was chosen assuming that the 06.01.1999 image more closely matched the 07.19.1999 vegetation phenology and degree of post-hurricane vegetation recovery.

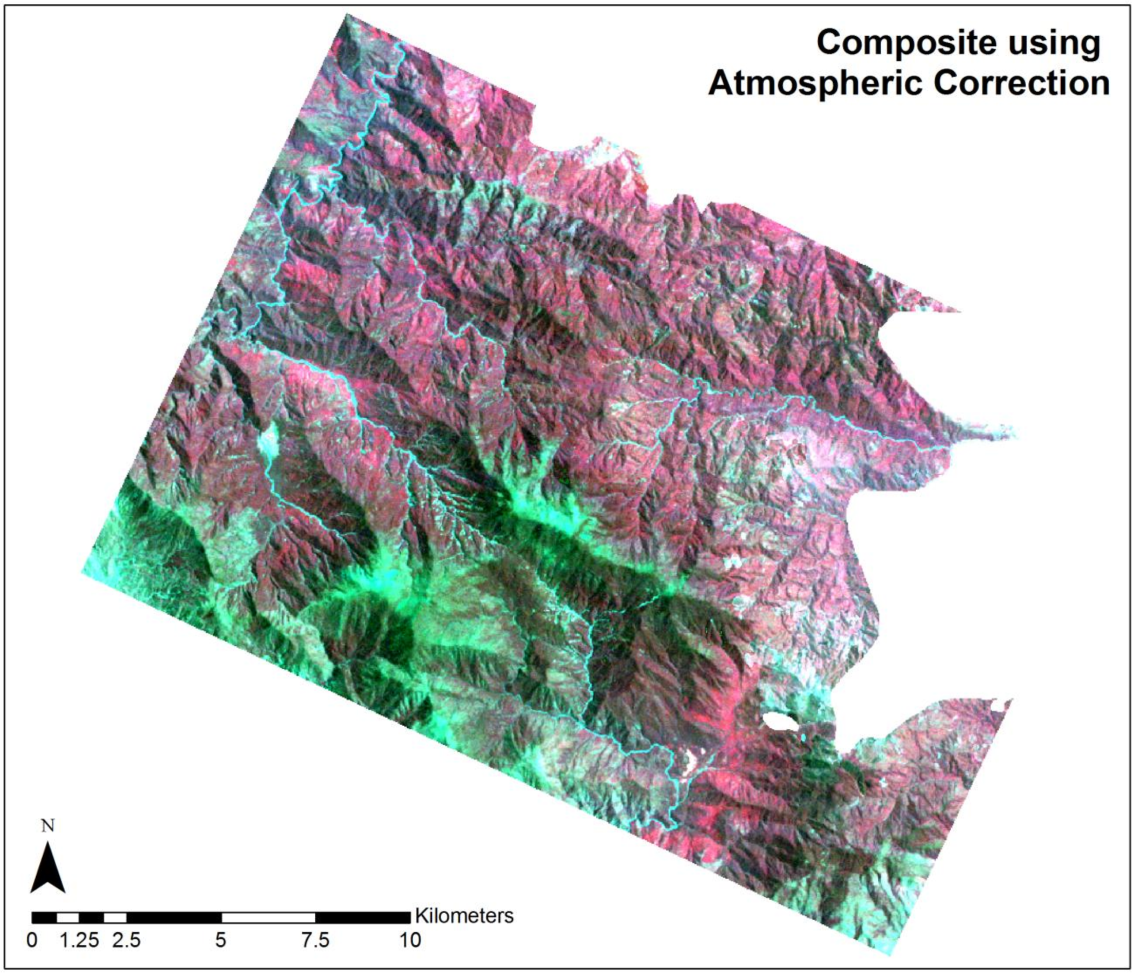

Figure III-3: CIR composite developed by gap-filling 07.19.1999 with 06.01.1999 and then 05.16.1999 atmospherically corrected using DOS.

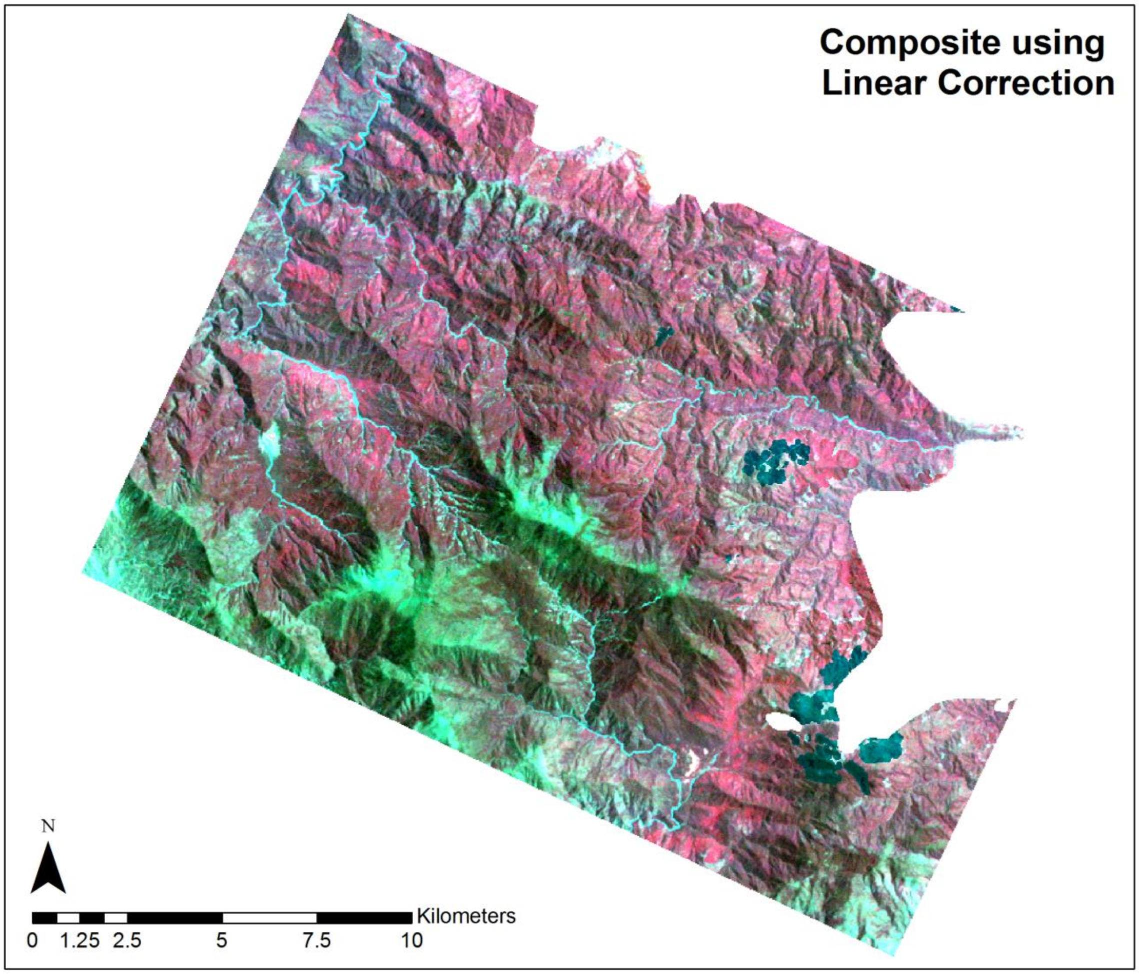

Figure III-4: CIR composite developed by gap-filling 07.19.1999 with 06.01.1999 and then 05.16.1999 that were corrected to 07.19.1999 using linear models.

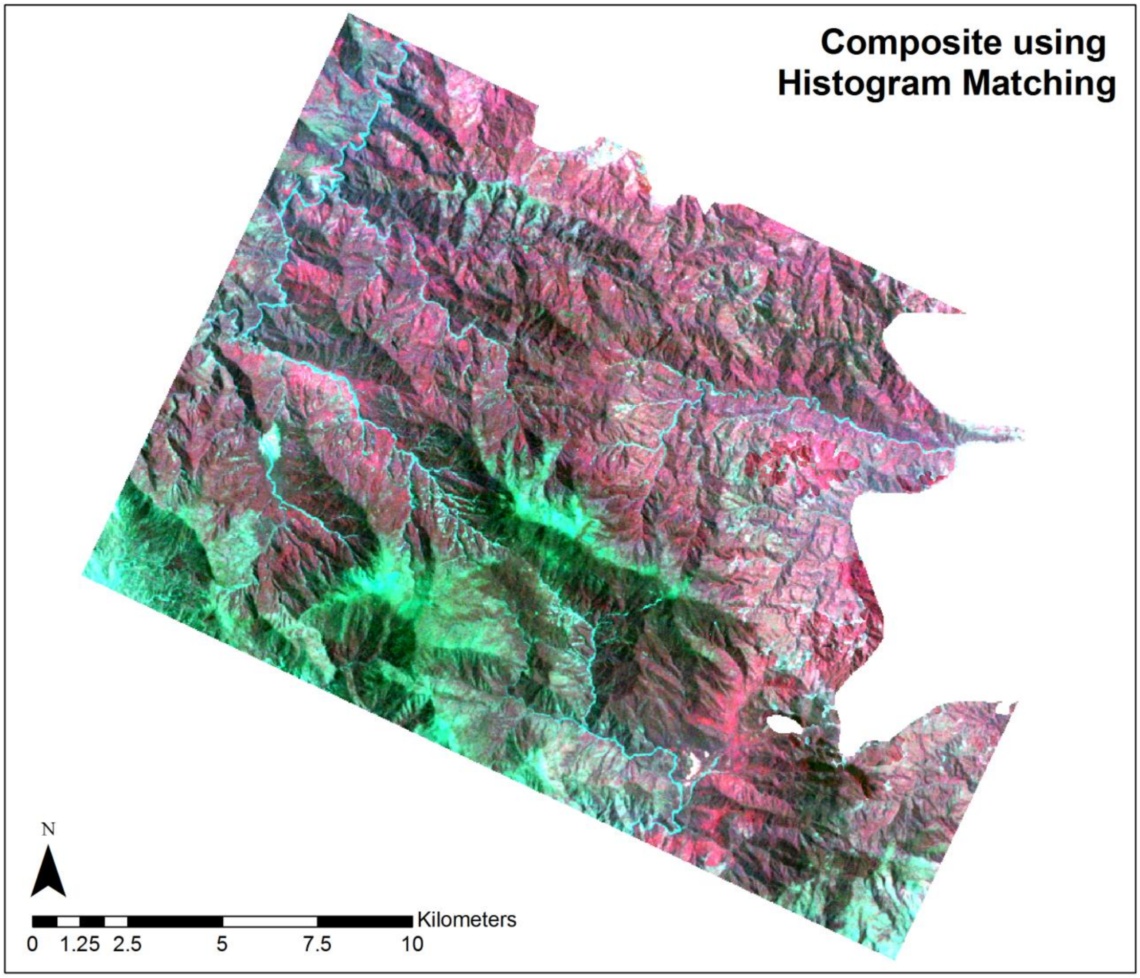

Figure III-5: CIR composite developed by gap-filling 07.19.1999 with 06.01.1999 and then 05.16.1999 that were corrected to 07.19.1999 using histogram matching.

Appendix IV – Details on Stream Scouring and Landslide Classification

Stream scouring and landslide features were easily interpreted from the CIR OM, providing training and testing data for the Landsat-based classification (Table IV-1).

Table IV-1: Training and testing data points (n) used in the stream scouring and landslide classification.

Class	Scour/Landslide	Vegetation
Training	172	343
Testing	86	172
Total	258	515

The raster predictor variables used in the analysis (Table IV-2) were selected from a spectral bands and indices taken from the post-hurricane composite and change in greenness indices from the change detection analysis. The change in greenness indices highlighted the drastic and long-lasting reductions in vegetative cover associated with stream scouring and landslides.

Table IV-2: Predictor variables used in the stream scouring and landslide classification.

Raster Layer	Notes
Change NDVI	Post-hurricane NDVI minus pre-hurricane NDVI
Change TCG	Post-hurricane TCG minus pre-hurricane TCG
Landsat Band 1	Reflectance from post-hurricane composite
Landsat Band 2	Reflectance from post-hurricane composite
Landsat Band 3	Reflectance from post-hurricane composite
Landsat Band 4	Reflectance from post-hurricane composite
Landsat Band 5	Reflectance from post-hurricane composite
Landsat Band 7	Reflectance from post-hurricane composite
NDVI	Normalized Difference Vegetation Index = (B4 – B3)/(B4 + B3)
NDII	Normalized Difference Infrared Index = (B4 – B5)/(B4 + B5)
TCB	Tasseled Cap Brightness from Crist *et. al* 1986
TCG	Tasseled Cap Greenness from Crist *et. al* 1986
TCW	Tasseled Cap Wetness from Crist *et. al* 1986
PCA 1	Principal components analysis of post-hurricane composite bands 1-5,7
PCA 2	Principal components analysis of post-hurricane composite bands 1-5,7
PCA 3	Principal components analysis of post-hurricane composite bands 1-5,7

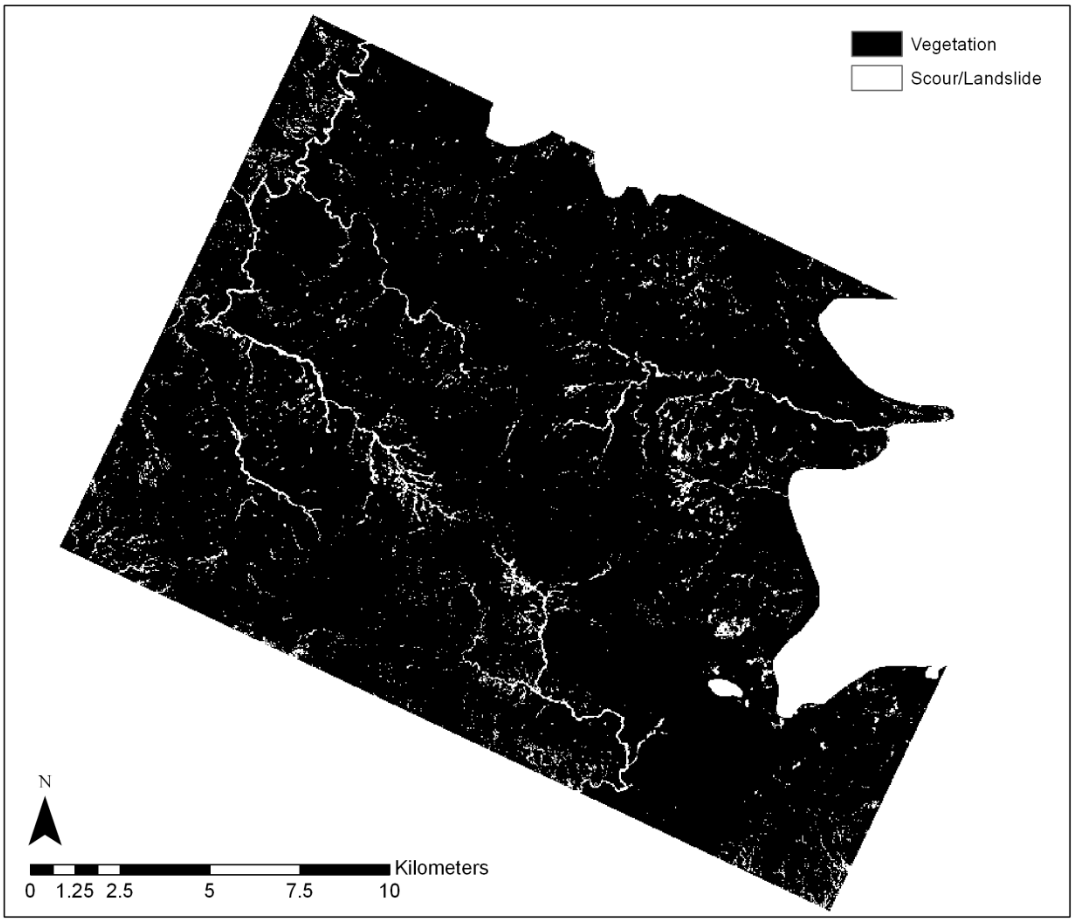

Figure IV-1: Stream scouring and landslide classification.

Table IV-3: Percent of study site area by class.

Class	**Percent of Site**
Vegetation	95.7
Scour/Landslide	4.3

Table IV-4: Confusion matrix of stream scouring and landslide classification.

Predicted

Actual

	Scour/ Landslide	**Vegetation**	**Producer's Accuracy %**
Scour/ Landslide	78	8	**90.7**
Vegetation	4	168	**97.7**
User's Accuracy %	**95.1**	**95.5**	

Appendix V – Collection Protocols and Analysis of Fire Impacted Stands

In pure and mixed pine forest plots which burned in a fire in 2005, cause of death for all dead stems was recorded: dead stems with charred wood (below the bark) were assumed to be dead before the fire; dead stems with charred bark (but not charred wood) were assumed to be killed by the fire. If a dead stem was broken, the type of break was described. Snap refers to a break that is splintered, indicating that the break occurred when the stem was still alive and tissue was sound. Brash failure refers to a break that is blunt, blocky, or smooth, indicating that the break occurred when the stem was dead and tissue was decayed. The cause of death was added as an extra attribute for stems in fire-impacted plots. Most often, multiple indicators, including presence and position of charring, stem position, root exposure, and break type were used to assign the cause of death.

Inventory of understory for these plots was performed the same, except with the addition of a category of cause of death for those stems killed by the fire. Pine germinant (any stem < 0.2m in length) frequency was also collected.

All stems considered to be killed by the fire were treated as live undamaged trees in the analysis.

Appendix VI – Vegetation Indices Used in the Change Detection

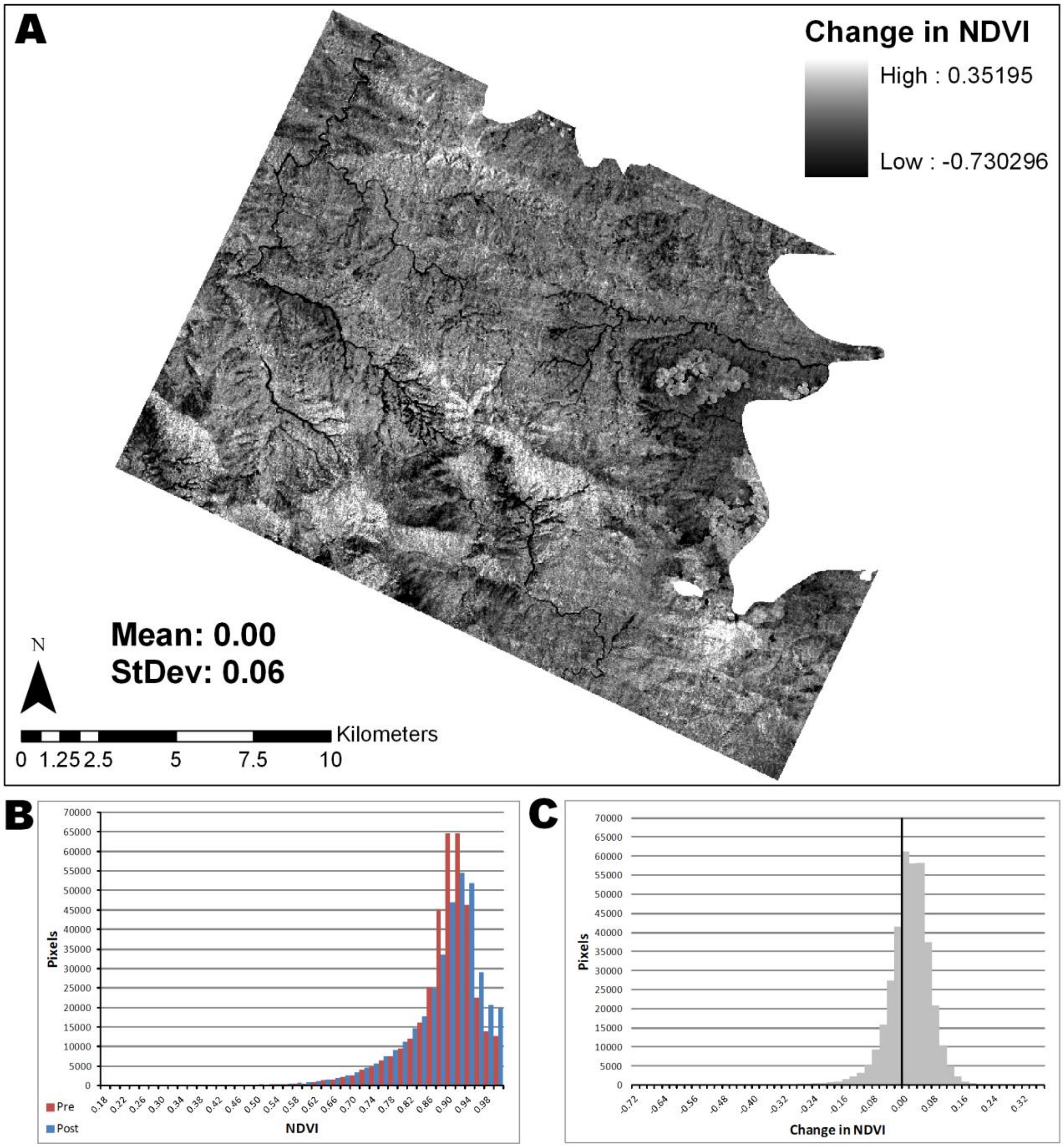

Figure VI-1: Change detection (post – pre) using NDVI reported as a) change image, b) histogram of pre- and post-image values, and c) histogram of change image values.

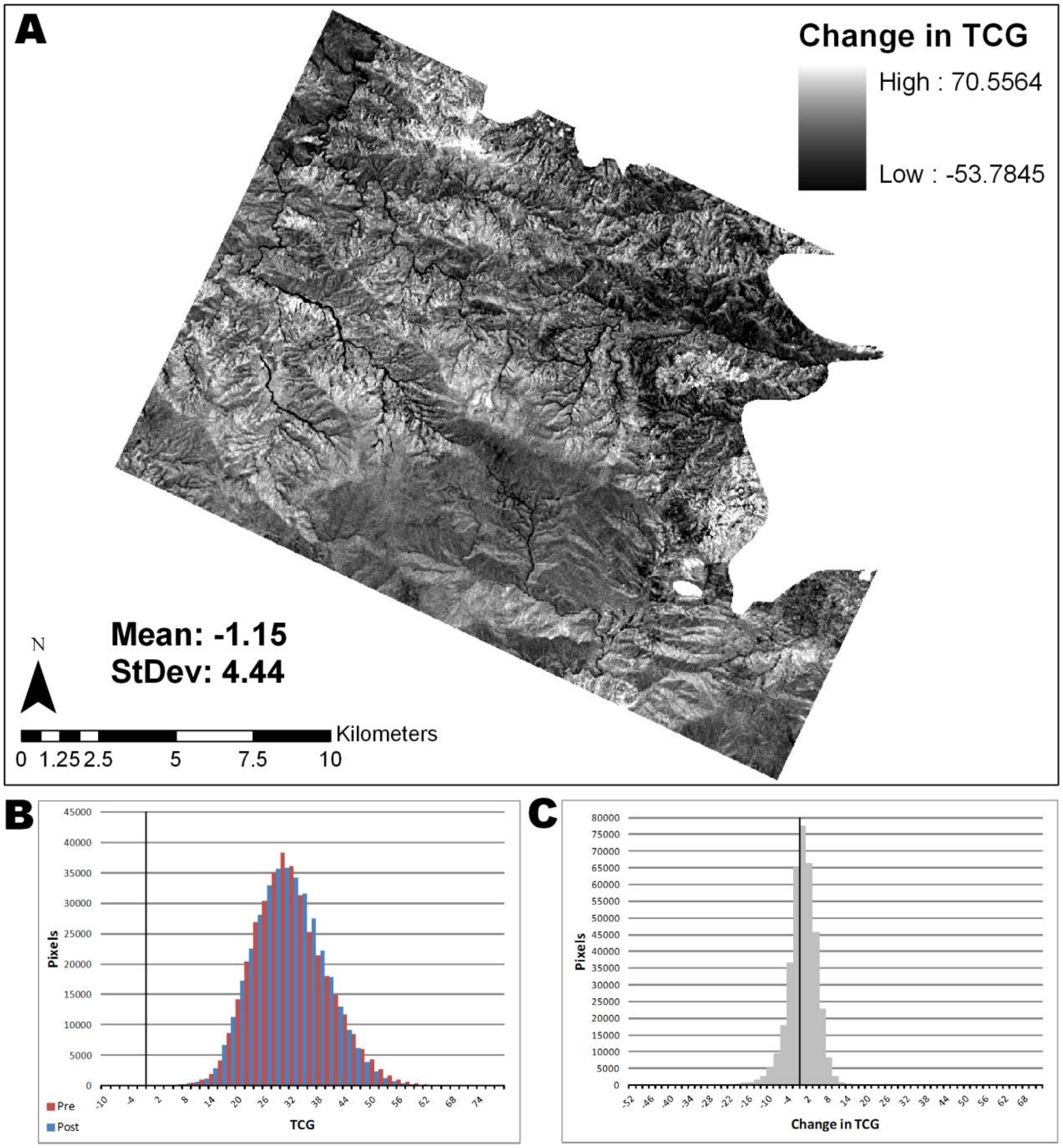

Figure VI-2: Change detection (post – pre) using TCG reported as a) change image, b) histogram of pre- and post-image values, and c) histogram of change image values.

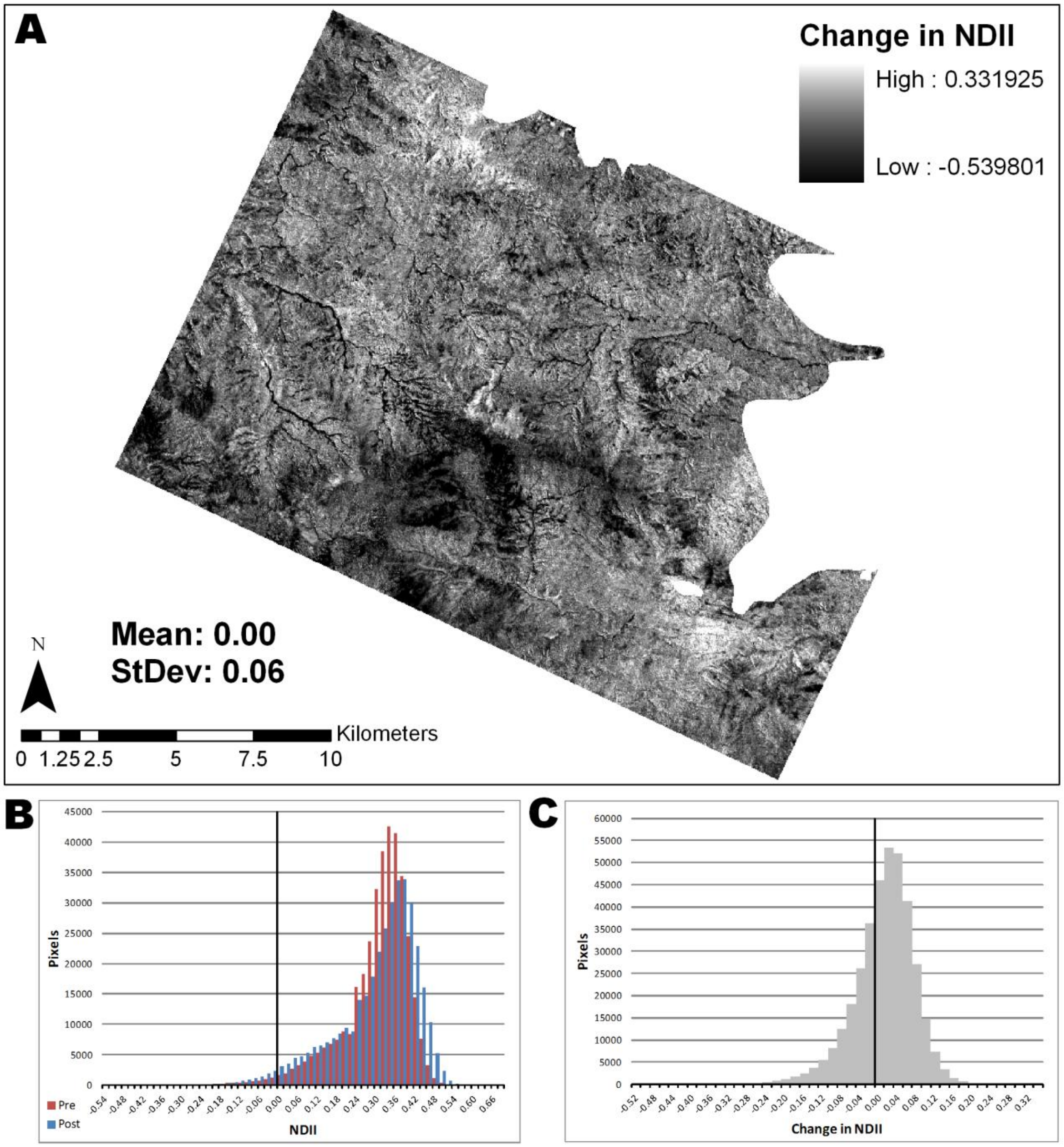

Figure VI-3: Change detection (post – pre) using NDII reported as a) change image, b) histogram of pre- and post-image values, and c) histogram of change image values.

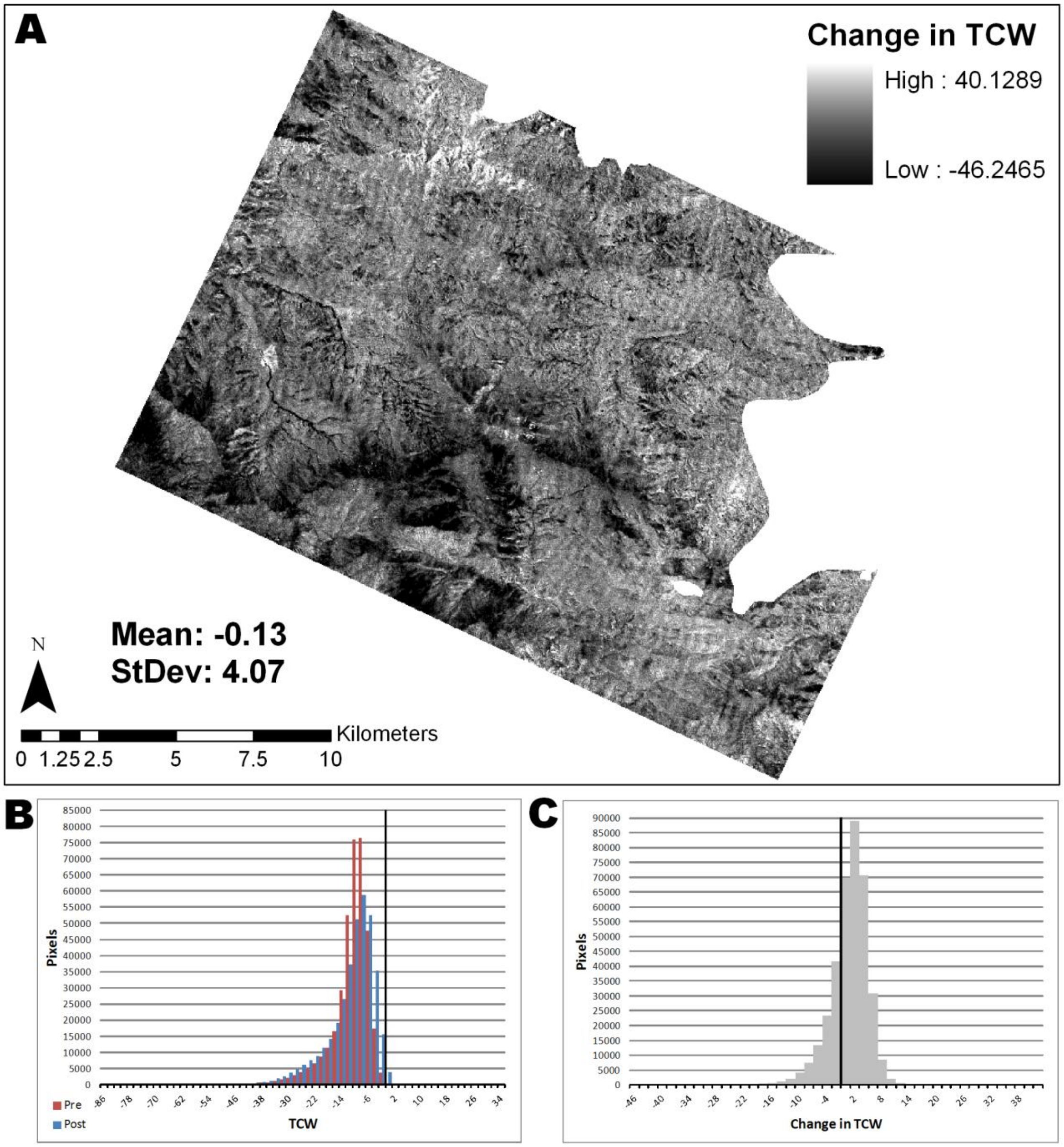

Figure VI-4: Change detection (post – pre) using TCW reported as a) change image, b) histogram of pre- and post-image values, and c) histogram of change image values.

Appendix VII – Initial Classification of Change Detection Results

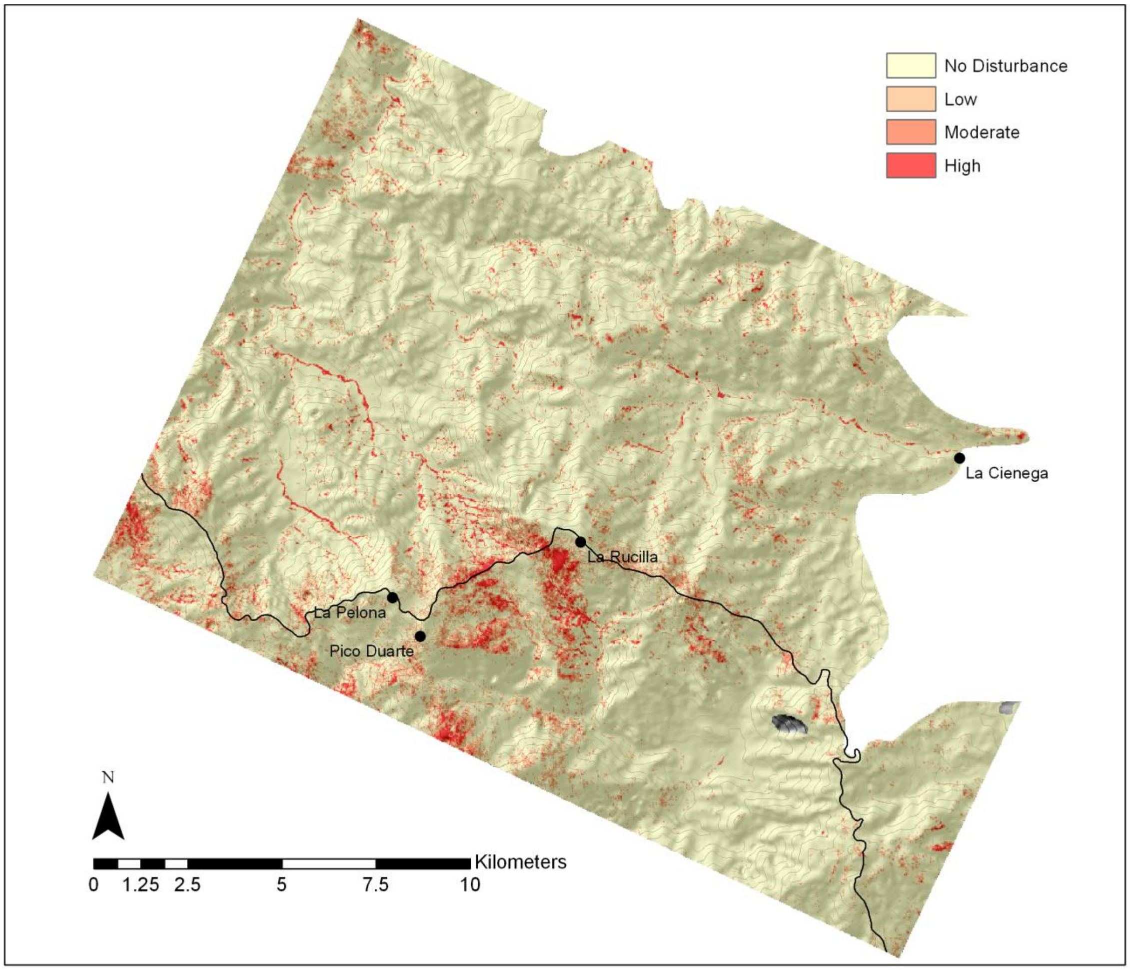

Figure VII-1: Classified NDII change detection results.

Table VII-1: Percent of study site area by damage class.

Disturbance Class	**Percent of Study Site**
Undisturbed	86.1
Disturbed	13.9
Low severity	10.0
Moderate severity	2.8
High severity	1.1