©2014

Irene Zager

ALL RIGHTS RESERVED

ANALYZING THE RELATIONSHIP BETWEEN FOREST FRAGMENTATION AND POST-HURRICANE DAMAGE AND RECOVERY: THE CASE OF HURRICANE DEAN IN THE CALAKMUL-SIAN KA'AN BIOLOGICAL CORRIDOR, YUCATÁN, MEXICO

by

IRENE ZAGER

A dissertation submitted to the

Graduate School-New Brunswick

Rutgers, The State University of New Jersey

In partial fulfillment of the requirements

For the degree of

Doctor of Philosophy

Graduate Program in Geography

Written under the direction of

Laura. C. Schneider

And approved by

_____

_____

_____

_____

New Brunswick, New Jersey

OCTOBER, 2014

ABSTRACT OF THE DISSERTATION

Analyzing the relationship between forest fragmentation
and post-hurricane damage and recovery: The case of Hurricane Dean
in the Calakmul – Sian Ka'an biological corridor, Yucatán, Mexico

By IRENE ZAGER

Dissertation Director:

Laura C. Schneider

Tropical forests are subject to disturbance regimes that occur across a range of temporal and spatial scales, and that are important drivers of land change. Understanding the effect of anthropogenic and natural disturbances, as well as their synergies, on forest change dynamics is essential for informing policy and management programs that seek to achieve sustainability and reduce human and ecological vulnerability. This is particularly true in the face of increasing pressures from growing populations, accelerated rates of deforestation and forest degradation, and global environmental change.

The impact of hurricane Dean on the forests of the Yucatán peninsula, Mexico, in August 2007 provided a unique opportunity to address some relevant questions on this topic. The Yucatán forests play a critical ecological and social role in Mexico and Mesoamerica, and amount for the largest expanse of mature forest left in the region.

However, they are in a continuous process of change due to a long history of anthropogenic and natural disturbances, including the periodic impact of hurricanes, which has raised concerns about their persistence and their ability to provide goods and ecosystem services in the future.

Given these concerns, this dissertation aims to advance our understanding of ongoing changes to the spatial configuration of the tropical forests of the Calakmul – Sian Ka'an biological corridor located in the southern Yucatán peninsula, and the relationship between human-driven forest fragmentation and forest vulnerability and resilience to the impact of hurricane Dean at different spatial (from the regional to the forest stand) and temporal (immediate to 5 years) scales. Embedded within the Land Change Science research agenda, a combination of temporal analysis of remotely sensed data, available land cover products and socio economic data, as well as field sampling of forest stands, were used to address this broad research question.

Acknowledgements

I would like to thank my advisor, Laura Schneider, who has guided, encouraged and supported me through the long process of completing the PhD program. Thank you for not giving up on me!

To my wonderful committee members: John Rogan, Tom Rudel and Tania Lopez-Marrero, I am very thankful for your encouragement and guidance through this process, and for the time you took to help me improve this research. I would also like to thank David Robinson and Ming Xu, who provided valuable comments during the development of the research proposal.

I am also very grateful to Zachary Christman, who provided support, encouragement and suggestions in the field as well as during the development of the proposal and initial analysis of the remotely sensed data.

Doing field research is always challenging, but even more so when it is conducted in a country that is not your own. Therefore, I would like to give a heartfelt "¡Gracias!" to El Colegio de la Frontera Sur (ECOSUR) for receiving me and being my "home" during fieldwork, and to its students and researchers, who helped and guided me through the innumerable acronyms that characterize Mexico's institutions, the local costumes, and more importantly, who made my life in Mexico so pleasant. Special thanks to my friends: Crisol Méndez, Birgit Schmook, René Foster, Karla Infante and Nancy Mercado. And to all who braved the mosquitoes and tábanos to help me complete the fieldwork, for their invaluable help: Alejandro Aragón, Colleen Earp, Karen Vandecar, Ángel Gómez, José

Ortiz, Crisol Méndez, María Manzón, Cornelio Poot, John Rogan, Juan Pablo Ramírez, Mazen Labban, and the ejidatarios of Quintana Roo and Campeche.

I was very fortunate to receive financial support for the entire extend of my studies, and I would like to thank the persons and institutions that made this possible: to Laura Schenider and the Gordon and Betty Moore Foundation (Grant #1697), for funding the first four years of my studies, as well as field work expenses, and to the Geography Department of Rutgers University, for providing me with TA funding for the last two years. I also want to acknowledge the support of the Center for Latin American Studies at Rutgers University, through the 2012 CLAS Travel Fund that allowed me to conduct additional field research.

I express my sincerest gratitude to the staff of the Geography Department, present and past: Mike Siegel, Kelly Bernstein, Johnny Nunez, Theresa Kirby, Michelle Martel, Cleo Bartos, and Betty Ann Abbatemarco, for their help to navigate the Rutgers' administrative and work challenges, the many enjoyable luncheons, and their constant friendship and encouragement. I will miss you all very much!

As an international student, my Rutgers friends became my family, and provided me with constant friendship, encouragement and support, without which it would have been rather impossible to make it through the last few years. There are so many of you that have made a huge impact during my time in the U.S. and in my life, but I want to give special thanks to: Colleen (the best sidekick and cheerleader ever!), Abidah and Debby (who have gone above and beyond the call of duty many times over these past years), Kalpana (for her continuous encouragement and always being there to listen), Za, Ali,

Diya, Jen, Aude, Vitor and Purba. I look forward to meeting again in distant locations of the world!

I am equally grateful to my dear friends, Beatriz, Tina, Rosa and Gaby, who managed to be there for me despite the distance. I am extremely fortunate to have you in my life.

Last but not least, I want to thank my family, who has always been there for me, with their love and encouragement: Mom, Dad, Ingrid, Alberto, Carlos, you helped me get here and carried me through the most difficult times, and I cannot wait to be in the same country as you again!

Dedication

This dissertation is dedicated to:

my grandparents, who left before I could return

&

to my parents, Gisela and Anton

Table of contents

Dissertation Abstract ..... **ii**

Acknowledgements ..... **iv**

Dedication ..... **vii**

Table of contents ..... **viii**

List of tables ..... **xiii**

List of illustrations ..... **xvi**

Chapter 1: Introduction **1**

1.1: The land change science approach **3**

1.2: Forest fragmentation **4**

1.2.1: Edge effects 7

1.2.2: Trends of forest fragmentation in the tropics 8

1.3: Synergies of forest fragmentation and hurricane disturbances in the Calakmul - Sian Ka'an corridor, Yucatán peninsula, México **10**

1.3.1: The Mesoamerican Biological Corridor 11

1.3.2: Hurricane disturbances in the Yucatán peninsula 12

1.4: Research goals and objectives **17**

1.5: Study area **19**

1.6: Dissertation overview **22**

Chapter 2: Measuring forest fragmentation in the Calakmul - Sian Ka'an corridor and its effects on forest damage caused by Hurricane Dean (2007) 26

2.1: Introduction 26

2.1.1: Forest loss and fragmentation in the southern Yucatán peninsula 27

2.1.2: Hurricanes in the Mexican Yucatán 28

2.1.3: Relation between forest fragmentation and wind disturbances 29

2.1.4: Research objectives 32

2.2: Methods 33

2.2.1: Data used 33

2.2.2: Forest loss and fragmentation in the corridor from 1976 to 2010 41

2.2.3: Measuring the relation between forest fragmentation and land use 47

2.2.4: Relation between forest fragmentation and hurricane damage 47

2.3: Results 48

2.3.1: Forest loss and fragmentation in the corridor from 1976 to 2010 48

2.3.2: Measuring the relation between forest fragmentation and land use 54

2.3.3: Relation between forest fragmentation and hurricane damage 54

2.4: Discussion 56

2.4.1: Significant forest loss and fragmentation 56

2.4.2: Relation between hurricane damage and forest fragmentation 60

2.5: Conclusion 62

Chapter 3: Measuring forest fragmentation at the stand level and its effect on forest damage caused by hurricane Dean within the Calakmul – Sian Ka'an corridor 64

3.1: Introduction 64

3.1.1: Catastrophic wind disturbances and forest damage 66

3.1.2: Factors that influence forest susceptibility to wind disturbances 66

3.1.3: Research objectives 69

3.2: Data and Methods 69

3.2.1: Field data collection of hurricane damage 70

3.2.2: Characterizing forest damage at the stand level 74

3.2.3: Characterizing forest fragmentation at the stand level 76

3.3: Results 82

3.3.1: Characterization of field plots 82

3.3.2: Forest fragmentation and hurricane damage at the stand level 85

3.3.3: Characterizing forest damage at the stand level 86

3.3.4: Characterizing forest fragmentation at the stand level 95

3.3.5: Forest fragmentation and hurricane damage at the stand level 101

3.4: Discussion 106

3.4.1: Forest damage at the stand level 107

3.4.2: Characterizing forest fragmentation at the stand level 111

3.4.3: Forest fragmentation and hurricane damage at the stand level 113

3.4.4: Added human impacts and conclusions 115

Chapter 4: Structural forest recovery after hurricane Dean's impact within the Calakmul – Sian Ka'an corridor 117

4.1: Introduction 117

4.1.1: Paths to forest recovery after catastrophic wind disturbances 118

4.1.2: Metrics of forest recovery 121

4.1.3: Does forest fragmentation affect forest recovery? 122

4.1.4: Research objectives 124

4.2: Data and Methods 125

4.2.1: Field assessment of forest recovery 125

4.2.2: Characterizing forest recovery at the stand level 128

4.2.3: Forest fragmentation and recovery at the stand level 128

4.3: Results 129

4.3.1: Overall patterns of forest recovery 129

4.3.2: Characterizing forest recovery at the stand level 140

4.3.3. Forest fragmentation and forest recovery at the stand level 143

4.4: Discussion 146

4.4.1: Overall patterns of forest recovery 146

4.4.2: Forest recovery at the stand level 151

4.4.3. Forest fragmentation and forest recovery at the stand level 152

4.4.4. Conclusion 154

Chapter 5: Conclusions 156

5.1: Disturbances and forest sustainability: a general overview 156

5.2: A Land Change Science approach to assess the effects of hurricanes on forests 159

5.3: Lessons learned: Forest damage and recovery after a hurricane impact within the Cakalmul – Sian Ka'an biological corridor 163

5.4: Further implications for the future of the forests of Southern Yucatán 167

Appendix A.1: Frequency of the most common species recorded in the 28 plots (2009-2012)..... 170

Appendix A.2: Frequency of the most common plant families recorded in the 28 plots (2009-2012). 171

Appendix A.3: Characterization of forest type, age, total number of stems and species found in the field plots in 2009 172

Appendix A.4: Number of stems, mean DBH and basal area per fiel plot in 2009. 174

Appendix A.5: Number of stems, mean DBH and basal area per monitoring plot in 2012..... 176

Bibliography 178

List of tables

Table 1.1: The Saffir-Simpson hurricane intensity scale (Sims and Vogelmann 2002; NOAA 2012)..... 14

Table 2.1: Land cover hierarchical classification used for the 1976 and 2000 land cover maps, and equivalency used for the binary forest/non forest map (NF: reclassified as Non Forest; F: reclassified as Forest). 36

Table 2.1: (Cont.)..... 37

Table 2.2: Land cover classification used for the 2010 land cover map, and equivalency used for the binary forest/non forest map (NF: reclassified as Non Forest; F: reclassified as Forest). The land cover equivalencies from the 1976 and 2000 hierarchical classification system were included for comparison (see Table 2.1)..... 38

Table 2.3: Change in forest extent and fragmentation indicators within the Calakmul – Sian Ka'an biological corridor from 1976 to 2010. 49

Table 2.4: ANOVA results of the fragmentation indicators in 2010 by land use type at the *ejido* level (Agricultural, N=34; Forestry, N=12). 54

Table 2.5: Pairwise correlations of the fragmentation indicators and the average hurricane damage for the *ejidos* of the study area. 55

Table 3.1: Description of the damage categories and their assigned coefficients for the calculation of the Damage Indices. 76

Table 3.2: Land cover classification used for the pre-hurricane 2007 land cover map, and equivalency used for the binary forest/non forest map (NF: reclassified as Non Forest; F: reclassified as Forest)..... 80

Table 3.3: List of SPOT images used for the accuracy assessment of the 2007 forest/non-forest map..... 81

Table 3.4: Characterization of the 91 plots by forest type, number of stems, DBH and basal area in 2008. The number of plots of each type is indicated in parentheses. 83

Table 3.5: Characterization of the28 plots by forest type, number of stems, DBH and basal area in 2009. The number of plots of each type is indicated in parentheses. 84

Table 3.6: Average percent of stems and basal area (BA) affected by a certain damage category in each field plot (corresponding to the maximum damage recorded per stem). For the 2012 column, only stems that were tagged in 2009 were included. For 2008 *N*= 6,312; for 2009 and 2012 *N*=2938. 86

Table 3.7: Number of stems that died between 2009 and 2012 by hurricane damage class. Percentages in relation to the total number of stems recorded within a given damage class are shown in parentheses. 92

Table 3.8: Survival and mortality rates by damage category and overall for the period 2007-2012. 93

Table 3.9: Average values of the MAX Damage Index per plot in 2008, by forest type and age. 94

Table 3.10: Mean, maximum and minimum values of the pre-hurricane fragmentation indicators at the stand level for the 91 field plots from 2008, by buffer size. 99

Table 3.11: Pairwise correlations of hurricane damage measured by MAX Index and fragmentation indicators by buffer area for the 91 plots (Pearson correlation coefficients with Bonferroni-correction, significant p = 0.05). 102

Table 3.12: Pairwise correlations of the MAX Damage Index and fragmentation indicators by buffer area and wind speed zone for the 91 plots (Pearson correlation coefficients with Bonferroni-correction, significant p = 0.05). 104

Table 3.13: Pairwise correlations of the MAX Damage Indices and fragmentation indicators by buffer area for the 20 damage plots located within wind speed zone 4 (Spearman's rank correlation coefficients with Bonferroni-correction, significant p = 0.05). 106

Table 4.1: Description of the recovery categories used in the field assessments. 125

Table 4.2: Importance values and ranks (in parentheses) for the 15 most important species recorded within 26 plots in 2009 and 2012. Species are in descending IV rank for 2009..... 133

Table 4.3: Percent of stems by resprouting category for all live stems recorded in the field plots one, two and five years after the impact of hurricane Dean (in 2008, 2009 and 2012, respectively). Individual stems might experience more than one type of resprouting. Therefore, adding up the percentages across recovery categories could lead to a value greater than 100%..... 134

Table 4.4: Average percent of live stems per plot with each type of resprouting one, two and five years after the impact of hurricane Dean (in 2008, 2009 and 2012, respectively). For 2008 *N*= 6,055; for 2009 *N*=2,678; for 2012 *N*=2,268..... 140

Table 4.5: Average percent of live stems per plot with each type of resprouting by forest type one, two and five years after the impact of hurricane Dean (in 2008, 2009 and 2012, respectively). The number of plots in each sample in indicated in parenthesis..... 142

Table 4.6: Average percent of live stems per plot with each type of resprouting by forest age one, two and five years after the impact of hurricane Dean (in 2008, 2009 and 2012, respectively). The number of plots in each sample in indicated in parenthesis..... 142

Table 4.7: Pairwise correlations between the proportion of stems with crown recovery (RC) in 2008 and fragmentation indicators by buffer area and forest type for 91 field plots..... 144

Table 4.8: Pairwise correlations between the proportion of stems with crown recovery (RC) in 2008 and fragmentation indicators by buffer area and forest type for 91 field plots..... 145

Table 4.9: Pairwise correlations between the proportion of stems with crown recovery (RC) in 2009 and fragmentation indicators by buffer area and forest type for 28 field plots. (Spearman's rank correlation coefficients with Bonferroni-correction, significant $p = 0.05$)..... 145

Table 4.10: Pairwise correlations between the proportion of stems with crown recovery (RC) in 2009 and fragmentation indicators by buffer area and forest age for 28 field plots. (Spearman's rank correlation coefficients with Bonferroni-correction, significant $p=0.05$). ……145

List of illustrations

Figure 1.1: Tracks of Atlantic Hurricanes making landfall in the Yucatán peninsula between 1851 and 2008 (figure by E. Rossi) 13

Figure 1.2: MODIS-aqua satellite image (250 m resolution) of hurricane Dean as it moved across the Yucatán peninsula on August 21st 2007 (Source: NASA's Earth Observing System Data and Information System, https://earthdata.nasa.gov/). 16

Figure 1.3: Calakmul – Sian Ka'an biological corridor study area in the Yucatán peninsula, México, showing the north-western path followed by hurricane Dean (August 2007). 20

Figure 1.4: Wind speed zones across the Calakmul – Sian Ka'an biological corridor study area, based on hurricane Dean's reported wind speeds. Polygons outlined in black correspond to *ejidos*. Stripped polygons correspond to the biosphere reserves. 22

Figure 2.1: Hurricane damage map for the Calakmul-Sian Ka'an corridor based on MODIS EVI data (Rogan et al. 2011). 39

Figure 2.2: *Ejidos* within the Calakmul – Sian Ka'an biological corridor for which additional land use and management information was available. 40

Figure 2.3: Thematic classes of forest fragmentation resulting from MSPA (Vogt 2010) 44

Figure 2.4: Forest losses and gains within the Calakmul – Sian Ka'an corridor from 1976 to 2010. 50

Figure 2.5: Forest fragmentation in the Calakmul – Sian Ka'an biological corridor between 1976 and 2010. 51

Figure 2.6: Area of core forest lost (in km^2) between 1976 and 2010. 52

Figure 2.7: Proportion of core forest (grey) and proportion of fragmented forest (black) per *ejido* for 1976, 2000 and 2010. 53

Figure 3.1: Location of the 2008 and 2009-2012 field plots across the study region. 71

Figure 3.2: Coverage of Landsat-7 ETM+ satellite images used for mapping pre-hurricane 2007 land cover in the region. West (blue): Path 20, Row 47; East (red): Path 19, Row 47. 77

Figure 3.3: Landsat 7 ETM+ satellite images used to map the pre-hurricane 2007 land cover of the eastern portion of the study region. To reduce missing data due to cloud coverage, two different corrected images were created by using each of the satellite images as the main data (wide arrow) and the other as the filler data (thin arrow). The

area of the masks used for wind speed zone 5 (blue) and wind speed zone 4 (red) is indicated. 78

Figure 3.4: Landsat 7 ETM+ satellite images used to map the pre-hurricane 2007 land cover of the western portion of the study region, and the resulting merged image created by filling the scan line errors of the image from February 27 2007 with data from the image from 07 January 2006. The area of the mask used for wind speed zone 3 (yellow) is indicated. 79

Figure 3.5: Plots of proportion of stems affected by damage (x-axis) versus proportion of biomass within a plot affected by the same type of damage (y-axis) for the damage field plots assessed in 2008. Each point represents one 0.05 ha plot (*N*=91) (modified from McGroddy et al 2013 to include palms). Asterisks indicate slopes significantly different from 1 ($\alpha = 0.05$). 90

Figure 3.6: Plots of proportion of stems affected by damage (x-axis) versus proportion of biomass within a plot affected by the same type pf damage (y-axis) for the monitoring field plots assessed in 2009. Each point represents one 0.05 ha plot (N=28). Asterisks indicate slopes significantly different from 1 ($\alpha = 0.05$). 91

Figure 3.7: Estimated BA Damage Index for each of the 91 plots in 2008 and the 28 plots in 2009 based on damage recorded in the field. 94

Figure 3.8: Pre-hurricane land cover and land use map for 2007, based on the interpretation of Landsat ETM+ data. 96

Figure 3.9: Pre-hurricane forest/non forest map for 2007, showing the location of the 150 validation points used for the accuracy assessment. 97

Figure 3.10: Representation of the size of buffer zones used to characterize forest fragmentation at the stand level (i.e., around the field damage plots). In each row, from left to right: False color composite of the Landsat ETM+ images (RGB:453), 2007 LC map and 2007 reclassified MSPA map. Plot ID is indicated on the top left of each set of images. Forest fragmentation indicators increase from top to bottom. 98

Figure 3.11: Pre-hurricane (2007) forest fragmentation within the Calakmul – Sian Ka'an biological corridor. 99

Figure 3.12: Change in the *edge/core* indicator with increasing buffer size for 41 field plots located within wind speed zone 4. Each line corresponds to a different field plot. 102

Figure 3.13: Scatter plot of the MAX Damage Index and three fragmentation indicators for the 2 km (top) and the 4 km (bottom) Buffer zones. 105

Figure 4.1: Total number of live stems (left) and basal area (right) between 2009 and 2012 in 26 field plots. "Pre-Dean" data corresponds to the estimated pre-hurricane conditions, based on the 2009 data. 130

Figure 4.2: Total number of live stems (top) and basal area (bottom) by DBH class from 2008 through 2012 in 26 field plots. "Pre-Dean*" data corresponds to the estimated pre-hurricane conditions based on field data from 2009. 132

Figure 4.3: Percent of stems within each resprouting category (RO: no resprouting apparent, RB: basal resprouting, RT: resprouting on the main trunk, RC: crown recovery) by DBH class for all live stems in the field plots from 2008, 2009 and 2012. 135

Figure 4.4: Percent of stems with resprouts in 2008, 2009 and 2012 for 9 of the most common species recorded in the field plots. 136

Figure 4.5: Percent of stems with resprouts for 26 of the less common species recorded in the field plots. Species are ordered by their frequency in 2009. Only species with at least five stems per year are included. 138

Figure 4.6: Percent of stems within each resprouting category (RO: no resprouting apparent, RB: basal resprouting, RT: resprouting on the main trunk, RC: crown recovery) by damage category. The 2012 recovery data is based on the damage recorded in 2009. For 2008 *N*=6,055; for 2009 *N*=2,672; for 2012 *N*=2,264. 139

Figure 4.7: Proportion of stems with crown recovery (RC) within 26 field plots in 2009 and 2012. 140

Chapter 1: Introduction

Ensuring the sustainability of Earth's ecosystems, i.e. reconciling over the long term societal development goals with the planet's limits, has become one of the biggest challenges currently faced by human societies (Clark and Dickson 2003), particularly in the face of increasing pressures from growing populations and global environmental change (Turner et al. 2007; Turner 2010a). Nonetheless, the concept of sustainability has proven to be problematic. There exist many discrepancies in terms of individual and institutional perceptions of what, where and how are ecosystems to be sustained, as well as by/for whom and for how long (e.g. Amaranthus 1997). Despite these difficulties, sustainability science has emerged in recent years as a flourishing interdisciplinary effort that embraces local and global perspectives (Clark and Dickinson 2003) in the search of understanding the coupled human-environment system in ways that can be used by the different communities of stakeholders (Turner et al. 2003). The path to sustainability first requires understanding the changes that are taking place in the world's ecosystems, their drivers, as well as the complex interactions that affect a community's or ecosystem's vulnerability (i.e. the propensity to suffer damage) and resilience (i.e. the ability to recover after a disturbance).

Particular attention is being paid to the sustainability of tropical forests (FAO 2012). It has been estimated that at least two-thirds of all terrestrial species of plants and vertebrates may be endemic to tropical forests, many of them being concentrated within a few "biodiversity hotspots", which have become the target of significant conservation efforts (Myers et al. 2000; Mittermeier et al. 2004). Furthermore, tropical forests provide

essential local, regional and global benefits to human populations through the provision of economic goods and ecosystem services (Gardner et al. 2009). These services include carbon sequestration, erosion control, regulation of water quality and flow, and biodiversity conservation (Chazdon 2003). A large proportion of the world's population also depends directly or indirectly on forest goods for their subsistence needs. For example, in Mexico, the approximately 64.2 million hectares of temperate and tropical forests which cover more than 33% of the country's land surface, provide essential environmental services and subsistence resources for the estimated 12 million people that live in or around them (Klooster 2003). This population is in large part composed of indigenous and mestizo peasants (Taylor and Zabin 2000), who obtain from forests firewood, construction materials, medicinal plants, and food, as well as timber and non-timber products that can be commercialized for cash income (Cabarle et al. 1997). However, it is widely recognized that tropical forests are currently threatened worldwide as a result of accelerated deforestation and degradation rates (FAO 2012), which often are associated to the subdivision or "fragmentation" of these ecosystems (Rudel and Poper 1997; Wade et al. 2003). Nonetheless, there are still significant uncertainties pertaining the specific rates and spatial patterns of change taking place (Achard et al. 2002; DeFries et al. 2002; Ramankutty et al. 2006).

Anthropogenic impacts are not the only threats currently faced by tropical forests worldwide. Natural disturbances such as wind storms, fires and drought, also have a significant role in shaping the structure and composition of these ecosystems. Furthermore, there is mounting evidence that human and natural disturbances act in synergy, with their combined effects resulting in accelerated or more intense rates of

species declines and loss of forest functions (Laurance et al. 2006; Brook et al. 2008). That is, the interactions of these processes result in greater effects than would be expected from the sum of the individual effects alone (Brook et al. 2008). Understanding the synergies between land use and land cover change and the occurrence and impact of natural disturbances has been recognized as a pressing research need (Foster et al. 1999; Chazdon 2003; Uriarte et al. 2004; Alcántara-Ayala and Dykes 2010).

In contribution to this need for further research, this dissertation aims to advance our understanding of ongoing changes to the spatial configuration of the tropical forests of the Calakmul – Sian Ka'an biological corridor of the Yucatán peninsula, Mexico, and the relationship between human-driven forest fragmentation and forest vulnerability and resilience to large scale wind disturbances (i.e., hurricanes).

1.1: The land change science approach

The human, environmental and geographic information-remote sensing research communities that have undertaken the challenges posed by global environmental change and sustainability have found a meeting point within the broader boundaries of land change (or land system) science. Broadly speaking, the agenda of land change science seeks to improve: 1) the observation and monitoring of land use and land cover changes taking place around the world, 2) understanding these changes as part of a coupled human-environment system, 3) modelling of land changes in a spatially explicit way, and 4) assessing the outcomes of land change, including vulnerability, resilience and sustainability (Turner et al. 2007).

This dissertation is embedded within the land change science research agenda, broadly drawing from the methods and theories of the geographic, ecological and landscape ecology traditions to better characterize patterns of forest change and possible interactions between the forests' spatial configuration and their responses to a hurricane disturbance, at different spatial scales. In doing so, I aim to provide one more piece to the puzzle of the complex interactions of the human-environment system of the tropical forests of the Yucatán peninsula.

The sections bellow will provide some of the necessary background on the topics of forest fragmentation, hurricane disturbances and the Calakmul – Sian Ka'an biological corridor, to ground the research questions and the rest of the dissertation chapters.

1.2: Forest fragmentation

"Forest fragmentation" usually refers to the process of both forest cover loss and subdivision into smaller fragments, which become isolated from each other by a matrix of a different land cover. According to this definition, a forested landscape can be categorized either as continuous (i.e., containing continuous forest) or fragmented, where forest remnants of different size and shape are dispersed within a non-forest matrix (Fahrig 2003). Under this framework, forest fragmentation is a process that results in both a decrease in extent and a change in the spatial configuration of the forest (Lindenmayer and Fischer 2007).

Fragmented forest ecosystems are not uncommon in natural systems as a result of the differential biophysical characteristics of the landscape. However, the more dramatic changes in the spatial configuration of forests that have taken place over the last decades

are more closely associated to anthropogenic causes, such as agricultural and urban expansion, and road development (Rudel and Roper 1997; Riitters et al. 2002; Wade et al. 2003). Indeed, tropical forests have become subject to deforestation and fragmentation rates unprecedented in their evolutionary history (Bierregaard et al. 1992; Turner 1996). This has resulted in a global pattern of habitat mosaics, characterized by the presence of semi-natural fragments immersed within a matrix of habitats with different types and levels of disturbance (Wilcove et al. 1986; Matthews et al. 2000; Wade et al. 2003).

Forest fragmentation research has received particular attention over the last decades from disciplines such as landscape ecology and conservation biology (Haila 2002; Fahrig 2003; Fischer and Lindenmayer 2007). The results of these endeavors have highlighted the close linkages between ecological pattern and process (Kupfer and Franklin 2009). Numerous studies have shown that forest fragmentation can have severe impacts on the population dynamics of local biota at finer scales, resulting in changes to species abundance, richness and diversity, changes in mortality, immigration and colonization rates, and altered interspecies interactions (such as predation and competition), among other. These differential effects have been empirically associated to several factors, mainly: to changes of forest area and isolation, habitat availability and quality, properties of the surrounding matrix and edge effects (Turner 1996; Fahrig 2003; Laurance et al. 2006; Kupfer and Franklin 2009).

One of the most dramatic results of forest fragmentation is the local extinction of species (Terborgh 1992; Turner 1996). This collapse of the biota can take place immediately after fragmentation occurs, or it can extend along temporal scales of up to 10^4 years (Wilcox and Murphy 1985; Andrén 1994). Due to the aggregated distribution of

many species, some of them will become locally extinct as a result of fragmentation simply because all of their habitats within the landscape will be destroyed (Bierregaard et al. 1992; Turner 1996). In addition, fragmentation is frequently accompanied by a reduction of habitat heterogeneity, which will negatively impact species that require a large diversity of microhabitats (Wilcove et al. 1986). Furthermore, during and after isolation occurs, human activity usually increases and often involves harvesting of vegetal products, hunting, disturbance of water bodies, and increased intrusion of fire and smoke into the remnant fragments, all of which will impact the local biodiversity (Turner 1996; Turner and Corlett 1996). Finally, the nature of the matrix can play a significant role in allowing species' movements between remnant fragments. When inhospitable for a particular animal species, a matrix can effectively prevent immigration of individuals between the fragments (Wilcove et al. 1986; Turner 1996). This, in turn, can reduce the immigration of plant species when the animals that have become isolated include pollinators and seed dispersers (Turner 1996).

Not all species are negatively affected by forest fragmentation. In some cases, population size might not be affected at all or even increase. This is usually the case for species that can effectively exploit edge habitats or that are dependent of habitat mosaics. Alternatively, fragmentation can promote a "competitive liberation", allowing the growth of populations competitively inferior.

Fragmentation can also significantly affect forest function and their ability to provide valuable ecosystem services (Fahrig 2003; Kupfer and Franklin 2009). Furthermore, forest fragmentation can significantly increase the vulnerability of the ecosystem to the effects of anthropogenic and natural disturbances (including hurricanes), as well as affect

the recovery rates after the disturbance (Fahrig 2003; Catteral et al. 2008; Laurance and Curran 2008).

1.2.1: Edge effects

Edge effects have received particular attention within forest fragmentation research. An "edge" refers to the boundary, or part of the boundary, that separates two adjacent habitats or patches that differ in one or more aspects (Forman 1995; Fagan et al. 2003; Harper et al. 2005). As the process of forest fragmentation progresses, a disproportionate increase in the proportion of edge *vs.* core habitat occurs. In this dissertation, forest edge will be used to refer to a sharp boundary between a forest ecosystem and an adjacent less vegetated, non-forest habitat (Fagan 2003).

"Edge effects" in turn refer to the diverse environmental changes that are associated with these abrupt forest boundaries (Murcia 1995; Laurance et al. 2006). Edge effects have been identified as the most important drivers of ecological change in fragmented forests, at least during the initial decades immediately following fragmentation (Laurance et al. 2006). They include abiotic effects that result in steep microclimatic gradients between the edge and the forest interiors, mostly as a result of increased exposure to sun and wind than the forest interior. As a result, air humidity, soil moisture, temperature, radiation levels and wind speeds along the edge differ from the conditions found in the forest interior (Chen et al. 1993; Murcia 1995). The higher desiccation stress and exposure to wind disturbances have been associated to higher tree mortalities within the first meters of forest edges, particularly for large trees (Laurance et al. 1998; Zeng et al. 2004). This differential mortality along edges in turn reduces forest biomass, and

promotes the creation of forest gaps, increased wood debris and colonization by invasive species (Chen et al. 1993; Laurance et al. 2006).

The microclimatic and structural changes along forest edges in turn have considerable consequences for faunal and floristic species composition and biodiversity patterns in the landscape, as well as their interactions (i.e. predation, competition, herbivory, pollination and dispersal). Species responses to edges can be positive, negative or neutral, and are in many cases site-specific (Jansson 2009). For example, in the case of plants, early successional or exotic species might find the conditions of forest edges more favorable, while the abundance of understory plants has been found to be lower in edges than interiors (Murcia 1995).

1.2.2: Trends of forest fragmentation in the tropics

The quantification and characterization of the trends of forest fragmentation share some of the challenges associated to the characterization of deforestation rates, such as the spatial and temporal limitations of available data (Rudel and Roper 1997), as well as the complexities of accurately mapping forests, particularly at large geographic scales (Wade et al. 2003).

Nonetheless, several efforts have provided some insights into the trends and patterns of tropical forest fragmentation in recent decades around the world. Rudel and Roper (1997) conducted a study to quantify the degree of rain forest fragmentation of 51 nations from Asia, Africa and the Americas, which together contain 83 percent of the world's tropical forests. To achieve this goal, the authors used maps produced by the World Conservation Monitoring Centre (WCMC) in Cambridge, England, most of which were

based on the interpretation of satellite images from the period between 1985 and 1990, although part of the sample corresponded to prior or later years. Fragmentation was quantified as the ratio of the perimeter (i.e., edge) to the total forest area in a country, normalized by the scale of the map. Results suggest that during the time period considered, West Africa and Central America had the most fragmented tropical forests in the world, while the Amazon forest contained the least fragmented. Furthermore, their analysis suggests that deforestation driven by smallholders is most likely to produce highly fragmented forest habitats.

More recently, Riitters et al. (2000) used 1 km resolution land cover maps derived from AVHRR satellite imagery to map and compare global patterns of forest fragmentation in the early 1990s. A novelty of their analysis was the application of a moving "window" of fixed-area that allowed them to characterize different types of forest fragmentation (i.e., interior, perforated, edge, transitional, patch, and undetermined). Their results show that the characterization of fragmentation types was highly dependent on the size of the window used for the analysis. Overall, tropical rain forest fragmentation was found to be most severe in North America and least severe in Europe-Asia. Five additional forest types were found to be highly fragmented in North America and four additional types in Europe-Asia.

Finally, Wade et al. (2003) complemented the previous work of Riitters et al. (2000) to differentiate between natural and anthropogenic forest fragmentation for biomes worldwide. Their results show that over half of the temperate broadleaf and mixed forest biomes and nearly one quarter of the tropical rainforest biome have been lost or fragmented due to anthropogenic impacts. Meanwhile, only 4% of the boreal forest

showed anthropogenic fragmentation. Overall, Europe was the continent displaying the most human-caused fragmentation and South America the least.

Overall, these results suggest that tropical forests in North and Central America, presumably including the forests of the Yucatán peninsula, are indeed undergoing a significant process of forest fragmentation.

1.3: Synergies of forest fragmentation and hurricane disturbances in the Calakmul - Sian Ka'an corridor, Yucatán peninsula, México

Research on forest fragmentation is very relevant for the seasonal tropical forests of the Yucatán peninsula. This is the largest expanse of mature forest remaining in Mexico and one of the largest left in Mesoamerica (Ramírez 2004; Vester et al. 2007). However, with a long history of human and natural disturbances, the Yucatán forests are far from "pristine." For centuries, these forests were extensively cleared and modified by the ancient Mayas, until this civilization's collapse about 1,100 years ago. A long period of forest recovery followed, although probably with significant changes in species abundances (Turner et al. 2001; Vester et al. 2007).

In the mid-20th century, a new period of significant land cover and land use change started in the region as a result of accelerated population growth rates and the decision of the federal government to open the area for timber extraction, specifically mahogany (*Swietenia macrophyla*) and Spanish cedar (*Cedrela odorata*) (Turner et al. 2001; Schneider and Geoghegan 2006). By the end of the 1960s, the completion of highway 186 connected the region to the capitals of the states of Quintana Roo (Chetumal) and Campeche (Campeche) as well as to continental Mexico, and a significant, permanent

occupation by migrant population began, further promoted by a key process of land reform and redistribution. Currently, most of the region corresponds to communally-managed lands known as *ejidos* (Turner et al. 2001). The dominant land uses include agriculture, which is predominantly subsistence, as well as cattle ranching, forestry, ecotourism and conservation, although the presence and extent of these land uses varies across the region (Turner et al. 2001; Roy Chowdhury 2006). As a result of these anthropogenic disturbances, much of the southern Yucatán has undergone a dynamic change pattern of forest cover, structure and composition over the last decades (Turner et al. 2001; Vester et al. 2007).

1.3.1: The Mesoamerican Biological Corridor

Over the last decades, several conservation efforts have been undertaken in the region, such as the establishment of the Sian Ka'an and Calakmul Biosphere Reserves in 1986 and 1989, respectively. These are the two most important reserves in the country, and together with the area that connects them, they constitute one of the four corridors that compose the Mesoamerican Biological Corridor (MBC) in Mexico, a regional conservation program aimed at conserving biological diversity while fostering sustainable development in Central America and southern Mexico (Miller et al. 2001; Ramírez 2004). Specifically, the MBC aims to:

> "a) protect key biodiversity sites; b) connect these sites with corridors managed in such a way as to enable the movement and dispersal of animals and plants; and c) promote forms of social and economic development in and around these areas that conserve biodiversity while being socially equitable and culturally sensitive." (Miller et al. 2001, p.1).

Vegetation within the Calakmul – Sian Ka'an portion of the corridor is characterized by a mosaic of seasonally dry mid-statured and low-statured forests (Vester et al. 2007), which are home to a large portion of Mexico's animal and plant species and are part of one of the world's biodiversity hot spots (Ramamoorthy et al. 1998). Despite the undertaken conservation efforts, land use and land cover changes are still common both within and beyond the borders of the reserves (Vester et al. 2007), and the corridor has been identified as the fastest-disappearing tract of tropical forest in Central America (Lawrence et al. 2004).

1.3.2: Hurricane disturbances in the Yucatán peninsula

Land cover change dynamics in the Yucatán are further complicated by the periodic effects of tropical storms and hurricanes, which can significantly affect local communities, infrastructure, and coastal morphology, as well as result in substantial blow down of forest areas and changes to forest structure and composition (Clifton 1991; Whigham et al. 1991, 2003; Boose et al. 2003; Vandecar et al. 2011; Bonilla-Moheno 2012; McGroddy et al. 2013).

The peninsula extends across one of the main hurricane paths in the world, being regularly impacted by hurricanes originating in the Atlantic Ocean, the Caribbean, or the southern Gulf of Mexico (Clifton 1991; Boose et al. 2003). Over the last 150 years, more than 60 hurricanes have made landfall in the Yucatán, most of them in the northern portion of the peninsula, in the state of Quintana Roo (Boose et al. 2003; Whigham et al. 2003; see Figure 1.1). It is expected that the effects of these natural events on forest dynamics in the region will become even more important in the 21st century, as recent

modeling studies predict an increase in hurricane intensity in the Atlantic basin due to global environmental change (Elsner 2006; Bender et al. 2010), although this prediction is still subject to much debate. Even if hurricane frequency and/or intensity do not increase in the future, it is undeniable that these natural disturbances will continue to periodically impact the region, and are therefore an inevitable threat to the peninsula (Clifton 1991; Boose et al. 2003).

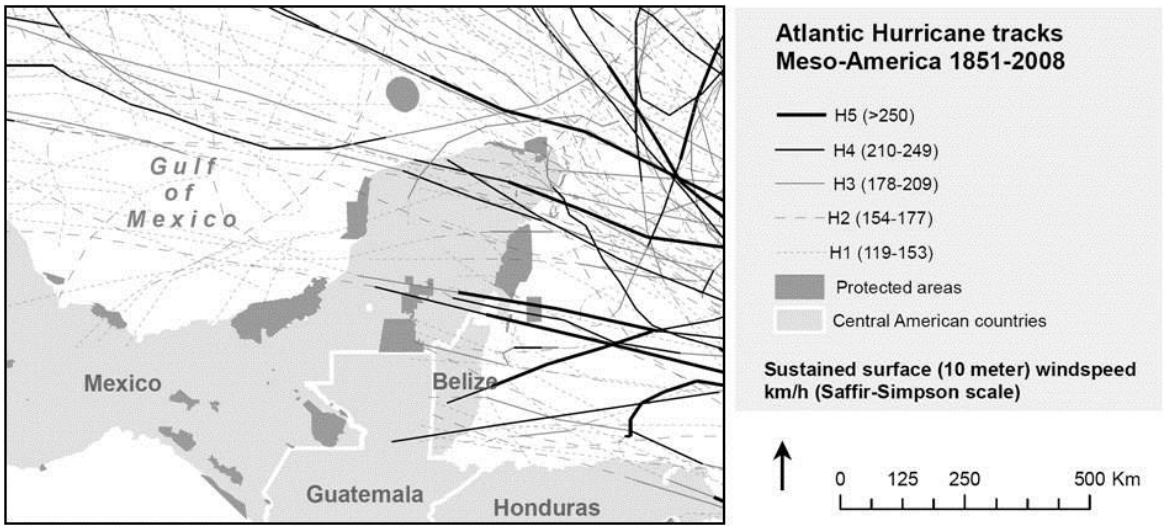

Figure 1.1: Tracks of Atlantic Hurricanes making landfall in the Yucatán peninsula between 1851 and 2008 (figure by E. Rossi)

The Saffir-Simpson hurricane scale rates hurricane intensity on a scale from one to five ratings, and it is used to estimate the potential coastal property damage and flooding expected from a hurricane landfall, with wind speed as the principal factor in the scale (Table 1.1).

Table 1.1: The Saffir-Simpson hurricane intensity scale (Sims and Vogelmann 2002; NOAA 2012)

Hurricane category	Winds (km/h)	Storm Surge	Expected damage
1	119–153	Up to 1.5 m above normal	Low damage due to very dangerous winds. Damage mostly to mobile homes, poorly constructed infrastructure, shrubbery, and trees. Significant damage to power lines and poles. Coastal roads may be flooded.
2	154–177	1.8–2.4 m above normal	Extensive damage due to extremely dangerous winds. Substantial risk of injury or death caused by flying and falling debris. Considerable damage to older mobile homes, signs and fences. Moderate damage to roofs and buildings. Trees and shrubbery may be knocked down or snapped. Bear-total power loss expected. Coastal and low-lying routes may be inundated up to four hours prior to the eye of the storm.
3	178–208	2.7–3.7 m above normal	Devastating damage. High risk of injury or death caused by flying and falling debris. Small buildings may suffer structural damage. Mobile homes and signs are destroyed. Electricity and water will not be available for several days to weeks after the storm. Flooding may occur in areas lower than 1.5 m above sea level and up to 13 km from the coastline.
4	209–251	4–5.5 m above normal	Catastrophic damage. Very high risk of injury or death caused by flying and falling debris. Homes, industrial buildings and infrastructure face severe damage. Shrubs, trees and signs are flown away. Lower floors of coastal structures are subject to extensive damage; flooding is likely in terrain less than 3 m above sea level. Power outages will last weeks to months.
5	>252	Up to 5.5 m above normal	Catastrophic damage. Very high risk of injury or death caused by flying and falling debris. Mobile homes and a high percentage of framed homes are destroyed. Nearly all trees snapped or uprooted. Many roofs cave in and smaller buildings may collapse or blow away, especially structures within 450m of the shoreline. Power outages will last weeks to months.

Of the hurricanes that have impacted Quintana Roo over the past century, only three made landfall as the most destructive category 5 hurricanes: Dean in 2007, Gilbert in

1988 and Janet in 1955. An additional four made landfall as category 4 hurricanes: Emily in 2005, Wilma 2005, Carmen in 1974 and Charlie in 1951 (NOAA Historical Hurricane Tracks, http://coast.noaa.gov/hurricanes/). These high intensity storms have resulted in the loss of thousands of lives and several billion dollars in costs across the peninsula. Just Gilbert caused significant beach erosion and destruction of the tourism infrastructure in the north-east of the peninsula, with damage estimates above 1.2 billion dollars (Clifton 1991).

Despite the significant effects of hurricanes in the Yucatán, research on their direct impacts on the deciduous and semi deciduous forests of this region has been scarce. Only in recent years has this type of research start to grow, particularly after the impact of hurricane Gilbert, and more significantly after hurricane Dean (e.g., Clifton 1991; Whigham et al 1991, 2003; Sánchez-Sánchez and Islebe1999; Garrido-Pérez et al. 2008; Islebe et al. 2009; Vandecar et al. 2011; Bonilla-Moheno 2012; Navarro-Martínez et al. 2012; McGroddy et al. 2013). Efforts to understand additional social (Clifton 1991; DiGiano and Racelis 2012; Schramski and Keys 2013) and ecological (Hernández-Díaz et al. 2012; Ramírez-Barajas et al. 2012a, b) impacts and responses after the disturbance have also emerged in recent years.

Hurricane Dean: On August 21st 2007, hurricane Dean made landfall in south-eastern Quintana Roo, as a category 5 hurricane in the Saffir-Simpson wind scale with sustained winds of 278 km/h, and then moved inland following a northwestern path towards the state of Campeche (Franklin 2008; Brennan et al. 2009) across the center of the corridor that connects the Calakmul and Sian-Ka'an Biosphere Reserves in the southern Yucatán peninsula (Figure 1.2).

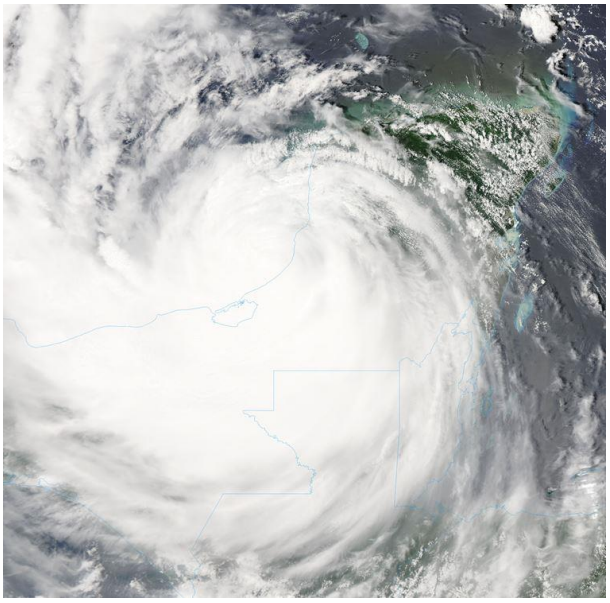

Figure 1.2: MODIS-aqua satellite image (250 m resolution) of hurricane Dean as it moved across the Yucatán peninsula on August 21st 2007 (Source: NASA's Earth Observing System Data and Information System, https://earthdata.nasa.gov/).

The first category 5 hurricane to make landfall in the Atlantic basin since hurricane Andrew (1992), Dean entered the Caribbean Sea on August 17, and rapidly strengthened from a category 1 hurricane to a category 5 hurricane as it moved westerly. It affected the islands of Martinique (over which the northern eye wall passed directly), St. Lucia, Jamaica and Haiti, before making landfall near the Mexican coastal town of Mahahual. Dean's barometric pressure at the time of landfall was estimated at 905 mb, which is the third-lowest landfall pressure on record for the Atlantic basin, behind hurricane Gilbert (1988) and the 1935 Labor Day hurricane (Brennan et al. 2009).

Despite its strength, hurricane Dean caused a significantly lower loss of human lives than other recent high magnitude hurricanes, such as Katrina and Ike, as it struck areas of relatively low population densities (DiGiano and Racelis 2012). A total of 32 fatalities

were directly associated to hurricane Dean across the Atlantic basin. Twelve of these deaths occurred in Mexico, but none of them within the Yucatán peninsula. Still, the damage caused by Dean was extensive across the impacted region, and has been estimated over €550 million overall. Martinique suffered extensive flooding, and infrastructure was severely damaged in the island, as well as in parts of Guadalupe, Haiti and Jamaica. Damage was also reported in St. Lucia, St. Vincent, Dominica, Barbados, and Belize. The banana and sugar cane industries in particular suffered significant losses across the region, and in some cases, plantations were entirely lost (Brennan et al. 2009). In Mexico, hurricane Dean also caused extensive damage. The National Forestry Commission (Comisión Nacional Forestal, CONAFOR) estimated that 1.4 million hectares of forests and more than 6,000 households dependent on forest resources were affected (CONAFOR 2007 cit. DiGiano and Racelis 2012).

1.4: Research goals and objectives

Despite the valuable information that previous studies have provided on the general trends of deforestation rates and the main land conversions taking place in Mexico (e.g. Turner et al. 2001; Díaz-Gallegos et al. 2008, 2010; Ramírez-Delgado et al. 2014), information on the specific patterns of spatial configuration that have characterized these forests over the last decades, how they are changing and the synergistic effects of anthropogenic and natural disturbances is still lacking. The impact of hurricane Dean on the Yucatán peninsula provided an excellent opportunity to fill part of this void and investigate the relationship between forest fragmentation and forest damage and recovery after a catastrophic wind storm.

Therefore, this dissertation seeks to quantify and characterize the patterns of extent and spatial configuration ("fragmentation") of the tropical forests of the Calakmul-Sian Ka'an Biological Corridor over the last 40 years, as well as the effect of the predominant land uses as proximate causes of fragmentation changes. Furthermore, it aims to understand the effect of the fragmentation pattern on the impact and initial recovery of the forests after a major natural disturbance, hurricane Dean (2007).

More specifically, this dissertation investigates the following sub-research questions:

1. How have the patterns of forest loss and fragmentation changed in the Calakmul – Sian Ka'an corridor over the last four decades? How do these changes relate to different land uses in the region? What is the relationship between forest fragmentation and the damage caused by hurricane Dean in 2007 at the regional and *ejido* level?
2. How much structural damage was caused by hurricane Dean to the forest stands of the Calakmul - Sian Ka'an corridor at the short (1-2 years) and medium term (5 years)? What is the relationship between pre-hurricane forest fragmentation and the damage observed at the stand level?
3. To what degree have the forests of the Calakmul - Sian Ka'an corridor recovered within the first 5 years after the impact of hurricane Dean? What is the relationship between forest fragmentation and forest recovery at the stand level?

To answer these questions, a combination of temporal analysis of remotely sensed data, available land cover products and socio economic data, as well as field sampling of forest stands, were used.

1.5: Study area

The Yucatán peninsula is a low lying limestone shelf comprising the Mexican states of Yucatán, Campeche and Quintana Roo, the northern part of Belize and the northern portion of El Petén, Guatemala. Within this region, the Calakmul – Sian Ka'an corridor occupies an area of approximately 26,870 km^2 of southwestern Quintana Roo and southeastern Campeche (Figure 1.3).

The area is characterized by a mostly flat terrain occasionally interrupted by low undulating hills (Foster and Turner 2004; Ellis and Porter-Bolland 2008). Drainage in this region is subterraneous, except when temporary surface water courses form during the rainy season after storms or flooding events (Ellis and Porter-Bolland 2008). Soils across the peninsula are for the most part very shallow (<10 cm in depth) above the underlying limestone (Bonilla-Moheno 2012).

The climate is classified as Aw (hot sub-humid), with a southeast-northwest precipitation gradient that results in some variability across the region (Giddings and Soto 2003). Most of the precipitation throughout the peninsula falls during the wet season (mid-May through October), with mean annual precipitation ranging from 1,000 to 1,500 mm, with strong seasonal and interannual variability (Foster and Turner 2004; Ellis and Porter-Bolland 2008). There is a marked dry season from December through April, with water deficits occurring during the final months, which creates stressing conditions for the vegetation, wildlife, livestock, agricultural activities, and human settlements (Foster and Turner 2004). Mean annual temperatures range from 24 to 26 °C (Giddings and Soto 2003).

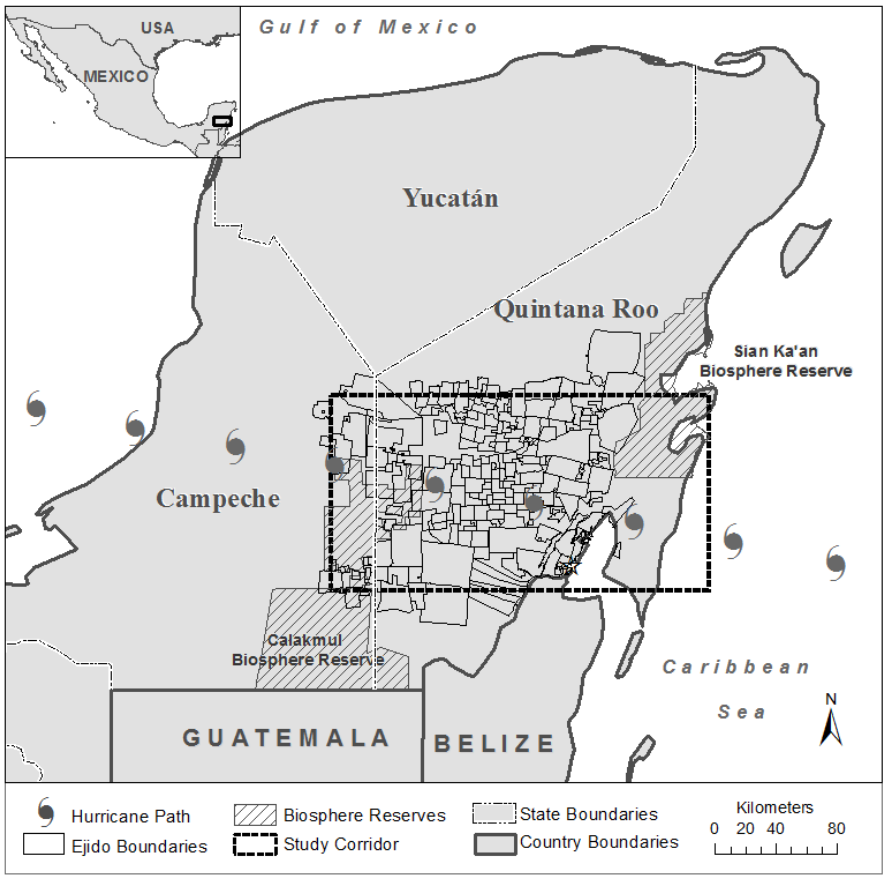

Figure 1.3: Calakmul – Sian Ka'an biological corridor study area in the Yucatán peninsula, México, showing the north-western path followed by hurricane Dean (August 2007).

The region is characterized by a mosaic of forest types that differ in structural appearance, deciduousness and successional stage. Deciduous and semi-deciduous mid-statured (*selva mediana*) and low-statured (*selva baja* or *bajos*) forests predominate inland (Vester et al. 2007), with mid-statured forests usually growing on the tops and sides of hills and on well drained terrain, and low-statured forests growing on low-lying terrain, mostly sinks and depressions that waterlog during the rainy season (Pérez-Salicrup 2004; Vester et al. 2007). Wetlands, mangroves and coastal vegetation predominate in the eastern side of Quintana Roo, mainly within the Sian Ka'an biosphere

reserve (Ellis and Beck 2004; Vester et al. 2007). Further differences in structure and composition have been associated to historic patterns of anthropogenic land use, as well as the impact of natural disturbances, particularly hurricanes and fires (Snook 1998; Boose et al. 2003; Whigham et al. 2003; Hernández-Stefanoni et al. 2011).

Within the Calakmul – Sian Ka'an corridor, most of the land outside of the biosphere reserves is characterized by the presence of *ejidos*, communally-managed land units within which all main decisions, including those pertaining to land management, are made by the members of the community at large (Turner et al. 2001; Roy Chowdhury 2010; Rueda 2010). Currently, there are approximately 170 *ejidos* and *ejido extensions* located within the study area, ranging in size from 10 to 850 km^2, with an average size of 91 km^2. Agriculture is widespread and predominantly semi-subsistence, consisting of a polyculture system that uses traditional slash-and-burn techniques of temporary cultivation and continuous rotation through forest fallow, with maize as the main crop (Schneider and Geoghegan 2006; Ellis and Porter-Bolland 2008; Schneider 2008). Forestry is an important activity for many of the communities in the region (Bray et al. 2008). Additionally, cattle ranching, ecotourism and conservation are also practiced across the peninsula (Turner et al. 2001; Roy Chowdhury 2006; Ellis and Porter-Bolland 2008). As a result, the study area is currently a mosaic landscape of agricultural plots, pasture lands, human settlements and forest fragments of a wide range of sizes and successional stages (Turner et al. 2001; Vandecar et al. 2011), ranging from heavily used stands to relatively preserved ones (Urquiza-Haas et al. 2007).

On August 21st 2007, hurricane Dean made landfall in the south-east of the Calakmul – Sian Ka'an corridor as a category 5 hurricane in the Saffir-Simpson. As it moved inland

following a north-west path Dean lost intensity, becoming a category 4 hurricane before the eye crossed over most of the Zona Maya, and a category 3 hurricane before it reached the state of Campeche state line. As a result, three different zones can be defined within the study area based on the intensity of the hurricane's winds: zone 5 in the coast experienced wind speeds ≥249 km/h; zone 4 in the center with wind speeds 210-248 km/h; and zone 3 inland with wind speeds 178-209 km/h (based on Franklin 2008; see Figure 1.4).

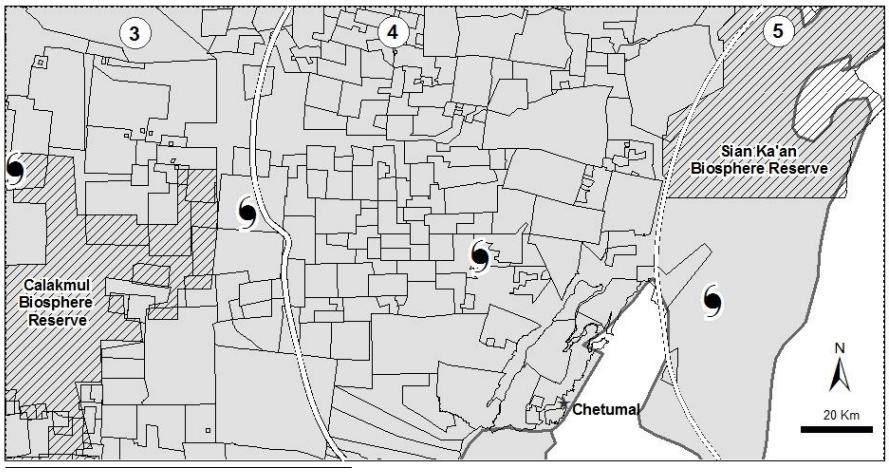

Figure 1.4: Wind speed zones across the Calakmul – Sian Ka'an biological corridor study area, based on hurricane Dean's reported wind speeds. Polygons outlined in black correspond to *ejidos*. Stripped polygons correspond to the biosphere reserves.

1.6: Dissertation overview

Each of the following chapters aims to address individually the specific research questions identified above:

Chapter 2 focuses on measuring forest fragmentation in Mexico's Calakmul –Sian Ka'an biological corridor over 34 years, determining the difference in fragmentation

indicators under different predominant land uses, mainly forestry and cultivation, and characterizing the relation between forest fragmentation and wind damage caused by hurricane Dean at the regional and *ejido* level. Understanding the relationship between land use, forest fragmentation and wind disturbances at the *ejido* level is particularly important because this is the level at which land management decisions and policies that result in land use and land cover changes are implemented (Turner et al. 2007). Results obtained through the spatial analysis of available land cover maps for three time periods (1976, 2000 and 2010) indicate that forest fragmentation increased significantly in the corridor in the last 34 years, particularly within agricultural *ejidos.* Furthermore, land management mediated forest loss and fragmentation was significantly correlated to high forest damage caused by the hurricane winds at the *ejido* level, which suggests that forest fragmentation does render forests more vulnerable to the impact of hurricanes at the *ejido* level.

Chapter 3 focuses on determining the relationship between forest fragmentation and forest damage due to the impact of hurricane Dean at the level of forest stands. Adding this local scale of analysis is important to investigate if the effects of wind disturbances on forest ecosystems vary with scale. Specifically, this chapter's objectives were to: 1) assess short and medium term forest damage at the forest stand level in the Calakmul - Sian Ka'an biological corridor (2008-2012); 2) characterize pre-hurricane forest fragmentation at the forest stand level; and 3) examine the relationship between forest fragmentation status and the damage caused by hurricane Dean in 2007 at the forest stand level. A combination of field surveys of hurricane damage, remote sensing, Morphological Spatial Pattern Analysis (MSPA) and correlation analysis were used to

accomplish these objectives. Results show a large spatial variability in both immediate and medium term forest damage across the region, as well as in forest fragmentation indicators at the stand level. No significant correlations were found between the pre hurricane fragmentation indicators and forest damage, either at the short (1 year) or medium (5 years) terms after hurricane Dean's impact, which is consistent with previous research on forest damage after large scale wind disturbances at the stand level.

Chapter 4 aims to determine the relationship at the stand level between forest fragmentation and forest recovery after the damage caused by the impact of hurricane Dean. Specifically, this chapter's objectives were: 1) to assess short and medium term recovery at the species level in the Calakmul - Sian Ka'an biological corridor (2008-2012); 2) to assess short and medium term recovery at the plot level in the Calakmul - Sian Ka'an biological corridor (2008-2012); and 3) to determine the relationship between forest fragmentation status and forest recovery at the forest stand level. A combination of field surveys of forest recovery, analysis of remotely sensed data, MSPA and correlation analysis were used to accomplish these objectives. Significant forest recovery was observed within the forests of the Calakmul – Sian Ka'an corridor just a couple of years after the extensive damage caused by hurricane Dean in 2007, mostly through forest regrowth (i.e., resprouting of the remaining living stems and their increase in width). No significant correlations were found between the forest fragmentation indicators and forest recovery at the short term (in 2008), but significant correlations with recovery in 2009 were found for older and medium-statured forests at the stand level.

Finally, **Chapter 5** presents some concluding remarks, with emphasis on the contributions of this research to the Land Change Science research agenda and the

possible implications of the dissertation findings regarding the resilience of the forests of Yucatán peninsula to hurricane impacts as well as their future in the face of continuing anthropogenic and natural disturbances.

Chapter 2: Measuring forest fragmentation in the Calakmul - Sian Ka'an corridor and its effects on forest damage caused by Hurricane Dean (2007)

2.1: Introduction

As discussed in the previous chapter, accelerated deforestation and forest fragmentation rates are widely recognized as one of the main threats to tropical forests' biodiversity and to the ability of these ecosystems to supply essential goods and services (Schmitt et al. 2009). Understanding the patterns of forest loss and fragmentation, their drivers and feedbacks with global climate change, as well as their ecological effects, is thus critical for any effort aimed to achieve the sustainable utilization of forest resources and the conservation of species and ecosystems (Lindenmayer and Fischer 2007; Kupfer and Franklin 2009). Furthermore, understanding the synergies between anthropogenic and natural disturbances (such as fires and hurricanes) on forest change dynamics across space, time, and scale is also essential for informing policy and management programs that seek to achieve sustainability and reduce human and ecological vulnerability (Foster et al. 1999; Chazdon 2003; Uriarte et al. 2004; 2009, 2010; Catterall et al. 2008; Alcántara-Ayala and Dykes 2010).

Research on forest fragmentation is very relevant for the seasonal tropical forests of the Yucatán peninsula, Mexico. These forests play a critical ecological and social role in Mexico and Mesoamerica (Ramírez 2004), yet surprisingly little is known about the recent trends of forest loss and fragmentation in the region. Even less is known regarding the relationship between forest fragmentation and other anthropogenic and natural disturbances, and how these interactions affect forest dynamics in the short and long

term. This chapter investigates some of these issues within the Calakmul – Sian Ka'an biological corridor.

2.1.1: Forest loss and fragmentation in the southern Yucatán peninsula

To date, most of the studies conducted to quantify and characterize the processes of land use and land cover change within the southern Yucatán region have been restricted to the area comprised by the Calakmul biosphere reserve (Figure 1.3) and the surrounding *ejidos*, with a large emphasis on the effects of anthropogenic disturbances (e.g. Turner et al. 2001; Roy Chowdhury 2006; Vester et al. 2007; Ramírez-Delgado et al. 2014). In comparison, very limited information is available about the changes that have taken place across the corridor that connects the Calakmul and Sian Ka'an biosphere reserves. Even less information is available regarding the effects of natural disturbances in this area.

Some evidence suggests that forest loss and fragmentation are a concern for the sustainable persistence of the tropical forests of the southern Yucatán. A regional analysis focused on the deforestation trends in southeast Mexico (which includes the Yucatán peninsula) suggests an average annual deforestation rate of 1.1 percent between the 1980's and 2000 (Díaz-Gallegos et al. 2010). This represents an average annual loss of 190,000 ha of forest. Deciduous and sub deciduous forests were the most affected, with the dominant process of change being the conversion of forests to grasslands and irrigation, followed by deforestation from slash-and-burn agriculture (Díaz-Gallegos et al. 2010). Similarly, a deforestation analysis for the Mesoamerican Biological Corridor-Mexico (MBCM) for the same time period conducted by Díaz-Gallegos et al. (2008), estimated that deforestation across the Calakmul – Sian Ka'an corridor occurred at a rate

of 0.6% over the 20 year period. The main cause of forest loss was identified in this study as expansion of temporal agriculture (slash-and-burn) (Díaz-Gallegos et al. 2008).

More recent and detailed information is needed in order to understand how these deforestation rates vary across the region, and how they relate to anthropogenic activities. Beyond quantifying the amount of forest that has been lost and the rates at which this is happening, it is important to understand the main mechanisms behind these changes and the resulting change in the spatial configuration of these ecosystems. Are forests becoming subdivided into smaller patches of different size and shape that become increasingly isolated from each other, or is forest loss concentrated only on the edges, resulting in smaller areas of continuous forest? Are forests becoming perforated (as would be expected from slash and burn agriculture)? That is, is the number of clearings within continuous forests increasing? Similarly, it is important to understand how anthropogenic activities relate to the new forest configurations, and if different land management practices result in different rates of forest loss and patterns of forest configuration. Finally, research should address how changes to the spatial configuration of forests may result in further structural and compositional changes as a result of the interaction with other disturbances in the region, which might affect their long term persistence and sustainability.

2.1.2: Hurricanes in the Mexican Yucatán

Forests in the Mexican Yucatán have not only been affected by anthropogenic disturbances, but also by large-scale natural disturbances such as hurricanes and fires. Hurricanes periodically affect the Yucatán's ecosystems, wildlife and human populations.

More than 60 hurricanes have made landfall in the Yucatán in the past 150 years (Figure 1.1; Boose et al. 2003). With wind speeds of over 100 km/h often accompanied by strong rains, and paths that are usually close to fifty kilometers wide, with areas of influence of hundreds of kilometers, the impacts of hurricanes are noticeable from regional to local scales. These impacts often include structural changes in vegetation, landslides, large debris accumulations, and altered topographic features (Lugo 2008; Xi and Peet 2011). More specifically, in forested ecosystems, immediate hurricane damage often results in widespread defoliation, biomass loss due to snapped stems and branches, as well as tree bending, uprooting and death (Everham and Brokaw 1996). At longer time scales, additional structural and compositional changes can occur as the altered environmental conditions impact competitive dynamics and forest succession, which in turn can alter ecosystem processes and function (Everham and Brokaw 1996; Vandecar et al. 2011; Xi and Peet 2011).

Among the abiotic factors that have been suggested to play a role in the effects of hurricanes on tropical forests is their spatial configuration as result of forest fragmentation (Fahrig 2003; Catteral et al. 2008; Laurence and Curran 2008). However, the interactions between hurricane disturbances and forest fragmentation are still poorly understood (Van Bloem et al 2005; Catteral et al. 2008), particularly at scales above that of forest stands.

2.1.3: Relation between forest fragmentation and wind disturbances

In addition to the direct negative effects of fragmentation on forested ecosystems (e.g. forest loss, species isolation, change in microclimatic conditions), it has been widely hypothesized that fragmented forests are likely more vulnerable to the impacts of large

scale disturbances, and have lower rates of recovery than less fragmented or continuous forest cover (Fahrig 2003; Catteral et al. 2008; Laurance and Curran 2008). Of the two environmental factors that characterize hurricanes and that strongly interact with forests, rain and wind; it is the latter which would be expected to interact more directly with the effects of forest fragmentation.

The effects of wind damage on forests have long been recognized by ecologists and foresters (Moore et al. 2008, 2013; Xi and Peet 2011; Mitchell 2013). Previous research on forest fragmentation and its effects on tropical forests' dynamics have found that under normal (non-hurricane) conditions, wind damage near edges can result in higher rates of structural damage, windthrow and mortality than in forest interiors (e.g., Williams-Linera 1990; Laurance 1997). Fragmented forests are expected to be more vulnerable to wind disturbances for two reasons: 1) cleared lands either surrounding or in the midst of forests allow for accelerated wind speeds as they provide less resistance, and 2) fragmentation results in an increase in the proportion of abrupt forest edges, which are exposed to the direct effects of winds, including turbulence and vorticity (Laurance 1997; Laurance and Curran 2008).

In recent years, special attention has been paid to the ecological impacts of large scale infrequent catastrophic windstorms, such as hurricanes and tornados, due to the substantial tree damage and/or mortality than they can produce (Xi and Peet 2011). Indeed, low frequency catastrophic wind disturbances, such as hurricanes, have been found to account for most of the forest damage recorded over long periods of time. For example, Moore et al. (2013) found that the high levels of damage that occurred during three major events account for nearly two-thirds of all recorded forest damage in New

Zealand over a period of 65 years. These results highlight the importance of understanding the effect of large-scale infrequent wind disturbances on forest change dynamics.

Some of this research has been aimed to assess if forest fragmentation does indeed increase the impact of these disturbances on forests. Two main approaches have been used so far in the available literature: comparing forest damage close to edges and forest interiors (e.g., Grimbacher et al. 2008; Pohlman et al. 2008), and comparing forest damage in patches of different size and large continuous forests (e.g., Laurance 1991; Van Bloem et al. 2005; Caterall et al. 2008; Grimbacher et al. 2008). In all cases, damage was assessed at the local scale within transects or plots of different size.

To date, the results of research mostly contradict the expectation that forest fragments are more vulnerable than continuous forests to the damage caused by catastrophic windstorms. Van Bloem et al. (2005) found that continuous semi-deciduous forests of the Guánica Forest in Puerto Rico experienced similar overall rates of damage after hurricane Georges, a category 3 hurricane, than forest fragments located close by. Similarly, research conducted after cyclone Larry made landfall in the forests of northeastern Australia did not find evidence of heightened damage in small forest fragments or forest edges than large forest fragments or forest interior (Caterall et al. 2008; Grimbacher et al. 2008; Pohlman et al. 2008). Only Laurance (1991) has reported that forest edges in tropical rainforest of northern Australia were more severely damaged by a category 3 cyclone than the forest interior. A significantly higher percentage of study plots located within 150 m of forest edges showed severe structural canopy and subcanopy damage in comparison to sites located further in, thus supporting the

hypothesis that fragmented forests are more vulnerable to wind disturbances than unfragmented forests.

A possible explanation for these findings is that the effects of the high wind speeds and turbulence associated with cyclones are so severe that they overcome whatever protection forest continuity might provide (Caterall et al. 2008), resulting on similar patterns of heterogeneous damage in both fragmented and continuous forests. However, more research on the effect of other hurricane disturbances of different intensity on tropical forests across the world is needed to further understand any possible interactions of forest fragmentation and hurricane damage. In particular, an effort should be made to assess these possible interactions of forest fragmentation and wind disturbances at all the spatial scales at which hurricane effects are noticeable, from the local to the regional.

2.1.4: Research objectives

This chapter has three main objectives: 1) to characterize forest loss and fragmentation in the Calakmul - Sian Ka'an biological corridor between 1976 and 2010, 2) to explore if different land uses have resulted in different patterns of forest loss and fragmentation within the region, and 3) to examine the relationship between forest fragmentation status and the damage caused by hurricane Dean in 2007 at the regional and *ejido* level. I hypothesize that during the 34 years of the study period, forest fragmentation has increased within the Calakmul – Sian Ka'an corridor as the result of anthropogenic activities, including slash-and burn and expansive agriculture and urban expansion, resulting in a significant increase of the proportion of forest edges and perforation. Furthermore, I expect these patterns to differ between *ejidos* depending on the

predominant land use, with forest fragmentation being more severe in agricultural *ejidos* than forestry *ejidos* over the last 34 years. Finally, I expect hurricane damage to have been significantly higher in *ejidos* with higher levels of forest fragmentation than *ejidos* with less fragmented forests.

Understanding the relationship between land use, forest fragmentation and wind disturbances at the *ejido* level is particularly important because this is the level at which land management decisions and policies that result in land use and land cover changes are implemented (Turner et al. 2007). Thus, if certain land uses and land management practices result in higher levels of forest fragmentation, and if more fragmented forests are more vulnerable to hurricane damage, this information could be useful for future management plans that seek to reduce vulnerability to hurricane impacts.

2.2: Methods

The study area for the analysis presented in this chapter corresponds to the entire Calakmul - Sian Ka'an corridor first described in Chapter 1 (Figure 1.3).

2.2.1: Data used

Land cover maps: Land cover maps for three time periods (circa 1976, 2000 and 2010), were used in order to estimate annual deforestation rates and characterize forest fragmentation in the corridor, covering a 34-year period.

The 1976 map, used as the reference dataset in the analysis, was produced by the Mexican National Institute of Statistics, Geography and Informatics (INEGI). This map, commonly known as the INEGI land use and vegetation map Series I, was based on the

visual interpretation by experts of aerial photographs acquired between 1968 and 1986 (Mas et al. 2002; INEGI 2005; Velázquez et al. 2010). The database was developed for the entirety of the country in analog format, and later digitized in vector format. The map was ground truthed using 10,000 field control points (Mas et al. 2002), although a value for the accuracy assessment was not available.

The 2000 map, known as the 2000 National Forestry Inventory map of Mexico, was produced by the Institute of Geography of the National Autonomous University of Mexico (IG-UNAM). This map was based on the previous INEGI maps and the visual interpretation by experts of Landsat ETM+7 images acquired between November 1999 and May 2000 (Palacio-Prieto et al. 2000; Velázquez et al. 2010). The accuracy of the map was evaluated for four ecogeographical areas located across Mexico (including a watershed in the southeastern Yucatán peninsula) using random control points from digital aerial photographs from the year 2000. Overall accuracy for these areas ranges between 64-78 percent (Couturier et al. 2010).

Both the 1976 and 2000 maps were created at a scale of 1:250,000. They follow a hierarchical system of classification with four aggregation levels: formations, vegetation types, communities and sub-communities (Palacio-Prieto et al. 2000). For the purposes of the analysis presented in this chapter, only the first three levels of aggregation were taken into consideration (i.e., the first three columns of Table 2.1).

The 2010 land cover map from Rogan et al. (*unpublished*) was based on the interpretation of four different satellite images: Landsat-5 TM from 26 January 2010 and Landsat-7 ETM+ 02 January 2010 (Path 20, Row 47), Landsat-7 ETM+ from 28 February 2010 and 08 September 2010 (Path19, Row 47). A line infilling algorithm was

used to correct for the Landsat-7 ETM+ scan line corrector error. Training sites were collected in the field during May 2009 and 2010. Sixteen land cover and land use classes were included in this map (Table 2.2). The classification process included several steps. First, an unsupervised classification was applied to separate vegetated and non-vegetated areas. Second, a classification tree algorithm was used to further separate the forested areas into subclasses (such as mid-statured forest and low-statured forests). Finally, a semi-unsupervised classification method was applied to further classify all non-forest areas into subclasses, by using the ISOCLUST module in Idrisi Taiga. A preliminary accuracy assessment of this map resulted in an 86% overall accuracy based on 136 random control points (N. Cuba, pers. comm.).

Given the intrinsic differences in the format of these maps, three main pre-processing steps were necessary to make them comparable for the analysis: reclassification, rasterization and generalization. First, the three land cover maps were reclassified to binary forest/non-forest maps. A detailed description of the equivalencies used for each map between the original land use/land cover classes and the final forest/non-forest map is presented in Tables 2.1 and 2.2.

Table 2.1: Land cover hierarchical classification used for the 1976 and 2000 land cover maps, and equivalency used for the binary forest/non-forest map (NF: reclassified as Non Forest; F: reclassified as Forest).

Land cover	Vegetation Type and Land Use	Plant community and other land covers	Forest/Non forest
I. Crops	1. Agriculture (irrigation and moisture)	Irrigation agriculture	NF
		Moisture agriculture	NF
		Suspended irrigation	
		Cropped pastures	NF
	2. Temporal agriculture	Temporal agriculture	NF
	3. Forest plantation	Forest plantation	F
II. Forests	4. Evergreen and semi-evergreen	High-statured and mid-statured evergreen forest[1]	F
		Low-statured evergreen forest[1]	F
		High-statured and mid-statured semi-evergreen forest[1]	F
		Low-statured semi-evergreen forest[1]	F
	5. Deciduous and semi-deciduous	Mid-statured deciduous and semi-deciduous forest[1]	F
		Low-statured deciduous and semi-deciduous forest[1]	F
		Low-statured spiny forest[1]	F
III. Grasslands	6. Grasslands	High-mountain prairie	NF
		Natural pastures (includes pastures-huizachal)	NF
		Savannah	NF
IV. Hydrophytic vegetation	7. Hydrophytic vegetation	Mangroves	F
		Popal-tular	NF
V. Other vegetation	8. Other vegetation	Palm grove	F
		Halophytic and gypsophile vegetation	NF
		Coastal dunes vegetation	NF
	9. Area without apparent vegetation	Area without apparent vegetation	NF

Table 2.1: (Cont.)

Land cover	Vegetation Type and Land Use	Plant community and other land covers	Forest/Non forest
VI. Other land covers	10. Human settlements	Human settlements	NF
	11. Water bodies	Water bodies	Water

[1:] Class includes two categories: primary vegetation and arboreous secondary vegetation, and shrubby secondary and herbaceous vegetation

Table 2.2: Land cover classification used for the 2010 land cover map, and equivalency used for the binary forest/non-forest map (NF: reclassified as Non Forest; F: reclassified as Forest). The land cover equivalencies from the 1976 and 2000 hierarchical classification system were included for comparison (see Table 2.1).

Land cover	**Vegetation Type and land use**	**Forest/Non forest**
I. Crops	1. Agriculture	NF
	2. Milpa	NF
	3. Pastures	NF
II. Forest	4. High- and mid-statured forest	F
	5. Mid-statured forest	F
	6. Low-statured forest	F
	7. Semi-deciduous forest	F
	8. Bajos	F
	9. Secondary forest	F
III. Hydrophytic vegetation	10. Mangroves	F
	11. Marsh	NF
IV. Other vegetation	12. Coastal vegetation	NF
	13. Bracken fern	NF
V. Other land covers	14. Urban settlements	NF
	15. Bare soil	NF
	16. Water	Water

Second, the 1976 and 2000 maps, originally available in vector format, were rasterized to a 30 m pixel spatial resolution in order to fit the 2010 land cover map pixel resolution. Finally, the 2010 raster map was generalized by applying two consecutive 7x7 window filters, in order to better match the mapping resolution of the older maps and reduce the impact of the different data sources in the estimation of forest fragmentation change through time due to differences in the minimum mapping units.

Damage map: A regional hurricane damage map (Rogan et al. 2011) was used to assess forest damage due to hurricane Dean within the Calakmul – Sian Ka'an corridor at the regional and e*jido* level (Figure 2.1). This map is based on the comparison of pre- and

post-hurricane 250-m Enhanced Vegetation Index (EVI) imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS). A simple subtraction of a pre-hurricane composite (5 August 2007) from a post-hurricane composite (6 September 2007) was calculated. Negative EVI pixel values in the resulting image were considered as indicative of hurricane damage. Damage values are expressed as a percentage of the decrease in EVI, with higher difference values indicating higher hurricane damage. This map was validated using field plot data, with accuracy varying by hurricane wind speed zone. The highest accuracy corresponds to areas within wind speed zone 5 (95%), followed by areas within wind speed zone 4 (92.9%) and the lowest accuracy corresponding to areas within wind speed zone 3 (87.1%) (Rogan et al. 2011).

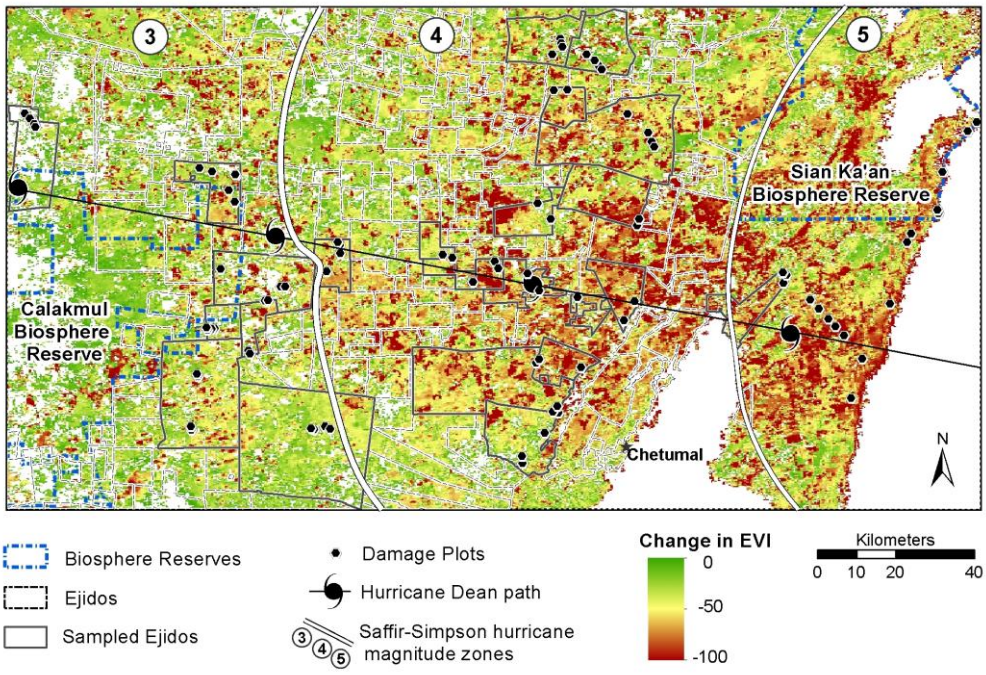

Figure 2.1: Hurricane damage map for the Calakmul-Sian Ka'an corridor based on MODIS EVI data (Rogan et al. 2011).

Ejido information: The predominant land use of the *ejidos* located within the study area was determined based on field surveys and their Community Land Management Plans

(CLMP) when available. CLMPs for the state of Quintana Roo were obtained from the National Forestry Commission (Comisión Nacional Forestal, CONAFOR). The CLMPs provide detailed information on the history of each of the *ejidos*, their population, and the main economic activities that take place within them, and establish the rules reached by the land holders in terms of the way the *ejido* land will be used. At the time this information was requested (January 2013), CLMPs were available for only 46 *ejidos* distributed across the biological corridor (Figure 2.2).

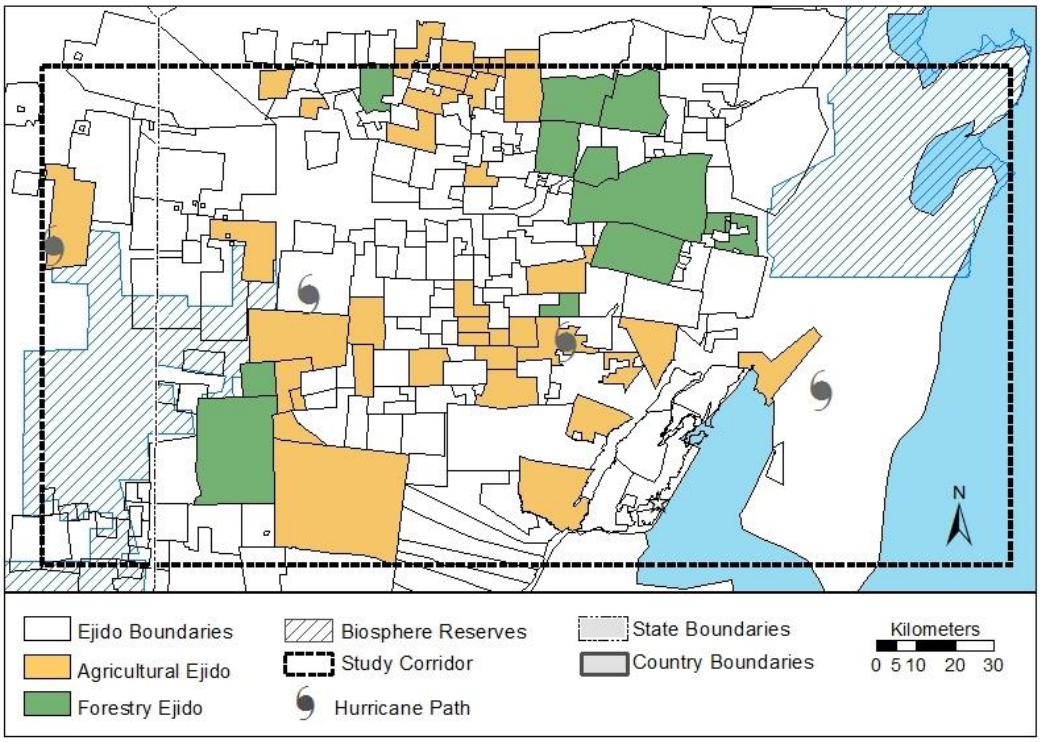

Figure 2.2: *Ejidos* within the Calakmul – Sian Ka'an biological corridor for which additional land use and management information was available. For the *ejidos* represented in white, no additional information on dominant land use was available.

Based on the information contained in the CLMP and the field surveys, 46 *ejidos* were classified as "Agricultural" or "Forestry." It is important to clarify that in the majority of the *ejidos* shifting cultivation is a common practice and forestry as an

exclusive activity is rare. Therefore, only *ejidos* described in the CLMP as dedicated mainly to agriculture (usually when more than 50% of the land owners depend on it as the main source of income) were characterized as "agricultural" (including subsistence, mechanized agriculture and pastures).

2.2.2: Forest loss and fragmentation in the corridor from 1976 to 2010

Data described above was analyzed in the following way:

a. Forest loss and annual deforestation rates: Annual deforestation rates were calculated for the entire region using the relationship of Puyravaud (2003):

$$P = \frac{100}{t_2 - t_1} ln \frac{A_2}{A_1}$$

where A_1 and A_2 are the forest cover at time t_1 and t_2 respectively, and P is the percentage of forest loss per year.

b. Forest fragmentation: In order to measure forest fragmentation within the Calakmul – Sian Ka'an corridor, a Morphological Spatial Pattern Analysis (MSPA) was conducted (Vogt 2010).

A vast number of different metrics and indices have been developed to characterize and quantify spatial heterogeneity and fragmentation from categorical maps (Riitters et al. 1995; Gustafson 1998; Neel et al. 2004). Available approaches fall within two main categories: those focused on evaluating landscape **composition**, which take into account the presence and amount of the different classes without being spatially explicit (e.g., number of classes in the map; proportion of each class in relation to the entire map,

diversity), and those focused on quantifying the **spatial configuration** of the system, which take into account the spatial distribution of the different elements and classes (Gustafson 1998; Griffith 2004). In turn, the spatial configuration metrics can be **patch-based** or **neighborhood-based**.

Patch-based measures of forest fragmentation focus on the spatial characteristics of individual patches, and include landscape-level statistics such as average patch area, number of patches, patch perimeter, and patch density. These statistics can be difficult to estimate for large areas where a great number of patches are present. Furthermore, since these measures result in summary numbers that are not spatially explicit, linking observed patterns to ecological processes can also be extremely difficult.

In contrast, the neighborhood-based approach focuses on the spatial relationships among different patches or alternatively, pixels, providing spatially-explicit measures of characteristics such as isolation, connectivity and aggregation (Gustafson 1998; Vogt et al. 2007b). In recent years, significant efforts have been made to develop pixel-based neighborhood methods for mapping and characterizing forest fragmentation (Riitters et al. 2000, 2002, 2007; Vogt et al. 2007a; Ostapowicz et al. 2008). These methods can be applied to raster maps derived from the interpretation of remotely-sensed satellite data, which have become the main inputs for forest fragmentation assessments over large geographic regions (Vogt et al. 2007a). Initial efforts were based on image convolution, a method that allows classifying each forest pixel into a fragmentation category by using a window of fixed area to measure the amount and adjacency of other forest pixels surrounding it (Riitters et al. 2000, 2002). However, this method can result in erroneous classifications because: 1) it is partly based on percolation theory, which only applies to

random images and not real landscapes, which are not random due in part to spatial auto-correlation; 2) the fragmentation classification is based on user-defined thresholds and is not directly related to ecological processes; and 3) only information from within the fixed window is considered, which can result in unreliable fragmentation estimates (Vogt et al. 2007). More recently, MSPA has been developed as an alternative methodology for classifying pixel-level fragmentation based on a series of operations derived from mathematical morphology (Riitters et al. 2007; Vogt et al. 2007; Ostapowicz et al. 2008).

MSPA describes the geometric arrangement and level of connectivity of the elements of the focal class of interest (foreground) in a binary map by assigning each pixel to mutually exclusive thematic categories. If the foreground corresponds to forests, there are seven possible thematic categories to which each forest pixel might be assigned (Figure 2.3): *Core*, forest pixels surrounded by forest pixels on all sides; *Edge*, pixels that form the transition between forest and non-forest areas; *Perforated*, pixels that form the transition between forest and non-forest areas within the interior of core areas; *Bridge*, forest pixels that connect two or more core areas; *Islet*, forest patches that are too small to contain core areas and are unconnected to core areas; *Loop*, forest pixels that connect a core area to itself; *Branch*, forest pixels that extent from a core area, but are not connected to other core areas (Ostapowicz et al. 2008; Riitters et al. 2009; Wickham et al. 2010).

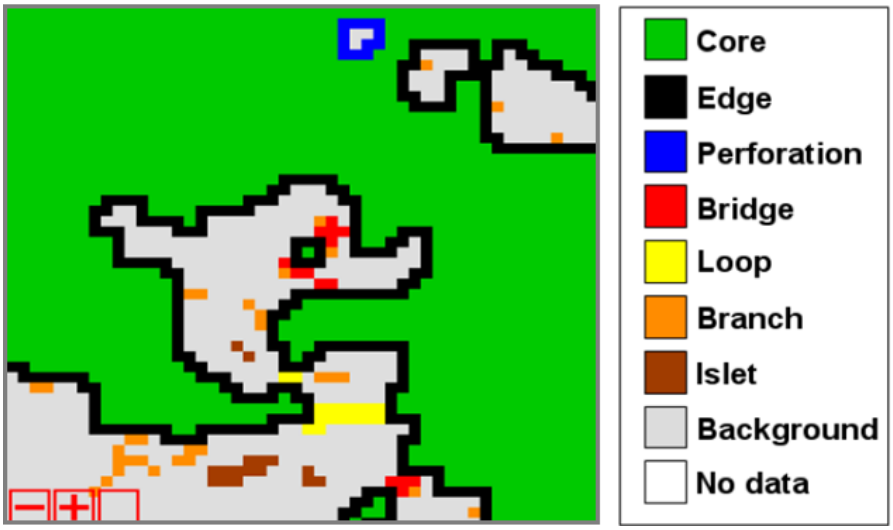

Figure 2.3: Thematic classes of forest fragmentation resulting from MSPA (Vogt 2010)

MSPA is especially useful when examining forested landscapes that have become more subdivided (i.e., have more edges) and isolated (Riitters et al. 2007; Ostapowicz et al. 2008) as it is expected to be the case for the forests in the corridor based on deforestation rates previously reported for the region (Roy Chowdhury 2006; Vester et al. 2007; Díaz-Gallegos et al. 2008, 2010). MSPA results have been found to be more consistent than traditional methods of pixel-level fragmentation classification because they are based on information from the entire landscape, resulting in fewer pixel misclassifications (Vogt et al. 2007). Additionally, MSPA presents the advantage of being spatially explicit regarding the locations where different patterns of fragmentation occur within the area of study (Saura et al. 2011).

It is important to point out that similarly to what occurs with more traditional patch-based measures, MSPA results are sensitive to the scale of the input raster maps used for the analysis. In general, the use of lower resolution maps result in data generalization which in turn results in the removal of the small scale non-core classes. The maximum

level of detailed fragmentation characterization for the landscape would be achieved with high resolution maps (Ostapowicz et al. 2008). This was a concern in this study, given the differences between the land cover maps used. However, since these were the best data available, the generalization of the more detailed, higher resolution map from 2010 through the application of consecutive filters was considered as an acceptable way to reduce any possible differences between years derived from differences in the resolution of the land cover maps.

In this chapter, MSPA was applied to each binary forest/non-forest map for 1976, 2000 and 2010 in order to measure forest fragmentation within the study region. A 30 m edge width, equivalent to the minimum pixel size of the 2010 land cover map, and an eight-neighbor connectivity rule were selected for the MSPA. Assigning the minimum possible edge width (30 m = 1 pixel) corresponds to a conservative assessment of forest fragmentation, as it allows detecting the maximum amount of core forest in the study area and avoiding overestimations of forest fragmentation. Larger edge widths would result in an increase of the amount of non-core classes at the expense of core areas (Vogt et al. 2007; Ostapowicz et al. 2008). In turn, an eight-neighbor connectivity rule means that two core forest pixels would be considered to be connected if they share either a common border or corner (Vogt 2010), reducing the risk of overestimating the amount of fragmented forest. The MSPA fragmentation analysis was applied for the entire study area, and for each of the *ejidos* found within the corridor (N= 173).

Four different indicators derived from MSPA were used to assess the patterns in forest fragmentation and spatial configuration for 1976, 2000 and 2010: *proportion core*,

proportion perforation, proportion edge and edge/core ratio. These indicators provide a measure of the amount of core and edge habitats in the landscape (Wright 2011):

Proportion Core: is an indicator of the abundance of core habitat. It provides an intuitive measure of the compactness of forests. It is calculated as:

$$\%\ Core = \frac{Total\ core\ forest\ pixels}{Total\ forest\ pixels}\ x\ 100$$

Values range from 0 to 100, with higher values corresponding to high levels of core forest, and therefore, lower levels of forest fragmentation.

Proportion Perforation: represents the amount of edge effects within forest interiors, as a result of the presence of non-forest patches within a mostly forested landscape.

$$\%\ Perforation = \frac{Total\ perforation\ pixels}{Total\ forest\ pixels}\ x\ 100$$

Values range from 0 to 100, with higher values corresponding to high levels of forest perforation, i.e., a large number of non-forest patches within the forest.

Proportion Edge: expresses the abundance of edge habitat in the landscape and the levels of edge effects present in the forests. Higher values indicate higher levels of forest fragmentation. In this chapter, the proportion edge is calculated as the sum of all MSPA forest classes except core forest.

$$\%\ Edge = \frac{Total\ forest\ pixels - Core\ forest\ pixels}{Total\ forest\ pixels}\ x\ 100$$

Edge/Core ratio: is an indicator of the relative abundance of edge versus core habitat, and it is a variation of the perimeter-edge ratio commonly used in past fragmentation research. High values indicate higher levels of forest fragmentation.

$$Edge/Core\ ratio\ = \frac{\%\ Edge}{\%\ Core}$$

All fragmentation indicators were calculated as a percent of the amount of forest present per unit of analysis (either the entire corridor or individual *ejidos*) in order to avoid the effect of differences in the initial amount of forest or *ejido* size on the fragmentation pattern analysis.

2.2.3: Measuring the relation between forest fragmentation and land use

The relation between land use and forest fragmentation patterns in the study region was explored through a series of one-way Analyses of Variance (ANOVA) in order to test for significant differences in the means of the fragmentation indicators between "Agricultural" and "Forestry" *ejidos*. Based on the information contained in the CLMPs (see data section), predominant land use activities were determined for a total of 46 *ejidos*, of which 34 were classified as agricultural and 12 as forestry (Figure 2.2).

2.2.4: Relation between forest fragmentation and hurricane damage

The statistical relation between pre-hurricane forest fragmentation and forest damage caused by hurricane Dean was measured for the entire corridor and at the *ejido* level.

For calculating the relationship within the entire corridor, the 2000 forest/non-forest map was rasterized to match the resolution of the regional damage map (Projection MODIS Sinusoidal; Pixel size: 231.66 m), and a MSPA was conducted. Next, a mask of all the edge forest pixels was created by grouping all non-core forest pixels, and edge density within a 3x3 pixel window was estimated. Finally, a simple linear regression analysis was conducted, using the damage values as the dependent variable, and edge density as the independent variable. For this regression, the unit of analysis was each

individual pixel in the hurricane damage and forest fragmentation maps for the entire area of the corridor (i.e., both *ejido* and *non ejido lands*, including the biosphere reserves).

To measure the statistical relation between forest fragmentation and forest damage caused by hurricane Dean at the *ejido* level, a pairwise correlation analysis between the fragmentation indicators from the MSPA and the regional hurricane damage (Rogan et al. 2011) was conducted. The 2000 data were used to characterize the pre-hurricane forest fragmentation conditions for each *ejido*. To characterize forest damage, the damage map was normalized to a scale from 0 to 1 and the result was aggregated at the *ejido* level by extracting the average hurricane damage in forest areas for each of the *ejidos* included in the fragmentation analysis.

In order to control for the effect of hurricane wind intensity in the analysis, only *ejidos* located within hurricane wind speed zone 4 were considered for the correlation analysis (N=118).

2.3: Results

2.3.1: Forest loss and fragmentation in the corridor from 1976 to 2010

a. Forest loss and annual deforestation rates: Approximately 13% (3,105 km^2) of the initial forest extent was lost in the study region between 1976 and 2010 (Table 2.3). The rate of deforestation over 34 years is 0.39%, whereas the rate of deforestation between 1976-2000 and 2000-2010 was 0.53% and 0.07%, respectively.

A comparison of the 1976 and 2010 forest maps shows that deforestation over the 34 year period occurred widely across the corridor, but was mostly concentrated within the southern and central sections (Figure 2.4). Noticeably, little forest loss has occurred

within the northern part of the Calakmul biosphere reserve, although some deforestation is evident towards the north-east as well as along highway 186 in the middle section of the reserve. In contrast, afforestation seems to have occurred in isolated patches across the corridor, and more significantly towards the coastal portion of the study area in the east, within and around the Sian Ka'an biosphere reserve.

Table 2.3: Change in forest extent and fragmentation indicators within the Calakmul – Sian Ka'an biological corridor from 1976 to 2010.

	1976	**2000**	**2010**
Extent of all Forest (km^2)	24,726	21,772	21,620
Percent of study area	92.8%	81.7%	81.2%
Fragmentation indicators (% of forest)			
Proportion Core	99.63	98.44	97.06
Proportion Perforation	0.22	1.07	1.93
Proportion Edge	0.36	1.56	2.95
Edge/Core Ratio	0.004	0.02	0.05

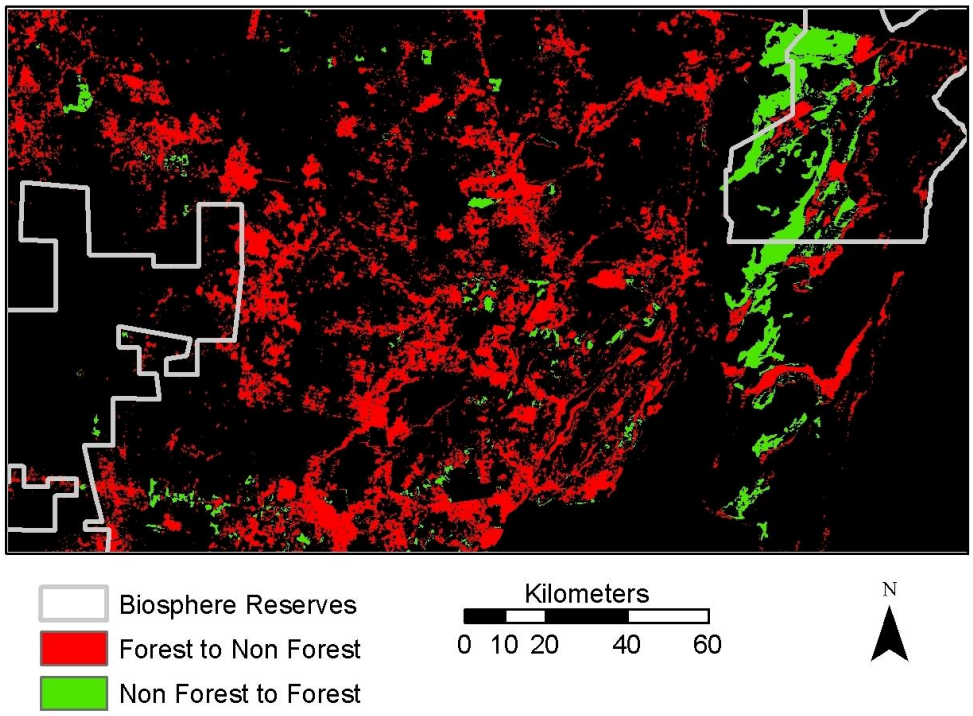

Figure 2.4: Forest losses and gains within the Calakmul – Sian Ka'an corridor from 1976 to 2010.

b. Forest fragmentation: MSPA results indicate a general trend of increased forest fragmentation within the Calakmul – Sian Ka'an biological corridor in recent decades (Table 2.3, Figure 2.5). Between 1976 and 2010, a 2.57% decrease in the *proportion core forest* and a 2.59% increase in the *proportion edge* forest occurred in the corridor. The other two fragmentation indicators considered also increased through time to a smaller degree: *proportion perforation* (1.71%), and *edge/core ratio* (0.05%).

During the 34 year time period covered by this analysis, rates of deforestation for *core forest* were higher than for all forest (by 10%). The major contributors to losses in *core forest* extent were *non-forest* (85.8%), *perforation* (9.9%) and *edge* (4.3%) (Figure 2.6).This trend is apparent for the individual time periods covered in the analysis.

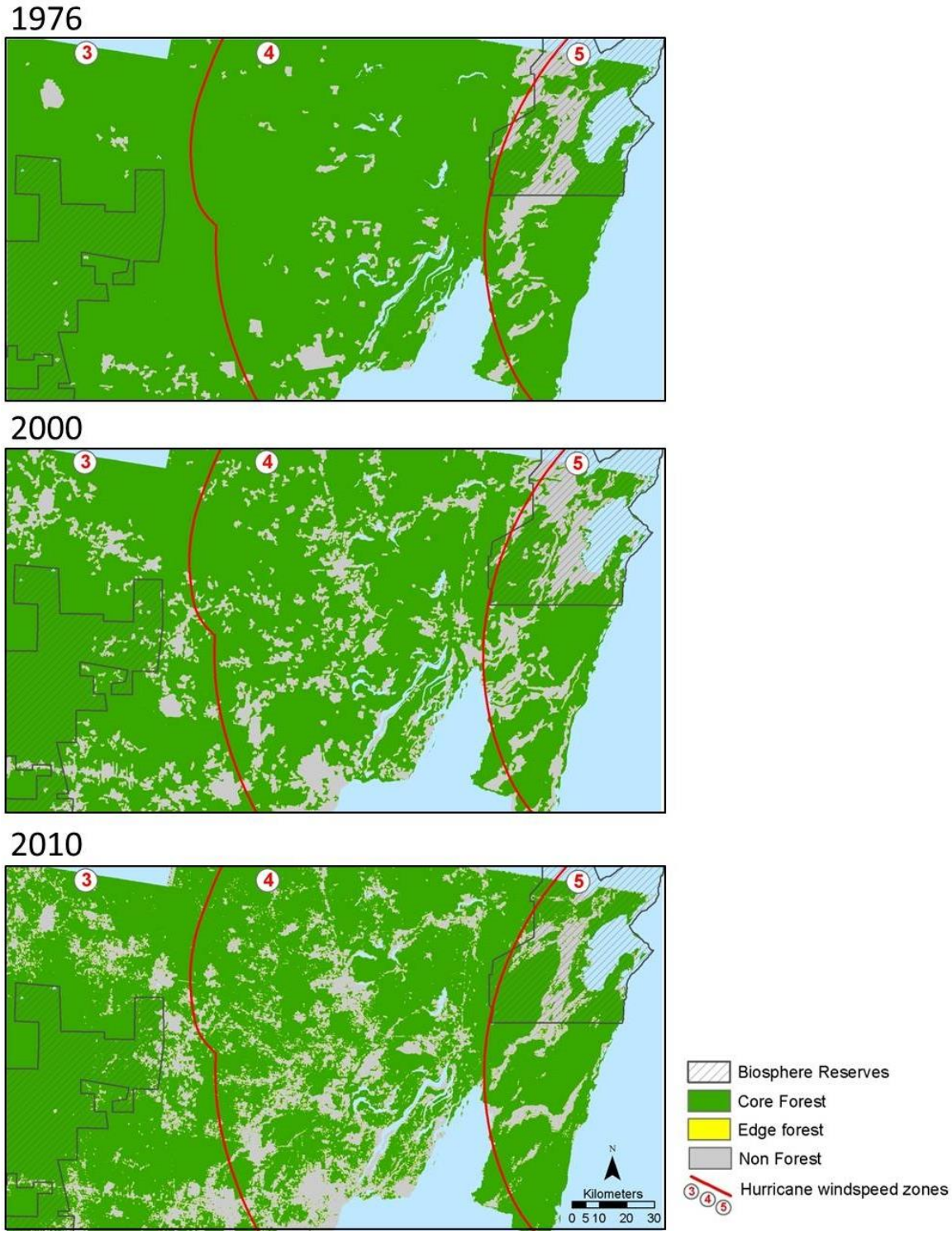

Figure 2.5: Forest fragmentation in the Calakmul – Sian Ka'an biological corridor between 1976 and 2010.

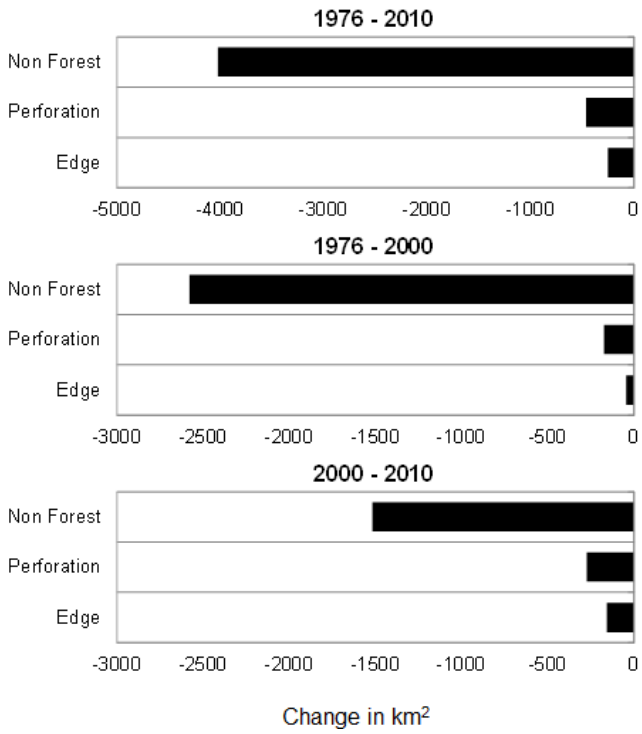

Figure 2.6: Area of core forest lost (in km^2) between 1976 and 2010.

Between 1976 and 2000 conversion of *core forest* to *non-forest* was highest (92.2%), while the conversion to *perforation* (6.0%) and *edge* (1.8%) was less pronounced. Between 2000 and 2010 the proportion of *core forest* that changed to *non-forest* was lower than during the 1976-2000 time period (52.2%), while the proportion that changed to *perforation* (34.4%) and *edge* (13.4.0%) increased.

At the *ejido* level there was also an increase in forest fragmentation through time. This is evident when looking at the changes in the proportion of *core* vs. *fragmented forest* by *ejido* (Figure 2.7). Almost all the *ejidos* located within the study area experienced a marked increase in the proportion of *fragmented forest* over the 34 year time period, as indicated by the increase in the number and length of black bars in this figure. Although these changes took place at different rates and to different degrees

amongst the different *ejidos*, the median of the proportion of *core forest* lost to *fragmented forest* between 1976 and 2010 was 5%, with 88 (53%) *ejidos* experiencing loss above this value. As *fragmented forest* include all non-core forest classes (i.e. edges and islets), these results clearly indicate that forests remaining within the *ejidos* in 2010 are overall more exposed to edge effects than the original forests from 1976.

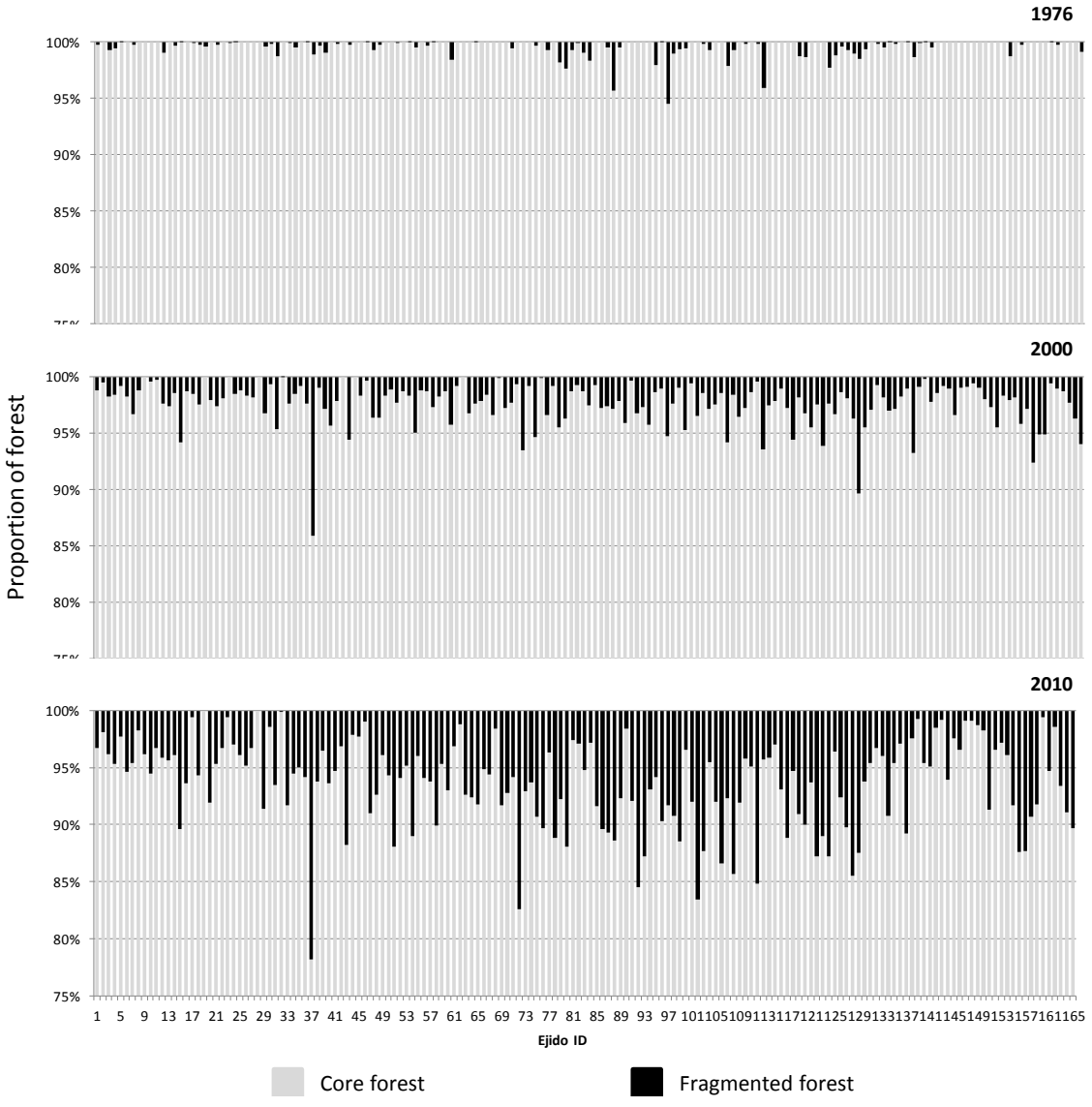

Figure 2.7: Proportion of core forest (grey) and proportion of fragmented forest (black) per *ejido* for 1976, 2000 and 2010.

2.3.2: Measuring the relation between forest fragmentation and land use

Different land uses and land management practices could explain at least in part the different rates and extent of forest fragmentation for the *ejidos* of the Calakmul – Sian Ka'an corridor between 1976 and 2010 (Table 2.4). In 2010, *ejidos* dominated by agricultural activities (e.g., shifting cultivation, pastures, mechanized agriculture; N=34) have significantly higher proportions of *edge forest*, higher ratios of *edge/core*, and lower proportions of *core forest*, than *ejidos* predominantly dedicated to forestry (e.g., timber management; N=12). On average, agricultural *ejidos* have 1.87% less *core* forest than forestry *ejidos*, and 1.86% more *edge* forest.

Table 2.4: ANOVA results of the fragmentation indicators in 2010 by land use type at the *ejido* level (Agricultural, N=34; Forestry, N=12).

Fragmentation Indicator	Mean Percent Agricultural (s.d.)	Mean Percent Forestry (s.d.)	F	Prob > F
Proportion Core	95.88 (±2.91)	97.75 (±1.54)	4.44	0.04*
Proportion Perforated	1.20 (±1.38)	0.68 (±0.93)	0.50	0.48
Proportion Edges	4.11 (±2.90)	2.25 (±1.55)	4.43	0.04*
Edge/Core Ratio	0.04 (±0.03)	0.02 (±0.02)	4.44	0.04*

2.3.3: Relation between forest fragmentation and hurricane damage

For the entire corridor, the results of the linear regression, do not point to a significant correlation between forest fragmentation (measured as edge density) and damage caused by hurricane Dean ($Y = -0.241856 – 0.044337 X$; $R= -0.0418$, $t = -20.5$).

However, at the *ejido* level, the pair wise correlation results do show a significant positive correlation between fragmentation indicators and hurricane damage within wind speed zone 4 (Table 2.5). Hurricane damage was negatively correlated with *proportion core forest* (β = -0.259), and positively correlated with the *proportion perforation* (β = 0.063), *edges* (β = 0.241) and the *edge/core ratio* (β = 0.236). Only for the indicator *proportion perforation* was the relationship not significant. This result suggests that not all forest edges are the same in terms of how they relate to damage caused by a hurricane: there is a difference between "long, exterior edges" and "shorter, interior edges."

Table 2.5: Pairwise correlations of the fragmentation indicators and the average hurricane damage for the *ejidos* of the study area.

	Average Forest Damage	
	Wind speed Zone4 (N=118)	
Fragmentation Indicator	**Coeff.**	**Prob>|t|**
Proportion Core	-0.259	0.005*
Proportion Perforation	0.063	0.496
Proportion Edges	0.241	0.009*
Edge/Core Ratio	0.236	0.010*

2.4: Discussion

The purpose of this chapter was to measure forest fragmentation in Mexico's Calakmul – Sian Ka'an biological corridor over 34 years, to determine the difference in fragmentation indicators under different land uses, mainly forestry and cultivation, and characterize the relation between forest fragmentation and wind damage caused by hurricane Dean. Results obtained through spatial analysis indicate that forest fragmentation increased significantly in the corridor in the last 34 years, and that land management mediated loss of core forest and increase in edge forest are significantly correlated to high forest damage by hurricane winds.

2.4.1: Significant forest loss and fragmentation

From 1976 to 2010, the Calakmul – Sian Ka'an biological corridor lost 13% of its original forest extent, at an annual rate of 0.39%. This result falls within previous estimates of annual deforestation for the Yucatán peninsula, which range from 0.1% to 1.9%, depending on the specific location (Cairns et al. 2000; Bray et al. 2004; Turner et al. 2004; Vester et al. 2007; Díaz-Gallegos et al. 2008). The loss in forest extent within the study area is congruent with previous studies that have identified southern tropical forests in Mexico as a deforestation 'hot spot' (Achard et al.1998; Turner et al. 2001), mostly as a result of the expansion of pasturelands and agriculture (Bray et al. 2004; Lawrence et al. 2004; Díaz-Gallegos et al. 2008). This expansion is taking place in parallel to significant increases in human population in the region, which grew from 2,174 to approximately 40,000 between 1960 and 2000 according to census data (Klepeis

2003). Such a rapid population growth has markedly increased anthropogenic pressures on forests.

It is important to point out that the spatial analysis also shows a limited amount of forest growth between 1976 and 2010 within specific locations of the study region (Figure 2.4). Most of the new forest areas located within the central region are likely the result of: 1) forest regrowth within abandoned agricultural plots and pastures; and 2) young agroforestry plantations established after 1976 and identified as forests in the 2010 map. A more significant forest expansion seems to have taken place in the eastern portion of the corridor, within and around the Sian Ka'an Biosphere Reserve. However, when looking at the original forest classes in the three lands cover maps used for the analysis it becomes evident that this new forested area is likely a byproduct of differences in the classification of mangrove forests and other hydrophilic vegetation between 1976 and 2010. If this is the case, forest expansion within the reserve would have been overestimated, and the overall deforestation rate for the corridor would have been underestimated. Although this is a concern, it is a limitation of the data and could not be avoided. Nonetheless, the effect of these differences in classification is expected to be less significant within the rest of the corridor, where seasonal deciduous forests predominate and most of the *ejidos* are located.

Understanding the extent and location of deforestation in the southern Yucatán peninsula is certainly important, as previous research has found that forest loss directly impacts aboveground biomass (Read and Lawrence 2003; Eaton and Lawrence 2009), soil nutrients (Lawrence et al. 2007), biodiversity and faunal movements, as well as increases vulnerability to other disturbances such as hunting (Escamilla et al. 2000), fires,

and invasive species (Schneider 2004; Schneider and Geoghegan 2006). However, understanding the changes in the spatial structure of the remaining forests is also essential. Forest subdivision and perforation introduce fragmentation impacts (mostly in the form of edge effects) deeper into forest interiors than would be the case if forest loss occurred consistently only in the outer forest boundaries (Riitters et al. 2002). In other words, not all forests are the same, and it would be expected that all things being equal, a forest remnant with larger amounts of *core* vs. *edge forest* would fare better in the long term than a similar extent of forest characterized by a larger proportion of *edge forest*. Therefore, being able to characterize these two main types of forest, as allowed by MSPA, is very valuable.

Forest fragmentation in the biological corridor increased significantly between 1976 and 2010. The results presented in this chapter suggest that between 1976 and 2010, *core forest* was lost at an annual rate of 0.62% while fragmented forest was gained at an annual rate of 16.9%. The majority of the *core forest* lost (85.6%) transitioned to agricultural, pasture and urban areas; while the remaining 14.6% became *edge forest* (which includes small forest patches). These results clearly indicate that forests remaining in 2010 are overall more exposed to edge effects than the original forests from 1976.

Even though not all species respond in the same way to edge effects, overall the evidence suggests that the abrupt, artificial edges resulting from forest fragmentation have negative impacts on many forest species and ecological processes (Murcia 1995; Laurance and Bierregaard 1997; Laurance 2000, 2002; D'Angelo 2004). Direct effects of new edges include: 1) physical disturbance of vegetation and soils, 2) changes in the microclimatic conditions (including light, wind and moisture), and 3) increased

accessibility for mobile organisms, materials such as seeds and pollutants, and energy (Harper et al. 2005). The microclimatic changes near edges usually result in increased desiccation and temperature variability, which negatively affect many animal and plant species associated with mature forests resulting in changes to the composition of the community. Similarly, the increased openness associated to forest edges has been linked to increased predation of bird nests, while limiting the movement of forest interior species. Finally, forest fragmentation has been found to also impact ecological processes such as pollination, seed dispersal and nutrient and carbon cycling (Laurance 1997, 2000; Laurance and Bierregaard 1997). Therefore, given the increased forest fragmentation found within the Calakmul – Sian Ka'an corridor, it seems clear that these forests and their associated biodiversity are becoming more vulnerable and their long term persistence might become at risk.

Noticeably, the increase in amount of fragmented forest occurred at different rates among different *ejidos* and was significantly linked to the predominant land use within these management units. *Ejidos* dedicated mainly to forestry had significantly higher proportions of *core* forest and lower proportions of fragmented forest. A similar result was reported by Bray et al. (2004) for the *ejidos* of the *Zona Maya* in central Quintana Roo. In their research, *ejidos* more engaged in timber management tended to have larger proportions of forest area and decreasing rates of forest loss. This finding relates to a number of institutional and organizational factors of community forestry programs in Mexico (Bray et al. 2004). First, even though the majority (98%) of the timber production is associated to the exploitation of mature forests (Cabarle et al. 1997), timber extraction is predominantly selective, and must comply with strict regulations (Antinori and Rausser

2007). Second, the administration of forestry activities is controlled by the *ejidal* authorities, who act on behalf of the community as a whole and are in charge of ensuring that timber extraction complies with what was established in the forestry management plan (Bray et al. 2006; Antinori and Rausser 2007). Finally, in an effort to maintain their forest resources, many forestry *ejidos* have opted for establishing Permanent Forest Areas (PFA), that is, forest areas which were declared by the community as not subject to land use change. Bray et al. (2004) found that PFAs effectively served as a barrier to the internal agricultural frontier within *ejidos*, limiting their expansion.

2.4.2: Relation between hurricane damage and forest fragmentation

Hurricane Dean severely impacted the seasonally dry forests of the Calakmul – Sian Ka'an biological corridor in 2007. Since this was a mostly dry hurricane, most of the effects on the forests were directly associated to winds, whereas under different circumstances, rainfall-soil interactions could have also resulted in significant tip up or landslides. Therefore, this event provides an excellent opportunity to explore the relationship between forest damage caused by hurricane winds and pre-existing forest fragmentation.

An analysis of remotely sensed data pre- and post-storm mapped significant forest damage (linked to defoliation) in 83% of the biological corridor, although significant spatial variability was observed (Rogan et al. 2011). This is not surprising given the fact that the geographical patterns of structural damage and mortality after severe windstorms have been shown to be very heterogeneous across landscapes (Walker 1991; Bellingham et al. 1992; Pohlman et al. 2008) as a result of the complex interaction of different abiotic

(e.g., winds, topography, soil) and biotic (e.g., tree species, tree characteristics, stand attributes) factors (Everham and Brokaw 1996; Foster et al. 1998; Xi and Peet 2011). Results presented in this chapter suggest that forest fragmentation could explain in part this spatial variability in forest damage within the Calakmul – Sian Ka'an corridor.

Results from the correlation analysis between fragmentation indicators and forest damage show that at the *ejido* level, arguably the landscape level (i.e., ~tens of km), hurricane damage was positively correlated to the *proportion of edges*, *perforation* and the *edge/core ratio*. Therefore, unlike previous studies looking into the differences in damage near edges versus the interior (Van Bloem et al. 2005; Caterall et al. 2008; Grimbacher et al. 2008; Pohlman et al. 2008), these results suggest that fragmentation does play a role in determining forest damage due to catastrophic wind disturbances at a scale above the stand level. By aggregating the data at the *ejido* level, a pattern emerges above the large spatial variability of forest damage usually observed at the stand level due to the very variable wind gusts and turbulence experienced by the unprotected edge vegetation (Laurance 1997). However, this relationship is lost when looking at even larger scales, as indicated by a lack of a significant correlation between forest fragmentation (measured as edge density) and damage caused by hurricane Dean at the regional level (i.e., for the entire corridor). The difference between the results at the two scales of analysis might be associated to the fact that they do not correspond to the same area of extent. As stated above, the linear regression was calculated with data from the entire corridor, including both *ejidos* and surrounding areas such as the biosphere reserves, while the other analysis focused exclusively on *ejidos.*

It has been previously recognized that forest damage due to catastrophic wind disturbances is a scale-dependent phenomenon, and both spatial and temporal scales are important in understanding these effects (Xi and Peet 2011). Given the broad range of spatial scales at which the effects of hurricanes occur, the novel approach used in this chapter provides valuable insights into the relationship between forest fragmentation and wind damage to forests at a larger scale than has traditionally been used. More studies at a similar scale are necessary in the future to test if this relationship holds for similar landscapes and disturbances in other regions of the world.

Stand level studies are still important, and will be addressed for the case of the Mexican Yucatán in the next chapter.

2.5: Conclusion

The Mexican Yucatán has been subjected to a long struggle between social development and resource conservation (Klepeis 2003; Schmook and Vance 2009). The significant effects of large scale disturbances, such as hurricanes, only complicate this relationship. Understanding the linkages between land use and land management practices, natural disturbances, and land cover change will prove essential for any effort that aims to achieve sustainability and reduce vulnerability in the region. As a contribution to this effort, the results presented here suggest that forests remaining within agricultural *ejidos* may be more severely affected by the large scale storms that periodically impact the region. Therefore, preventing further forest fragmentation might reduce the damage caused by hurricane impacts. This is crucial as even in agricultural *ejidos*, local communities are highly dependent on their forests as sources of fuel wood,

construction material, medicines, fruits, animals and other economically important goods (Porter-Bolland et al. 2007).

Chapter 3: Measuring forest fragmentation at the stand level and its effect on forest damage caused by hurricane Dean within the Calakmul – Sian Ka'an corridor

3.1: Introduction

Wind disturbances are an important natural phenomenon in forests (Everham and Brokaw 1996; Ulanova 2000). Their effects vary widely in both spatial and temporal scales, ranging from brief localized perturbations that operate at the scale of individual trees or forest stands, up to large scale catastrophic events, which operate at the landscape and regional levels and can last for several hours (Foster et al. 1998; Ulanova 2000). Furthermore, the effects of any single event, particularly in the case of large scale disturbances such as hurricanes, can result in very heterogeneous patterns of damage across the impacted landscapes (Walker 1991; Bellingham et al. 1992; Everham and Brokaw 1996). Both immediate and long term effects on forest structure, composition and dynamics can result from these disturbances (Everham and Brokaw 1996; Lugo 2008).

The effect of wind disturbances on trees is relevant to a large number of disciplines, and as such has long been investigated through the lenses of botany and theoretical biology, forestry, and disaster and emergency management, among many others (Cullen 2002). Particular attention has long been paid to the effects of wind disturbances on forest plantations. Years of research have provided valuable insights on the influence of factors such as species composition, tree size, topography, soil characteristics and previous disturbances on the spatial distribution and severity of damage on forests due to chronic wind effects. However, in recent decades a shift of focus has occurred towards

understanding the effects of less frequent large scale catastrophic wind disturbances on natural forests (Everham and Brokaw 1996).

In forestry areas, wind damage can severely affect land owners as a result of the reduced revenues from damaged trees, as well as the increased management costs associated to timber salvaging, cleaning operations and altered cutting schedules (Zeng et al. 2007, 2009; Moore et al. 2013). Records show that in New Zealand approximately 63,000 ha of planted forest suffered catastrophic damage over a 65 year period as a result of 62 discrete storm events, with the extent of damage ranging from 2.8 up to 25,692 ha for individual storms (Moore et al. 2013). In Western Europe, close to 200 million m^3 of timber were levelled by storms that occurred in December of 1999, with the most affected countries losing the equivalent of two years' harvest (UNECE/FAO 2000). In the Caribbean, Lugo et al. (1983) estimated that 5 million trees died in 10 hours in Dominica due to the impact of Hurricane David. Given these impacts, researchers have aimed to understand the susceptibility of planted forest stands to catastrophic wind damage, and how to reduce this vulnerability through different management practices (e.g.; temporal and spatial patterns of clear-cuts) (Zeng et al. 2007; Moore et al. 2013).

Even though harder to quantify from an economic point of view, the damage caused by large scale wind disturbances on natural forests is equally important, and understanding the relation between the effects of this disturbances on forest damage and recovery is essential for effective forest management and conservation (Xi and Peet 2011).

3.1.1: Catastrophic wind disturbances and forest damage

The immediate effects of hurricanes on forests include widespread defoliation, biomass loss due to snapped stems and branches, as well as tree bending, uprooting and death. The latter can take place immediately after the disturbance, or be delayed for several years (Everham and Brokaw 1996; Webb et al 2014).

In addition to the direct impacts to individual trees, ecosystem dynamics are also affected as a result of the creation of light-gaps in the tree canopy, increases in the nutrient availability in the forest floor due to the fallen biomass, the creation of a patchwork pattern of forest age and height, and changes to topography (e.g., uproot mounds) (Foster et al. 1998; Ulanova 2000; Xi and Peet 2011). At longer time scales, these altered environmental conditions can impact competitive dynamics and forest succession, which in turn can alter ecosystem processes and function and result in additional structural and compositional changes (Everham and Brokaw 1996; Xi and Peet 2011).

3.1.2: Factors that influence forest susceptibility to wind disturbances

Forest damage that results from a catastrophic wind disturbance can vary widely in terms of extent and severity. Previous research has identified that the factors that determine forest susceptibility to wind damage include: 1) meteorological conditions associated to the disturbance (including duration and intensity); 2) topography, 3) stand characteristics, such as tree density and average height; 4) individual tree characteristics such as species, height, diameter, crown area, rooting depth and width; and 5) soil and

terrain conditions, such as moisture and slope (Mayer et al. 1989; Everham and Brokaw 1996; Boose et al. 2003; Zeng et al. 2007, 2009; Marra et al. 2014).

The relevance of each of these factors varies with the scale of analysis. For example, in their review of the literature, Foster et al. (1998) summarize that at the regional scale (100-500 km) the main factors that account for forest damage include: 1) the wind gradients associated to the hurricane's intensity, size and track; 2) topography, particularly large features such as coastlines and mountains; and 3) regional vegetation types. At the landscape scale (~10 km), damage is mostly determined by: 1) changes in wind speed and direction, as well as gusts and downburst; 2) topographic exposure; and 3) the specific stand characteristics such as structure, composition and history of natural and anthropogenic disturbance. The number of possible interactions of these biotic and abiotic factors is large, and in consequence the possible patterns of resulting damage are varied (Foster et al. 1998).

The ensuing complexity has rendered the search for general patterns between the different factors and measured damage rather difficult, especially when looking at natural forests (instead of forest plantations) (Everham and Brokaw 1996). For example, some studies have found that fast growing pioneer species characterized by low wood densities suffered greater damage than slower growing species with high wood densities (Zimmerman et al. 1994; Curran et al. 2008), but not others (Bellingham et al. 1995; Ostertag et al. 2005; Van Bloem et al. 2005). Many studies have found that hurricane damage generally increases with tree height and diameter (e.g., Walker 1991; Ostertag et al. 2005; Van Bloem et al. 2006; Vandecar et al. 2011; McGroddy et al. 2013), although

others have not found a significant relation between tree size and damage patterns (Zimmerman et al. 1994; Bellingham et al. 1995; Metcalfe et al. 2008).

What is the role of forest fragmentation? Forest fragmentation is an additional factor affecting forest vulnerability to the damaging impacts of wind disturbances. Specifically, fragmented forests (characterized by larger edge/core ratios) are theorized to be more vulnerable than less fragmented or continuous forests to wind damage (Fahrig 2003; Catteral et al. 2008; Laurance and Curran 2008). It has been found that under normal conditions (i.e., when no catastrophic wind storms occur), wind damage near edges can result in higher rates of structural damage, windthrow and mortality than in forest interiors (e.g. Williams-Linera 1990; Laurance 1997). This relation does not seem to hold for the less frequent and more intense catastrophic wind storms such as hurricanes (Caterall et al. 2008; Grimbacher et al. 2008; Pohlman et al. 2008; but see Laurance 1991). However, research on the synergies between forest fragmentation and catastrophic wind damage has been limited. Given the global trends of increasing forest loss and fragmentation, and the predicted increase in hurricane frequency and/or intensity, more research is needed to understand the interactions of forest fragmentation and hurricane damage. In particular, it is important to conduct research that considers different spatial scales (from the local to the regional), as both forest fragmentation and wind damage effects vary by scale, as well as address both short and long term effects after the disturbance.

3.1.3: Research objectives

This chapter is focused on determining the relationship between forest fragmentation and forest damage due to the impact of hurricane Dean at the stand level. Adding this local scale of analysis complements the results at the regional and *ejido* level presented in Chapter 2, by permitting to explore if the effects of wind disturbances on forest ecosystems vary with scale. The objectives are: 1) to assess short and medium term forest damage at the forest stand level in the Calakmul - Sian Ka'an biological corridor (2008-2012); 2) to characterize pre-hurricane forest fragmentation at the forest stand level; and 3) to examine the relationship between forest fragmentation status and the damage caused by hurricane Dean in 2007 at the forest stand level. "Stand level" refers to a scale of a few hundred meters, within which relatively homogeneous units of continuous forests can be found. I hypothesize that a significant component of stand level damage was only noticeable several years after the hurricane impact due to the lagged mortality of stems. I expect overall damage was higher in forest stands located in areas of higher forest fragmentation (i.e., surrounded by more and larger non-forest areas, with higher ratios of edge/core forest).

A combination of field surveys of hurricane damage, remote sensing, MSPA and correlation analysis were used to accomplish these objectives.

3.2: Data and Methods

The study area for the analysis presented in this chapter corresponds to the Calakmul - Sian Ka'an corridor first described in Chapter 1 (Figure 1.3).

3.2.1: Field data collection of hurricane damage

Damage caused by Hurricane Dean to the forests of the Calakmul-Sian Ka'an corridor was first evaluated at the scale of individual forest stands by means of a field-based plot assessment conducted between May and July 2008, approximately nine months after the hurricane impacted the region (Vandecar et al. 2011; McGroddy et al. 2013). A total of 91 plots of 500 m^2 (5 m x 100 m) were established across the corridor (Figure 3.1) according to a stratified sample limited by forest presence, type and potential damage (as defined by the linear differencing of Normalized Difference Vegetation Index MODIS products obtained prior and immediately after the hurricane impacted the region), road access and permission from local communities (Rogan et al. 2011; McGroddy et al. 2013). The field damage plots were distributed across three wind speed zones based on models of hurricane dynamics: zone 5 with winds ≥ 249km/h, zone 4 with winds 210-248 km/h and zone 3 with winds 178-209 km/h (Franklin 2008; see Figure 1.4). A total of 19 plots were located near the coast, in the zone of greatest hurricane intensity (wind speed zone 5), 42 were located inland in the zone of intermediate hurricane intensity (wind speed zone 4) and 30 were located further inland, in the zone of lower hurricane intensity (wind speed zone 3) (Figure 3.1).

It is important to note that access to the forest stands was an important consideration during the selection of the plot locations, particularly since they would be revisited every year to evaluate long term damage and recovery. Therefore, all the plots were established in close proximity to roads. As a result, there is admittedly a selection bias in the forest areas evaluated, and for most of the cases there was at least some edge effect. Nonetheless, because road characteristics varied significantly throughout the study area

from broad interstate paved roads to small dirt roads surrounded by forest (for the most part not distinguishable in Landsat satellite images; Figure 3.2), the location of the forest plot does indeed account for significantly different fragmentation conditions (i.e., from high fragmentation to continuous forest, respectively).

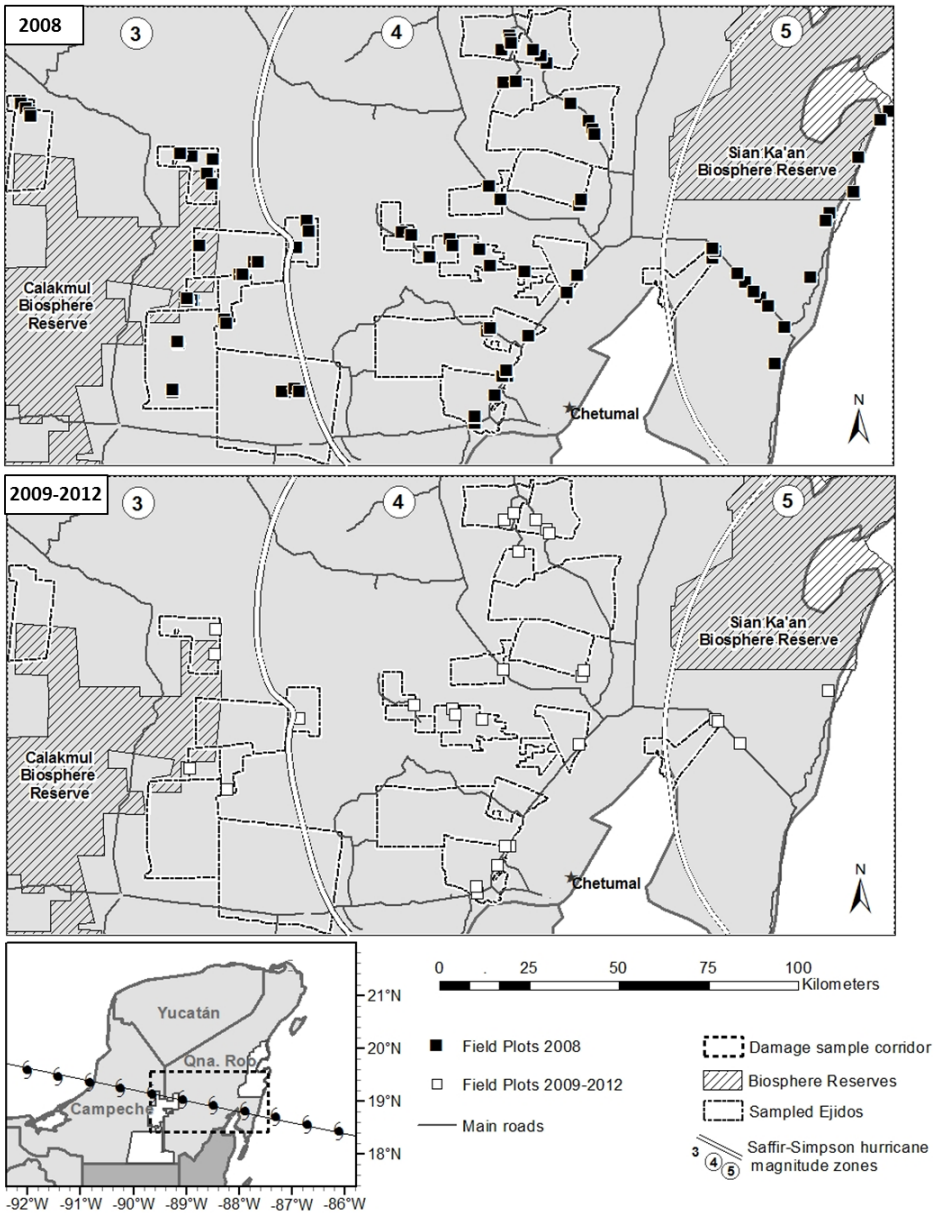

Figure 3.1: Location of the 2008 and 2009-2012 field plots across the study region.

Figure 3.2: All sampling plots were located in close proximity to roads, but these differed significantly from broad paved roads (A) to small dirt roads surrounded by vegetation (C).

In each plot, trees with a diameter at breast height (DBH) of 5 cm or more were identified to species, DBH was measured, and branch and trunk damage was qualitatively evaluated as it was readily evident even several months after the disturbance due to the substantial force of winds associated to the hurricane. Scientific names and classifications followed Arellano et al. (2003). Damage to trees was assessed using the following seven categories: no damage apparent (O), small branch damage (SB), medium branch damage (MB), bent stem (B), tree stem snapped (SS), tree uprooted (TU), and dead (D). Trees were only classified as dead when there were no signs of sprouting and the stem appeared to be dry (Vandecar et al. 2011; McGroddy et al. 2013).

A subset of 28 of the 91 forest stands sampled in 2008 was selected for revisiting and monitoring from 2009 to 2012. The selection process for the 28 plots was based on three main criteria: 1) stands of different forest types (mid-statured and low-statured forests) and with different land use histories (both based on type of use and time since last use), 2) stands that showed the highest plot basal area estimations from the 2008 data, and 3) location within the hurricane wind zones. To address the first criterion, the available 2000 LC map was used to estimate the proportion of low- and mid-statured forest, agricultural fields and pasturelands surrounding the 2008 sampling localities within a 2 km buffer, as well as to characterize the forest stands according to their age as young-secondary, old-secondary or mature. Taking into account the second criterion, when two localities shared similar landscape characteristics, priority was given to those with the largest basal area estimates from 2008. Finally, special attention was given to localities within the zone of intermediate hurricane wind speeds (wind speed zone 4).

Based on this selection, between May and July 2009, 20 plots of 500 m^2 (5 m x 100 m) were established within the area of wind speed zone 4, and four such plots within wind sped zones 3 and 5, for a total of 28 plots (Figure 3.1). The same methodology used for the damage assessment of the 91 plots from 2008 was implemented, with the addition that all stems greater than 5 cm in diameter were tagged to facilitate their location in the future. For trees that branched below 1.3 m height (i.e., multi-stem trees), each stem was recorded and measured individually and a unique numbered tag was tied around the largest stem. For all 28 plots, an effort was made to establish them within 150 m of the respective damage plots from 2008 (based on the recorded GPS locations) so that they would correspond to the same MODIS pixel in the damage maps.

The 28 plots were revisited in 2010 (May-June), 2011 (May-July) and 2012 (May-July) to record information on each of the tagged stems' DBH, current damage (particularly in the case of dead stems) and recovery. Each year, if new stems reached a DBH $\geq$ 5 cm, they were tagged, measured and incorporated into the database.

Finally, in order to further characterize forest type, successional stage and past land use of the forest stands in which the plots were located, a field survey was conducted in the summer of 2010. All the original locations of the damage plots from 2008 were revisited with local land owners, who provided information on the type of land use that had characterized the area in the past (either agriculture, pastureland, timber extraction, conservation or none) and at the time the survey was conducted (mainly fire wood and/or timber extraction, conservation or none). Forest type was determined on site primarily based on the structure and species assemblage (Vester et al. 2007).

3.2.2: Characterizing forest damage at the stand level

Basic damage statistics were estimated for each of the 91 plots from 2008 as well as for the 28 plots from 2009 and 2012. These include percent of stems and percent of basal area affected within each damage class. Since any given stem could show more than one type of hurricane damage (e.g., a stem might have experienced trunk snapping and uprooting), damage statistics are based on the most severe damage observed per stem. Damage severity was ordered as follows: small branch damage (SB) < medium branch damage (MB) < bent stem (B) < tree stem snapped (SS) < tree uprooted (TU) < dead (D) (McGroddy et al. 2013).

The analysis presented here considers all the stems recorded in the field, including palms, and counts each recorded stem separately (even if they are part of a multi-stem individual). This differs slightly from the analysis conducted by Vandecar et al. (2011) and McGroddy et al. (2013), as these authors excluded palms from their analysis and for some purposes grouped stems from the same individual.

Survival and mortality rate: The data from the 28 plots was used to estimate the five-year survival after the hurricane impact for: 1) all stems in the plots, 2) stems sustaining significant damage from the hurricane (TU, SS, B and MB), and 3) stems sustaining minimum or no damage (SB and O). Since there are no data available on the number of trees that were alive in the field plots prior to the impact of the hurricane (2007), an estimate was calculated as the number of stems recorded as alive in 2009 plus those that were recorded as dead due to the hurricane impact. The five-year survival was then calculated as the percentage of stems presumed alive in 2007 that were still alive in 2012 (Webb et al. 2014). Additionally, the overall annual mortality rate (AMR) for the period 2007- 2012 was calculated as a percentage using the following equation:

$$m = \frac{\ln(N\,o) - \ln(Nt)}{t}\, x\ 100$$

where N_0 is the number of stems alive in 2007, *Nt* is the number of stems alive in 2012, ln(*N*) is the natural logarithm of *N* and *t* is 5 (i.e., 2012-2007) (Condit et al. 1995).

Mortality rate calculations consider only those deaths presumably resulting from damage associated to the hurricane impact, and do not include mortality resulting from anthropogenic impacts (such as cutting or fire, which were also recorded in several instances when the plots were revisited).

Damage Indices: The percent of stems and percent of basal area within each damage class were used to estimate two separate overall Damage Indices for each plot (MAX Damage Index and BA Damage Index, respectively). This was done both for the 91 plots from 2008 and for the 28 plots from 2009. The indices were calculated using a weighted linear combination algorithm using the WEIGHT function in IDRISI Selva (Eastman 2012). Weights were estimated by pairwise comparisons of the impact of the different types of recorded damage in order to establish their relative importance (based on the same severity order from above). This resulted in a set of eigenvalue weights, one for each damage category (Table 3.1). The resulting indices ranged from 0 to 1, with larger values indicating a greater general level of recorded damage across the plot.

Table 3.1: Description of the damage categories and their assigned coefficients for the calculation of the Damage Indices.

Damage category	Description	Coeff. for Index
None (O)	Non damage apparent	0.000
Small branch damage (SB)	Branches< 5cm broken	0.0267
Medium branch damage MB)	Branches > 5cm broken	0.0361
Bend (B)	Bend (leaning) tree	0.0708
Tree snapped (SS)	Stem snapped (crown missing)	0.1369
Tree uprooted (TU)	Tree uprooted	0.2589
Dead (D)	Tree dead (suspected by hurricane)	0.4705

3.2.3: Characterizing forest fragmentation at the stand level

Mapping pre-hurricane land cover and land use: In order to characterize forest fragmentation at the stand level, a pre-hurricane 2007 land cover map (2007 LC map from now on) was produced, focusing on identifying forest *vs.* non-forest areas. This map is based on the interpretation of four different satellite images: Landsat-7 ETM+ from 07

January 2006 and 27 February 2007 (Path 20, Row 47; western part of the study region), Landsat-7 ETM+ from 09 April 2007 and 25 April 2007 (Path19, Row 47; eastern part of the study region) (Figure 3.3). These dates correspond to the second half of the dry season in this region, which usually extends from November to mid-May (Foster and Turner 2004). The classification process included the following steps.

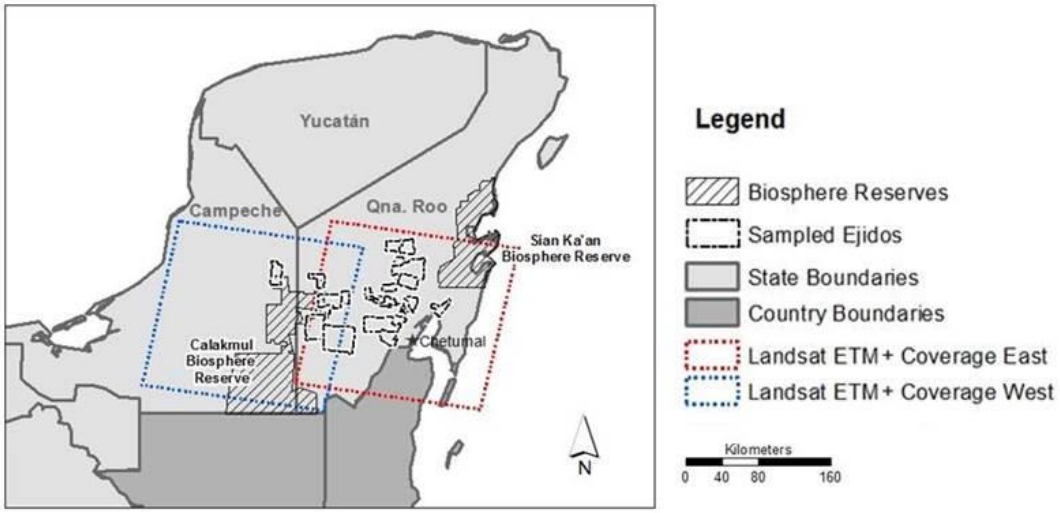

Figure 3.3: Coverage of Landsat-7 ETM+ satellite images used for mapping pre-hurricane 2007 land cover in the region. West (blue): Path 20, Row 47; East (red): Path 19, Row 47.

First, a line infilling algorithm was used to correct for the Landsat-7 ETM+ scan line corrector error. To reduce missing data due to cloud cover, two different corrected images were created for the eastern portion of the study region, and only one corrected image for the western portion of the region (Figures 3.4 and 3.5, respectively).

Second, a mask that only covered the ejidos where damage plots were established in 2008 was applied to the corrected images to reduce the extent of the study area, and therefore, to reduce the landscape variability that had to be considered in the

classification. This was done to improve the accuracy of the resulting classification, which was crucial in order to characterize forest fragmentation at a local scale (i.e., stand level).

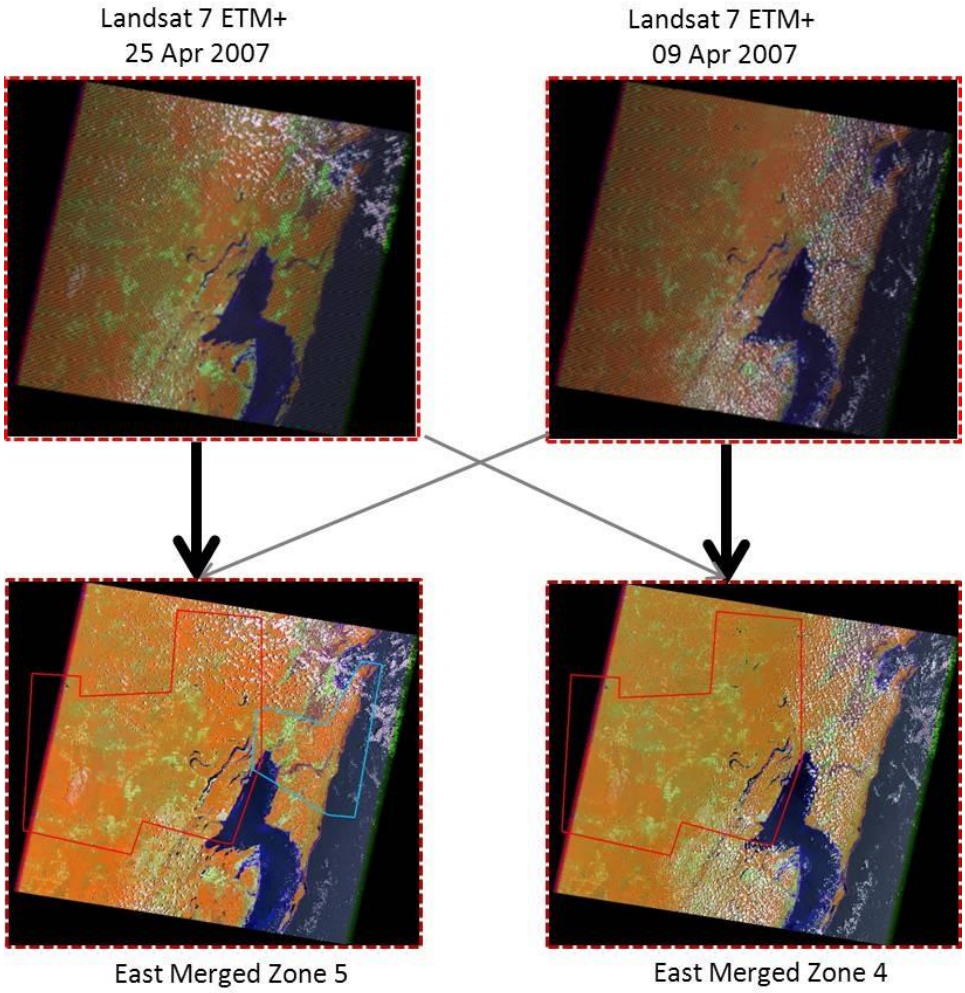

Figure 3.4: Landsat 7 ETM+ satellite images used to map the pre-hurricane 2007 land cover of the eastern portion of the study region. To reduce missing data due to cloud coverage, two different corrected images were created by using each of the satellite images as the main data (wide arrow) and the other as the filler data (thin arrow). The area of the masks used for wind speed zone 5 (blue) and wind speed zone 4 (red) is indicated.

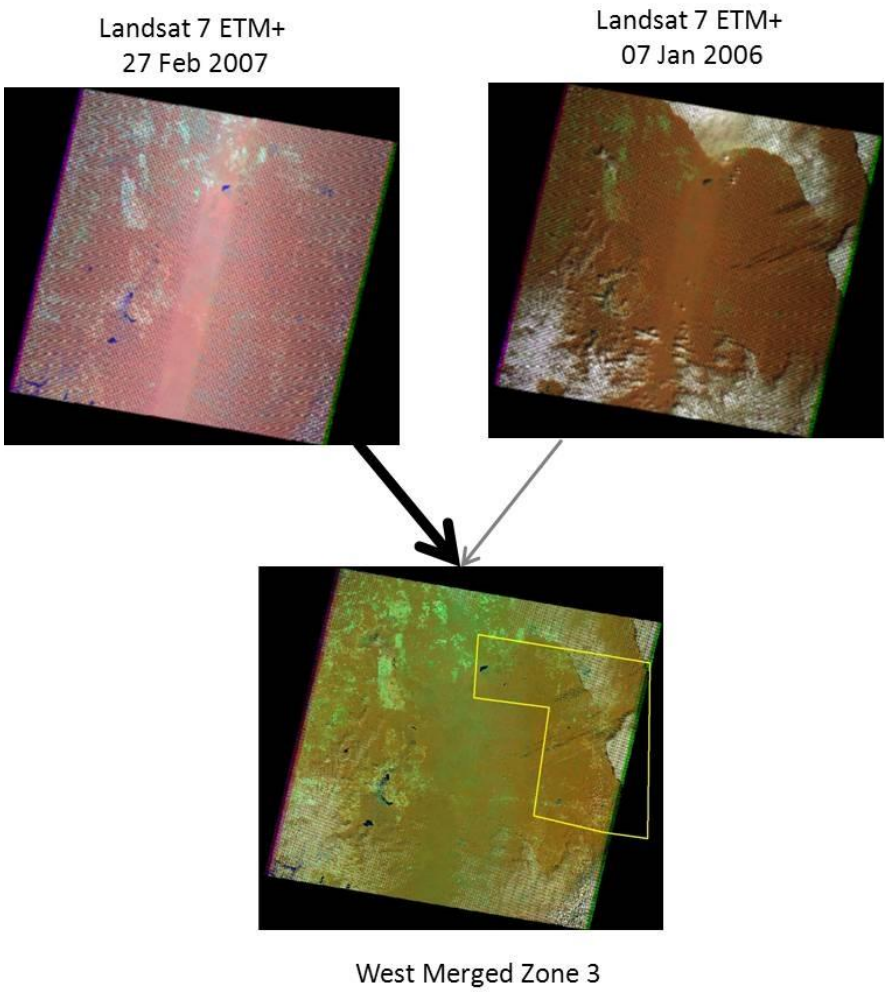

Figure 3.5: Landsat 7 ETM+ satellite images used to map the pre-hurricane 2007 land cover of the western portion of the study region, and the resulting merged image created by filling the scan line errors of the image from February 27 2007 with data from the image from 07 January 2006. The area of the mask used for wind speed zone 3 (yellow) is indicated.

Third, each masked image was then classified separately by conducting an unsupervised classification using the ISOCLUST classification module in IDRISI Selva (Eastman 2012), and matching the resulting clusters with one of six predefined land use and land cover classes (Table 3.2). For this classification, all the different forest types (e.g., low-statured, medium-statured, mangrove) were grouped into a general "forest" class.

Table 3.2: Land cover classification used for the pre-hurricane 2007 land cover map, and equivalency used for the binary forest/non-forest map (NF: reclassified as Non Forest; F: reclassified as Forest).

Vegetation Type and land use	Forest/Non forest
0. Clouds and shadows	Background
1. Forest (including mangroves)	F
2. Marsh and coastal vegetation	NF
3. Agriculture, pastures and bare soil	NF
4. Urban settlements	NF
5. Water	Background

Fourth, clusters corresponding to mixed land cover classes (e.g., cloud shadows, marsh and low-statured inundated forests) were isolated and further separated by conducting a supervised classification using the MAXLIKE classification module. Training sites were defined based on familiarity with the landscape through field work and examination of higher resolution images available in Google Earth.

Finally, a mosaic of the three separate land cover and land use maps was created using the module CONCAT in IDRISI Selva (Eastman 2012). For overlapping areas, priority was given to the map that had the least amount of missing data due to cloud cover.

The pre-hurricane 2007 LC map was then reclassified to a binary forest/non-forest map (Table 3.2) for use in a forest fragmentation analysis at the stand level. The accuracy of this map was evaluated using seven SPOT satellite images acquired between March 2006 and April 2007 as reference (Table 3.3). The seven images were geo-rectified to match the Landsat TM and ETM+ images used for the land cover classification using a

1st polynomial bilinear interpolation transformation, with at least 8 ground control points and an overall RMS error <10 (i.e., less than half a pixel) in each case. The SPOT images have a pixel resolution of 20m, and it is possible to differentiate forested *vs.* non forested areas through visual inspection. A total of 150 points were chosen with the SAMPLE module in IDRISI Selva (Eastman 2012) using a stratified random sampling scheme, and the cover compared between the 2007 forest/non-forest map and the satellite images. It is important to note that no SPOT images were available for the western most part of the study area. Therefore, the location of the reference points for the accuracy assessment was limited to wind speed zones 3 and 4.

Table 3.3: List of SPOT images used for the accuracy assessment of the 2007 forest/non-forest map.

Date acquired	Reference Grid	
	K (column)	J (row)
16 March 2001	607	311
11 April 2007	610	311
16 April 2007	607	312
17 April 2007	609	312
11 April 2007	610	312
17 April 2007	609	313
06 March 2006	611	313

Quantifying forest fragmentation at the stand level: In order to quantify forest fragmentation locally at the stand level (i.e., around each field damage plot), the 2007 forest/non-forest map was used to conduct a MSPA using the software Guidos 1.4 (Vogt

2010). A 30 m edge width, equivalent to the minimum pixel size, and an eight-neighbor connectivity rule were selected for the analysis.

Three different indicators derived from MSPA, similar to those used to characterized forest fragmentation in Chapter 2, were used to assess the patterns in forest fragmentation and spatial configuration around each field damage plot: *proportion forest*, *proportion edge* and *edge/core ratio*. These indicators provide a measure of the amount of core and edge habitats in the landscape (Wright 2011), as well as of the extent of non-forest areas around the forest stands, which might facilitate wind effects associated to the hurricane impact.

Each of these indicators was estimated within five different circular buffer zones around the starting point of each plot, the area of which was determined by the following radiuses: 250m (Buffer area: 0.20 km^2), 500m (Buffer area: 0.79 km^2), 1km (Buffer area: 3.15 km^2), 2 km (Buffer area: 12.57 km^2), and 4 km (Buffer area: 50.28 km^2). All fragmentation indicators were calculated as a percent of the amount of forest present in the different sized buffer zones in order to avoid the effect of differences in the initial amount of forest on the fragmentation pattern analysis. This is particularly important to account for differences due to missing data in the 2007 LC map, mostly because of the effect of clouds and the remaining missing pixels from Landsat7 ETM+ scan line error.

3.3: Results

3.3.1: Characterization of field plots

A total of 6,312 stems were recorded for the 91 plots during the damage assessment of 2008. In 2009, a total of 2,938 stems were tagged and recorded within the 28 plots.

This number increased to 3,155 stems by 2012, due to the incorporation of new stems that reached a DBH ≥5cm.

Note that given the slightly different samples, the values reported here for the 91 plots from 2008 are somewhat different from the values reported by Vandecar et al. (2011) and McGroddy et al. (2013). Nonetheless, the patterns are very similar.

The forest stands assessed in this study are heterogeneous, encompassing a variety of forest types and successional stages. Among the 91 field plots from 2008, five main different forest types were identified (Table 3.4), while three forest types were identified for the 28 monitoring plots in 2009 (Table 3.5). In both cases, most forest stands correspond to medium-statured forests (s*elva mediana*), followed by low-statured forests (*selva baja* and *selva baja inundable*). A few field plots showed mixed elements of more than one forest type, particularly along the coast (within wind speed zone 5), where transitional forest types that combine mangroves and some other type of forest or coastal vegetation where found. Common species within the field plots include *Piscidia piscipula* ("Jabín"), *Bursera simaruba* ("Chacá"), *Croton reflexifolius* ("P'erezkuts"), *Metopium brownie* ("Chechem"), *Vitex gaumeri* ("Yaxnik"), *Lonchocarpus xuul* ("Xu'ul"), *Luehea speciosa* ("Kaskat") and *Lysiloma latisiliquum* ("Tzalam ") (see Appendix A.1). The most common plant family in the field plots was Fabaceae, corresponding to 20% of the identified stems, followed by the families Polygonaceae and Sapotaceae, each corresponding to 8% of the identified stems (Appendix A.2)

Table 3.4: Characterization of the 91 plots by forest type, number of stems, DBH and basal area in 2008. The number of plots of each type is indicated in parentheses.

Forest Type	**Total No.**	**Mean**	**Mean BA**

	of Stems	DBH (cm)	(m^2/ha)
Mangrove (3)	98	17.2	22.5
Mangrove - Selva baja (3)	180	12.7	23.7
Selva baja (9)	690	11.3	21.0
Selva baja inundable (14)	967	11.7	21.1
Selva mediana (62)	4377	14.3	35.2

Table 3.5: Characterization of the28 plots by forest type, number of stems, DBH and basal area in 2009. The number of plots of each type is indicated in parentheses.

Forest Type	Total No. of Stems	Mean DBH (cm)	Mean BA (m^2/ha)
Selva baja (1)	104	9.0	16.8
Selva baja inundable (4)	623	8.7	22.9
Selva mediana (23)	2211	10.8	25.8

The land use field survey conducted in 2010 indicates the majority of forest stands assessed in the study correspond to mature or secondary forests over 20 years old: 66 (73%) of the 91 plots measured in 2008, and 19 (68%) of the plots measured in 2009-2012. The rest of the field plots were located in forest stands younger than 20 years old, and in at least one case, younger than 10 years old (see Appendix A.3 and A.4 for a detailed description of the 28 field plots established in 2009). As is very common in the region, most of the areas where the field plots were located had been subjected to previous use by local communities in recent decades, predominantly agriculture/pastures (40% of the 91 plots and 50% of the 28 plots), and timber extraction (33% and 36%, respectively). A smaller number of plots had no registered previous land use (27% and 14%, respectively).

Trees sampled in 2008 were on average larger than those sampled in 2009 (Tables 3.4 and 3.5). Average plot basal areas were also higher in 2008 than 2009. In 2012, a small percentage of the trees tagged in 2009 (2.4%) had been cut as a result of deforestation associated to road clearing and timber extraction, and in one case, in order to clear the land for building houses. In addition, a plot burned down during the summer of 2011 due to a forest fire. At the end of 2012 summer field season, only 26 of the 28 monitoring plots remained.

3.3.2: Forest fragmentation and hurricane damage at the stand level

Correlation analyses were used to determine the statistical relationship between forest fragmentation and hurricane damage at the stand level (i.e., around each field damage plot). This was done using the damage indicators at the plot level (percent of stems affected within each damage class and MAX Damage Index) and the three fragmentation indicators derived from the 2007 forest/non-forest map: *proportion forest, proportion edge* and *edge/core ratio*. The correlations were estimated for each of the buffer zones used to characterize forest fragmentation at the stand level (250m, 500m, 1km, 2 km and 4 km), and the sample was adjusted to include all plots or stratified by wind speed zones, the latter in order to account for differences in the strength of hurricane winds.

For the 91 plots from 2008, the statistical significance of the correlations was tested using Pearson correlation coefficients (r) with Bonferroni-adjusted P values for significance levels at a = 0.05. A similar analysis was conducted for the 28 plots using both the damage indicators at the stand level estimated from 2009 and 2012. Given the

small sample size, the non-parametric Spearman's rank correlation coefficients (*rho*) with Bonferroni-adjusted *p* values for significance levels at a = 0.05 were used instead. All statistical analyses were conducted with Stata/MP 13.1for Windows.

3.3.3: Characterizing forest damage at the stand level

The 2008 field damage assessment indicates that more than half (51%) of the stems recorded suffered moderate to severe damage (i.e., major branch damage or higher) as a result of the impact of hurricane Dean (Table 3.6). This level of damage was still evident in 2009, almost two years after the hurricane made landfall (Table 3.6). Results on the average percent of stems and basal area affected by the storm are consistent between both years. In 2008, stem snapping was the most common severe damage recorded, followed by the loss of major branches, bending and tree uprooting. Death was the less common damage associated to the hurricane. A similar pattern was observed in 2009, with the exception of more dead than uprooted trees being recorded at this time. This difference signals lagged stem mortality after severe damage.

Table 3.6: Average percent of stems and basal area (BA) affected by a certain damage category in each field plot (corresponding to the maximum damage recorded per stem). For the 2012 column, only stems that were tagged in 2009 were included. For 2008 *N*= 6,312; for 2009 and 2012 *N*=2938.

	Average % of affected stems			**Average % of affected BA (m^2/ha)**		
Damage Class	**2008**	**2009**	**2012**	**2008**	**2009**	**2012**
None or SB	48.8	53.2	58.1	43.5	42.9	53.5
MB	11.0	8.2	5.1	15.5	20.7	9.6
B	10.4	10.9	7.8	5.8	7.4	5.5
SS	17.5	16.1	5.3	22.2	17.5	5.5

TU	6.5	2.7	1.8	7.3	2.5	1.1
D	5.6	8.7	14.6	5.5	8.7	21.8
DNH	0.2	0.1	4.6	0.2	0.1	3.0
CUT/FIRE	0	0.2	2.7	0	0.1	0.1

For individual field plots, a large variability in sustained damage was observed both in 2008 and 2009. In 2008, moderate to severe maximum damage (≥MB) of at least 80% of stems was recorded in 13 of the 91 plots, while 54 of them had at least 50% of stems with this type of damage. The most common major damage reported was stem snapping, occurring on average on 17.5% of stems per plot. At least 25% of stems had suffered snapping in almost a third of the 91 plots, and in the most severely damaged plot, 56% of stems had been snapped. There were on average more uprooted (6.5%) than dead (5.6%) stems per plot, and 22 of the 91 plots had over 10% of uprooted stems. Less than 5% of dead stems were recorded in 66 (73%) of the plots, but in one plot 80% of stems had died.

Two years after hurricane Dean's impact, the storm's damage on the forests was still quite evident. In 2009, the average percent of stems per plot with snapping reported as the maximum damage was 16.1%. Only a fourth of plots showed snapping in more than 25% of stems as the most severe damage recorded, with the maximum damage observed in a plot where 38% of stems had been snapped. None of the 28 plots showed moderate to severe damage to more than 70% of stems. However, 16 plots had at least 50% of stems that had lost major branches or were more severely affected, and only 1 plot had less than 20% of stems with this type of damage. The average number of stems for which uprooting was the most severe damage recorded was lower than the previous year (2.7%);

but there were a higher proportion of dead stems per plot (8.7%). Only 8 (29%) of the 28 plots had less than 5% of dead stems,

Five years after the disturbance, in 2012, the storm's legacy on forest structure was still evident as bending, stem snapping and uprooting were recorded for an average 15% of stems in the field plots. Nevertheless, at this time, the most significant observation was that a large proportion of the stems that had survived the immediate impact of the hurricane had subsequently died. On average, 14.6% of stems per plot were reported as dead in 2012, in comparison to only 5.6% of stems in 2008 and 8.7% of stems in 2009. The dead stems accounted on average for 21.8% of the basal area of each plot. Only 2 (8%) of the 28 plots had less than 5% of dead stems, and the highest mortality was recorded in a plot were 46% of stems had died. The results of a more detailed analysis of this delayed mortality are presented in the next section.

For all damage classes, there was a positive linear correlation between the proportion of stems and the proportion of basal area affected by field plot (Figure 3.6 and 3.7). The slope of these correlations provides information on how a given type of damage varied by stem size (DBH). Slopes >1 suggest that larger stems were more affected in the plots, while slopes <1 suggest that smaller stems were disproportionally affected. A slope of 1 suggests damage was evenly distributed across all stem sizes (McGroddy et al. 2013).

Results suggest than in the 91 plots from 2008, the slope of the relationship between basal area and stem number is greater than one for major branch damage, snapped, uprooted and dead; that is, stems with larger DBH were more likely to be affected by these types of damage. In contrast, for bent stems the slope of the relationship was significantly less than one, indicating that stems with smaller DBH were most likely to be

affected. For the remaining damage classes (no damage, small branch) the slope did not differ from one, suggesting damage was evenly distributed among the diameter classes.

For the 28 plots from 2009, somewhat different results were obtained. For stems recorded that year, results suggest that larger stems were more likely to have suffered major branch damage, or no damage, as the slope of the relationship between basal area and stem number was significantly greater than one. Meanwhile, the slope was significantly less than one for the small branch, and bend damage categories, suggesting that smaller stems were more likely affected. The slope of the relationship did not significantly differ from one for any of the major damage classes (stem snapped, uprooted, dead), suggesting that within the field plots sampled , these types of damage were evenly distributed among stems with different DBH sizes.

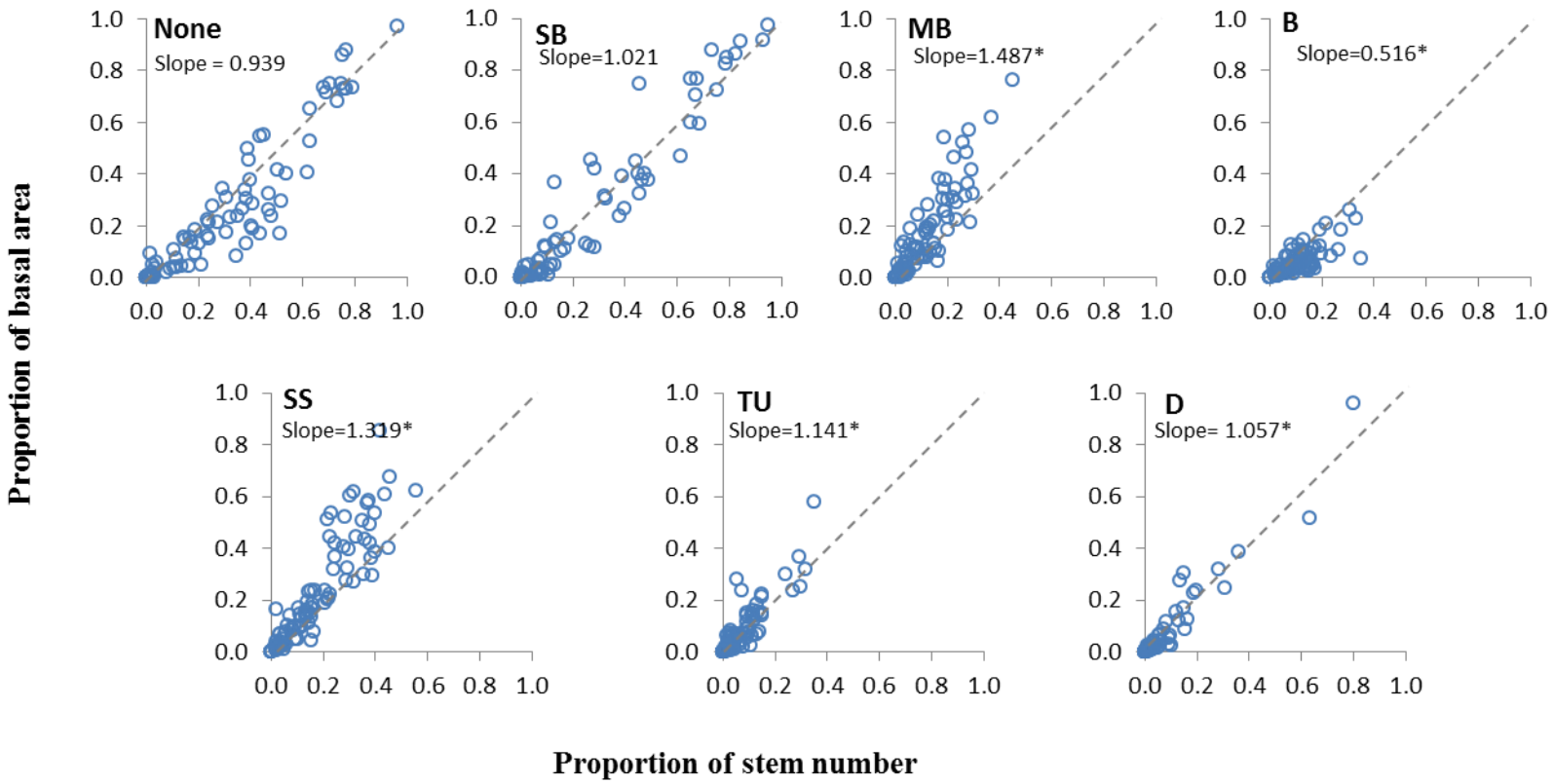

Figure 3.6: Plots of proportion of stems affected by damage (x-axis) versus proportion of biomass within a plot affected by the same type of damage (y-axis) for the damage field plots assessed in 2008. Each point represents one 0.05 ha plot (*N*=91) (modified from McGroddy et al 2013 to include palms). Asterisks indicate slopes significantly different from 1 (α = 0.05).

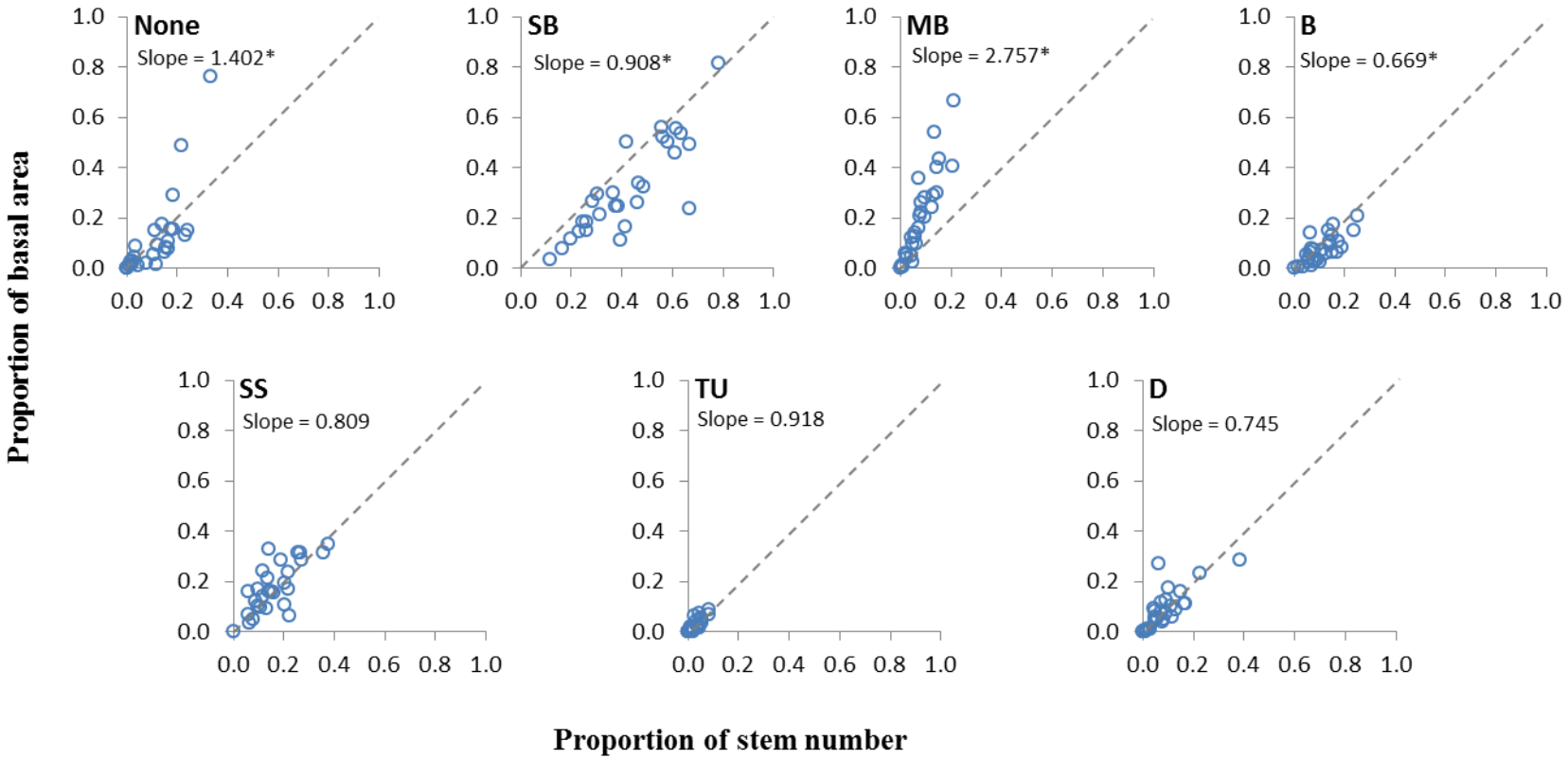

Figure 3.7: Plots of proportion of stems affected by damage (x-axis) versus proportion of biomass within a plot affected by the same type pf damage (y-axis) for the monitoring field plots assessed in 2009. Each point represents one 0.05 ha plot (N=28). Asterisks indicate slopes significantly different from 1 ($\alpha = 0.05$).

Survival and mortality rates: Death of stems after a storm like hurricane Dean can take place within the first year, or several years after the damage occurred. The data recorded from 2009 to 2012 provides valuable insights into this issue (Table 3.7). In 2009, the highest stem mortalities were associated to uprooting and trunk snapping. Out of the 256 dead stems reported that year, 78.5% had been uprooted or snapped. In fact, up to 34.4% of all the stems that were uprooted and 26.0% of the stems that suffered snapping had died in 2009, two years after the hurricane struck the forests of the Calakmul – Sian Ka'an corridor. By 2012, five years after the hurricane impacted the region, an additional 22.4% of the uprooted trees and 10.2% of the snapped stems had died.

Bent stems also experienced higher mortality than stems for which none or only branch damage was reported in 2009 (Table 3.7). Bend damage was associated to 7.4% of stem deaths that year. Overall, 5.1% of all bend stems had died by 2009, while a further 7.8% died between 2010 and 2012.

Table 3.7: Number of stems that died between 2009 and 2012 by hurricane damage class. Percentages in relation to the total number of stems recorded within a given damage class are shown in parentheses.

Damage Class	No. of stems alive in 2009	No. of dead stems in 2009	No. of stems that died between 2010-2012
None	287	15 (5.0)	10 (3.3)
SB	1272	16 (1.2)	29 (2.3)
MB	229	5 (2.1)	6 (2.6)
B	352	19 (5.1)	29 (7.8)
SS	450	158 (26.0)	62 (10.2)
TU	82	43 (34.4)	28 (22.4)
TOTAL	**2,672**	**256 (8.7)**	**164 (5.6)**

The overall five-year survival rate was 85.7%, corresponding to an annual mortality rate of 3.1% (Table 3.8). As mentioned before, stem survival and mortality varied markedly depending on the maximum damage that it had suffered, with uprooted trees having the lowest survival at 43.2% (AMR = 16.8%), followed by snapped stems at 63.8% (AMR = 9%). In contrast, stems that only lost small branches or that showed no apparent damage had a survival of 95.6% (AMR = 0.9%).

Table 3.8: Survival and mortality rates by damage category and overall for the period 2007-2012.

Damage Class	Survival 2007-2012	Mortality rate
None or SB	95.6	0.9
MB	95.3	1.0
B	87.1	2.8
SS	63.8	9.0
TU	43.2	16.8
Overall	**85.7**	**3.1**

Damage Indices: The values of the weighted damage indices also showed high variability among plots (Figure 3.8). In 2008 (*N=91*), the MAX Damage Index ranged between 0.005 and 0.389 (average = 0.084), while the BA Damage Index ranged between 0.004 and 0.453 (average = 0.090). In 2009 (*N=28*), the MAX Damage Index ranged between 0.018 and 0.216 (average = 0.087), while the BA Damage Index ranged between 0.006 and 0.197 (average = 0.093).

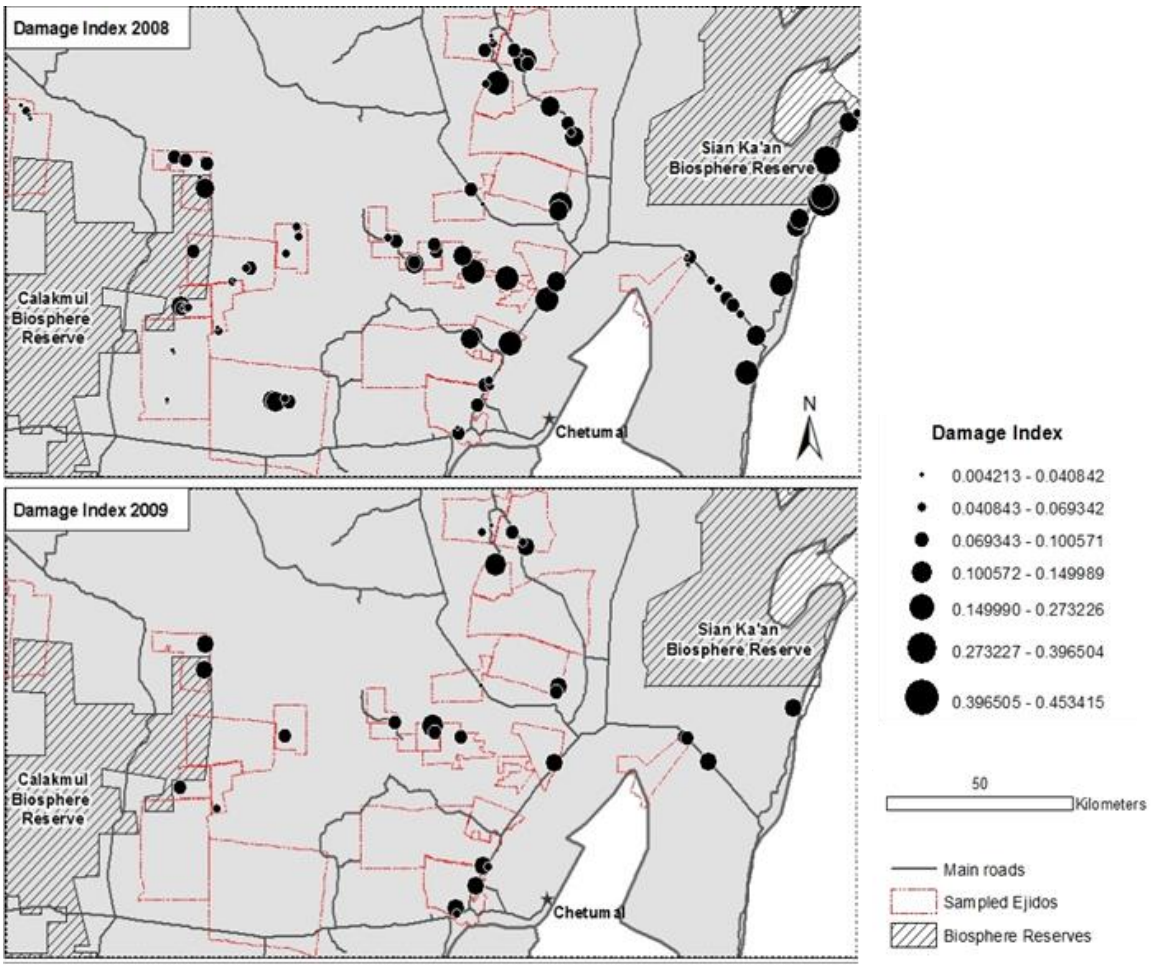

Figure 3.8: Estimated BA Damage Index for each of the 91 plots in 2008 and the 28 plots in 2009 based on damage recorded in the field.

Overall, data from the 91field plots assessed in 2008 suggests that forest stands older than 20 years old suffered on average higher damage, as reported by the MAX Damage Index, than younger forest stands ($t(89)=2.91$, $p<0.05$). Similarly, damage was reportedly higher within medium-statured forests than low-statured forests ($t(89)=1.05$, $p<0.05$) (Table 3.9).

Table 3.9: Average values of the MAX Damage Index per plot in 2008, by forest type

and age.

Forest Type/Age	No. of Plots	Mean (s.d.)
Forest < 20 years old	25	0.056 (0.028)
Forest >20 years old	66	0.095 (.065)
Low-statured forest	23	0.067 (0.032)
Medium-statured forest	62	0.078 (0.044)

3.3.4: Characterizing forest fragmentation at the stand level

Mapping pre-hurricane land cover and land use: The 2007 LC map (Figure 3.9) shows that forests are the dominant land cover in the study area, followed by agriculture, pastures and bare soil. Marshes and coastal vegetation are the third dominant land cover; while urban settlements occupy the least extend of area, with Chetumal in the south east being the largest city found in this area.

Once reclassified to a binary forest/non-forest map, the overall accuracy was found to be 93.4% (Figure 3.10). The user's accuracy, the probability that the classes in the map accurately represent the ground land covers, was 95.2% for the forest class and 83.3% for non-forest. Finally, the producer's accuracy, the probability that ground land covers where correctly classified in the map, were 96.8% and 87.0%, respectively.

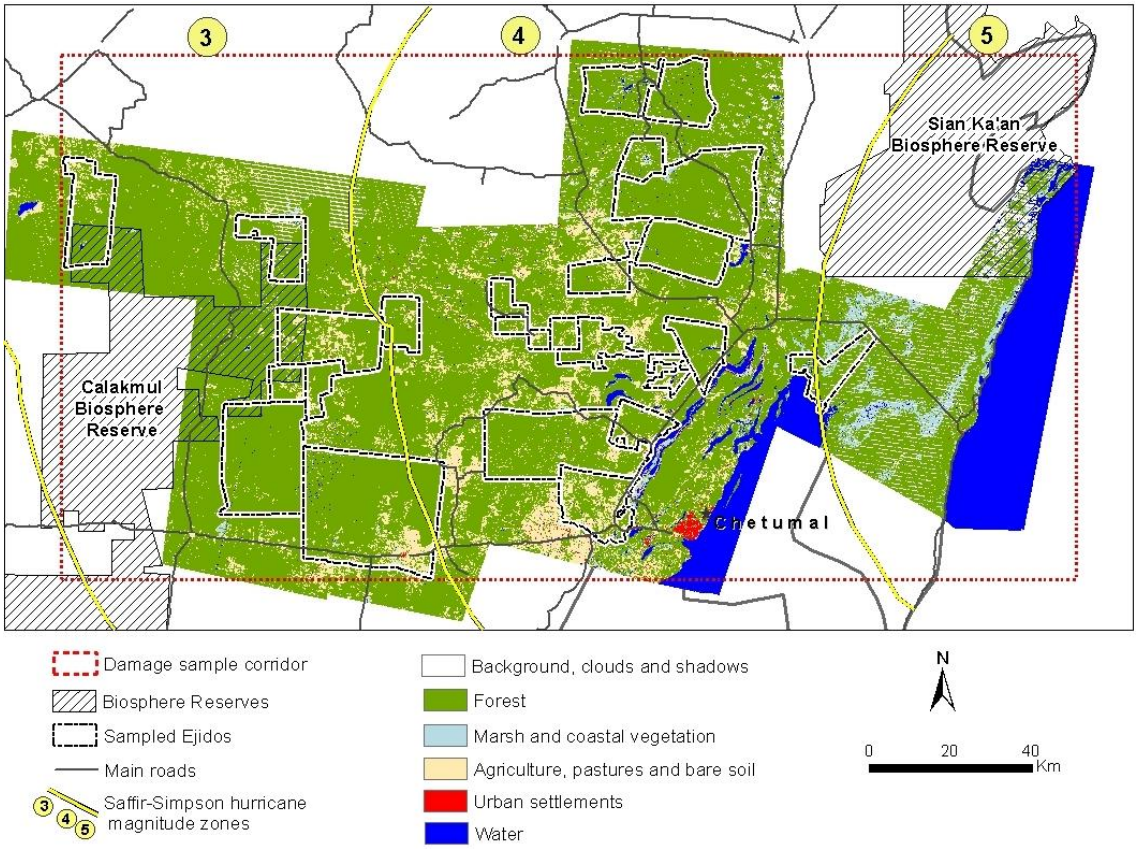

Figure 3.9: Pre-hurricane land cover and land use map for 2007, based on the interpretation of Landsat ETM+ data.

The high overall accuracy of the forest/non-forest classification was apparent at the forest stand level, when comparing the original Landsat satellite data, with the 2007 LC map and the 2007 reclassified MSPA map (Figure 3.11). As shown in this example, non-forest areas corresponding to agricultural lands and bare soil (seen as green or pinkish areas in the Landsat composites) are reflected in the land cover classification as yellow patches in the 2007 LC map, and as grey non-forest areas in the MSPA map.

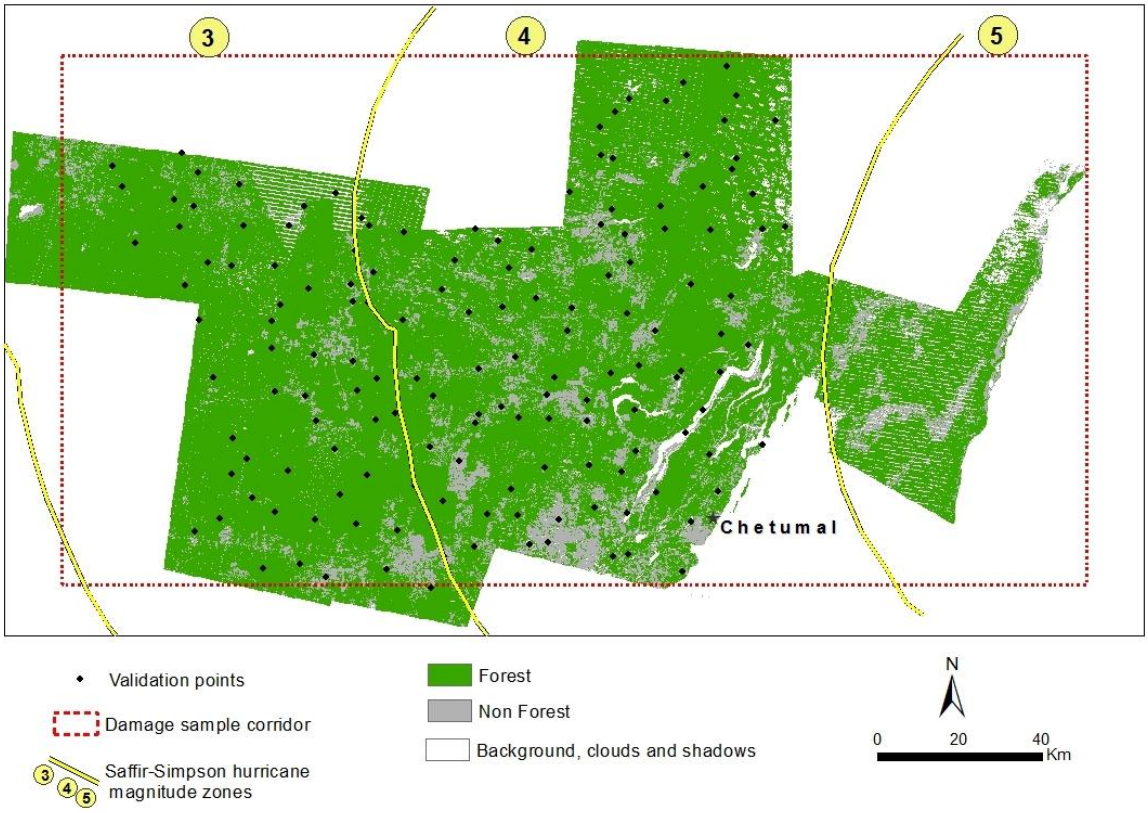

Figure 3.10: Pre-hurricane forest/non-forest map for 2007, showing the location of the 150 validation points used for the accuracy assessment.

The results of the MSPA characterize and quantify the pre-hurricane fragmentation conditions in the study area. Forests covered 86.1% of the mapped area, with only 13.9% of the area corresponding to non-forest (i.e. marsh and coastal vegetation, agriculture, pastures, bare soil and urban settlements). Of the total forest extent, 89.2% corresponded to *core forest*, 4.4% to *perforation* and 4.9% to other types of *edge forest* (Figure 3.12).

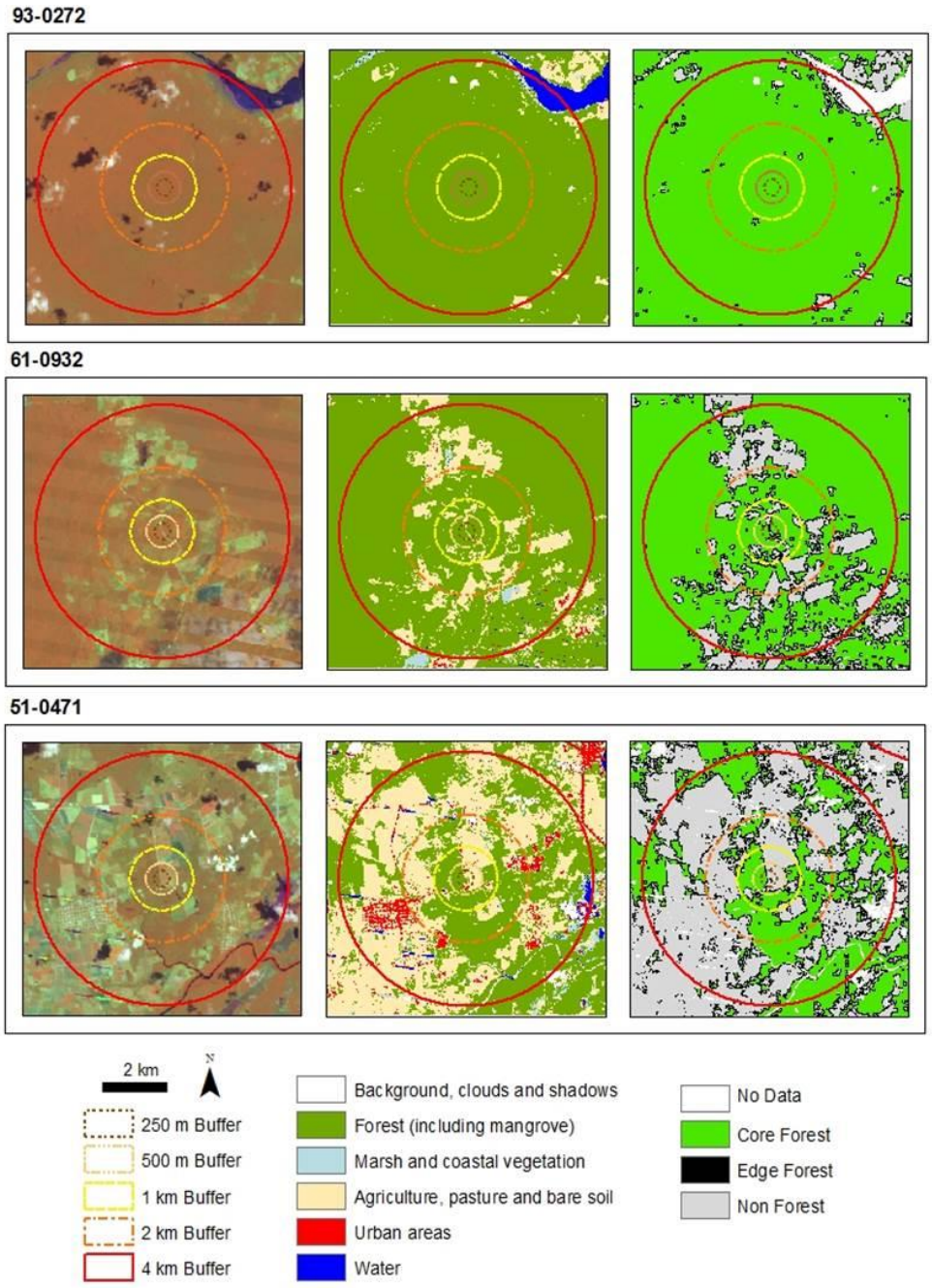

Figure 3.11: Representation of the size of buffer zones used to characterize forest fragmentation at the stand level (i.e., around the field damage plots). In each row, from left to right: False color composite of the Landsat ETM+ images (RGB: 453), 2007 LC map and 2007 reclassified MSPA map. Plot ID is indicated on the top left of each set of images. Forest fragmentation indicators increase from top to bottom.

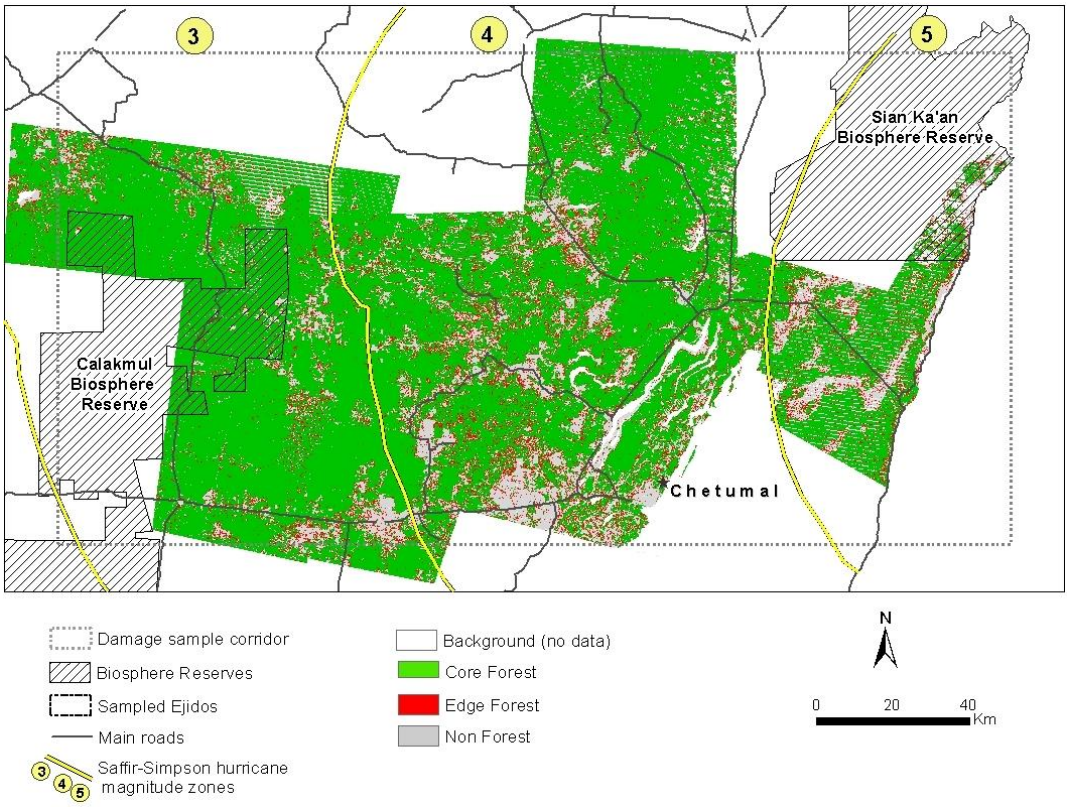

Figure 3.12: Pre-hurricane (2007) forest fragmentation within the Calakmul – Sian Ka'an biological corridor.

A large variability in forest fragmentation indicators was observed at the stand level for the field plots prior to the impact of hurricane Dean (Table 3.10). The standard deviations were large, with marked differences between the maximum and minimum values reported within each buffer size. However, average values were consistently similar between the different buffer sizes.

Table 3.10: Mean, maximum and minimum values of the pre-hurricane fragmentation indicators at the stand level for the 91 field plots from 2008, by buffer size.

Fragmentation Indicator	Mean Percent (s.d.)	Min	Max
250m Buffer			
Proportion Forest	85.2 (17.9)	100.0	36.2
Proportion Edge	21.9 (19.8)	75.9	0.0
Edge/Core Ratio	0.4 (0.6)	3.1	0.0
500m Buffer			
Proportion Forest	85.1 (17.6)	100.0	26.2
Proportion Edge	19.1 (17.6)	82.8	0.0
Edge/Core Ratio	0.3 (0.6)	4.8	0.0
1 km Buffer			
Proportion Forest	84.9 (16.7)	100.0	31.8
Proportion Edge	17.8 (15.9)	76.6	0.0
Edge/Core Ratio	0.3 (0.5)	3.3	0.0
2 km Buffer			
Proportion Forest	84.8 (15.5)	100.0	23.2
Proportion Edge	15.9 (13.9)	84.3	0.1
Edge/Core Ratio	0.3 (0.6)	5.4	0.0
4 km Buffer			
Proportion Forest	84.0 (14.2)	99.7	28.7
Proportion Edge	14.3 (11.4)	72.6	0.7
Edge/Core Ratio	0.2 (0.3)	2.6	0.0

Although indicative of the large variability of fragmentation patterns around forest stands within the study region, these summary statistics do not provide information on the specific trends of forest fragmentation observed for individual plots as different scales (i.e., buffer sizes) are considered. In order to look into these differences, the change in the fragmentation indicator *edge/core ratio* by buffer size was plotted for 41 of the field plots from 2008 that were located within wind speed zone 4 (Figure 3.13). Three main trends become evident from this graph. First, for 19 (46%) of the plots, the *edge/core* indicator remains below a value of 0.2 for all buffer sizes. Second, for 13 (32%) of the plots, the

edge/core ratio remains relatively stable around 0.2 for all buffer sizes. Finally, for 8 (20%) of the plots the values of the *edge/core ratio* indicator show a marked decrease as buffer size increases. Only for one plot did the *edge/core ratio* significantly increase with buffer size. These differences suggest that increasing the buffer size did not have the same effect on the values of the fragmentation indicators for different field plots, as the configuration of the landscape surrounding them varies with scale.

3.3.5: Forest fragmentation and hurricane damage at the stand level

For all but the smallest of the buffer areas considered, the results of the pair wise correlation analysis show a significant positive correlation between two pre-hurricane fragmentation indicators, *proportion edge* and the *edge/core ratio*, and two of the damage indicators: overall damage index and the proportion of dead stems, when all 91 plots from 2008 are considered (Table 3.11). The strength of the correlation seems to increase with buffer size. Additionally, there was a significant negative correlation between the *proportion forest* and the proportion of dead stems per plot, but only for the two largest buffer sizes (2 km and 4 km).

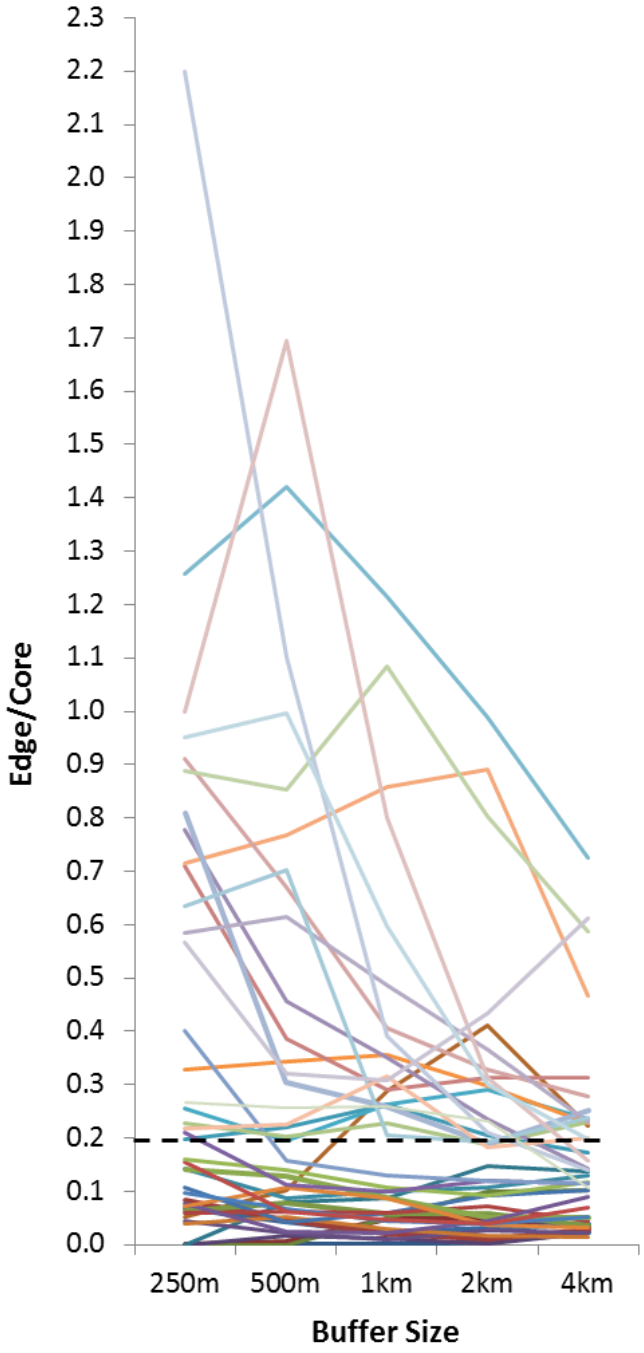

Figure 3.13: Change in the *edge/core* indicator with increasing buffer size for 41 field plots located within wind speed zone 4. Each line corresponds to a different field plot. The dotted line corresponds to a threshold value of 0.2, which was chosen based on the distribution of the data to differentiate between trends in forest fragmentation with increasing buffer sizes.

Table 3.11: Pairwise correlations of hurricane damage measured by MAX Index and

fragmentation indicators by buffer area for the 91 plots (Pearson correlation coefficients with Bonferroni-correction, significant p = 0.05).

Fragmentation Indicator	MAX Damage Index		Proportion of Dead Stems	
250m Buffer	**Coeff.**	**Prob>|t|**	**Coeff.**	**Prob>|t|**
Proportion Forest	-0.139	1.000	-0.215	0.244
Proportion Edge	0.227	0.183	0.297	0.026*
Edge/Core Ratio	-0.008	1.000	0.096	1.000
500m Buffer				
Proportion Forest	-0.160	0.775	-0.204	0.313
Proportion Edge	0.289	0.033*	0.341	0.006*
Edge/Core Ratio	0.432	0.000*	0.498	0.000*
1 km Buffer				
Proportion Forest	-0.163	0.743	-0.199	0.350
Proportion Edge	0.303	0.021*	0.364	0.002*
Edge/Core Ratio	0.457	0.000*	0.504	0.000*
2 km Buffer				
Proportion Forest	-0.246	0.113	-0.304	0.020*
Proportion Edge	0.389	0.001*	0.470	0.000*
Edge/Core Ratio	0.474	0.000*	0.571	0.000*
4 km Buffer				
Proportion Forest	-0.261	0.074	-0.336	0.007*
Proportion Edge	0.381	0.001*	0.480	0.000*
Edge/Core Ratio	0.450	0.000*	0.560	0.000*

However, when the 91plots are disaggregated by wind speed zone to control for the effect or hurricane wind intensity in the analysis, significant correlations between the fragmentation and damage indicators were only found within wind speed zone 5 (Table 3.12). Furthermore, the values of the correlation coefficients were noticeably higher within wind speed zone 5, than within wind speed zones 3 and 4. Surprisingly, in this analysis the signs of the correlations between the forest fragmentation indicators and the damage index are negative within wind speed zone 3 and 4, for all buffer sizes.

Table 3.12: Pairwise correlations of the MAX Damage Index and fragmentation indicators by buffer area and wind speed zone for the 91 plots (Pearson correlation coefficients with Bonferroni-correction, significant p = 0.05).

Fragmentation Indicator	Wind speed zone 3 (*N*= 30)		Wind speed zone 4 (*N*=42)		Wind speed zone 5 (*N*=19)	
250m Buffer	**Coeff.**	**Prob>|t|**	**Coeff.**	**Prob>|t|**	**Coeff.**	**Prob>|t|**
Proportion Forest	0.227	1.000	0.089	1.000	-0.468	0.262
Proportion Edge	-0.193	1.000	-0.115	1.000	0.459	0.289
Edge/Core Ratio	-0.188	1.000	-0.303	0.308	0.624	0.026*
500m Buffer						
Proportion Forest	0.149	1.000	0.060	1.000	-0.453	0.311
Proportion Edge	-0.189	1.000	-0.014	1.000	0.474	0.241
Edge/Core Ratio	-0.179	1.000	-0.023	1.000	0.548	0.091
1 km Buffer						
Proportion Forest	0.148	1.000	0.123	1.000	-0.556	0.081
Proportion Edge	-0.172	1.000	-0.111	1.000	0.618	0.029*
Edge/Core Ratio	-0.143	1.000	-0.137	1.000	0.678	0.009*
2 km Buffer						
Proportion Forest	0.174	1.000	0.103	1.000	-0.582	0.054
Proportion Edge	-0.205	1.000	-0.114	1.000	0.674	0.009*
Edge/Core Ratio	-0.206	1.000	-0.155	1.000	0.582	0.054
4 km Buffer						
Proportion Forest	0.134	1.000	0.068	1.000	-0.439	0.360
Proportion Edge	-0.206	1.000	-0.104	1.000	0.558	0.078
Edge/Core Ratio	-0.233	1.000	-0.116	1.000	0.534	0.112

An inspection of the scatter plots of the fragmentation and damage indicators for which significant correlations were found suggests that these results might be heavily influenced by the values of two specific field plots found within wind speed zone 5, which correspond to a mangrove plot and a transitional coastal vegetation-mangrove plot for which both damage and fragmentation indicators had much higher values than the other 89 plots (Figure 3.14).

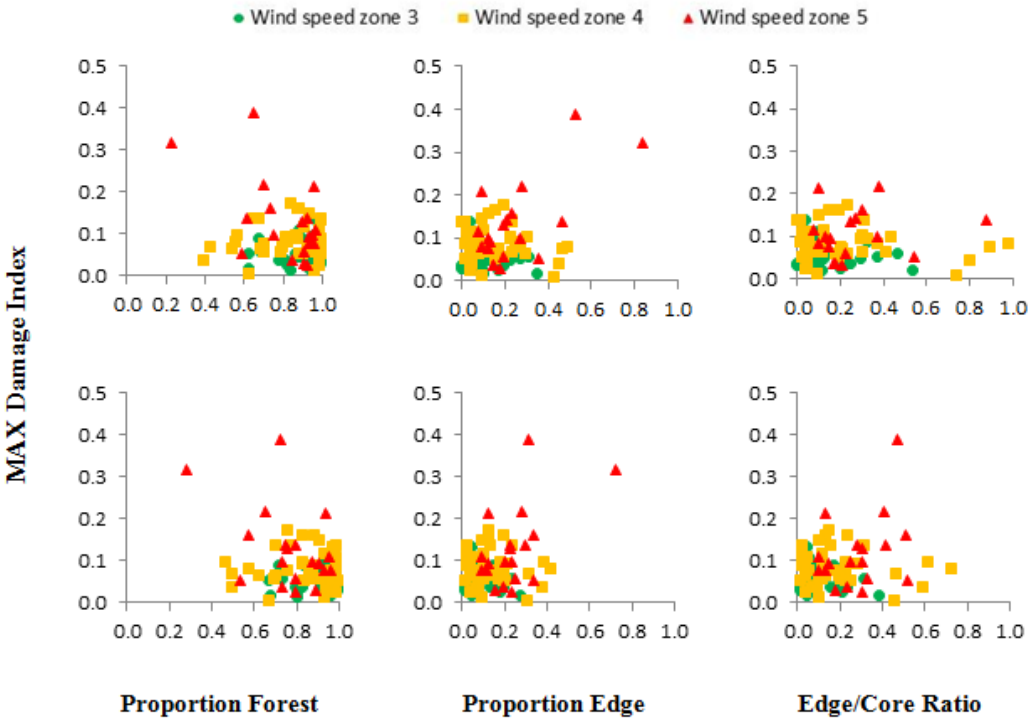

Figure 3.14: Scatter plot of the MAX Damage Index and three fragmentation indicators for the 2 km (top) and the 4 km (bottom) Buffer zones.

Using the data collected in 2009 and 2012, no significant correlations were found between any of the damage and fragmentation indicators, both when all plots were grouped together or when only considering those plots located within wind speed zone 4 (Table 3.13). For the 2009 data, similarly to what was observed for the 91 plots from 2008, the signs of the correlations between the forest fragmentation indicators and the Damage Index are negative within wind speed zone 4, for all buffer sizes considered. More variability is observed in the signs of the correlations for the 2012 data, with positive correlations between damage and the *proportion edge* and *edge/core* indicators

for the three smallest (250m, 500m and 1km) and the largest (4km) buffer sizes, but negative correlations for the 2km buffer.

Table 3.13: Pairwise correlations of the MAX Damage Indices and fragmentation indicators by buffer area for the 20 damage plots located within wind speed zone 4 (Spearman's rank correlation coefficients with Bonferroni-correction, significant p = 0.05).

Fragmentation Indicator	**MAX Damage Index 2009**		**MAX Damage Index 2012**	
250m Buffer	***rho***	**Prob>|t|**	***rho***	**Prob>|t|**
Proportion Forest	0.162	1.000	0.062	1.000
Proportion Edge	-0.020	1.000	0.030	1.000
Edge/Core Ratio	-0.020	1.000	0.030	1.000
500m Buffer				
Proportion Forest	0.134	1.000	0.092	1.000
Proportion Edge	-0.011	1.000	0.030	1.000
Edge/Core Ratio	-0.011	1.000	0.030	1.000
1 km Buffer				
Proportion Forest	0.126	1.000	0.119	1.000
Proportion Edge	-0.030	1.000	0.024	1.000
Edge/Core Ratio	-0.030	1.000	0.024	1.000
2 km Buffer				
Proportion Forest	0.152	1.000	0.161	1.000
Proportion Edge	-0.188	1.000	-0.129	1.000
Edge/Core Ratio	-0.188	1.000	-0.129	1.000
4 km Buffer				
Proportion Forest	0.005	1.000	-0.108	1.000
Proportion Edge	-0.044	1.000	0.250	1.000
Edge/Core Ratio	-0.044	1.000	0.250	1.000

3.4: Discussion

The field plots assessed in this research are a sample of the large variability of forest types and successional stages which characterize the Calakmul – Sian Ka'an corridor in

the Southern Yucatán peninsula (Read and Lawrence 2003; Perez-Salicrup 2004; Vester et al. 2007). In this region, in addition to the variability of forest types associated to changes in climate, topography and soil conditions, forest structure, age and composition have also been affected by a long history of human use and natural disturbances (Perez-Salicrup 2004; Vester et al. 2007), resulting in a complicated temporal and spatial mosaic of forests that is continuously changing. The results of this chapter provide valuable insights into the specific role played by damage caused by catastrophic hurricane winds into contributing to the complex dynamics of forest change within the corridor, and how it might interact with the spatial pattern of forest configuration.

3.4.1: Forest damage at the stand level

Hurricane Dean caused severe structural damage to the forests of the Calakmul – Sian Ka'an corridor. In fact, over half of the stems recorded almost one year after the hurricane impacted the region showed moderate to severe damage (i.e., broken major branches or higher) as a result of the impact of the storm.

In the short term, stem snapping was the most common severe damage recorded within the forest stands across the corridor, followed by the loss of major branches, bending and tree uprooting. The results of the correlations between the proportion of stems and proportion of basal area per plot affected by these types of damage suggest that at least in the short term, stems with a larger DBH were more likely to suffer severe damage as a result of the impact of the hurricane, with the exception of bending, which affected mostly stems with smaller DBH. A possible explanation for these results is that stems with larger DBH are presumably taller, and might have been emergent within the

forest canopy. Consequently, they would have been more exposed to the direct impact of the hurricane winds than the shorter surrounding stems (McGroddy et al. 2013). Additionally, stems or large diameter tend to be less flexible than their smaller counterparts, and are therefore more likely to suffer snapping and/or uprooting, while the smaller, more flexible stems are able to better sustain the intense winds and thus are more likely to suffer bending rather than actual breakage (Van Bloem et al. 2005).

Interestingly, similar higher likelihoods for larger stems to register more severe damage were not observed within the 2009 field plot data. This might be due to the fact that by this time, two years after the disturbance, it is very likely that surviving stems might have experienced additional damage, associated or not to the hurricane impact. For example, stems with smaller DBH that were leaning in 2008 as result of the impact of the strong hurricane winds might have completely fallen down by 2009 as the result of the impact of additional wind disturbances, heavy rains, or the additive effect of neighboring falling tree tops and branches, thus resulting uprooted or dying . This additive damage could have resulted in a homogenizing effect of severe hurricane damage across the different DBH size classes at a longer temporal scale. Alternatively, these results might also reflect structural differences between the forest stands sampled in 2008 and 2009, and the patchwork nature of catastrophic wind damage on forests depending on a number of additional variables besides stem size.

As has been reported to be the case for other tropical forests impacted by hurricanes, a large spatial variability in the severity of the structural damage after the disturbance was observed within the forest stands of the Sian Ka'an – Calakmul biological corridor. Several factors have been identified that explain, at least in part, this damage variability.

These factors include those associated to structural characteristics of the forest stands (such as canopy height, median DBH and basal) as well as the intensity of the storm. Indeed, an analysis of multiple regression models found that wind speed was the main determinant of the severe damage (≥MB) observed within the 91 field plots from 2008 (McGroddy et al. 2013). In addition, species may exhibit differential susceptibility to hurricane wind damage (Everham and Brokaw 1996). In the case of the forests stands assessed in this study, it was found that higher damage was associated to rare species (less than 50 individuals recorded within all plots), while species with lower wood density were more likely to be snapped or uprooted within wind speed zones 4 and 5 one year after the impact of hurricane Dean (Vandecar et al. 2011).

Survival and mortality rate: The results from the field assessments also point to the fact that a relatively low proportion of stems (5.6%) died within the year immediately following the disturbance. This value is towards the lower end of the wide range that has been reported for tropical forests after catastrophic wind disturbances (1-58%, Everham and Brokaw 1996), but about twice as high as results that have been reported for other tropical dry forests of the Caribbean region affected by hurricanes (<2%, Van Bloem et al. 2006; 3% Frangi and Lugo 1991). Nonetheless, field data collected between 2009 and 2012 shows that the overall five-year annual mortality rate of 3.1% associated to hurricane Dean's impact was six times higher than background mortality rates (0.5%/y) reported by Whigham et al. (1991) for the forests of the northeastern Yucatán peninsula. The background mortality refers to mortality that results from the natural death of tress as well as from low-intensity disturbances (such as the formation of canopy gaps) (Lugo and Waide 1993; Lugo and Scatena 1996); in other words, it is the mortality that would be

expected under "normal" forest conditions. The results presented in this chapter indicate an important lagged effect of the hurricane impact on forest structure.

Immediate and longer term mortality within the field plots was associated to the type of damage, particularly tree uprooting and snapping, which is consistent with previous research (e.g., Whigham et al. 1991). Uprooting effectively reduces tree height to ground level and exposes roots, therefore limiting the tree's ability to access resources both above- and belowground, while snapped trees will likely only be able to survive if the species has resprouting abilities along with shade tolerance (Bellingham et al. 1994; Curran et al. 2008; Webb et al 2014).

Besides the delayed mortality of severely damaged stems, additional mortality was observed among the stems that experienced lower levels of damage (i.e., small branch breakage) or no apparent damage in the years following the hurricane (5.6%). At least part of these deaths might have also been related to the stress caused by the impact of the hurricane, although other factors, such as disease, drought and natural senescence likely also played a role.

Damage Indices: The weighted indices calculated based on the proportion of stems with each type of damage within individual field plots provide a useful measure for contrasting the intensity of hurricane damage between stands of different characteristics (such as forest type, age and level of forest fragmentation).

Based on these indices, in 2008 (*N=91*) the highest damage was recorded within the plots located along the coast, in wind speed zone 5. This is not surprising considering that this was the area affected by the strongest hurricane winds, and as mentioned previously, wind speed was the main determinant of the severe damage observed in the field plots

(McGroddy et al. 2013). However, within any given wind speed zone there were plots with both low and high values of damage. In 2009 (*N=28*), a large spatial variability of damage was still evident in the field plots, although in general, damage values were lower than those recorded within the damage plots the previous year. In 2009, the highest damage was recorded in plots located within wind speed zone 4, where a larger proportion of plots were located that year.

Overall, results suggest that in 2008 hurricane damage was higher in older and medium-statured forest stands. This coincides with previous analysis which point towards a higher susceptibility to damage for stems of larger diameter and height (Vandecar et al. 2011), which are more abundant in later successional forest stages and in medium-statured forests in this region (Perez-Salicrup 2004; Vester et al. 2007).

3.4.2: Characterizing forest fragmentation at the stand level

A large variability in forest fragmentation prior to the impact of hurricane Dean was observed at the stand level for the damage and monitoring plots (Table 3.10, Figure 3.13). Some of this variability was evident in the trends in the values of a fragmentation indicator across different buffer sizes for 41 of the field plots from 2008 located in wind speed zone 4 (Figure 3.13). As this data suggests, some plots were effectively located within relatively continuous tracts of *core forest*. For these plots, an increase in buffer size does not result in large changes in the *edge/core ratio* indicator, which remains below 0.2 for all buffer sizes. Other field plots were located within areas dominated by *edge forest* and non-forested areas, surrounded by larger extends of *core forest*. For these, plots, an increase in buffer size resulted in decreasing values of the *edge/core ratio*, as a

larger proportion of *core* than *edge* forest was incorporated into the calculation as the area increased. Finally, some of the field plots were located within areas dominated by *edge forest*, furthermore surrounded by large extents of non-forested areas and *edge forest*. For these plots, an increase in the buffer size does not result in a significant change in the values of the *edge/core ratio* indicator (which remains relatively stable around 0.2 for all buffer sizes).

The highest variability in fragmentation indicators was observed for plots located within wind speed zones 4 and 3. Most of the extent of the study area located within these wind speed zones corresponds to *ejidal* lands, and urban settlements and anthropogenic disturbances are much more common and heterogeneous across them. Subsistence and extensive agriculture, cattle ranching, forestry, and tourism have all left their mark on the landscape (Turner et al. 2001; Roy Chowdhury 2006; Schneider and Geoghegan 2006; Schneider 2008), affecting forest configuration (Turner et al. 2001; Vester et al. 2007), and therefore, the proportions of *core* and *edge forest* across the region

Plots located within wind speed zone 5, many of them within the area of the Sian Ka'an biosphere reserve or the Uaymil protected area, showed much less variability among them in terms of fragmentation indicators, with overall high *proportions of core forest* and low *edge/core* ratios. Along the coast, anthropogenic clearings are much less frequent than inland and most non-forest areas correspond to marsh lands and coastal vegetation. Therefore, in this area most forest edges correspond to the actual coastline boundary, or the boundary between forests and coastal vegetation.

It is worth noting that the estimation of the fragmentation indicators is dependent on the accuracy of the 2007 pre-hurricane LC map. The main difficulty encountered when

mapping the pre-hurricane land cover was the missing data due to cloud cover in the original satellite data. This problem was most severe along the coast, within wind speed zone 5, which resulted in a grainy classification for this zone. Additionally, close inspection of the original satellite data and the final classification shows that pixels with mixed spectral signatures in the borders of clouds tended to be classified as "non-forest," which could potentially increase estimates of *forest edges* and *perforation* in the MSPA results. Unfortunately, no SPOT data was available to assess the accuracy of the classification within wind speed zone 5 and to quantify the seriousness of this problem on the estimation of the fragmentation indicators.

3.4.3: Forest fragmentation and hurricane damage at the stand level

The results of the pair wise correlation analysis showed a significant positive correlation between two pre-hurricane fragmentation indicators, *proportion edge* and the *edge/core ratio*, and two of the damage indicators: overall damage index and the proportion of dead stems, when all 91 plots from 2008 were considered (Table 3.11). However, this correlation was lost for wind speed zones 3 and 4 when the data was disaggregated to account for differences in wind intensity. Significant correlations were only found within wind speed zone 5. This zone is characterized by both high levels of forest damage due to the intense category 5 hurricane winds that impacted it and relatively high values of the *edge/core ratio* because the coastline creates a fairly large proportion of natural *forest edge*. Thus, the fact that a significant correlation between fragmentation indicators and hurricane damage was only found within this area might be

more the result of the effect of a few field plots with extreme values, than an overall pattern for all the coastal forest stands.

Furthermore, when using the data collected in 2009 and 2012, no significant correlations were found between any of the damage and fragmentation indicators, both when all plots were grouped together or when only considering those plots located within wind speed zone 4. This result is consistent with previous research which found no relationship between forest fragmentation and forest vulnerability to large scale wind disturbances (e.g., Van Bloem et al. 2005; Caterall et al. 2008; Grimbacher et al. 2008; Pohlman et al. 2008). As suggested in the introduction, this has previously been associated to the fact that even if forest edges are more vulnerable to wind effects, if a storm is too intense or lasts long enough, the trees located inside the forest will also likely experience severe damage (Mayer et al. 1989; Ulanova 2000; Zeng et al 2007). It is possible that this explanation applies to the case of the forests of the Calakmul – Sian Ka'an corridor. However, the significant correlations that were found at even larger scales within this area (i.e., at the *ejido* level) warrant additional analysis before discarding a significant correlation between forest fragmentation and hurricane damage at the stand level. It might be that the high variability of the landscape (and field plots) in terms of the additional factors that are known to affect forest damage after catastrophic wind disturbances (including structural characteristics, forest type, species, and successional stage) are contributing to mask any possible impact of forest fragmentation. Applying a modeling approach that simultaneously incorporates these additional factors and the level of forest fragmentation when trying to explain the observed patterns of damage would help determine is that is the case.

3.4.4: Added human impacts and conclusions

Even though assessing the impacts of land use on forest change was not the goal of this chapter, the field data from the monitoring plots indicate an important human influence on the amount and spatial configuration of the forests of the study region, which add to the changes caused by hurricane Dean. The number of stems lost since the permanent plots were first established in 2009 due to land clearings and timber and fire wood extraction (2.4%) show how agriculture and forestry are common anthropogenic impacts within the Calakmul – Sian Ka'an corridor. Over a period of four years, two of the 28 plots were lost: one as the direct result of deforestation in order to build houses, and a second plot burned. In the latter case, a fire spread from an agricultural area to nearby forest and resulted in the loss of approximately 2,000 ha of prime old forest within the *ejido* of Noh Bec (A. Tadeo, pers. comm.). Forestry in this *ejido* has a long tradition, and it has become one of the most successful community forestry enterprises in the state of Quintana Roo, providing the main livelihood for community members (DiGiano and Racelis 2012). The forest that burned in 2011 was part of the Permanent Forestry Area of the *ejido*, where timber extraction is carried out periodically according to the extraction program pre-established in the Forestry Management Plan (FMP). It is expected that the loss of such a large extension of old forest will have affected forest management in this community, not only because of the expense of putting out the fire and cleaning operations, and the actual value of the timber lost, but also because it would require a modification of the FMP to account for the forest area lost. In addition, the 2010 land-use history field assessment indicated that at least five other plots from 2008 had been lost

either to deforestation or forest fires within the two years that followed the first field assessment.

These results highlight the dynamic changes that take place within the forested landscape of the Calakmul - Sian Ka'an corridor, and the importance for future research to consider both natural and anthropogenic disturbances and their synergies, when trying to understand changes in forest structure, composition and landscape configuration in this region.

Chapter 4: Structural forest recovery after hurricane Dean's impact within the Calakmul – Sian Ka'an corridor

4.1: Introduction

Large, infrequent disturbances can severely affect the structure and function of forests (Boucher 1990; Peterson and Pickett 1991; Zimmerman et al. 1994; Foster et al. 1998; Turner and Dale 1998; Turton and Stork 2008). Forest communities are in large part the result of differential responses of species to disturbance, both in terms of the types of damage experienced and mortality, and in the differential ability of tree species to recover and grow after the impact of the disturbance (Zimmerman et al. 1994). In the Yucatán peninsula and other Caribbean regions, hurricanes are among the main disturbances shaping forest structure (Walker et al. 1991; Islebe et al. 2009; Ramírez-Barajas et al. 2012a).

The areas affected by the damaging effects of hurricanes are usually much larger than those affected by other natural disturbances, such as landslides and earthquakes (Lugo et al 1983; Lugo and Waide 1993; Lugo and Scatena 1996; Foster et al. 1998). However, the recovery time after a hurricane impact seems to take place much faster than with other disturbances (Lugo 2008; Xi and Peet 2011), although estimates of recovery times vary tremendously, depending on how recovery is quantified, the frequency of disturbances in the region, storm intensity and vegetation characteristics (Everham and Brokaw 1996). Although there has been a significant amount of research aimed at understanding the damage caused by catastrophic wind disturbances on forests all over the world, less attention has been paid to the recovery process that follows (Zimmerman

et al. 1994; Everham and Brokaw 1996). Nevertheless, a number of studies on this topic have been conducted in the last several years (e.g. Zimmerman et al. 1994; Imbert and Portecop 2008; Crk et al. 2009; Heartsill Scalley et al. 2010).

Understanding the recovery process of tropical forests after hurricane disturbances is important not only to guide conservation efforts but also proper sustainable management by the human populations that depend on forest resources for their subsistence (Imbert and Portecop 2008; Ramírez-Barajas et al. 2012a). This is especially relevant in the context of ongoing climate change and predictions for higher frequency and intensity of hurricanes in the Atlantic basin (Elsner 2006; Bender et al. 2010).

4.1.1: Paths to forest recovery after catastrophic wind disturbances

Forest recovery from catastrophic wind disturbance might follow different routes, depending on a combination of biotic and abiotic factors, including soil characteristics, species, disturbance history, as well as the severity of damage (Everham and Brokaw 1996; Chazdon 2003). Everham and Brokaw (1996) describe four possible paths of recovery: 1) regrowth, (2) recruitment, (3) release, and (4) repression.

Regrowth refers to the vegetative recovery (i.e. resprouting) of surviving trees. Its prevalence depends on the type and extent of structural damage, and tends to decline as stem mortality increases. Recovery through resprouting has also been referred to in the literature as “direct regeneration” (Boucher 1990) and “direct species recovery” (Walker 1991), among others. Recovery through **recruitment** refers to the establishment of seedlings of early successional species, which can take place as a “shortened” succession than that described by traditional models of secondary succession. In this case, short-

lived or shade-intolerant pioneer species are briefly established after the disturbance, and then suppressed by primary-forest species. **Release** refers to the rapid growth or previously "suppressed" subcanopy trees or saplings. These might correspond to individuals of the dominant canopy species, or different ones, which in turn could potentially alter species composition significantly. Finally, **repression** is the path in which secondary succession is suppressed as certain plants, often herbs and vines, or heavy litter, restrict the regrowth or recruitment of trees (Everham and Brokaw 1996).

In any given case, forest recovery after a wind disturbance might take place through more than one path, particularly at very local scales. However, one path tends to dominate. The prevalence of each of these paths will determine if the forest community will experience a shift in structure or composition in the future (Everham and Brokaw 1996).

The evidence suggests that in the case of hurricanes, regrowth is usually the predominant path to forest recovery, especially in the tropics (Basnet 1993; Vandermeer et al. 1995; Van Bloem et al. 2006; Imbert and Portecop 2008, Poorter et al. 2010). Hurricanes can cause significant structural damage to forested ecosystems, but the resulting tree mortality tends to remain low to moderate (Frangi and Lugo 1991; Everham and Brokaw 1996; Van Bloem et al. 2006). Even when trees are seriously damaged, a majority of the stems survive and retain at least some live root and stem material from which new stems and branches can sprout (Paciorek et al 2000). The access to substantial energy reserves allows sprouts to grow quickly and rapidly reenter the canopy following the disturbance (Putz and Brokaw 1989; Dietze and Clark 2008). Therefore, sprouting of damaged trees can be considered as a demographic shortcut that allows regeneration to

occur much more quickly than by seed after a disturbance (Dietze and Clark 2008), minimizing the effects of the disturbance, reducing population turnover and the dependence on seeds for population maintenance (Bond and Midgley 2001).

Since recovery through resprouting depends on vegetation already in place at the time of the disturbance, it could be expected that it leads towards a forest composition that closely resembles pre-disturbance conditions (Boucher et al. 1994). Nonetheless, that is not always necessarily the case. This is partly due to the fact that not all species have the same ability to resprout (Basnet 1993; Bellingham et al. 1994; Zimmerman et al. 1994; Salk and McMahon 2011), and for the ones that do, resprouts might show differential mortality over time (Paciorek et al 2000). Similarly, species often have different sprouting abilities at different life history stages. For example, in some species the capacity to resprout increases with size until it reaches a maximum at adult stages, while in other species resprouting is common in juveniles but not in adults (Bond and Midgley 2001). Trees that resprout might have a competitive advantage and reoccupy the canopy space faster than non-resprouting trees. Although this might not affect species richness, it can modify their relative abundances in the forest stand (Zimmerman et al. 1994). Furthermore, species with sprouts that are able to survive could become dominant over non-sprouting species, or species for which a large proportion of sprouts die in the medium to long term after the disturbance.

In addition, forest recovery through resprouting can also affect forest structure. On one side, the type and location of sprouts has been found to depend on the type of damage experienced by the tree (Whigham et al 1991; Yih et al 1991; Bellingham et al 1994), but only sprouts located at the base of the trunk (i.e., basal resprouting) will affect stem

density. On the other side, differential survival of resprouting trees can also affect tree density and forest basal area. For example, Putz and Brokaw (1989) found that in Barro Colorado Island, Panama, the smaller trees that sprouted after breaking were more likely to survive than larger trees that sprouted, resulting in an overall reduction of basal area in the years following the disturbance.

4.1.2: Metrics of forest recovery

Quantitative and qualitative assessments of the timing, extent and speed of forest recovery after a disturbance will depend on the variables used to measure it. In the case of hurricanes, for which extensive defoliation is one of the most evident impacts in forested ecosystems, most authors have described the recovery process as occurring rapidly, since many of the impacted trees produce new leaves within a few weeks (Lugo et al. 1983; Whigham et al.1991) or months (Bellingham 1991; Yih et al. 1991; Walker 1991; Bellingham et al. 1992; Basnet 1993). However, differences in the duration of the recovery process start to become evident when using additional variables of measurement, such as canopy structure and light levels in the understory, stem density, amount of standing biomass and rates of species accumulation (Everham and Brokaw 1996; Chazdon 2003). When these more complex variables are taken into account, forest recovery might not be considered to be complete for several decades (Chazdon 2003; Turton and Stork 2008).

Many recent studies of forest recovery after the impact of a hurricane have focused on structural measures, such as basal area, tree height and stem density, which are closely

related to measures of ecosystem function. Furthermore, these characteristics often experience rapid change after a disturbance, and are easily measurable (Chazdon 2003).

4.1.3: Does forest fragmentation affect forest recovery?

In recent years, research conducted in order to assess the relationship between forest fragmentation and catastrophic wind disturbances, such as hurricanes, has been mostly focused on forest damage (e.g., Laurance 1991; Van Bloem et al. 2005; Caterall et al. 2008; Grimbacher et al. 2008; Pohlman et al. 2008). Significantly less information is available regarding the relationship of forest fragmentation and forest recovery after catastrophic winds and other large disturbances, and almost all of it has been focused on recovery within forest gaps.

Most of the research on forest recovery within forest gaps has been focused on the recruitment of pioneer species and the release of seedlings as the main paths of recovery, particularly within large gaps created after the blowdown of extensive forested areas (Putz and Brokaw 1989; Everham and Brokaw 1996; Bond and Midgley 2001). Under these circumstances, traditional gap theory would suggest that shade-intolerant species with abundant seed production and fast growing, light-demanding seedlings would be the best suited to exploit the newly created high-light environment, while shade-tolerant species would be at a disadvantage (Bond and Midgley 2001; Dietze and Clark 2008). If this is the case, recovery within large gaps could potentially result in a shift of forest composition towards early successional species, and a net loss of shade-tolerant species (Everham and Brokaw 1996; Dietze and Clark 2008).

Even though the expectations from traditional gap theory are reasonable, recent research on forest dynamics after disturbances suggests that even within larger gaps, sprouting plays a larger role than previously thought, and that shifts of forest composition do not always occur as a result of the recovery process. For example, Dietze and Clark (2008) assessed the importance of tree survival and resprouting for forest recovery within experimental gaps in the southeastern United States, where strong winds, primarily associated to hurricanes, are the main disturbance. They found that overall, the growth rates of sprouts were considerably higher than that of saplings and that sprouts constituted a substantial fraction of new stems. Resprouting accounted from 26-87% of early gap regeneration, and for some species, it was the dominant path of regeneration (Dietze and Clark 2008).

In forest edges, microclimatic gradients can be dramatically different from forest interiors, similarly to what occurs in forest gaps. In general, forest edges have been found to experience greater exposure to sunlight and extremes of temperature, humidity and winds, although the extent of these effects into the forest interior varies significantly with forest type and time since edge/gap creation (Kapos et al. 1997; Laurance 2000), as well as with the surrounding matrix (Harper et al. 2005). These factors in turn can affect species regeneration and growth after a large wind disturbance. For example, increased light conditions at the edge can promote the recruitment of light-demanding pioneer species, while seed dispersal from the surrounding matrix can result in the establishment of new species, resulting in changes to species abundance and composition at the edge (Harper et al.2005). In addition, similar to what has been found to occur within forest

gaps, resprouting could also be expected to play a significant role in forest recovery along forest edges.

More detailed insights into the role that vegetative regrowth plays in the process of forest recovery after hurricane disturbances within fragmented forests will greatly improve our understanding of what to expect in terms of changes to forest structure, composition and dynamics after these large disturbances.

4.1.4: Research objectives

This chapter aims to determine the relationship at the stand level between forest fragmentation and forest recovery after the damage caused by the impact of hurricane Dean. There are three main objectives: 1) to assess short and medium term recovery at the species level in the Calakmul - Sian Ka'an biological corridor (2008-2012); 2) to assess short and medium term recovery at the plot level in the Calakmul - Sian Ka'an biological corridor (2008-2012); and 3) to determine the relationship between forest fragmentation status and forest recovery at the forest stand level. I hypothesize that recovery capacity varies with species and stem size, and that it is more evident in the dominant forest species (i.e., common species) than in less common species. However, I do not expect that the differences are significant enough to have resulted in a change of species composition within the sampled forest stand within the first five years after the impact of hurricane Dean. I also hypothesize that the observed variability in forest recovery at the stand level was significantly correlated to the forest fragmentation conditions of the particular stands after the disturbance, and that overall recovery occurred faster in forest stands located in areas of higher forest fragmentation (i.e., where

light availability is higher). Furthermore, I expect that overall forest recovery five years after the disturbance has been significant across the entire study area.

A combination of field surveys of forest recovery, analysis of remotely sensed data, MSPA and correlation analysis were used to accomplish these objectives.

4.2: Data and Methods

The study area for the analysis presented in this chapter corresponds to the Calakmul - Sian Ka'an corridor first described in Chapter 1 (Figure 1.3).

4.2.1: Field assessment of forest recovery

The initial forest recovery after the damage caused by hurricane Dean was evaluated at the scale of individual forest stands within the 91 plots first described in Chapter 3 (Figure 3.1). A field-based plot assessment was conducted between May and July 2008, approximately nine months after the hurricane impacted the region (Vandecar et al. 2011; McGroddy et al. 2013). In each plot, trees with a diameter at breast height (DBH) of 5 cm or greater were identified to species, DBH was measured, and for each stem recovery was qualitatively evaluated in terms of observed resprouting on the trunk and branches. Four different resprouting categories were used: no resprouting apparent (RO), basal resprouting (RB), trunk resprouting (RT), and crown recovery (RC) (Table 4.1).

Table 4.1: Description of the recovery categories used in the field assessments.

Resprouting category	Description
None (RO)	No resprouting apparent
Basal resprouting (RB)	Basal trunk ≤50 cm from ground
Resprouting on trunk (RT)	Resprouting on trunk > 50 cm from ground or lateral branches from the trunk
Crown (RC)	Resprouting from lateral branches, closed crown

A similar assessment was conducted in 28 plots in the summers of 2009 (May-July), as well as in the remaining 27 plots in 2010 (May-June) and 2011 (May-July), and the 26 plots remaining in 2012 (May-July). Every year, if new stems reached a DBH ≥ 5 cm, they were tagged, measured and incorporated into the database as new recruits.

Tree density, basal area and species change: Recovery data for the entirety of stems recorded within the field plots from 2009 to 2012 were grouped by year and used to compare forest recovery in terms of the number of live stems (including recruits that reached the 5cm DBH threshold in between field assessments) and basal area. Because there is no previous information for these plots, the 2009 data was used to estimate pre-hurricane conditions for some of the comparisons. This was done by adding the total number of live stems and dead stems assumed to have died due to hurricane Dean's impact, as well as their total basal area.

In order to evaluate if the recovery process resulted in any significant species changes within the first 5 years after the disturbance caused by hurricane Dean, the importance values (IVs) and ranks of all species were calculated for 2009 and 2012. Each IV was calculated as the sum of the relative frequency, relative density and relative abundance of each species recorded in the field (Bonilla-Moheno 2012), where:

$$\textbf{Relative Frequency specie } i = \frac{\frac{No.\,of\ plots\ where\ species\ i\ is\ found}{Total\ No.\,of\ plots}}{Sum\ of\ frecuencies\ of\ all\ species} \times 100$$

$$\textbf{Relative Density specie } i = \frac{\frac{Total\ No.\,individuals\ tallied\ for\ specie\ i}{Toal\ area\ of\ plots\ in\ ha}}{Sum\ of densities\ of\ all\ species} \times 100$$

$$\textbf{Relative Dominance specie } i = \frac{\frac{Total\ basal\ area\ of species\ i\ in\ all\ plots}{Toal\ area\ of\ plots\ in\ ha}}{Sum\ of basal\ areas\ of\ all\ species} \times 100$$

For this analysis, only data from the 26 plots that remained standing through the entirety of field surveys was considered, in order to focus on the potential impacts of the hurricane disturbance on changes to species composition rather than on the impact of other disturbances (i.e., deforestation and fires). The data from 2009 was used as the baseline of the comparison since no pre-hurricane data was available for the field plots. The total area covered by the 26 field plots considered in the analysis was 1.3 ha, with each individual plot covering 0.05 ha. The maximum IV for any given species is 300, with higher numbers corresponding to species that dominate within the forest community.

Resprouting capacity: Forest recovery was further assessed in terms of resprouting. The field data was used to compare stem resprouting by DBH class (A: 5–7.4, B: 7.5–9.9, C: 10–12.4, D: 12.5–14.9, E: ≥15 cm; following Vandecar et al. 2011), species, type of damage and time after the disturbance. In the latter case, particularly attention was paid to data from 2008, 2009 and 2012, in order to characterize forest recovery one year, two years and five years after the hurricane disturbance; respectively.

4.2.2: Characterizing forest recovery at the stand level

The percent of stems with each type of resprouting was estimated for each of the 91 plots from 2008 as well as for the 28 plots from 2009. The recovery of all stems tagged in 2009 that were still alive five years after the hurricane impact was further assessed within the 26 plots remaining in 2012. Differences in the mean proportion of resprouting at the forest stand level by forest type and successional stage were explored for 2008, 2009 and 2012.

4.2.3: Forest fragmentation and recovery at the stand level

Correlation analyses were used to explore the statistical relationship between forest fragmentation and forest recovery at the stand level (i.e., for each field damage plot). This was done using the proportion of stems with crown resprouting (RC) as an indicator of forest recovery at the plot level and two fragmentation indicators derived from the 2010 forest/non-forest map: *proportion forest* and *edge/core ratio* (see Chapter 2).

The 2010 LC map was used instead of the 2007 LC map for this analysis as it was the closest available representation of post hurricane forest configuration conditions. In doing so, the analysis takes into account both the impact of the actual hurricane damage as well as anthropogenic disturbances on forest fragmentation.

The correlations were estimated only for the three smallest buffer zones used to characterize forest fragmentation at the stand level in Chapter 3 (250 m, 500 m, 1 km), as I only expect fragmentation to affect forest recovery through regrowth at local scales, at which light conditions would be affected. For the analysis, plots were grouped by forest

type (low-statured *vs*. mid-statured) and by forest age (younger than 20 years old *vs.* older than 20 years old).

For the 91 plots from 2008, the statistical significance of the correlations was tested using Pearson correlation coefficients (r) with Bonferroni-adjusted P values for significance levels at a = 0.05. A similar analysis was conducted for the 28 plots from 2009. In this case, given the small sample size, the non-parametric Spearman's rank correlation coefficients (*rho*) with Bonferroni-adjusted P values for significance levels at a = 0.05 were used instead. All statistical analyses were conducted with Stata/MP 13.1for Windows.

4.3: Results

4.3.1: Overall patterns of forest recovery

Regrowth and significant structural recovery of the forests of the Calakmul – Sian Ka'an corridor were evident within the first five years after the damage caused by hurricane Dean.

Tree density, basal area and species change: Data from 26 plots provides valuable information of forest recovery after the hurricane in terms of changes in tree density and basal area between 2009 and 2012.

As was expected, an initial decline in the number of live stems and their total basal area was observed within the field plots after the impact of hurricane Dean. This decline reached its lowest point three years after the disturbance, in 2010 (Figure 4.1). In subsequent years, an increase in both the number of live stems and total basal area was

recorded, and by 2012 both measurements had surpassed the values recorded in 2009, when the field plots were first established. That is, by 2012, the number of stems and basal area that had been lost since 2009 due to delayed hurricane mortality had been regained and surpassed. However, 2012 values are still below estimations of the pre-hurricane conditions (Figure 4.1).

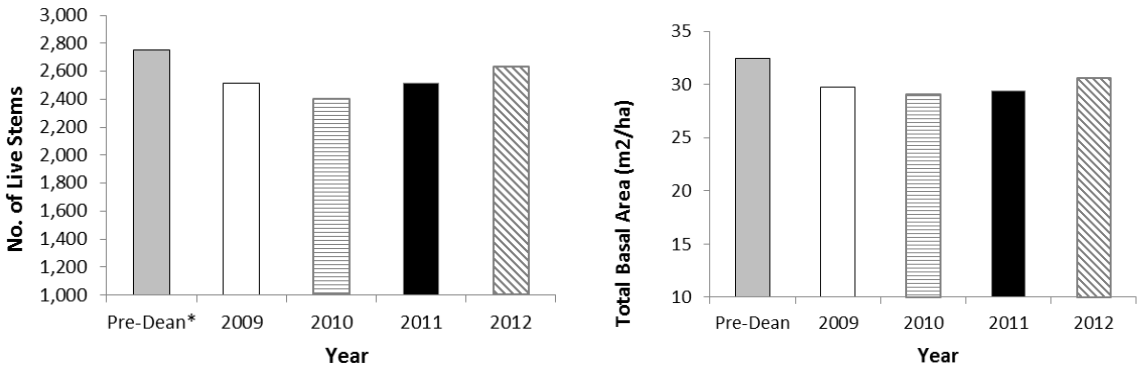

Figure 4.1: Total number of live stems (left) and basal area (right) between 2009 and 2012 in 26 field plots. "Pre-Dean" data corresponds to the estimated pre-hurricane conditions, based on the 2009 data.

The observed increase in the number of live stems in the field plots is a direct result of the incorporation into the database of stems as they reached a DBH of 5 cm or more. The smallest DBH size class (5.0-7.5 cm) experienced the most noticeable increase between 2009 and 2012, actually reaching similar values to those estimated for the pre-hurricane conditions (Figure 4.2, Appendix A5). Stem growth within the intermediate and larger DBH classes has also contributed to the increase in basal area in the 26 plots in the years following the hurricane impact, but at a slower rate. Noticeably, the largest DBH size class (>15 cm) has experienced the lowest recovery in basal area when compared to the estimated pre-hurricane conditions.

In the years following the impact of hurricane Dean, the total number of species recorded in the 26 field plots that remained standing was similar (132 in 2009 and 2010; 131 in 2011 and 130 in 2012). When comparing the abundance of live stems recorded in 2009 and 2012, 56 species did not experience a change in stem frequency, 33 had a decline in the number of stems and 44 showed an increase. Of the latter, the most noticeable were *Vitex gaumeri* (24 new stems), *Piscidia piscipula* (23 new stems) and *Luehea speciosa* (18 new stems). It is worth pointing out that the number of stems that could not be identified increased from 12 in 2009 to 63 in 2012, which corresponds to 0.5% and 2.4% of the total number of live stems for each year, respectively. New recruits were in some cases particularly difficult to identify. Only three species recorded in 2009 had disappeared from the 2012 sample: *Cordia gerascanthus, Trema micrantha* and *Pimenta dioica*. All of them were represented by three stems or less in 2009. By contrast, only one species not recorded in 2009 was incorporated into the sample in 2010, *Hyptis pectinata,* for which five stems were recorded in 2012.

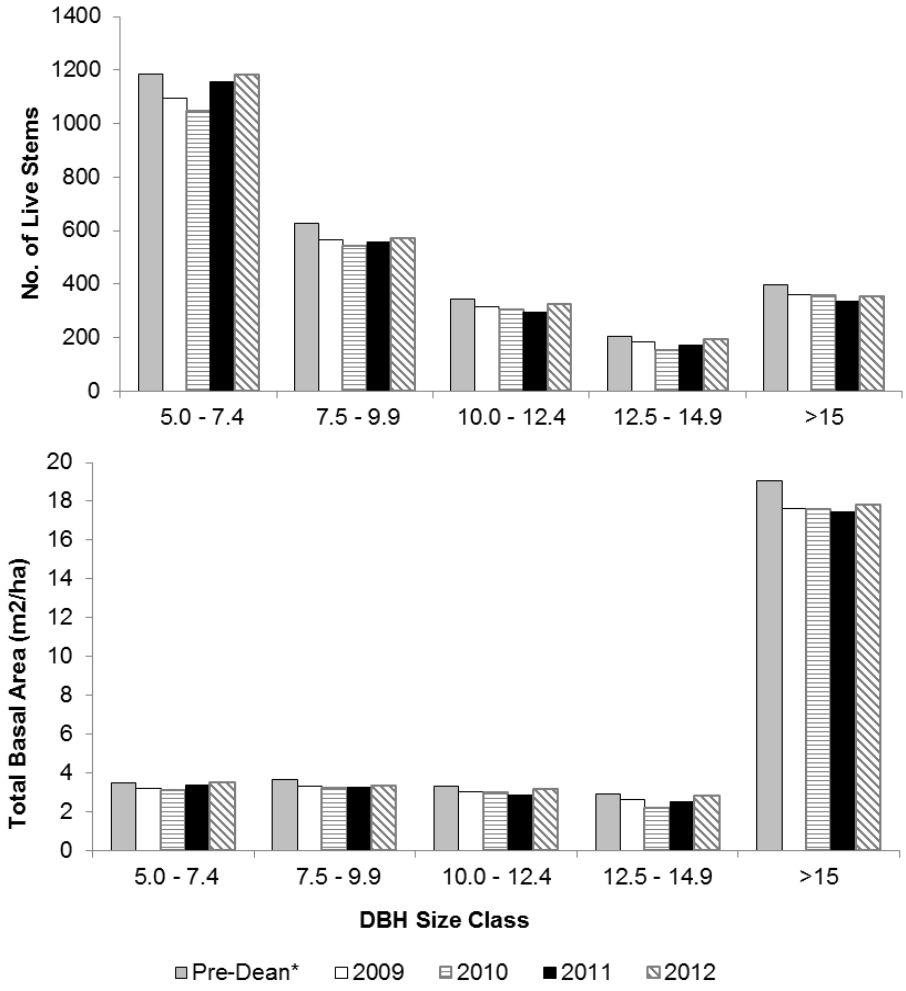

Figure 4.2: Total number of live stems (top) and basal area (bottom) by DBH class from 2008 through 2012 in 26 field plots. "Pre-Dean*" data corresponds to the estimated pre-hurricane conditions based on field data from 2009.

In general, the IVs for most species remained similar across years, with most of the 15 dominant species from 2009 retaining their dominance in 2012 (Table 4.2). In both years, the three most dominant species were *Bursera simaruba*, *Piscidia piscipula* and *Lysiloma latisiliquum*. Only the palm *Sabal mexicana* experienced a noticeable shift in IV ranking, moving from position 13 in 2009 to position 25 in 2012.

Table 4.2: Importance values and ranks (in parentheses) for the 15 most important species recorded within 26 plots in 2009 and 2012. Species are in descending IV rank for 2009.

Species	Family	2009	2012
Bursera simaruba	Burseraceae	18.66 (1)	17.68 (2)
Piscidia piscipula	Fabaceae	17.50 (2)	18.42 (1)
Lysiloma latisiliquum	Fabaceae	14.69 (3)	13.66 (3)
Metopium brownei	Anacardiaceae	12.41 (4)	11.79 (6)
Manilkara zapota	Sapotaceae	11.90 (5)	11.84 (5)
Vitex gaumeri	Verbenaceae	11.27 (6)	12.13 (4)
Croton reflexifolius	Euphorbiaceae	8.54 (7)	8.24 (7)
Pseudobombax ellipticum	Bombacaceae	6.89 (8)	6.91 (9)
Spondias mombin	Anacardiaceae	6.51 (9)	6.49 (10)
Luehea speciosa	Tiliaceae	6.50 (10)	7.49 (8)
Lonchocarpus xuul	Fabaceae	6.13 (11)	5.86 (11)
Gymnopodium floribundum	Polygonaceae	5.59 (12)	5.44 (12)
Sabal mexicana	Arecaceae (Palmae)	5.51 (13)	3.51 (25)
Coccoloba diversifolia	Polygonaceae	5.30 (14)	5.23 (13)
Coccoloba spicata	Polygonaceae	5.18 (15)	5.09 (14)
Alseis yucatanensis	Rubiaceae	4.99 (18)	4.76 (15)

Resprouting capacity: Almost one year after the hurricane impact, in 2008, stem damage was still very noticeable (Chapter 3) and only 42.3% of all live stems recorded within the 91 plots showed some type of resprouting (Table 4.3), with 7.3% of stems showing sprouts in more than one area of the stem (e.g., base and lateral branches). In the following years, the percent of stems with sprouts increased significantly, reaching 86.1% of the live stems recorded in 2009 and 98.1% of live stems in 2012.

Table 4.3: Percent of stems by resprouting category for all live stems recorded in the field plots one, two and five years after the impact of hurricane Dean (in 2008, 2009 and 2012, respectively). Individual stems might experience more than one type of resprouting. Therefore, adding up the percentages across recovery categories could lead to a value greater than 100%.

Resprouting category	% of stems		
	2008	2009	2012
None	57.7	13.7	1.8
RB	3.3	3.5	5.7
RT	14.2	53.9	57.1
RC	33.7	56.9	86.1
Total No. of Live Stems	6,055	2,678	2,268
Total No. of Stems	6,312	2,938	2,749

For all years, the largest percent of recovering stems corresponds to those which had recovered a closed crown (RC) as assessed by field observers from the forest ground. The percent of stems showing this type of recovery had increased from 33.7% to 56.9% between 2008 and 2009, and had reached 86.1% of all live stems recorded in 2012, five years after the disturbance caused by hurricane Dean. The percent of stems with sprouts on the main trunk and on lateral branches from the trunk (RT) also increased significantly with time (Table 4.3). The percent of stems with resprouting at the base of the trunk (RB) remained low throughout the field assessment, although it also increased in the years following the disturbance.

These general trends were consistent for all the different DBH size classes (Figure 4.3). Vandecar et al. (2011) found that in 2008, sprouting capacity was significantly correlated to tree diameter. In general, sprouting was less common in the smallest DBH class, and more common in the intermediate and largest DBH classes (particularly above

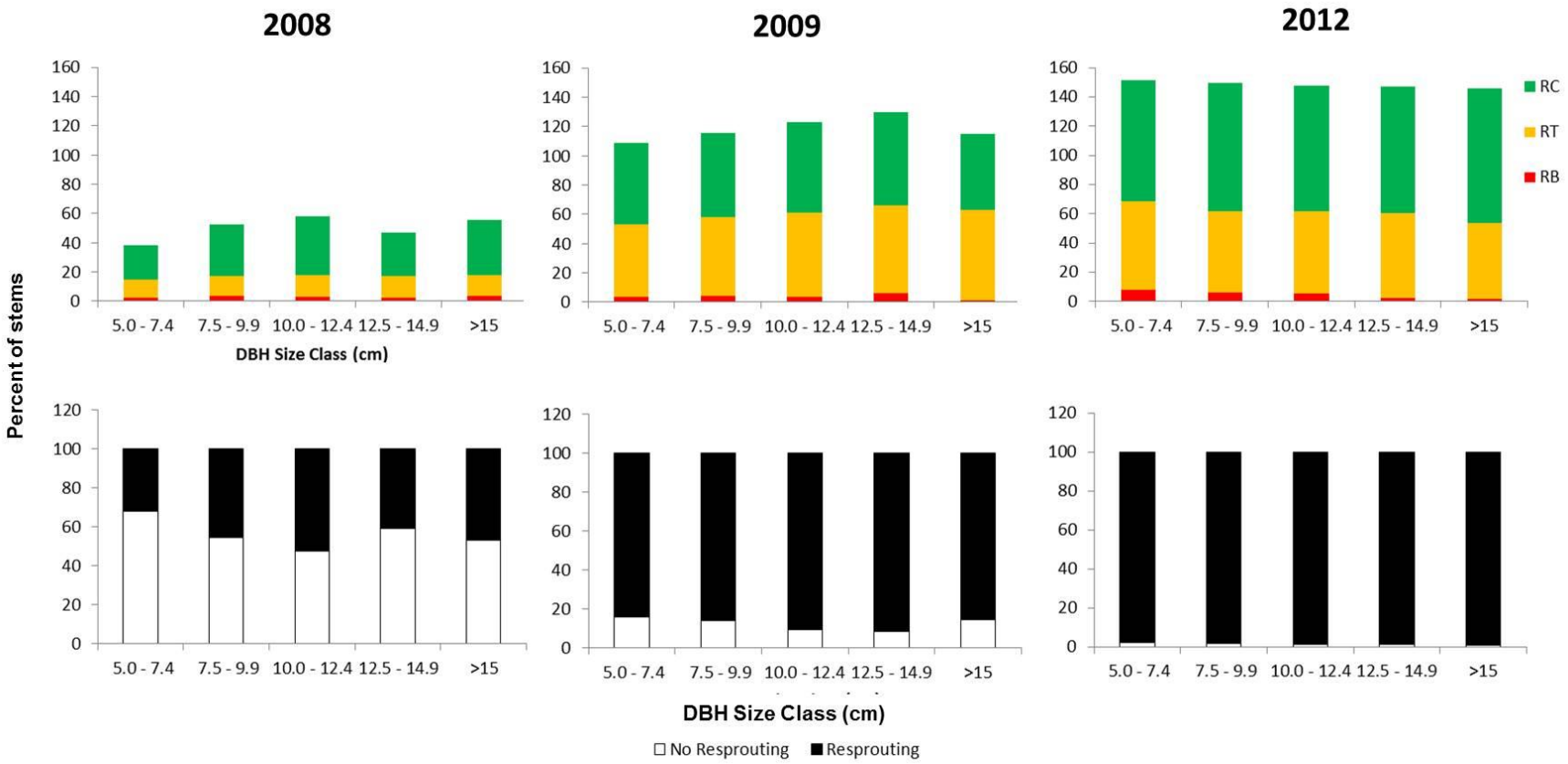

Figure 4.3: Percent of stems within each resprouting category (RO: no resprouting apparent, RB: basal resprouting, RT: resprouting on the main trunk, RC: crown recovery) by DBH class for all live stems in the field plots from 2008, 2009 and 2012.

10 cm). However, these differences in resprouting capacity are not evident in subsequent years, with more than 80% of stems within all DBH size classes resprouting in 2009, and more than 95% of all stems resprouting in 2012 (Figure 4.3).

When comparing the resprouting capacity of the common and less common species recorded within the 91 plots from 2008, Vandecar et al. (2011) did not find differences in the proportions of stems with sprouting 9-11 months after the impact of hurricane Dean. Data from 26 plots further complemenrs these results. Changes in resprouting patterns through time for 9 of the most common species in the sample (at least 48 stems recorded each year) are similar, with a moderate proportion of stems showing resprouting in 2008 (28 – 56%) , and marked increases in subsequent years (all above 70%) (Figure 4.4)

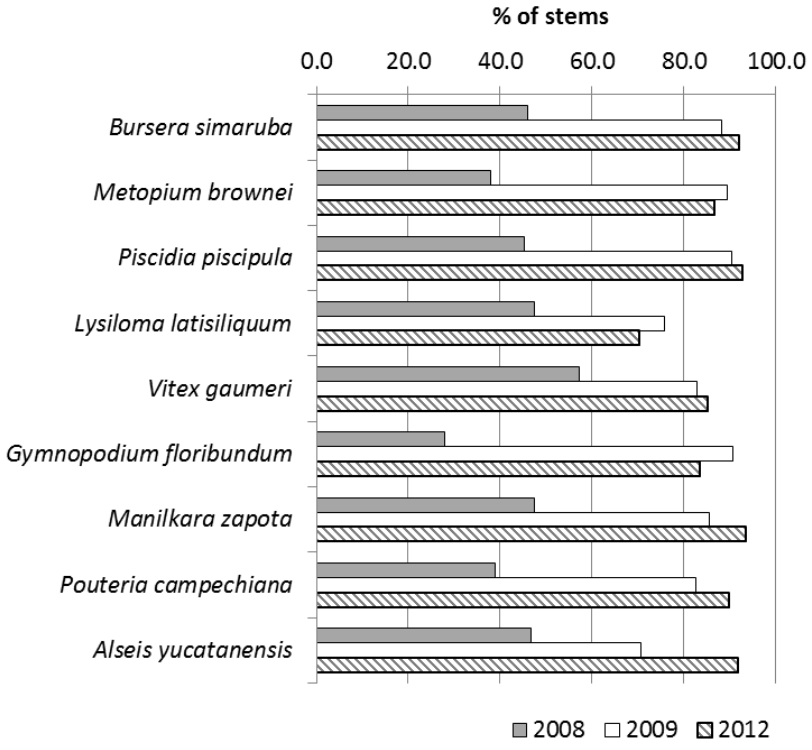

Figure 4.4: Percent of stems with resprouts in 2008, 2009 and 2012 for 9 of the most common species recorded in the field plots.

The resprouting pattern of the less common species is similar, although more variation was observed (Figure 4.5). Most of the 26 species with at least five but less than 48 stems recorded between 2008 and 2012 show an increase in the proportion of stems with sprouts in the years following the impact of hurricane Dean. By 2012, resprouting in more than 70% of all live stems was recorded for 22 of the 26 species. However, the proportion of stems with resprouting decreased in at least four species: *Nectandra coriacea, Chrysophyllum cainito, Hampea trilobata* and *Psidium satorianum.*

Finally, in 2008, resprouting capacity was also found to vary with the most severe damage recorded for the stem, with a lower percentage of individuals sprouting in the no damage category than expected, and a greater than expected number of individuals sprouting in the SB category (Vandecar et al. 2011). In 2009, sprouting was still significantly lower among the stems that did not suffer hurricane damage, but similar among all the other damage categories (Figure 4.6). By 2012, almost all live stems had sprouts, independently of the damage originally suffered by the stem.

The location of resprouting on the stem also seems to depend on the type of damage incurred by the stem (Figure 4.6). Thus, crown recovery (RC) and resprouting on the trunk (RT) occur commonly across all the different damage categories. However, resprouting at the base of the trunk (i.e., basal resprouting, RB) most commonly occurs in uprooted trees, and to a lesser degree in bend trees, while it is much less frequent within the other damage categories. In 2008, 14.4% of all uprooted trees had RB. This proportion increased to 23.2% in 2009 and 36.1% in 2012 (Figure 4.6). In contrast, the proportion of uprooted trees still alive and with a healthy crown decreased noticeably between 2009 and 2012, from 73.2% to 33.3% respectively.

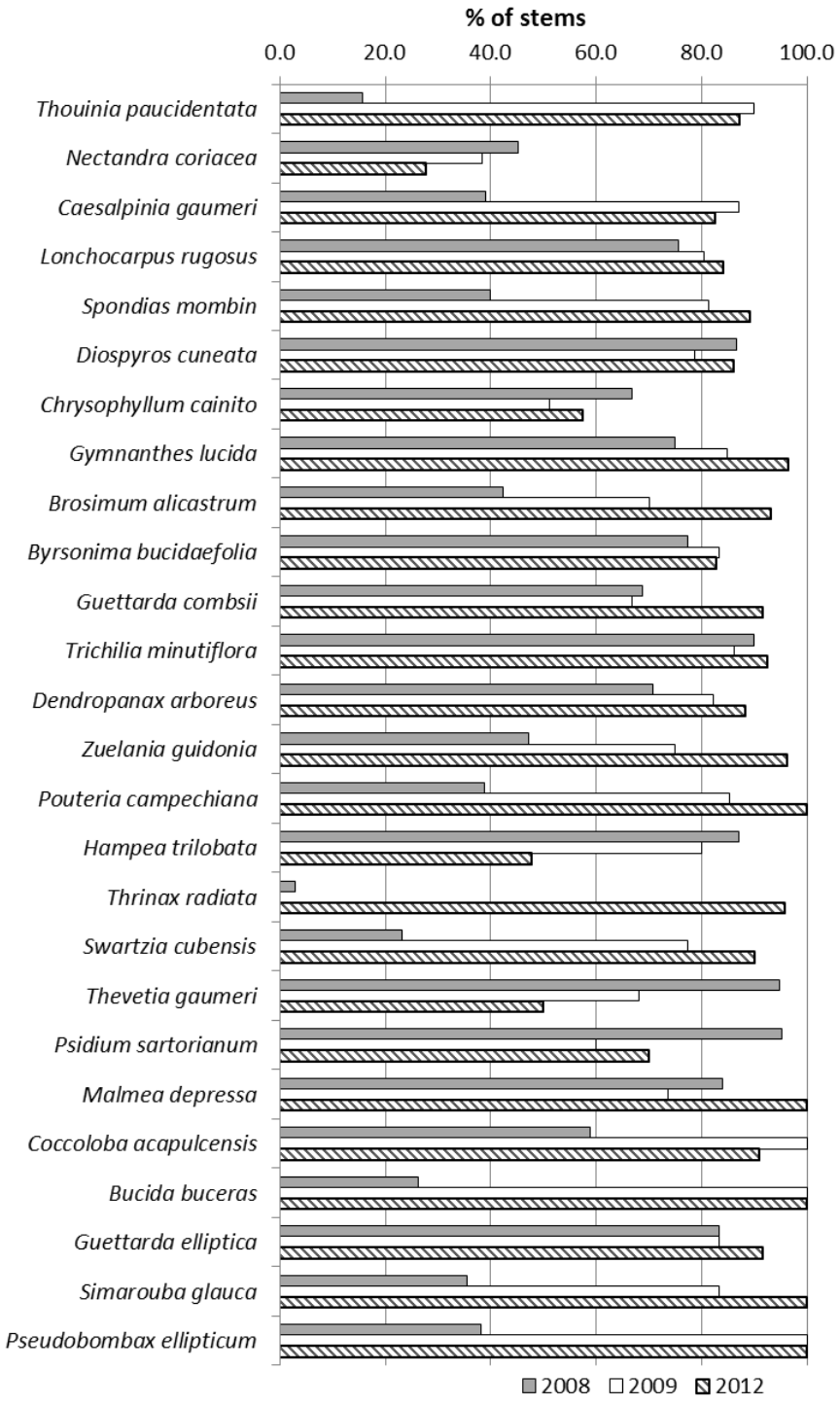

Figure 4.5: Percent of stems with resprouts for 26 of the less common species recorded in the field plots. Species are ordered by their frequency in 2009. Only species with at least five stems per year are included.

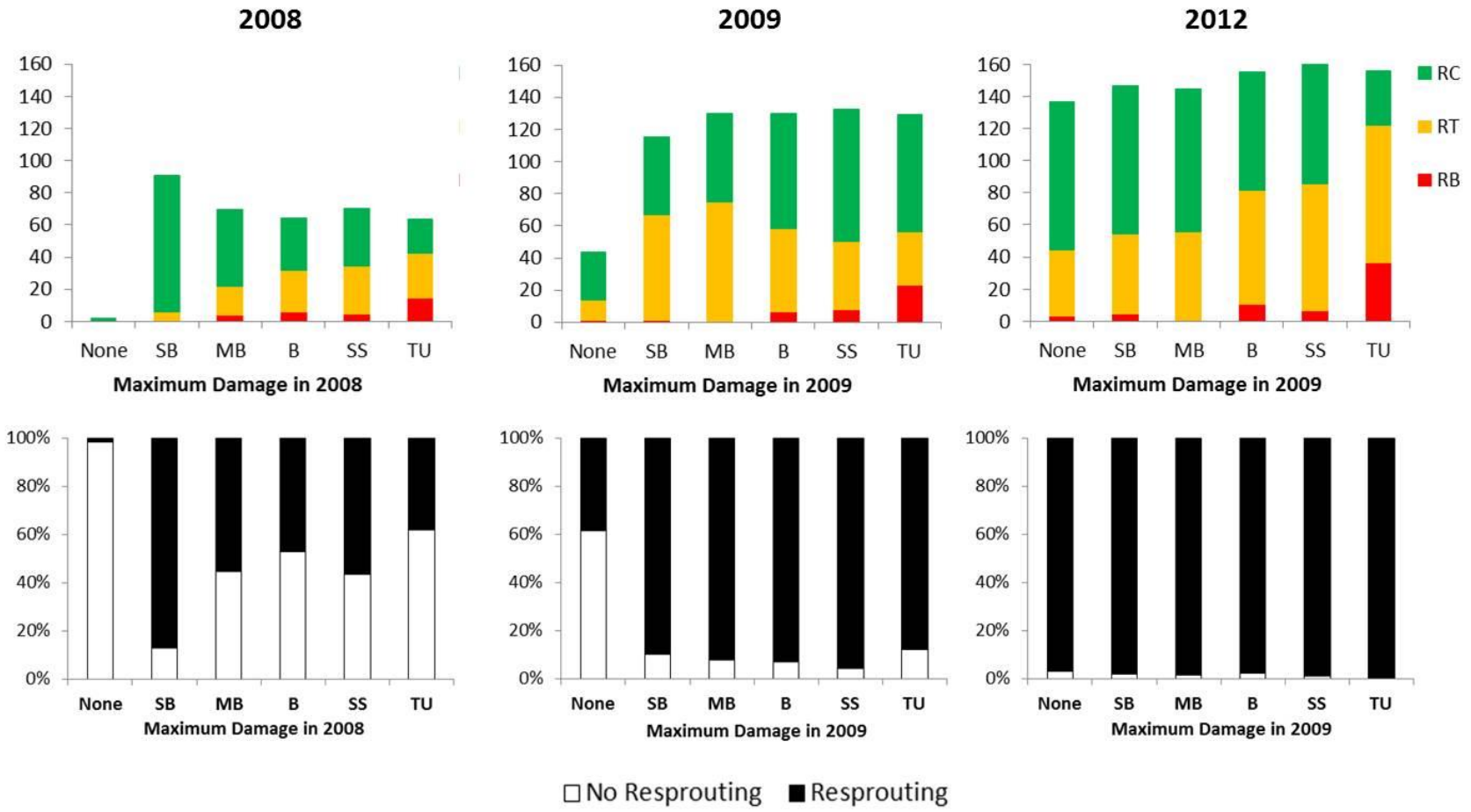

Figure 4.6: Percent of stems within each resprouting category (RO: no resprouting apparent, RB: basal resprouting, RT: resprouting on the main trunk, RC: crown recovery) by damage category. The 2012 recovery data is based on the damage recorded in 2009. For 2008 *N*=6,055; for 2009 *N*=2,672; for 2012 *N*=2,264.

4.3.2: Characterizing forest recovery at the stand level

Forest recovery after the impact of hurricane Dean varied widely among forest stands within the Calakmul – Sian Ka'an corridor, both spatially and temporally (Figure 4.7). The average percent of stems per plot for which resprouting was recorded follows the same pattern of the overall stem sample, with a marked increase from 2008 through 2012 (Table 4.4). On average, in 2012, five years after the disturbance, the vast majority of stems had recovered a closed crown (average of 86.5% per plot) resulting in largely closed forest canopies, while only an average 1.5% of stems per plot did not show any type of resprouting.

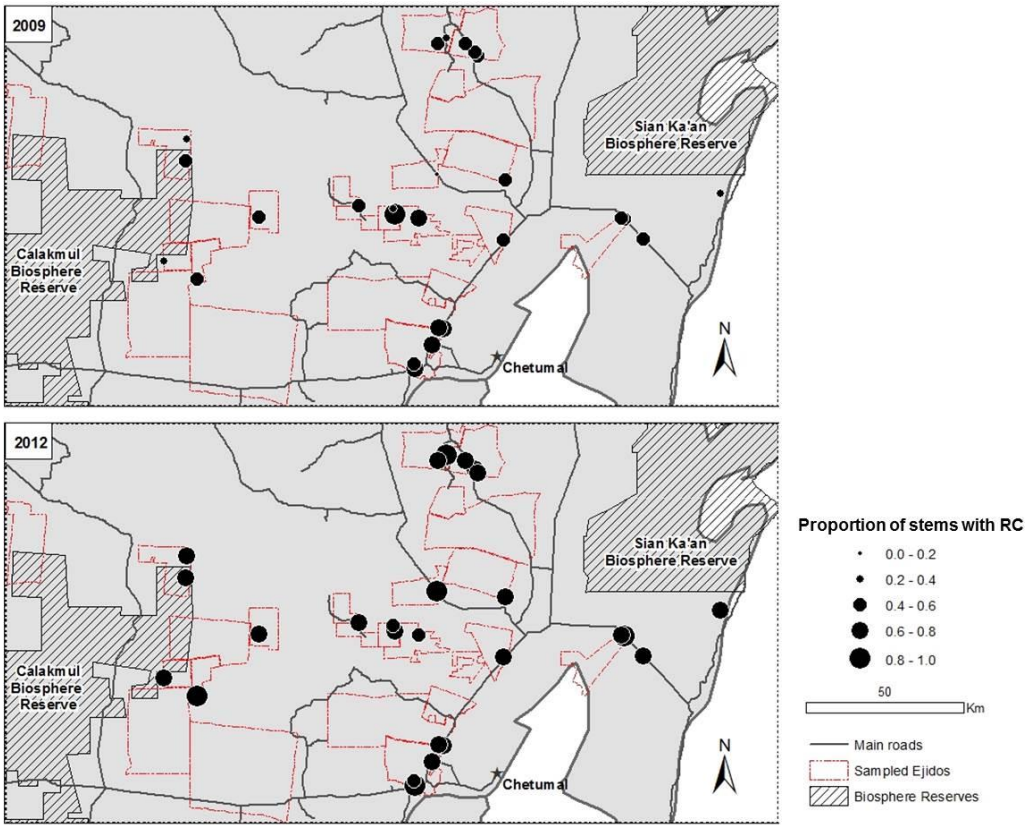

Figure 4.7: Proportion of stems with crown recovery (RC) within 26 field plots in 2009 and 2012.

Table 4.4: Average percent of live stems per plot with each type of resprouting one, two

and five years after the impact of hurricane Dean (in 2008, 2009 and 2012, respectively). For 2008 *N*= 6,055; for 2009 *N*=2,678; for 2012 *N*=2,268.

Resprouting Category	Average % of stems		
	2008	2009	2012
RO	60.6	15.5	1.5
RB	4.7	3.3	5.9
RT	15.5	53.1	57.0
RC	41.9	55.6	86.5

When dissagregating the data by forest type (Table 4.5) and succesional stage (Table 4.6), differences in the resprouting response within the field plots become apparent. Even though within all the plots the proportion of live stems with resprouting increased between 2008 and 2012, in 2009 the average proportion of live stems with RT recorded in low-statured forests (80.8%) was almost twice that of medium-statured forests (47.1%). This value is also much higher than the proportions for the same tipe of forests from 2008 (12.9%) and 2012 (57.2%). Similarly, in 2009, 96.3% of all live stems showed some type of resprouting in low-statured forests, and 5.9% had basal resprouting. In comparison, that same year only 82.0% of live stems from mid-statured forests had resprouts, with only 2.7% of them occuring at the base of the trunks (Table 4.5).

Likewise, when the field plots are separated by forest age, a similar pattern of higher average proportion of stems with RT was recorded in young forests in 2009 than in mature forests, or in other years (Table 4.6). Differences are also observed in terms of the average proportion of stems with RB, which was higher in 2008 and 2009 in mature forests, but noticeably larger in younger forests in 2012. Finally, the average proportion

of stems with a healthy crown in 2012 was slightly lower in mature forests than in younger forests.

Table 4.5: Average percent of live stems per plot with each type of resprouting by forest type one, two and five years after the impact of hurricane Dean (in 2008, 2009 and 2012, respectively). The number of plots in each sample in indicated in parenthesis.

	Average % of stems					
	Low-statured forests			**Medium-statured forests**		
Resprouting Category	**2008 (*N*=23)**	**2009 (*N*=5)**	**2012 (*N*=5)**	**2008 (*N*=62)**	**2009 (*N*=23)**	**2012 (*N*=21)**
RO	61.3	3.7	2.0	51.3	18.0	1.3
RB	3.4	5.9	8.1	4.3	2.7	5.4
RT	12.9	80.8	57.2	15.6	47.1	57.0
RC	35.7	48.8	88.0	43.2	57.1	86.1

Table 4.6: Average percent of live stems per plot with each type of resprouting by forest age one, two and five years after the impact of hurricane Dean (in 2008, 2009 and 2012, respectively). The number of plots in each sample in indicated in parenthesis.

	Average % of stems					
	Forest < 20 years old			**Forest >20 years old**		
Resprouting Category	**2008 (*N*=25)**	**2009 (*N*=9)**	**2012 (*N*=9)**	**2008 (*N*=60)**	**2009 (*N*=19)**	**2012 (*N*=17)**
RO	59.3	16.0	1.1	51.8	15.2	1.7
RB	2.0	1.8	7.3	4.9	4.0	5.2
RT	10.4	60.2	51.5	16.7	49.7	59.9
RC	36.4	50.3	90.1	43.2	58.2	84.6

4.3.3. Forest fragmentation and forest recovery at the stand level

Results of the correlation analysis show no significant correlations between the proportion of stems with crown resprouting (RC) in 2008 and the fragmentation indicators for any of the buffer sizes, either when considering the effect of forest type or forest age (Tables 4.7 and 4.8). Interestingly, the interaction of the variables is exactly the opposite in low-statured and mid-statured forests (Table 4.7). In low-statured forests, the proportion of stems with RC is positively correlated to the *proportion forest* and negatively correlated with the *edge/core ratio* at all scales, while the opposite is true for mid-statured forests. Although similarly non-significant, the interaction of the recovery and fragmentation variables shows more variation when contrasting young *vs.* old forests. Thus, within a buffer of 250 m, the proportion of stems with RC is negatively correlated with the *proportion forest* indicator and positively correlated to the *edge/core ratio* in both young and old forests. However, for the two larger buffer sizes, the direction of the correlations varies both between forests of different age groups and within forests of the same age groups.

For the 2009 field data, the correlation analysis does show significant correlations between the proportion of stems with crown resprouting (RC) and the fragmentation indicators for both medium-statured and old forests (>20 years old) within the 250 m buffer size (Table 4.9 and Table 4.10). In medium-statured forests, the proportion of stems with RC has a significant negative correlation with the *proportion forest* (*rho* = -0.4421, p=0.0347), and an almost significant positive correlation with the *edge/core ratio* (*rho* = 0.3977, p=0.0602). Similar interactions are seen for the larger buffer sizes and for low-statured forests at the 250 m buffer size, but these are not significant (Table

4.9). Similarly, in forests older than 20 years, the proportion of stems with RC has a significant negative correlation with the *proportion forest* (*rho* = -0.4820, *p*=0.0366), and a significant positive correlation with the *edge/core ratio* (*rho* = 0.5212, *p*=0.0221). At the next buffer size considered (500 m), these correlations are almost significant (*rho* = -0.4253, *p*=0.0695 and *rho* = -0.4236, *p*=0.0708, respectively). In younger forests (<20years old), none of the correlations were significant, and their sign changed between the 250 m buffer and the larger buffers.

Table 4.7: Pairwise correlations between the proportion of stems with crown recovery (RC) in 2008 and fragmentation indicators by buffer area and forest type for 91 field plots.

Fragmentation Indicator	**Low-statured forests**		**Medium-statured forests**	
250 m Buffer	**Coeff.**	**Prob>|t|**	**Coeff.**	**Prob>|t|**
Proportion Forest	0.0783	1.0000	-0.2075	0.6339
Edge/Core Ratio	-0.1220	1.0000	0.1351	1.0000
500 m Buffer				
Proportion Forest	0.1621	1.0000	-0.1389	1.0000
Edge/Core Ratio	-0.2677	1.0000	0.0677	1.0000
1 km Buffer				
Proportion Forest	0.1577	1.0000	-0.1123	1.0000
Edge/Core Ratio	-0.2549	1.0000	0.0204	1.0000

Table 4.8: Pairwise correlations between the proportion of stems with crown recovery (RC) in 2008 and fragmentation indicators by buffer area and forest type for 91 field plots.

Fragmentation Indicator	**Forest <20 years old**		**Forest >20 years old**	
250 m Buffer	**Coeff.**	**Prob>|t|**	**Coeff.**	**Prob>|t|**
Proportion Forest	-0.2560	1.0000	-0.1018	1.0000
Edge/Core Ratio	0.0284	1.0000	0.1253	1.0000
500 m Buffer				
Proportion Forest	-0.3187	0.7233	0.0076	1.0000
Edge/Core Ratio	-0.0018	1.0000	0.0431	1.0000
1 km Buffer				
Proportion Forest	-0.3209	0.7066	0.0285	1.0000
Edge/Core Ratio	-0.0069	1.0000	-0.0313	1.0000

Table 4.9: Pairwise correlations between the proportion of stems with crown recovery (RC) in 2009 and fragmentation indicators by buffer area and forest type for 28 field plots. (Spearman's rank correlation coefficients with Bonferroni-correction, significant p= 0.05).

Fragmentation Indicator	**Low-statured forests**		**Medium-statured forests**	
250 m Buffer	**Coeff.**	**Prob>|t|**	**Coeff.**	**Prob>|t|**
Proportion Forest	-0.6000	0.2848	-0.4421*	0.0347
Edge/Core Ratio	0.5000	0.3910	0.3977	0.0602
500 m Buffer				
Proportion Forest	0.3000	0.6238	-0.3386	0.1140
Edge/Core Ratio	-0.5000	0.3910	0.2840	0.1891
1 km Buffer				
Proportion Forest	0.3000	0.6238	-0.2631	0.2251
Edge/Core Ratio	0.1000	0.8729	0.2433	0.2632

Table 4.10: Pairwise correlations between the proportion of stems with crown recovery

(RC) in 2009 and fragmentation indicators by buffer area and forest age for 28 field plots. (Spearman's rank correlation coefficients with Bonferroni-correction, significant p=0.05).

Fragmentation Indicator	**Forest <20 years old**		**Forest >20 years old**	
250 m Buffer	**Coeff.**	**Prob>|t|**	**Coeff.**	**Prob>|t|**
Proportion Forest	-0.1695	0.6628	-0.4820*	0.0366
Edge/Core Ratio	0.1356	0.7279	0.5212*	0.0221
500 m Buffer				
Proportion Forest	0.0586	0.8810	-0.4253	0.0695
Edge/Core Ratio	-0.0251	0.9489	0.4236	0.0708
1 km Buffer				
Proportion Forest	0.0667	0.8647	-0.3168	0.1863
Edge/Core Ratio	-0.0500	0.8984	0.3554	0.1354

4.4: Discussion

Hurricane Dean caused extensive structural damage to the Mexican forests of the Calakmul – Sian Ka'an corridor. However, regrowth and significant structural recovery through resprouting of surviving stems have taken place within the first five years after the disturbance, resulting in forest stands with a high proportion of stems with healthy crowns and mostly closed canopies. Nonetheless, this recovery has not yet brought back the structure of these forest stands to the inferred pre-hurricane conditions.

4.4.1: Overall patterns of forest recovery

In the years following the impact of hurricane Dean, average basal area in the 26 forest plots increased from 24.9 m^2ha^{-1} in 2009 to 29.5 m^2ha^{-1}in 2012, which indicates that forest regrowth is ongoing. However, forest structure has not yet reached the

estimated pre-hurricane conditions. It is important to note that it is not possible to establish a clear "threshold" for this estimated pre-hurricane condition for all plots, since structural measures such as mean DBH and basal area estimates for the forests of the Yucatán Peninsula vary significantly, depending on factors such as forest type and age, and history of previous disturbances, particularly clear-cutting and fire. For example, Urquiza-Haas et al. (2007) found that basal area in the region varied from 1.6 to 23.8 m^2ha^{-1} in mid-successional stands (<30 years), while in late-successional stands (30-50 years) it ranged from 7.8 to 46.3 m^2ha^{-1}. In old-growth forest plots that had not been affected by natural or anthropogenic disturbance events for at least 50 years, basal area was consistently higher ranging from 23.2 to 46.3 m^2ha^{-1}.

In the post-hurricane forests of the study area, smaller-sized tree stems (DBH: 5.0-7.5 cm) have become more abundant, with their relative contribution to overall forest basal area reaching inferred pre-disturbance levels by 2011, four years after Dean's impact (Figure 4.2). Meanwhile, the density and basal area of large trees (DBH>15 cm) remains below the inferred pre-hurricane conditions. This is not surprising considering that larger stems where more severely affected by the intense winds associated to the hurricane (Chapter 3; Vandecar et al. 2011), and many of them were uprooted or died. As a result, average stem size for forest stands is still below estimated pre-hurricane levels.

In the forests of the Calakmul – Sian Ka'an biological corridor impacted by hurricane Dean, the growth of stems within the smaller DBH size classes, and the incorporation of new individuals reaching the 5 cm DBH threshold seems to be occurring at a faster rate than the growth of larger, mature stems (Figure 4.2). Under certain conditions, this result may partly be due to an increased contribution of pioneer and early

successional species among recruited stems, which generally exhibit a maximum growth rate at small size classes (Uriarte et al. 2004; Imbert and Portecop 2008). Alternatively, the growth of juveniles of the dominant forest species might have been "released" after the disturbance, as canopy cover dramatically decreased and competitive dynamics were altered within the forest understory (Everham and Brokaw 1996). The latter case seems to explain more appropriately field observations from the forests of the Yucatán peninsula, as there were no significant changes to species richness and dominance within the first five years after hurricane Dean's impact. The largest number of stems that were incorporated into the plots as they reached a DBH of 5 cm over a period of four years corresponded to three of the dominant forest species (*Vitex gaumeri, Piscidia piscipula* and *Luehea speciosa*).

In addition, slower growth of the larger surviving stems might be associated to the loss of part of their crown or root system, and therefore, to an allocation of resources towards sprouting rather than diameter growth in the first years after the disturbance, resulting in slower increases to DBH (Paciorek et al 2000; Imbert and Portecop 2008). This result is not surprising, given that in order to be able to sprout after suffering damage, a tree needs to use stored reserves to support regrowth. This in turn carries a cost traded off against growth (Bond and Midgley 2001). Furthermore, the crowns play an essential role in the photosynthesis process that allows for the building of carbohydrates needed for tree growth. Therefore, their absence will at the very least slow down this process.

Interestingly, as reported for other tropical forests recovery (Imbert and Portecop 2008), drought might also have partially delayed forest recovery in the first couple of

years after the hurricane impact. A small decrease in DBH was noticed for many stems in 2010 and 2011 from the previous year. Data from meteorological stations from across the study region indicates that the 2-3 years immediately following the impact of hurricane Dean were drier than average in this region (see Mardero et al. *submitted*).

Resprouting capacity: As has been widely reported in the literature, the production of new leaves seems to be the first step in the recovery process of tropical forests structure and function after a catastrophic wind disturbance (Imbert and Portecop 2008). Islebe et al. (2009) found that approximately 70-80% of the stems in plots of medium-statured forests located along the coast of the Calakmul – Sian Ka'an corridor (within wind speed zone 5) had already produced new leaves only one month after hurricane Dean's impact, even though defoliation was almost 90%-100% immediately after the disturbance.

The sprouting of new branches and stems quickly followed within the next months and years, with almost all the surviving stems showing some resprouting in 2012, five years after the hurricane impact. Crown recovery was by far the most common and fastest occurring type of resprouting observed within the study plots. This is probably related to the characteristics of the species found within this area and their resprouting ability, and the fact that they probably present more mersistems (i.e., tissue of undifferentiated cells where growth can take place) towards the apice of the trunk, which are essential for a plant's resprouting response after an injury (Bond and Midgley 2001). In addition, the extent of crown resprouting might be a response to the fact that the dominant types of damage caused by hurricane Dean to the trees left most of the surviving trees erect and able to resprout from the top (e.g., stem snapping and branch loss; see Chapter 3).

Of the different types of resprouting considered in this assessment, only basal sprouts could potentially contribute to an increase in stem density and basal area; while sprouts locater higher along the trunk will help fill in canopy gaps (Van Bloem et al. 2005).

Almost all species resprouted to varying degrees, with no significant differences observed in the proportion of stems with sprouts for either the common or less common species (Vandecar et al. 2011). Similar high resprouting capacities have been observed in other tropical forests periodically affected by hurricanes (e.g. Van Bloem et al 2005, 2006), which might be an indication of species adaptation to this type of disturbance in the region. The main exceptions to this pattern were palm species, which in general lack the ability to resprout (Frangi and Lugo 1991). As a result, palm trees that are severely affected by hurricanes and lose their crowns due to the high winds can die in the medium to long term. This in turn would lead to a reduction of their relative abundance in the forest stands (as was the case of *Sabal mexicana* in this study).

Given these results, it is expected that species dominance and composition within the group of dominant species will not be significantly altered within the study area in the years following the impact of hurricane Dean as a result of the recovery process, with the possible exception of palm species. Results of the species IV analysis support this expectation, at least for the period 2009-2012. In the future, this should still hold true as long as there are no significant differences in sprout survival through time, which was not directly assessed in this study but has been found to vary between 40.5% and 74% in other studies, with no significant differences regardless of location on the trunk (Peterson and Pickett 1991; Van Bloem et al 2006). Qualitative observations during field work suggest a high rate of resprout survival within the Calakmul – Sian Ka'an forests. In fact,

by 2012 a few basal sprouts had become large enough to be included in the database as they reached the minimum diameter class (≥5 cm DBH).

Nonetheless, it is important to note that Vandecar et al. (2011) identified a notably higher mortality rate as a result of the impact of hurricane Dean for the less abundant species in the region when a larger sample was considered (91 plots). If this trend is typical of hurricane damage in the Yucatán forests, the added impact of these natural disturbances might effectively reduce the presence of rare species within these forests in the future, even if any surviving stems have the potential to recover through resprouting. The continuing monitoring of the study plots in the future will help determine if this is the case.

4.4.2: Forest recovery at the stand level

Forest recovery after the impact of hurricane Dean varied widely among forest stands within the Calakmul – Sian Ka'an corridor, both spatially and temporally. Some of these differences seem to be related in part to forest type.

Overall, tree stems in low-statured (*selva baja*) forests seemed to resprout faster than stems in medium-statured forests (*selva mediana*), showing a noticeably larger proportion of stems with resprouting in 2009 (Tables 4.5). These differences, however, become less evident with time. Although the sample of low-statured forests for 2009 and 2012 is small, this result is still somewhat surprising, given that these forest types differ mostly in structural appearance rather than species composition (Vester et al. 2007), and no significant differences on the capacity to resprout were found for species within the study area. One possible explanation is that damage was higher in medium-statured forests,

which are characterized by taller and wider trees. In this case, it would be expected that a longer time would be required for the more severely impacted trees to resprout.

Water availability might also have played a role in the observed differences in early sprouting capacity. Low-statured forests are mostly found in low-lying areas, with less water run-off (Pérez-Salicrup 2004; Vester et al. 2007). As a result, it would be expected that in particularly dry years, such as those that followed hurricane Dean's impact, low-statured forests would have a hydric advantage over mid-statured forests, which would favor their resprouting capacity. However, this is only speculation, and further data would be needed to test it.

4.4.3: Forest fragmentation and forest recovery at the stand level

Contrary to what was expected, results of the correlation analysis suggest that forest fragmentation was not significantly correlated with forest recovery at the stand level in the year immediately following the impact of hurricane Dean within the Calakmul – Sian Ka'an corridor (Tables 4.7 and 4.8). This might be due in part to the fact that severe damage caused by hurricanes in tropical forests can significantly alter the light environment within the forest for over a year after the disturbance (Fernández and Fetcher 1991; Bellinghmam et al. 2006). In this case, the differences between edge habitat and forest interior that may result in different rates of recovery under normal circumstances might not be significant. In addition, stem resprouting in 2008 was still limited within the forest stands of the study area (average of 42.9% of stems per plot), and thus the variability in values of the proportion of stems with RC used in the correlation analysis was limited.

In contrast, correlation analysis between the proportion of stems which had recovered a closed canopy by 2009 and the fragmentation indicators did result in significant correlations within the smaller buffer size used for the analysis (250m) for both medium-statured and older forests (Tables 4.9 and 4.10). In particular, the proportion of stems with RC was negatively correlated to the *proportion forest* indicator, and in the case of older forests, it was positively correlated with the *edge/core ratio*. This result coincides with what would be expected. Forest fragmentation effectively results in a change in microclimatic conditions in forest stands, including an increase in light availability along forest edges. In turn, light availability can promote the resprouting response. However, the results suggests that in low-statured and younger secondary forests which are naturally characterized by a more open canopy and where light availability is overall higher, any possible effects of the light gradient partitioning resulting from forest fragmentation on resprouting rates are lost. A similar explanation was proposed by Poorter et al. (2010) to explain the differences in regeneration of forest species in moist versus dry tropical forests in Bolivia. It is worth pointing out that these results do not suggest that forest fragmentation is "good" for the recovery of medium-statured and old forests after a hurricane impact, but are instead a reflection of the forest species characteristics, their resprouting capabilities and their light requirements.

An interesting point is that the resolution of the fragmentation analysis limits the type of fragmentation that is taken into account for the pairwise correlations with forest recovery. Field observations suggest that forest gaps presumably related to hurricane damage within the study plots were small in size, certainly smaller on average than the size of the Landsat image pixels used to map forest fragmentation (30 x 30 m). Therefore,

small sized perforations existing within the plots, mostly resulting from trees that fell after the impact of hurricane Dean or from extractive forestry activities, were not accounted for in the fragmentation measures. Instead, the fragmentation measures considered in this study account mostly for large edges in the boundary of forest *vs.* non forested areas, while "perforations" (i.e., gaps) correspond mostly to areas affected by human activities (e.g., subsistence agriculture and pastures) or to areas where non-forest vegetation is predominant. Nonetheless, the small forest gaps might effectively have influenced the rates of forest recovery within the forest stands, both by increasing light availability and by facilitating other paths to recovery to take place, such as the recruitment of early successional species and the release of sub canopy trees. A correlation analysis between forest recovery and fragmentation associated to gap size and number as measured in the field might help further characterize the relation between these two variables in the Yucatán forests.

4.4.4: Conclusion

The impact of hurricane Dean caused noticeable structural changes in the short and medium-term to the forests of the Calakmul – Sian Ka'an biological corridor. In particular, basal area and stem density (particularly of larger trees) have decreased. In addition, although not directly measured in the field, average forest height was also reduced, as many large trees were snapped, bent or fell down. Despite these significant changes, the forests in the study region seem to be recovering at a relatively fast pace, mostly through resprouting and growth. Furthermore, this recovery process does not

seem to be resulting in additional changes to forest composition that could add to those already caused by the original damage, at least at the short and medium terms.

Results from previous research suggest that in the long term, the reduction in basal area resulting from hurricane damage in the forests of the Yucatán peninsula is less significant than reductions resulting from other common disturbances that regularly affect these forests, particularly fire and clear-cutting. Therefore, if these forests are not affected by other disturbances, it is expected that continuous growth would eventually allow them to reach pre-hurricane conditions after a few decades (Urquiza-Haas et al. 2007).

Chapter 5: Conclusions

In a world where land use and land cover are changing at a very fast pace (Achard et al. 2002; DeFries et al. 2002; Ramankutty et al. 2006; Hansen et al. 2010), the sustainability of forests and their ability to provide goods and ecosystem services in the future are an important concern (Clark and Dickson 2003; Schmitt et al. 2009; FAO 2012). This dissertation contributes to current research agendas in Geography and Land Chance Science (LCS) aimed at understanding how disturbances affect tropical forests. This information is important to better understand the "environment" side of the complex socio-ecological systems that are tropical forests. In particular, this research expands on the current knowledge on how hurricanes, an important and recurrent disturbance in tropical regions, impact the forests of the southern Yucatán peninsula in the short and medium term, and how these impacts might be exacerbated by anthropogenically driven forest fragmentation at the landscape scale. These insights are complemented by an assessment of the recovery process after the disturbance, which allows important inferences regarding these forests' resilience and their future in the face on increased anthropogenic and environmental disturbances.

5.1: Disturbances and forest sustainability: a general overview

Most ecosystems are subject to disturbance regimes that occur across a range of temporal and spatial scales, and that are important drivers of land change (Turner 2010b). Large infrequent disturbances such as fires and hurricanes can dramatically alter the land surface, often within much shorter time frames and across larger areas than those

associated to anthropogenic activities (Dale et al. 1998; Foster et al. 1998; Negrón Juárez et al. 2008). Hurricanes in particular can impact land surfaces with effects that are noticeable from regional to local scales, as they can result in substantial blowdown of forest areas, landslides, large debris accumulations and altered topographic features (Lugo 2008; Xi and Peet 2011).

Hurricanes furthermore become an integral part of long-term ecosystem dynamics (Dale et al. 1998; Willig et al. 2007). They usually result in significant structural changes in vegetation, including widespread defoliation, biomass loss due to snapped stems and branches, as well as tree bending, uprooting and death. At longer time scales, additional structural and compositional changes can occur as the altered environmental conditions impact competitive dynamics and forest succession, which in turn can alter ecosystem processes and function (Everham and Brokaw 1996; Willig et al. 2007; Vandecar et al. 2011; Xi and Peet 2011), as well as the geochemical cycles of nutrients and trace gases (Lodge and McDowell 1991). Hurricanes can also induce changes to land use patterns, as the strong winds and heavy rainfall that usually characterize them can significantly affect urban and agricultural lands, resulting in crop loss, infrastructure collapse and landslides (e.g. Philpott et al. 2008).

In recent years concerns have been growing after studies have shown that the regimes of many of these disturbances are shifting, and their intensity and frequency will likely increase across a wide range of forest ecosystems as a result of global climate change (e.g., Dale et al. 2001; Elsner 2006; Flannigan et al. 2009; Bender et al. 2010). For example, in the western United States there has been a significant increase in the frequency of large wild-fires and their duration, in association with increasing

temperatures and earlier snowmelt (Westerling et al. 2006). Seven of the 10 most damaging hurricanes that affected the United States since the mid-20th century made impact over just two years of the last decade, 2004 and 2005 (Changnon 2009). These altered disturbance regimes could potentially result in significant changes in species composition, or the elimination of forests all together (Buma and Wessman 2011; Brown and Johnstone 2012). For example, Brown and Johnstone (2012) found that shortened fire return intervals severely affect seed availability and reduce recruitment in a black spruce boreal forest in Canada, disrupting the normal port-fire recovery process and reducing these forests' resilience to fire.

To further complicate the picture, the fast increase of anthropogenic disturbances such as agricultural and urban expansion is resulting in significant and accelerated land use and land cover changes worldwide (Lambin et al. 2006; Turner et al. 2007). These human driven changes are closely related to processes of land degradation, and loss of biological diversity and ecosystem services (Kok and Winograd 2002; Rindfuss et al. 2004).

Disturbances may interact and cause novel disturbances (Buma and Wessman 2011), affect forest recovery (Brown and Johnstone 2012) or result in accelerated or more intense rates of species declines and loss of forest functions (Dale et al. 2000; Laurance et al. 2006; Brook et al. 2008).

Given these facts, concerns about the long-term ability of forests to maintain their biodiversity and their provision of good and services to human societies, including food, clean water, timber, carbon storage and soil protection are well founded (Constanza et al. 2000; Thompson et al. 2009). Comprehensive studies of the patterns of disturbance

impacts on the landscape and the factors controlling them are essential to understand landscape dynamics. Understanding the complexities around disturbances regimes will help to inform resource managers and policy makers towards efforts of reducing human and ecological vulnerability, as well as achieving sustainability (Foster et al. 1998; Turner and Dale 1998; Lugo 2008; M. G. Turner 2010).

Such research is very relevant for the seasonal forests of the Yucatán peninsula, Mexico, given their long history of anthropogenic and environmental disturbances. Using a LCS approach, this dissertation tries to further complement our understanding of forest change within the Calakmul – Sian Ka'an biological corridor. This approach differs from the more traditional approaches of ecology and landscape ecology that have been applied to the study of hurricane disturbances in that it attempts to bring together very different data sets at different scales, but in particular the landscape scale, across a large geographic region, to address the research questions.

5.2: A Land Change Science approach to assess the effects of hurricanes on forests

Since its beginning, LCS has been concerned with how changes to land and ecosystems affect global environmental change and sustainability. So far, The LCS research community has addressed some of the major issues of land change in the modern world, including the causes of tropical deforestation and desertification, agricultural intensification, urban expansion and biodiversity loss. In doing so, it has provided an understanding of how land use and land cover change are affected by the behavior of people and society (agents and structure), the different levels at which decisions on land

management are made, and the ways in which people and their lands are connected to the broader world (Lambin et al. 2006; Rounsevell et al. 2012).

As important as these issues are, it is evident that most of these efforts have focused on land cover changes driven by human land use and other anthropogenic disturbances. That is, most of the focus has been on the "human" side of the "human-environment system." So far, environmental disturbances have received less attention in these studies, with the notable exception of fire (e.g., Rogan and Yool 2001; Balch et al. 2008; Bowman et al. 2011). Overall, environmental disturbances should be incorporated more broadly into the LCS research agenda in order to fully understand the socio-ecological systems where they occur.

Recognizing the above facts, the Global Land Project Science Plan and Implementation Strategy (Moran and Ojima 2005) identified almost a decade ago the establishment of research programs that quantify the impacts of hurricanes and other extreme climatic events as a key area of research for the following years. Such studies would complement the large body of research on the impacts of hurricanes on natural ecosystems and human societies that has been developed over the last decades (particularly since the early 1990s, after hurricane Hugo struck the Caribbean). These include studies carried out by ecologists focusing on plot level assessments and long term comparisons of pre- and post-hurricane conditions across different ecosystems (e.g. Walker et al. 1991; Sánchez- Sánchez and Islebe 1999; Whigham et al. 2003), as well as the work of geographers and other social scientists involved in hazards research, whom have greatly advanced the understanding on the social impacts and vulnerability caused by these disturbances (e.g. Alcántara-Ayala 2002; Pielke Jr. et al. 2003; Mas Bermejo

2006). These efforts have gathered a fairly large amount of information regarding the characteristics of hurricane effects on ecosystem and human societies at local scales, and in particular, of damage. For example, we know that in forested ecosystems immediate hurricane damage often results in widespread defoliation, biomass loss due to snapped stems and branches, as well as tree bending, uprooting and death (Everham and Brokaw 1996; Whigham et al. 2003). At longer time scales, additional structural and compositional changes can occur as the altered environmental conditions impact competitive dynamics and forest succession, which in turn can alter ecosystem processes and function (Everham and Brokaw 1996; Xi and Peet 2011). However, there is less information about the effects of these disturbances at the landscape scale, or of their interactions with other natural or anthropogenic disturbances (Lugo 2008).

Among the important questions that require additional research we can mention: How do different disturbances interact and how do those interactions affect ecosystems? How do these interactions and effects vary with scale? How do recovery patterns differ among disturbances? Which ecosystems are more vulnerable, and how can we reduce that vulnerability? Which systems are more resilient and why?

Within the framework of these remaining questions and LCS, this dissertation provides insights into the interaction of a natural and an anthropogenic disturbance on forest change, by looking at the relationship of hurricane impacts and the effects of a mostly human-driven forest fragmentation. The research presented here is an important contribution to understanding the impact of hurricanes on forests at different spatial (from the regional to the forest stand) and temporal (immediate to 5 years) scales. Incorporating these spatial and temporal scales to the analysis seemed essential for several reasons.

First, to incorporate the large spatial heterogeneity of hurricane damage that previous research has proven arises from the interaction of different biotic and abiotic factors (such as species composition, topography, and wind speed, among many others). Second, to assess if there are differences in the interactions between forest fragmentation and forest damage and recovery at different spatial scales. Third, in recognition that even though it is very important to understand what is happening at the very local scale of individual forest stands, we also need to address research scales that have more significance in terms of potential management decisions, such as those of states, municipalities, or as was the case of this dissertation, the land management units (i.e., *ejidos*).

Similarly, assessing both the immediate and medium term response of the forests to the hurricane disturbance is an important contribution of this dissertation. In the case of the impact of hurricanes on forests, this includes addressing both damage and recovery at different points in time, since changes to forest dynamics as result of these natural disturbances cannot be understood solely by looking at the immediate time after the disturbance. In particular, the assessment of forest recovery several years after a hurricane disturbance contributes to the limited available data on the topic. This is especially important given that the response of forests to global change will greatly depend on its ability to regenerate following a disturbance (Dietze and Clark 2008). As will be discussed in the following section, limiting the assessment of the impacts of hurricane Dean to the year immediately following the disturbance would have resulted in missing significant information regarding the lagged-mortality of trees in the following years.

5.3: Lessons learned: Forest damage and recovery after a hurricane impact within the Calakmul – Sian Ka'an biological corridor

In this dissertation, the effect of hurricane Dean on the forests of the Calakmul – Sian Ka'an biological corridor and its relationship with forest fragmentation was addressed from two different perspectives: the direct damage caused by the strong hurricane winds on the forests, and the subsequent recovery of surviving trees.

Forest damage: Overall, the results of this dissertation show that hurricane Dean caused significant and extensive damage to the forests of the study region, both at the level of forest stands as well as at the *ejido* and regional levels. In the particular case of forest stands, results show a large spatial variability in both immediate and medium term forest damage across the region. Significant reductions in the number of live stems and basal area were observed overall. Noticeably, the most severe effects were not evident immediately following the disturbance, but a few years later. While stem mortality immediately after the hurricane impact was relatively low at 5.6%, field data from subsequent years highlights the delayed impact of forest damage in terms of lagged mortality. The number of dead stems presumably due to hurricane damage had reached an average of 14.6% of stems per plot five years after the disturbance, which corresponds to an average of a fifth of the estimated original standing tree basal area. Most of these deaths were associated to stems that had been uprooted or snapped. Similar observations that community level effects of hurricanes are more noticeable sometime after the

disturbance have been reported for other Caribbean forests (e.g. Bellingham et al. 1995; Tanner and Bellingham 2006; Imbert and Portecop 2008; Bonilla-Moheno 2012).

At the *ejido* level, land management mediated forest loss and fragmentation was significantly correlated to high forest damage by winds, which suggests that forest fragmentation does render forests more vulnerable to the impact of hurricanes at the landscape scale. However, at the stand level a significant correlation between forest fragmentation and hurricane damage was found only within the coastal wind speed zone 5, which sustained the highest wind speeds. Together, these results suggest that the effect of different biotic and abiotic factors, as well as the synergistic effects of disturbances do in fact differ with the spatial scale considered, and therefore, including the different scales of analysis is essential in order to obtain a complete understanding of the interactions within the system. Only with this complete information would we be able to infer future patterns of change resulting from similar disturbances.

Forest recovery: Despite the severe damage caused by hurricane Dean, the forests of the Calakmul – Sian Ka'an biological corridor have shown significant recovery in the years following the disturbance. This is not surprising given that the current stands that persist in the Yucatán peninsula are the product of centuries of selection by these environmental disturbances. The forests of the study region were able to achieve significant structural recovery through resprouting and growth of the surviving stems and the release of pre-established seedlings within the first five years after the disturbance impact, resulting in forest stands with a high proportion of stems with healthy crowns and mostly closed canopies. In fact, results from other studies suggest that the dry forests of the Yucatán

peninsula show a high degree of resprouting and recovery even after being affected by subsequent hurricanes over short periods of time (e.g. Sánchez-Sánchez and Islebe 1999; Bonilla-Maheno 2012). However, the recovery process has not yet brought back the structure of these forest stands to the inferred pre-hurricane conditions, and total basal area remained below the estimated pre-hurricane conditions, particularly for the largest DBH size classes (i.e., larger trees) five years after the disturbance.

This predominantly vegetative recovery has been widely reported as the main recovery path for tropical forests affected by hurricanes (Brokaw and Walker 1991; Yih et al. 1991; Bellingham et al. 1994; Boucher et al. 2001; Van Bloem et al. 2006).The predominance of this particular path to recovery has the important consequence that it has not resulted in significant changes to species composition, at least in the medium term. No noticeable changes in species dominance were observed between 2009 and 2012, particularly for the 15 most dominant species from 2009. Additionally, no significant differences were observed in the proportion of stems with sprouts between species, although overall, tree stems in low-statured (*selva baja*) forests seemed to resprout faster than stems in medium-statured forests (*selva mediana*), which could be linked to higher light and water availability in the former.

From the results presented in this dissertation I could infer that over the next decades, after a few more years of regrowth, the affected forests stands would look very similar to the pre-disturbance conditions, if they are not affected by additional disturbances. Any possible observed differences would likely be a result of the observed differential mortality rates of rare *vs*. abundant species from the direct impact of the

hurricane (Vandecar et al. 2011), rather than from differences derived from the recovery process.

Together these results indicate that the forests of the Calakmul – Sian Ka'an corridor are resilient to hurricane disturbances. Resilience has been defined as the ability of a system to recover to a state similar to the one that preceded the disturbance. This includes maintaining the essential structural, compositional and functional characteristics that determine its identity (Holling 1973; Thompson et al. 2009; Buma and Wessman 2013). In this sense, when subjected to a disturbance or perturbation, a resilient forest ecosystem will be able to absorb the impacts without suffering significant change. However, if the disturbance exceeds the capacity of the forest to recover, the system will shift to a different state that may or may not also be highly resilient, but which will probably not be able to provide the same type and level of goods and services (Thompson et al. 2009).

Resilience is an emergent property, and as such it is conferred at multiple scales by genes, species, functional groups of species, and processes within the forest ecosystem (Drever et al. 2006; Thompson et al. 2009). In this sense, resilience is related to the biological diversity in the system and the capacity that it confers to maintain ecosystem processes (Walker 1995; Peterson et al. 1998; Drever et al. 2006). In the case of the forests of the Yucatán peninsula, it is very likely that the resilience of the systems is in large part related to its high species diversity (over 130 species were recorded within the 28 plots were recovery was assessed). No significant differences where observed in terms of the dominant species and their ability to recover, which suggests that they are all contributing to the overall resilience of the system.

Resilience is also a scale-dependent phenomenon. Therefore, defining the resilience of an ecosystem requires both a spatial and a temporal component that are related to the disturbance extent and frequency. For most forests, resilience tends to be considered over many decades to centuries (Thompson et al. 2009). In the case of this study, time constraints limited the analysis to just five years. Therefore, it is not surprising that the system had not yet returned to its previous state. However, as discussed above, it is inferred that after some more years, and in the absence of additional disturbances, it will do so.

Forest resilience to hurricane impacts observed within the Calakmul – Sian Ka'an forests is a desired quality given the high ecological and social value of these forests (Ramamoorthy et al. 1998; Klooster 2003; Vester et al. 2007). The results of this dissertation support observations from other areas of the world that suggest that most forests, particularly very diverse and productive ones, are overall resilient ecosystems, adapted to various kinds of perturbations and disturbance regimes (e.g., Holling 1973; Drever et al. 2006).

5.4: Further implications for the future of the forests of Southern Yucatán

Forest sustainability in the Calakmul – Sian Ka'an corridor within the goals of the Mesoamerican Biological Corridor seems to offer a particular challenge, given the increasing human pressures and the constant natural disturbances that affect this region.

Nonetheless, the results of this dissertation suggest that hurricanes are not the biggest threat against these forests, given their resilience to this type of disturbance. Of more concern seem to be the anthropogenic pressures that are resulting in an increased

deforestation and fragmentation of the forests within the corridor, and that facilitate and increase the incidence and extent of other catastrophic disturbances such as fires, which can effectively wipe out thousands of hectares of forests within a few days, leaving behind much less from which to start the forest recovery process than hurricanes (such as was observed for at least one of the study field plots). In support of this conclusion, other studies have found that the effects of hurricanes in tropical forests are usually less significant than those associated to human activities. For example, land-use changes were found to be the main determinant of forest composition in Puerto Rico, while hurricanes only had a small effect on the successional trajectories of the forests (Pascarella et al. 2004). Similarly, Boucher et al. (2001) found that in Nicaragua, post-hurricane forest stands were more similar in species composition to pre-hurricane sites than they were to young post-agricultural fields.

That being said, even if the forests of the Yucatán peninsula are able to recover relatively quickly from the direct impact of hurricane winds, these disturbances have an additional impact on the forests that needs to be characterized, as they can further increase anthropogenic impacts in the forests after the disturbance. Field observations and anecdotal evidence suggest that operations to salvage timber and dispose of woody debris after the hurricane resulted in a significant number of new roads being open, thus increasing forest perforation and overall fragmentation. Furthermore, the need to stop forest extraction after the impact of the hurricane until new Forestry Management Plans were approved resulted in some communities turning towards alternative sources of income, such as charcoal production (Schramski and Keys 2013). Even though this strategy can be seen as an example of the adaptive capacity of the inhabitants of the

Yucatán peninsula to natural hazards (Schramski and Keys 2013), local researchers and environmental authorities have expressed fear that such activities might further accelerate forest loss, degradation and fragmentation in the region in the future (B. Schmook, pers. comm.).

In the face on increasing disturbances and environmental change, it seems that the best approach to ensure the persistence of the world's forests and the valuable goods and services they provide is to maintain high levels of diversity within them. Such a strategy addresses the need to be prepared for any potential environmental changes that may take place, which is fundamental to the concept of resilience (Drever et al. 2006; Thompson et al. 2009). In this sense, it is likely important for the sustained resilience of the forests of the Calakmul – Sian Ka'an biological corridor that anthropogenic disturbances, such as selective timber extraction and small scale agriculture, do not significantly affect the species and genetic diversity of trees within the region.

Reducing forest loss and fragmentation should also reduce the vulnerability of forests to disturbances such as hurricanes, and very likely to other environmental disturbances, such as fires, as well. Furthermore, reducing forest fragmentation and other anthropogenic changes to the landscape will also reduce potential negative effects on seed dispersal and population genetic exchanges, which might affect the genetic pool of a forest's plant community, and therefore, their resilience.

Appendix A.1: Frequency of the most common species recorded in the 28 plots (2009-2012). Frequency is based on the cumulative tag ID, that is, it includes both live and death stems from previous years.

SCIENTIFIC NAME	No. of Stems 2009	% 2009	No. of Stems 2012	% 2012
Piscidia piscipula	207	7.05	239	7.19
Bursera simaruba	202	6.88	215	6.47
Croton reflexifolius	132	4.49	146	4.39
Metopium brownei	124	4.22	131	3.94
Vitex gaumeri	81	2.76	108	3.25
Lonchocarpus xuul	89	3.03	102	3.07
Luehea speciosa	78	2.65	101	3.04
Lysiloma latisiliquum	95	3.23	99	2.98
Gymnopodium floribundum	86	2.93	91	2.74
Cecropia peltata	66	2.25	78	2.35
Unknown	19	0.65	78	2.35
Manilkara zapota	69	2.35	77	2.32
Pouteria reticulata	69	2.35	75	2.26
Coccoloba spicata	64	2.18	70	2.11
Coccoloba diversifolia	61	2.08	67	2.02
Alseis yucatanensis	58	1.97	61	1.84
Thouinia paucidentata	49	1.67	53	1.59
Nectandra coriacea	47	1.60	50	1.5
Caesalpinia gaumeri	46	1.57	49	1.47
Chrysophyllum cainito	41	1.40	49	1.47
Lonchocarpus rugosus	46	1.57	49	1.47
Spondias mombin	43	1.46	46	1.38
Diospyros cuneata	42	1.43	44	1.32
Cupania glabra	37	1.26	37	1.11
Total Stems	**2,938**	**100.00**	**3,324**	**100**

Appendix A.2: Frequency of the most common plant families recorded in the 28 plots (2009-2012). Frequency is based on the cumulative tag ID, that is, it includes both live and death stems from previous years

FAMILY	No. of Stems 2009	% 2009	No. of Stems 2012	% 2012
Fabaceae	591	20.12	664	19.98
Polygonaceae	249	8.48	271	8.15
Sapotaceae	230	7.83	267	8.03
Euphorbiaceae	222	7.56	240	7.22
Burseraceae	209	7.11	223	6.71
Anacardiaceae	167	5.68	177	5.32
Unknown	104	3.54	163	4.9
Sapindaceae	140	4.77	148	4.45
Verbenaceae	87	2.96	117	3.52
Rubiaceae	108	3.68	115	3.46
Tiliaceae	78	2.65	101	3.04
Myrtaceae	86	2.93	97	2.92
Arecaceae (Palmae)	78	2.65	80	2.41
Cecropiaceae	66	2.25	78	2.35
Moraceae	66	2.25	70	2.11
Flacourtiaceae	44	1.5	52	1.56
Lauraceae	47	1.6	50	1.5
Ebenaceae	42	1.43	44	1.32
Meliaceae	39	1.33	43	1.29
Annonaceae	39	1.33	41	1.23
Malpighiaceae	33	1.12	37	1.11
Nyctaginaceae	29	0.99	32	0.96
Araliaceae	28	0.95	29	0.87
Malvaceae	25	0.85	29	0.87
Apocynaceae	25	0.85	26	0.78
Simaroubaceae	19	0.65	22	0.66
Rutaceae	14	0.48	17	0.51
Total Stems	**2,938**	**100**	**3,324**	**100**

Appendix A.3: Characterization of forest type, age, total number of stems and species found in the field plots in 2009

Plot ID	*Ejido*	Wind speed zone	Forest Type	Successional Stage	No. Stems	No. Spp.
03-0061	Bacalar	4	Selva mediana	Secondary veg. >20 years	145	25
08-0071	El Bajio	4	Selva mediana	Secondary veg. <10 years	60	18
09-0072	El Bajio	4	Selva mediana	Secondary veg. 10-20 years	64	17
10-0881	Tolloacan	5	Selva baja	Secondary veg. <10 years	104	29
12-SK2?2	Carretera Cafetal (Sian K'aan)	5	Selva baja inundable	Mature forest	142	35
19-0883	Tolloacan	5	Selva baja inundable	Secondary veg. <10 years	112	20
28-SK18	Costa Mahahual	5	Selva mediana	Mature forest	115	22
30-0572	Laguna Kana	4	Selva mediana	Mature forest	39	20
32-0574	Laguna Kana	4	Selva mediana	Mature forest	91	27
33-0511	Yoactun	4	Selva mediana	Mature forest	86	22
34-0512	Yoactun	4	Selva mediana	Mature forest	70	19
36-0514	Yoactun	4	Selva mediana	Secondary veg. 10-20 years	114	39
38-0562	Santa Maria Poniente	4	Selva mediana	Mature forest	77	29
46-0354	El Gallito	4	Selva mediana	Secondary veg. 10-20 years	168	22
48-0322	Francisco J. Mujica	4	Selva baja inundable	Mature forest	181	37
51-0471	Juan Sarabia	4	Selva mediana	Secondary veg. >30 years	108	33
52-0472	Juan Sarabia	4	Selva mediana	Secondary veg. >30 years	119	28
53-0473	Juan Sarabia	4	Selva mediana	Mature forest	121	31
54-0474	Juan Sarabia	4	Selva mediana	Secondary veg. >20 years	99	22
55-0102	Buenavista	4	Selva mediana	Secondary veg. <10 years	82	21
56-0282	Los Divorciados	4	Selva mediana	Secondary veg. <10 years	15	13
58-0122	Blancaflor	4	Selva mediana	Secondary veg. >30 years	113	25

Appendix A.3: (Cont.)

Plot ID	*Ejido*	Wind speed zone	Forest Type	Successional Stage	No. Stems	No. Spp.
60-0931	Cinco de Mayo	3	Selva mediana	Secondary veg. <10 years	83	11
81-0052	Chun-Ek	3	Selva baja inundable	Mature forest	188	34
87-0534	Ricardo Flores Magon	3	Selva mediana	Mature forest	105	36
89-0056	Chun-Ek	3	Selva mediana	Mature forest	122	35
92-0271	Noh Bec	4	Selva mediana	Mature forest	103	33
93-0272	Noh Bec	4	Selva mediana	Mature forest	112	35

Appendix A.4: Number of stems, mean DBH and basal area per fiel plot in 2009

PLOT ID	*EJIDO*	Total Stems	Mean DBH (cm)	DBH Std. Dev (cm)	PLOT BA/ha (m^2/ha)
03-0061	Bacalar	145	7.8	2.8	15.39
08-0071	El Bajio	60	8.8	5.1	7.03
09-0072	El Bajio	64	9.6	3.5	10.42
10-0881	Tolloacan	104	9.1	4.5	15.85
12-SK2?2	Carretera Cafetal (Sian K'aan)	142	9.6	5.2	24.65
19-0883	Tolloacan	112	8.5	3.3	13.78
28-SK18	Costa Mahahual	115	11.2	4.5	20.12
30-0572	Laguna Kana	39	13.7	9.7	17.01
32-0574	Laguna Kana	91	15.7	10.4	50.50
33-0511	Yoactun	86	14.9	17.0	64.95
34-0512	Yoactun	70	14.7	10.0	28.77
36-0514	Yoactun	114	10.9	6.4	25.95
38-0562	Santa Maria Poniente	77	11.8	7.5	17.17
46-0354	El Gallito	168	8.4	3.8	20.32
48-0322	Francisco J. Mujica	181	8.5	3.9	23.51
51-0471	Juan Sarabia	108	11.6	6.3	29.15
52-0472	Juan Sarabia	119	9.5	5.2	18.53
53-0473	Juan Sarabia	121	12.3	7.4	34.02
54-0474	Juan Sarabia	99	10.2	5.3	18.32
55-0102	Buenavista	82	7.9	2.4	7.83
56-0282	Los Divorciados	15	7.9	5.7	2.18
58-0122	Blancaflor	113	8.8	3.7	15.14
60-0931	Cinco de Mayo	83	8.6	2.9	10.69
81-0052	Chun-Ek	188	8.2	4.4	23.72

Appendix A.4: (Cont.)

PLOT ID	*EJIDO*	Total Stems	Mean DBH (cm)	DBH Std. Dev (cm)	PLOT BA/ha (m^2/ha)
87-0534	Ricardo Flores Magon	105	10.7	6.3	24.39
89-0056	Chun-Ek	122	10.9	7.2	29.58
92-0271	Noh Bec	103	13.5	11.1	43.62
93-0272	Noh Bec	112	11.5	6.3	27.05
ALL PLOTS		**2938**	**10.3**	**6.8**	**22.84**

Appendix A.5: Number of stems, mean DBH and basal area per monitoring plot in 2012

PLOT ID	*EJIDO*	Total Stems	Mean DBH (cm)	DBH Std. Dev (cm)	PLOT BA/ha (m^2/ha)
03-0061	Bacalar	164	8.1	2.9	17.141
08-0071	El Bajio	105	8.0	3.1	8.276
09-0072	El Bajio	80	9.5	3.8	11.826
10-0881	Tolloacan	117	8.7	4.3	15.637
12-SK2?2	Carretera Cafetal (Sian K'aan)	160	9.1	4.9	23.449
19-0883	Tolloacan	123	8.4	3.2	14.901
28-SK18	Costa Mahahual	123	11.0	4.6	20.352
30-0572	Laguna Kana	41	14.1	9.8	16.81
32-0574	Laguna Kana	96	15.6	10.5	52.34
33-0511	Yoactun	90	15.0	17.7	70.32
34-0512	Yoactun	76	14.5	10.5	28.61
36-0514	Yoactun	122	11.1	6.8	25.76
46-0354	El Gallito	182	8.6	4.3	18.93
48-0322	Francisco J. Mujica	198	8.5	3.8	22.99
51-0471	Juan Sarabia	124	11.6	6.2	32.44
52-0472	Juan Sarabia	132	10.1	6.1	17.10
53-0473	Juan Sarabia	134	13.4	15.8	31.00
54-0474	Juan Sarabia	116	11.4	10.4	18.30
55-0102	Buenavista	97	9.2	5.3	9.22
56-0282	Los Divorciados	84	6.7	2.6	6.86
58-0122	Blancaflor	125	8.9	4.2	16.47
60-0931	Cinco de Mayo	93	10.0	3.3	15.11
81-0052	Chun-Ek	204	8.3	4.3	23.59

Appendix A.5: (Cont.)

PLOT ID	*EJIDO*	Total Stems	Mean DBH (cm)	DBH Std. Dev (cm)	PLOT BA/ha (m^2/ha)
87-0534	Ricardo Flores Magon	110	11.0	7.0	23.17
89-0056	Chun-Ek	130	11.0	7.0	27.27
92-0271	Noh Bec	106	14.3	12.7	44.60
ALL PLOTS		**3155**	**10.4**	**7.9**	**23.56**

Bibliography

Achard F., Eva H.D., Stibig H.-J., Mayaux P., Gallego J., Richards T., & Malingreau J. P. (2002) Determination of deforestation rates of the world's humid tropical forests. *Science*, **297**, 999–1002.

Achard F., Glinni A., Mayaux P., Richards T., & Stibig H. (1998) *Identification of deforestation hot spot areas in the humid tropics*. Trees Publication Series B. Research Report No. 4.

Alcántara-Ayala I. & Dykes A.P. (2010) Introduction - Land use change in the tropics: causes, consequences and monitoring in Mexico. *Singapore Journal of Tropical Geography*, **31**, 143–151.

Alcántara-Ayala I. (2002) Geomorphology, natural hazards, vulnerability and prevention of natural disasters in developing countries. *Geomorphology*, **47**, 107–124.

Amaranthus M.P. (1997) *Forest sustainability: an approach to definition and assessment at the landscape level. Gen. Tech. Rep. PNW-GTR-416.* U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Andrén H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355–366.

Antinori C. & Rausser G. (2007) Collective choice and community forestry management in Mexico: an empirical analysis. *Journal of Development Studies*, **43**, 512–536.

Arellano Rodríguez, J.A. Flores J.S., Tun Garrido J., & Cruz Bojórquez M.M. (2003) *Etnoflora yucatanense: nomenclatura, forma de vida, uso, manejo y distribución de las especies vegetales de la península de Yucatán.* Universidad Autónoma de Yucatán, Facultad de Medicina Veterinaria y Zootecnia, México.

Balch J.K., Nepstad D.C., Brando P.M., Curran L.M., Portela O., de CARVALHO O., & Lefebvre P. (2008) Negative fire feedback in a transitional forest of southeastern Amazonia. *Global Change Biology*, **14**, 2276–2287.

Basnet K. (1993) Recovery of a tropical rain forest after hurricane damage. *Vegetatio*, **109**, 1–4.

Bellingham P.J. (1991) Landforms influence patterns of hurricane damage: evidence from Jamaican montane forests. *Biotropica*, **23**, 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., & 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., & Healey J.R. (1994) Sprouting of trees in Jamaican montane forests, after a hurricane. *Journal of Ecology*, **82**, 747–758.

Bellingham P.J., Tanner E.V.J., & Healey J.R. (1995) Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology*, **76**, 2562–2580.

Bender M.A., Knutson T.R., Tuleya R.E., Sirutis J.J., Vecchi G.A., Garner S.T., & Held I.M. (2010) Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. *Science*, **327**, 454 – 458.

Bierregaard Jr. R.O., Lovejoy T.E., Kapos V., Dos Santos A.A., & Hutchings R.W. (1992) The biological dynamics of tropical rainforest fragments. *BioScience*, **42**, 859–866.

Bond W. & Midgley J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution*, **16**, 45–51.

Bonilla-Moheno M. (2012) Damage and recovery of forest structure and composition after two subsequent hurricanes in the Yucatán peninsula. *Caribbean Journal of Sciences*, **46**, 240–248.

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

Boose E.R., Foster D.R., & Hall B. (2003) Geographical and historical variation in hurricanes across the Yucatán peninsula. *The lowland Maya area. Three millennia at the human-wildland interface* (ed. by A. Gómez-Pompa, M. Allen, S. Fedick, and J. Jiménez-Osornio), pp. 495–516. Food Products Press, New York.

Boucher D.H. (1990) Growing back after hurricanes: catastrophes may be critical to rain forest dynamics. *BioScience*, **40**, 163–166.

Boucher D.H., Vandermeer J.H., Granzow de la Cerda I., Mallona M.A., Perfecto I., & Zamora N. (2000) Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest. *Plant Ecology*, **156**, 131–137.

Boucher D.H., Vandermeer J.H., Mallona M.A., Zamora N., & Perfecto I. (1994) Resistance and resilience in a directly regenerating rainforest: Nicaraguan trees of the Vochysiaceae after Hurricane Joan. *Forest Ecology and Management*, **68**, 127–136.

Bowman D.M.J.S., Balch J., Artaxo P., Bond W.J., Cochrane M. a, D'Antonio C.M., Defries R., Johnston F.H., Keeley J.E., Krawchuk M. a, Kull C. a, Mack M., Moritz M. a, Pyne S., Roos C.I., Scott A.C., Sodhi N.S., Swetnam T.W., & Whittaker R.

(2011) The human dimension of fire regimes on Earth. *Journal of biogeography*, **38**, 2223–2236.

Bray D.B., Antinori C., & Torres-Rojo J.M. (2006) The Mexican model of community forest management: the role of agrarian policy, forest policy and entrepreneurial organization. *Forest Policy and Economics*, **8**, 470–484.

Bray D.B., Duran E., Ramos V.H., Mas J., Velazquez A., McNab R.B., Barry D., & Radachowsky J. (2008) Tropical deforestation, community forests, and protected areas in the Maya forest. *Ecology and Society*, **13**, 56. [online] URL: http://www.ecologyandsociety.org.

Bray D.B., Ellis E. A., Armijo-Canto N., & Beck C.T. (2004) The institutional drivers of sustainable landscapes: a case study of the "Mayan zone" in Quintana Roo, Mexico. *Land Use Policy*, **21**, 333–346.

Brennan M.J., Knabb R.D., Mainelli M., & Kimberlain T.B. (2009) Atlantic hurricane season of 2007. *Monthly Weather Review*, **137**, 4061–4088.

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

Brook B.W., Sodhi N.S., & Bradshaw C.J. A (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453–60.

Brown C.D. & Johnstone J.F. (2012) Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *Forest Ecology and Management*, **266**, 34–41.

Buma B. & Wessman C.A. (2011) Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere*, **2**, art64.

Buma B. & Wessman C.A. (2013) Forest resilience, climate change, and opportunities for adaptation: A specific case of a general problem. *Forest Ecology and Management*, **306**, 216–225.

Cabarle B., Chapela F., & Madrid S. (1997) Introducción: El manejo forestal comunitario y la certificación. *El manejo forestal comunitario en México y sus perspectivas de sustentabilidad* (ed. by L. Merino), pp. 17–33. Centro Regional de Investigaciones Multidisciplinarias, UNAM, Cuernavaca, México.

Cairns M.A., Haggerty P.K., Alvarez R., De Jong B.H.J., & Olmsted I. (2000) Tropical Mexico's recent land-use change: a region's contribution to the global carbon cycle. *Ecological Applications*, **10**, 1426–1441.

Carpenter S., Walker B., Anderies J.M., & Abel N. (2014) From Metaphor to Measurement: Resilience of What to What? *Ecosystems*, **4**, 765–781.

Catterall C.P., Mckenna S., Kanowski J., & Piper S.D. (2008) Do cyclones and forest fragmentation have synergistic effects? A before–after study of rainforest vegetation structure at multiple sites. *Austral Ecology*, **33**, 471–484.

Changnon S.A. (2009) Characteristics of severe Atlantic hurricanes in the United States: 1949–2006. *Natural Hazards*, **48**, 329–337.

Chapman E.L., Chambers J.Q., Ribbeck K.F., Baker D.B., Tobler M.A., Zeng H., & White D.A. (2008) Hurricane Katrina impacts on forest trees of Louisiana's Pearl River basin. *Forest Ecology and Management*, **256**, 883–889.

Chazdon R.L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 51–71.

Chen J., Franklin J.F., & Spies T.A. (1993) Contrasting microclimates among clearcut edge and interior old-growth Douglas fir forest. *Agricultural and Forest Meteorology*, **63**, 219–237.

Clark W.C. & Dickson N.M. (2003) Sustainability science: the emerging research program. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 8059–61.

Clifton D. (1991) Yucatán after the wind: human and environmental impact of hurricane Gilbert in the central and eastern Yucatán peninsula. *GeoJournal*, **23**, 337–345.

Condit R., Hubbell S.P., & Foster R.B. (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs*, **65**, 419–439.

Costanza R., Daly H., Folke C., Hawken P., Holling C.S., Mcmichael A.J., Pimentel D., & Rapport D. (2000) Managing our environmental portfolio. *BioScience*, **50**, 149.

Couturier S., Mas J.-F., López-Granados E., Benítez J., Coria-Tapia V., & Vega-Guzmán Á. (2010) Accuracy assessment of the Mexican national forest inventory map: a study in four ecogeographical areas. *Singapore Journal of Tropical Geography*, **31**, 163–179.

Crk T., Uriarte M., Corsi F., & Flynn D. (2009) Forest recovery in a tropical landscape: what is the relative importance of biophysical, socioeconomic, and landscape variables? *Landscape Ecology*, **24**, 629–642.

Cullen S. (2002) Trees and wind: a bibliography for tree care professionals. *Journal of Arboriculture*, **28**, 41–51.

Curran T.J., Gersbach L.N., Edwards W., & Krockenberger A.K. (2008) Wood density predicts plant damage and vegetative recovery rates caused by cyclone disturbance in tropical rainforest tree species of North Queensland, Australia. *Austral Ecology*, **33**, 442–450.

D'Amato A.W., Fraver S., Palik B.J., Bradford J.B., & Patty L. (2011) Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *Forest Ecology and Management*, **262**, 2070–2078.

D'Angelo S.A., Andrade A.C.S., Laurance S.G., Laurance W.F., & Mesquita R.C.G. (2004) Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal of Tropical Ecology*, **20**, 243–246.

Dale V.H., Joyce L. a., Mcnulty S., Neilson R.P., Ayres M.P., Flannigan M.D., Hanson P.J., Irland L.C., Lugo A.E., Peterson C.J., Simberloff D., Swanson F.J., Stocks B.J., & Michael Wotton B. (2001) Climate change and forest disturbances. *BioScience*, **51**, 723.

Dale, V.H., Lugo A.E., MacMahon J.A., & Pickett S.T.A. (1998). Ecosystem management in the context of large, infrequent disturbances. *Ecosystems*, **1**, 546-557.

DeFries R.S., Houghton R. A, Hansen M.C., Field C.B., Skole D., & Townshend J. (2002) Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 14256–61.

Díaz-Gallegos J.R., Mas J.-F., & Velázquez A. (2010) Trends of tropical deforestation in southeast Mexico. *Singapore Journal of Tropical Geography*, **31**, 180–196.

Díaz-Gallegos J.R., Mas J.-F., & Velázquez Montes A. (2008) Monitoreo de los patrones de deforestación en el Corredor Biológico Mesoamericano, México. *Interciencia*, **33**, 882–890.

Dietze M.C. & Clark J.S. (2008) Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. *Ecological Monographs*, **78**, 331–347.

DiGiano M.L. & Racelis A.E. (2012) Robustness, adaptation and innovation: forest communities in the wake of hurricane Dean. *Applied Geography*, **33**, 151–158.

Drever C.R., Peterson G., Messier C., Bergeron Y., & Flannigan M. (2006) Can forest management based on natural disturbances maintain ecological resilience? *Canadian Journal of Forest Research*, **36**, 2285–2299.

Eastman J. (2012) IDRISI Selva.

Eaton J.M. & Lawrence D. (2009) Loss of carbon sequestration potential after several decades of shifting cultivation in the southern Yucatán. *Forest Ecology and Management*, **258**, 949–958.

Ellis E.A. & Beck C.T. (2004) Dinámica de la vegetación y uso del suelo en los bosques tropicales de la zona maya de Quintana Roo. *Uso, conservación y cambio en los*

bosques de Quintana Roo (ed. by N. Armijo and C. Llorens), pp. 203–230. Universidad de Quintana Roo, Chetumal.

Ellis E.A. & Porter-Bolland L. (2008) Is community-based forest management more effective than protected areas? *Forest Ecology and Management*, **256**, 1971–1983.

Elsner J.B. (2006) Evidence in support of the climate change–Atlantic hurricane hypothesis. *Geophysical Research Letters*, **33**, L16705.

Escamilla A., Sanvicente M., Sosa M., & Galindo-Leal C. (2000) Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, Mexico. *Conservation Biology*, **14**, 1592–1601.

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

Fagan W.F., Fortin M.-J., & Soykan C. (2003) Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. *BioScience*, **53**, 730–738.

Fahrig L. (2003) Effects of habitat fragmentation on biodiversity, *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

FAO (2012) *State of the world's forests.* Food and Agriculture Organization, Rome.

Fernandez D. & Fetcher N. (1991) Changes in light availability following hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica*, **23**, 393–399.

Fischer J. & Lindenmayer D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.

Flannigan, M.D., Krawchuk, M.A., Groot, W.J.D., Wotton, B.M., & Gowman, L. (2009). Implications of changing climate for global wildland fire. *International Journal of Wildland Fire* **18**, 483–507.

Flynn, D.F.B., Uriarte M., Crk T., Pascarella J.B., Zimmerman J.K., Aide T.M., & Caraballo Ortiz M.A.. (2010). Hurricane disturbance alters secondary forest recovery in Puerto Rico. *Biotropica*, **4**, 149-157.

Forman R.T.T. (1995) *Land mosaics. The ecology of landscapes and regions.* Cambridge University Press, Cambridge.

Foster D.R. & Turner II B. (2004) The long view: human-environment relationships in the region, 1000 BC-AD 1900. *Integrated land-change science and tropical deforestation in the southern Yucatán* (ed. by B.L. Turner II, J. Geoghegan, and D.R. Foster), pp. 23–37. Oxford University Press Inc., Oxford.

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

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

Frangi J. & Lugo A. (1991) Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica*, **23**, 324–335.

Franklin J.L. (2008) Tropical Cyclone Report - Hurricane Dean (AL042007) 13-23 August 2007. 23.

Gardner T.A., Barlow J., Chazdon R., Ewers R.M., Harvey C.A., Peres C.A., & Sodhi N.S. (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, **12**, 561–582.

Garrido-Pérez E.I., Dupuy J.M., Durán-García R., Ucan-May M., Schnitzer S. A., & Gerold G. (2008) Effects of lianas and hurricane Wilma on tree damage in the Yucatán peninsula, Mexico. *Journal of Tropical Ecology*, **24**, 559–562.

Giddings L. & Soto M. (2003) Rhythms of precipitation in the Yucatán peninsula. *The lowland Maya area. Three millennia at the human-wildland interface* (ed. by A. Gómez-Pompa, M.F. Allen, S.L. Fedick, and J.J. Jiménez-Osornio), pp. 77–89. Food Products Press, New York.

Goldenberg, S. B., C. W. Landsea, A. M. Mestas-Nuñez & Gray W.M. (2001). The recent increase in Atlantic hurricane Activity: Causes and implications. *Science*, **293**, 474-479.

Griffith J.A. (2004) The role of landscape pattern analysis in understanding concepts of land cover change. *Journal of Geographical Sciences*, **14**, 3–17.

Grimbacher P.S., Catterall C.P., & Stork N.E. (2008) Do edge effects increase the susceptibility of rainforest fragments to structural damage resulting from a severe tropical cyclone? *Austral Ecology*, **33**, 525–531.

Gustafson E.J. (1998) Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems*, **1**, 143–156.

Haila Y. (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications*, **12**, 321–334.

Hansen M.C., Stehman S. V, & Potapov P. V (2010) Quantification of global gross forest cover loss. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 8650–5.

Harper K.A., Macdonald S.E., Burton P.J., Chen J., Brosofske K.D., Saunders S.C., Euskirchen E.S., Roberts D., Jaiteh M.S., & Esseen P.-A. (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, **19**, 768–782.

Heartsill Scalley T., Scatena F.N., Lugo A.E., Moya S., & Estrada Ruiz C.R. (2010) Changes in structure, composition, and nutrients during 15 Years of hurricane-induced succession in a subtropical wet forest in Puerto Rico. *Biotropica*, **42**, 455–463.

Hernández-Díaz M., Ramírez-Barajas P.J., Chávez C., Schmook B., & Calmé S. (2012) Presencia y abundancia relativa de carnívoros en una selva dañada por el huracán Dean (2007). *Revista Mexicana de Biodiversidad*, **83**, 790–801.

Hernández-Stefanoni J.L., Dupuy J.M., Tun-Dzul F., & May-Pat F. (2011) Influence of landscape structure and stand age on species density and biomass of a tropical dry forest across spatial scales. *Landscape Ecology*, **26**, 355–370.

Holling C.S. (2014) Resilience and stability of ecological systems. *Annual review of Ecology and Systematics*, **4**, 1–23.

Imbert D. & Portecop J. (2008) Hurricane disturbance and forest resilience: assessing structural vs. functional changes in a Caribbean dry forest. *Forest Ecology and Management*, **255**, 3494–3501.

INEGI (2005) *Guía para la interpretación de cartografía - Uso de suelo y vegetación.* Instituto Nacional de Estadística, Geografía e Informática, México.

Islebe G.A., Torrescano-Valle N., Valdez-Hernandez M., Tuz-Novelo M., & Weissenberger H. (2009) Efectos del impacto del huracán Dean en la vegetación del sureste de Quintana Roo, México. *Foresta Veracruzana*, **11**, 1–6.

Jansson U. (2009) *Forest edges in boreal landscapes − factors affecting edge influence.* PhD Dissertation. Umea University, Swede.

Kapos V., Wandelli E., Camargo J., & Ganade G. (1997) Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. *Tropical forest remnants. Ecology, management, and conservation of fragmented communities* (ed. by W.F. Laurance and R.O. Bierregaard Jr.), pp. 33–44. The University of Chicago Press, Chicago.

Klepeis P. (2003) Development policies and tropical deforestation in the southern Yucatán peninsula: centralized and decentralized approaches. *Land Degradation & Development*, **14**, 541–561.

Klepeis, P. & B. L. Turner II. (2001).Integrated land history and global change science: the example of the Southern Yucatán Peninsular Region project. *Land Use Policy*, **18**, 27-39.

Klooster, D. (2003) Campesinos and the Mexican forest policy during the twentieth century. *Latin American Research Review*, **38,** 94-126.

Kok, K. & Winograd, M. (2002). Modelling land-use change for Central America, with special reference to the impact of hurricane Mitch. *Ecological Modelling*, **149**, 53-69.

Kupfer J. A. & Franklin S.B. (2009) Linking spatial pattern and ecological responses in human-modified landscapes: the effects of deforestation and forest fragmentation on biodiversity. *Geography Compass*, **3**, 1331–1355.

Lambin, E.F., H. Geist & R.R. Rindfus. (2006). Local processes with global impacts. In: *Land-Use and Land-Cover Change: Local processes and global impacts.* E.F. Lambin and H.J. Geist Editors. The IGBP Series. Springer. Pag. 1-8.

Laurance W. (1991) Edge effects in tropical forest fragments: application of a model for the design of nature reserves. *Biological Conservation*, **57**, 205–219.

Laurance W. (2000) Do edge effects occur over large spatial scales? *Trends in Ecology & Evolution*, **15**, 134–135.

Laurance W.F. & Bierregaard Jr. R.O. (1997) *Tropical forest remnants: ecology, management and conservation of fragmented communities.* University of Chicago Press, Chicago.

Laurance W.F. & Curran T.J. (2008) Impacts of wind disturbance on fragmented tropical forests: a review and synthesis. *Austral Ecology*, **33**, 399–408.

Laurance W.F. (1997) Hyper-disturbed parks: Edge effects and the ecology of isolated rainforest reserves in tropical Australia. *Tropical forest Remnants, Ecology, Management, and Conservation of Fragmented Communities* (ed. by W.F. Laurance and R.O. Bierregaard), pp. 71–83. The University of Chicago Press, Chicago.

Laurance W.F. (2002) Hyperdynamism in fragmented habitats. *Journal of Vegetation Science*, **13**, 595.

Laurance W.F., Ferreira L. V., Rankin-de Merona J.M., & Laurance S.G. (1998) Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*, **79**, 2032–2040.

Laurance W.F., Lovejoy T.E., Vasconcelos H.L., Bruna E.M., Didham R.K., Stouffer P.C., Gascon C., Bierregaard R.O., Laurance S.G., & Sampaio E. (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*, **16**, 605–618.

Laurance W.F., Nascimento H.E.M., Laurance S.G., Andrade A., Ribeiro J.E.L.S., Giraldo J.P., Lovejoy T.E., Condit R., Chave J., Harms K.E., & D'Angelo S. (2006)

Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 19010–4.

Lawrence D., D'Odorico P., Diekmann L., Delonge M., Das R., & Eaton J. (2007) Ecological feedbacks following deforestation create the potential for a catastrophic ecosystem shift in tropical dry forest. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 20696–701.

Lawrence D., Vester H.F.M., Pérez-Salicrup D., Ronald J., Ii B.L.T., & Geoghegan J. (2004) Integrated analysis of ecosystem interactions with land- use change: the southern Yucatán peninsular region. *Ecosystem Interactions with Land Use Change* (ed. by R. Defries and R. Houghton), pp. 277–292. American Geophysical Union, Washington, D.C.

Lindenmayer D.B. & Fischer J. (2007) Tackling the habitat fragmentation panchreston. *Trends in Ecology & Evolution*, **22**, 127–32.

Lodge, D.J. & Mc Dowell W. H. (1991). Summary of ecosystem-level effects of Caribbean hurricanes. *Biotropica*, **23**, 373-378.

Lugo A. & Scatena F. (1996) Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica*, **28**, 585–599.

Lugo A.E. & Waide R.B. (1993) Catastrophic and background disturbance of tropical ecosystems at the Luquillo experimental forest. *Journal of Biosciences*, **18**, 475–481.

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

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

Marra D.M., Chambers J.Q., Higuchi N., Trumbore S.E., Ribeiro G.H.P.M., Dos Santos J., Negrón-Juárez R.I., Reu B., & Wirth C. (2014) Large-scale wind disturbances promote tree diversity in a central Amazon forest. *PloS One*, **9**, e103711.

Mas Bermejo P. (2006) Preparation and response in case of natural disasters: Cuban programs and experience. *Journal of Public Health Policy*, **27**, 13–21.

Mas J., Velázquez A., Palacio J., Bocco G., Peralta A., & Prado J. (2002) Assessing forest resources in Mexico: wall-to-wall land use/cover mapping. *Photogrammetric Engineering and Remote Sensing*, **68**, 966–968.

Matthews E., Payne R., Rohweder M. & Murray S. (2000). *Pilot analysis of global ecosystems (PAGE): forest ecosystems.* Washington (DC): World Resources Institute.

Mayer H., Raupach M.R., Kohsiek W., Gardiner B., Clarke J.A., Amtmann R., Crowther J.M., Jarvis P.G., & Milne R. (1989) Windthrow. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **324**, 267–281.

McGroddy M., Lawrence D., Schneider L., Rogan J., Zager I., & Schmook B. (2013) Damage patterns after hurricane Dean in the southern Yucatán: has human activity resulted in more resistant forests? *Forest Ecology and Management*, **310**, 812–820.

Metcalfe D.J., Bradford M.G., & Ford A.J. (2008) Cyclone damage to tropical rain forests: species- and community-level impacts. *Austral Ecology*, **33**, 432–441.

Miller K., Chang E., & Johnson N. (2001) *Defining common ground for the Mesoamerican biological corridor.* World Resources Institute.

Mitchell S.J. (2013) Wind as a natural disturbance agent in forests: a synthesis. *Forestry*, **86**, 147–157.

Mittermeier R.A., Gil P.R., Hoffmann M., Pilgrim J., Brooks T., Mittermeier C.G., Lamoreux J., & Da Fonseca. G.A.B. (2004) *Hotspots: revisited.* Cemex books on Nature, Mexico City, D.F.

Moore J.R., Manley B.R., Park D., & Scarrott C.J. (2013) Quantification of wind damage to New Zealand's planted forests. *Forestry*, **86**, 173–183.

Moore J.R., Tombleson J.D., Turner J. A., & Van der Colff M. (2008) Wind effects on juvenile trees: a review with special reference to toppling of radiata pine growing in New Zealand. *Forestry*, **81**, 377–387.

Moran, E. & Ojima D. (2005). Global Land Project Science Plan and Implementation Strategy. IGBP-IHDP. Stockholm, Sweden.

Murcia C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*, **10**, 58–62.

Myers N., Mittermeier R. a, Mittermeier C.G., Da Fonseca G.A, & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–8.

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

Neel M.C., McGarigal K., & Cushman S. A. (2004) Behavior of class-level landscape metrics across gradients of class aggregation and area. *Landscape Ecology*, **19**, 435–455.

Negrón Juárez R.I., Chambers J.Q., Zeng H., & Baker D.B. (2008) Hurricane driven changes in land cover create biogeophysical climate feedbacks. *Geophysical Research Letters*, **35**, L23401.

Ostapowicz K., Vogt P., Riitters K.H., Kozak J., & Estreguil C. (2008) Impact of scale on morphological spatial pattern of forest. *Landscape Ecology*, **23**, 1107–1117.

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

Paciorek C.J., Condit R., Hubbell S.P., & Foster R.B. (2000) The demographics of resprouting in tree and shrub species of a moist tropical forest. *Journal of Ecology*, **88**, 765–777.

Palacio-Prieto J.L., Bocco G., Velazquez A., Mas J. F., Takaki-Takaki F., & Victoria (2000) La condición actual de los recursos forestales en México: resultados del inventario forestal nacional 2000. *Investigaciones Geográficas*, **43**, 183–203.

Pascarella J.B., Mitchell Aide T., & Zimmerman J.K. (2004) Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. *Forest Ecology and Management*, **199**, 379–393.

Pérez-Salicrup D. (2004) Forest types and their implications. *Integrated land-change science and tropical deforestation in the southern Yucatán* (ed. by B.L. Turner II, J. Geoghegan, and D.R. Foster), pp. 63–80. Oxford University Press Inc., New York.

Peterson C.J. & Pickett S.T.A. (1991) Treefall and resprouting following catastrophic wind throw in an old-growth hemlock-hardwoods forest. *Forest Ecology and Management*, **42**, 205–217.

Peterson G., Allen C.R., & Holling C.S. (1998) Ecological resilience, biodiversity, and scale. *Ecosystems*, **1**, 6–18.

Philpott, S.M., Lin B.M., Jha S., & Brines S.J. (2008). A multi-scale assessment of hurricane impacts on agricultural landscapes based on land use and topographic features. *Agriculture, Ecosystems and Environment*, 128: 12–20.

Pielke Jr R.A., Rubiera J., Landsea C., Fernández M.L., & Klein R. (2003) Hurricane Vulnerability in Latin America and The Caribbean : Normalized Damage and Loss Potentials. *Natural Hazards Review*, **4**, 101–114.

Pohlman C.L., Goosem M., & Turton S.M. (2008) Effects of severe tropical cyclone Larry on rainforest vegetation and under storey microclimate near a road, powerline and stream. *Austral Ecology*, **33**, 503–515.

Poorter L., Kitajima K., Mercado P., Chubiña J., Melgar I., & Prins H.H.T. (2010) Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance. *Ecology*, **91**, 2613–27.

Porter-Bolland L., Ellis E.A., & Gholz H.L. (2007) Land use dynamics and landscape history in La Montaña, Campeche, Mexico. *Landscape and Urban Planning*, **82**, 198–207.

Putz F.E. & Brokaw N.V.L. (1989) Sprouting of Broken Trees on Barro Colorado Island, Panama. *Ecology*, **70**, 508–512.

Puyravaud J.P. (2003) Standardizing the calculation of the annual rate of deforestation. *Forest Ecology and Management*, **177**, 593–596.

Ramamoorthy T.P., Bye R., Lot A., & Fa J. (1998) *Diversidad biológica de México: orígenes y distribución.* México.

Ramankutty, N., L. Graumlich, F. Achard, D. Alves, A, Chhabra, R. DeFries, J. Foley, H. Geist, R. Houghton, K. Goldewijk, E. Lambin, A. Millington, K. Rasmissen R.R. and B.T. (2006) Global land-cover change: recent progress, remaining challenges. *Land-use and land-cover change: local processes and global impacts* (ed. by E.F. Lambin and H.J. Geist), pp. 9–39. The IGBP Series. Springer, Berlin.

Ramírez G. (2004) El corredor biológico mesoamericano en México. *Biodiversitas*, **7**, 4-7.

Ramírez-Barajas P.J., Islebe G.A., & Calme S. (2012a) Impact of hurricane Dean (2007) on game species of the Selva Maya, México. *Biotropica*, **44**, 402–411.

Ramírez-Barajas P.J., Islebe G.A., & Torrescano-Valle N. (2012b) Post-hurricane Dean impact on habitat and its influence on the relative abundance of large vertebrates in the Selva Maya, Quintana Roo, México. *Revista Mexicana de Biodiversidad*, **83**, 1194–1207.

Ramírez-Delgado J.P., Christman Z., & Schmook B. (2014) Deforestation and fragmentation of seasonal tropical forests in the southern Yucatán, Mexico (1990-2006). *Geocarto International*, 1–38.

Read L. & Lawrence D. (2003) Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatán. *Ecological Applications*, **13**, 85–97.

Riitters K., Vogt P., Soille P., & Estreguil C. (2009) Landscape patterns from mathematical morphology on maps with contagion. *Landscape Ecology*, **24**, 699–709.

Riitters K., Wickham J., Neill R.O., Jones B., & Smith E. (2000) Global-scale patterns of forest fragmentation. *Conservation Ecology*, **4**, 3. [online] URL: http://www.consecol.org/vol4/iss2.

Riitters K.H., Neil R.V.O., Hunsaker C.T., Wickham J.D., Yankee D.H., & Timmins S.P. (1995) A factor analysis of landscape pattern and structure metrics. *Landscape Ecology*, **10**, 23–39.

Riitters K.H., Vogt P., Soille P., Kozak J., & Estreguil C. (2007) Neutral model analysis of landscape patterns from mathematical morphology. *Landscape Ecology*, **22**, 1033–1043.

Riitters K.H., Wickham J.D., Neill R.V.O., Jones K.B., Smith E.R., Coulston J.W., Wade T.G., & Smith J.H. (2002) Fragmentation of continental United States forests. *Ecosystems*, **5**, 815–822.

Rindfuss, R.R., Walsh S., Turner B.L. II, Fox J., & Mishra V. (2004) Developing a science of land change: Challenges andm methodological issues. *Proceedings of the National Academy of Sciences,* 101:13976-13981.

Rogan J. & Yool S.R. (2001) Mapping fire-induced vegetation depletion in the Peloncillo Mountains, Arizona and New Mexico. *International Journal of Remote Sensing*, **22**, 3101–3121.

Rogan J., Schneider L., Christman Z., Millones M., Lawrence D., & Schmook B. (2011) Hurricane disturbance mapping using MODIS EVI data in the southeastern Yucatán, Mexico. *Remote Sensing Letters*, **2**, 259–267.

Rounsevell M.D.A., Pedroli B., Erb K.-H., Gramberger M., Busck A.G., Haberl H., Kristensen S., Kuemmerle T., Lavorel S., Lindner M., Lotze-Campen H., Metzger M.J., Murray-Rust D., Popp A., Pérez-Soba M., Reenberg A., Vadineanu A., Verburg P.H., & Wolfslehner B. (2012) Challenges for land system science. *Land Use Policy*, **29**, 899–910.

Roy Chowdhury R. (2006) Landscape change in the Calakmul biosphere reserve, Mexico: modeling the driving forces of smallholder deforestation in land parcels. *Applied Geography*, **26**, 129–152.

Roy Chowdhury R. (2010) Differentiation and concordance in smallholder land use strategies in southern Mexico's conservation frontier. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 5780–5.

Rudel T. & Roper J. (1997) Forest fragmentation in the humid tropics: a cross-national analysis. *Singapore Journal of Tropical Geography*, **18**, 99–109.

Rueda X. (2010) Understanding deforestation in the southern Yucatán: insights from a sub-regional, multi-temporal analysis. *Regional Environmental Change*, **10**, 175–189.

Salk C.F. & McMahon S.M. (2011) Ecological and environmental factors constrain sprouting ability in tropical trees. *Oecologia,* **166**, 485–92.

Sánchez-Sánchez O. & Islebe G.A. (1999) Hurricane Gilbert and structural changes in a tropical forest in south-eastern Mexico. *Global Ecology and Biogeography*, **8**, 29–38.

Sánchez-Sánchez O. & Islebe G.A. (2002) Tropical forest communities in southeastern Mexico. *Plant Ecology*, **158**, 183–200.

Saura S., Vogt P., Velázquez J., Hernando A., & Tejera R. (2011) Key structural forest connectors can be identified by combining landscape spatial pattern and network analyses. *Forest Ecology and Management*, **262**, 150–160.

Schmitt C.B., Burgess N.D., Coad L., Belokurov A., Besançon C., Boisrobert L., Campbell A., Fish L., Gliddon D., Humphries K., Kapos V., Loucks C., Lysenko I., Miles L., Mills C., Minnemeyer S., Pistorius T., Ravilious C., Steininger M., & Winkel G. (2009) Global analysis of the protection status of the world's forests. *Biological Conservation*, **142**, 2122–2130.

Schmook B. & Vance C. (2009) Agricultural policy, market barriers, and deforestation: the case of Mexico's southern Yucatán. *World Development*, **37**, 1015–1025.

Schneider L. & Geoghegan J. (2006) Land abandonment in an agricultural frontier after a plant invasion: the case of bracken fern in southern Yucatán, Mexico. *Agricultural and Resource Economics Review*, **35**, 167–177.

Schneider L.C. (2004) Bracken fern invasion in southern Yucatán: a case for land-change science. *The Geographical Review*, **94**, 229–241.

Schneider L.C. (2008) Plant invasions in an agricultural frontier: linking satellite, ecological and household survey data. *Land-change science in the tropics: Changing agricultural landscapes* (ed. by A. Millington and W. Jepson), pp. 117–141. Springer, New York.

Schramski S. & Keys E. (2013) Smallholder response to hurricane Dean: creating new human ecologies through charcoal production. *Natural Hazards Review*, **14**, 211–219.

Sims H. & Vogelmann K. (2002) Popular mobilization and disaster management in Cuba. *Public Administration and Development*, **22**, 389–400.

Snook L.K. (1998) Sustaining harvests of Mahogany (*Swietenia macrophylla* King) from Mexico's Yucatán forests: past, present, and future. *Timber, tourists, and temples. Conservation and development in the Maya forest of Belize, Guatemala, and Mexico* (ed. by R.B. Primack, D.B. Bray, H.A. Galletti, and I. Ponciano), pp. 61–80. Island Press, Washington, DC.

Stork N.E., Coddington J. a, Colwell R.K., Chazdon R.L., Dick C.W., Peres C. A, Sloan S., & Willis K. (2009) Vulnerability and resilience of tropical forest species to land-use change. *Conservation Biology*, **23**, 1438–47.

Tanner E.V.J. & 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.

Taylor, P. L., & Zabin C. (2000) Neoliberal reform and sustainable forest management in Quintana Roo, Mexico: rethinking the institutional framework of the Forestry Pilot Plan. *Agriculture and Human Values*, 17: 141-156.

Terborgh J. (1992) Maintenance of diversity in tropical forests. *Biotropica*, **24**, 283–292.

Thompson I., Mackey B., McNulty S., & Mosseler A. (2009) *Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosyste*ms. Secretariat of the Convention on Biological Diversity, Montreal. Technical SeriesNno. 43, 67 pp.

Turner B.L. (2010a) Sustainability and forest transitions in the southern Yucatán: the land architecture approach. *Land Use Policy*, **27**, 170–179.

Turner B.L., Matson P. a, McCarthy J.J., Corell R.W., Christensen L., Eckley N., Hovelsrud-Broda G.K., Kasperson J.X., Kasperson R.E., Luers A., Martello M.L., Mathiesen S., Naylor R., Polsky C., Pulsipher A., Schiller A., Selin H., & Tyler N. (2003) Illustrating the coupled human-environment system for vulnerability analysis: three case studies. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 8080–5.

Turner BL II, Villar S., Foster D., Geoghegan J., Keys E., Klepeis P., Lawrence D., Mendoza P., Manson D., Ogneva-Himmelberger Y., Plotkin A., Salicrup D., Chowdhury R., Savitsky B., Schneider L., Schmook B., & Vance C. (2001) Deforestation in the southern Yucatán peninsular region: an integrative approach. *Forest Ecology and Management*, **154**, 353–370.

Turner I.M. & T Corlett R. (1996) The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends in Ecology & Evolution*, **11**, 330–3.

Turner I.M. (1996) Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology*, **33**, 200–209.

Turner II B.L., Lambin E.F., & Reenberg A. (2007) The emergence of land change science for global environmental change and sustainability. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 20666–20671.

Turner II, B. L., Moran, E. & Rindfuss, R. (2004). Integrated Land-Change Science and its relevance to the human sciences. In: *Land Change Science. Observing, monitoring and understanding trajectories of change on the Earth's surface* (Ed. by Gutman, G., Janetos, A. C., Justice, C. O., Moran, E. F., Mustard, J. F., Rindfuss, R. R., Skole, D., Turner II, B. L. & Cochrane, M. A.), pp. 431-447. NL: Kluwer Academic Publishers.

Turner M.G. & Dale V.H. (1998) Comparing large, infrequent disturbances: what have we learned? *Ecosystems*, **1**, 493–496.

Turner M.G. (2010b) Disturbance and landscape dynamics in a changing world. *Ecology*, **91**, 2833–2849.

Turton S. & Stork N. (2008) Impacts of tropical cyclones on forests in the wet tropics of Australia. *Living in a dynamic tropical forest landscape* (ed. by N.E. Stork and N. Turton), pp. 47–58. Blackwell Publishing, Malden, MA.

Ulanova N.G. (2000) The effects of windthrow on forests at different spatial scales: a review. *Forest Ecology and Management*, **135**, 155–167.

UNECE/FAO (2000) Forest products annual market review.

Uriarte M., Canham C.D., Thompson J., Zimmerman J.K., Murphy L., Sabat A.M., Fetcher N., & Haines B.L. (2009) Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. *Ecological Monographs*, **79**, 423–443.

Uriarte M., Rivera L.W., Zimmerman J.K., Aide T.M., Power A.G., & Flecker A.S. (2004) Effects of land use history on hurricane damage and recovery in a neotropical forest. *Plant Ecology*, **174**, 49–58.

Uriarte M., Schneider L., & Rudel T. (2010) Synthesis: land transitions in the tropics. *Biotropica*, **42**, 59–62.

Urquiza-Haas T., Dolman P.M., & Peres C. A. (2007) Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: Effects of forest disturbance. *Forest Ecology and Management*, **247**, 80–90.

Van Bloem S., Murphy P., Lugo A., Ostertag R., Rivera Costa M., Ruiz Bernard I., Molina Colon S., & Canals Mora M. (2005) The influence of hurricane winds on Caribbean dry forest structure and nutrient pools. *Biotropica*, **37**, 571–583.

Van Bloem S.J., Lugo A.E., & Murphy P.G. (2006) Structural response of Caribbean dry forests to hurricane winds: a case study from Guanica forest, Puerto Rico. *Journal of Biogeography*, **33**, 517–523.

Vandecar K.L., Lawrence D., Richards D., Schneider L., Rogan J., Schmook B., & Wilbur H. (2011) High mortality for rare species following hurricane disturbance in the southern Yucatán. *Biotropica*, **43**, 676–684.

Vandermeer J., Mallona M., Boucher D., Yih K., & Perfecto I. (1995) Three years of ingrowth following catastrophic hurricane damage on the Caribbean coast of Nicaragua—evidence in support of the direct regeneration hypothesis. *Journal of Tropical Ecology*, **11**, 465–471.

Velázquez A., Mas J.-F., Bocco G., & Palacio-Prieto J.L. (2010) Mapping land cover changes in Mexico, 1976-2000 and applications for guiding environmental management policy. *Singapore Journal of Tropical Geography*, **31**, 152–162.

Vester H., Lawrence D., Eastman R., Turner II B., & Calme S. (2007) Land change in the southen Yucatán and Calakmul biosphere reserve: effects on habitat and biodiversity. *Ecological Applications*, **17**, 989–1003.

Vogt P. (2010) MSPA Guide. Version 1.3.

Vogt P., Riitters K.H., Estreguil C., Kozak J., Wade T.G., & Wickham J.D. (2007a) Mapping spatial patterns with morphological image processing. *Landscape Ecology*, **22**, 171–177.

Vogt P., Riitters K.H., Iwanowski M., Estreguil C., Kozak J., & Soille P. (2007b) Mapping landscape corridors. *Ecological Indicators*, **7**, 481–488.

Wade T.G., Riitters K.H., Wickham J.D., & Jones K.B. (2003) Distribution and causes of global forest fragmentation. *Conservation Ecology*, **7**, 7. [online] URL: http://www.consecol.org/vol7/iss2.

Walker B. (1995) Conserving biological diversity through ecosystem resilience. *Conservation Biology*, **9**, 747–752.

Walker L. (1991) Tree damage and recovery from hurricane Hugo in Luquillo experimental forest, Puerto Rico. *Biotropica*, **23**, 379–385.

Walker L., Lodge D., Brokaw V.L., & Waide R. (1991) An introduction to hurricanes in the Caribbean. *Biotropica*, **23**, 313–316.

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

Webb E.L., Van de Bult M., Fa'aumu S., Webb R.C., Tualaulelei A., & Carrasco L.R. (2014) Factors affecting tropical tree damage and survival after catastrophic wind disturbance. *Biotropica*, **46**, 32–41.

Westerling a L., Hidalgo H.G., Cayan D.R., & Swetnam T.W. (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science*, **313**, 940–3.

Whigham D., Olmsted I., Cano E., & Harmon M. (1991) The impact of hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatán peninsula. *Biotropica*, **23**, 434–441.

Whigham D.F., Olmsted I., Cabrera Cano E., & Curtis A.B. (2003) Impacts of hurricanes on the forests of Quintana Roo, Yucatán peninsula, Mexico. *The lowland Maya area: three millennia at the human-wildland interface* (ed. by A. Gómez-Pompa,

M.F. Allen, S.L. Fedick, and J.J. Jiménez-Osornio), pp. 193–213. Food Products Press, Binghamton, NY.

Wickham J.D., Riitters K.H., Wade T.G., & Vogt P. (2010) A national assessment of green infrastructure and change for the conterminous United States using morphological image processing. *Landscape and Urban Planning*, **94**, 186–195.

Wilcove D.S., McLellan C.H., & Dobson A.P. (1986) Habitat fragmentation in the temperate zone. *Conservation biology: the science of scarcity and diversity* (ed. by M.E. Soulé), pp. 237–256. Sinnauer Associates Publishers, Massachusetts.

Wilcox B.A. & Murphy D.D. (1985) Conservation strategy: the effects of fragmentation on extinction. *The American Naturalist*, **125**, 879–887.

Williams-Linera G. (1990) Vegetation structure and environmental conditions of forest edges in Panama. *The Journal of Ecology*, **78**, 356–373.

Willig M.R., Bloch C.P., Brokaw N., Higgins C., Thompson J., & Zimmermann C.R. (2007) Cross-scale responses of biodiversity to hurricane and anthropogenic disturbance in a tropical forest. *Ecosystems,* **10**, 824–838.

Wright TM (2011) *A multitemporal assessment of forest fragmentation in Massachusetts (USA) using 1 remotely sensed data*. Honor Thesis, Clark University

Xi W. & Peet R.K. (2011) The complexity of catastrophic wind impacts on temperate forests. *Recent Hurricane Research - Climate, Dynamics, and Societal Impacts* (ed. by A. Lupo), pp. 503–534.

Yih K., Boucher D.H., Vandermeer J.H., & Zamora N. (1991) Recovery of the rain forest of southeastern Nicaragua after destruction by hurricane Joan. *Biotropica*, **23**, 106–113.

Zeng H., Peltola H., Talkkari A., Venäläinen A., Strandman H., Kellomäki S., & Wang K. (2004) Influence of clear-cutting on the risk of wind damage at forest edges. *Forest Ecology and Management*, **203**, 77–88.

Zeng H., Peltola H., Väisänen H., & Kellomäki S. (2009) The effects of fragmentation on the susceptibility of a boreal forest ecosystem to wind damage. *Forest Ecology and Management*, **257**, 1165–1173.

Zeng H., Pukkala T., & Peltola H. (2007) The use of heuristic optimization in risk management of wind damage in forest planning. *Forest Ecology and Management*, **241**, 189–199.

Zimmerman J., Everham III E.M., Waide R., Lodge D. Jean, Taylor C.M., & 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**, 911–922.