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RELATING ANCIENT MAYA LAND USE LEGACIES TO THE CONTEMPORARY
FOREST OF CARACOL, BELIZE

by

JESSICA N. HIGHTOWER
B.S. University of Central Arkansas, 2008

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Science
at the University of Central Florida
Orlando, Florida

Spring Term
2012

Major Professor: John F. Weishampel

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ABSTRACT

Human land use legacies have significant and long lasting impacts across landscapes. However, investigating the impacts of ancient land use legacies (>400 years) remains problematic due to the difficulty in detecting ancient land uses, especially those beneath dense canopies. The city of Caracol, one of the most important Maya archaeological sites in Belize, was abandoned after the collapse of the Maya civilization (ca. A.D. 900), leaving behind numerous structures, causeways, and agricultural terraces that persist beneath the dense tropical forest of western Belize. LiDAR (Light Detection and Ranging) technology enables detection of below canopy Maya archaeological features, providing an ideal opportunity to study the effects of ancient land use legacies on contemporary tropical forest composition. LiDAR also provided us with a detailed record of the 3-dimensional forest structure over the 200 km² study area. This allowed the investigation how ancient land uses continue to impact both forest composition, in terms of tree species, and forest structure.

I recorded tree species over four land use categories: 1) structures, 2) causeways, 3) terraced, and 4) non-terraced land. Using non-metric multidimensional scaling (NMS) and multi-response permutation procedures (MRPP) to test for differences between the classes, I found significantly distinct tree communities associated with the presence of terraces and the underlying topography. Terraced slopes appear to function as micro-valleys on the side of a hill, creating an environmental "bridge" between slope and valley tree communities. Tree species composition over causeways and structures was also found to be significantly different from terraced and non-terraced plots.

Forest structure was assessed by extracting LiDAR points for terraced (n=150) and non-terraced (n=150) 0.25 ha plots. I calculated average canopy height, canopy closure, and vertical diversity from the height bins of the LiDAR points, using slope, elevation, and aspect as covariates. Using PerMANOVA I determined that forest structure over terraces was significantly different from non-terraced land. Terraces appear to mediate the effect of slope, resulting in less structural variation between slope and non-sloped land. These results led to the conclusion that human land uses abandoned >1000 years ago continue to impact the contemporary forests.

ACKNOWLEDGMENTS

This thesis would not have been possible without the help of a number of people. First of all, I would like to thank my advisor, Dr. John Weishampel. I greatly appreciate the opportunity provided to work on such a great project. I would also like to thank Dr. Weishampel for all the assistance and guidance you have provided during my time at UCF. You have been an inspiration. I would also like to thank my committee, Dr. Pedro Quintana-Ascencio, Dr. Betsy Von Holle, and Dr. Arlen Chase, for their guidance and assistance on this project. I would like to thank Dr. Nicholas Brokaw for his advice on identifying tree species in Belize. I am very appreciative of Drs. Diane and Arlen Chase for welcoming me down to Caracol to conduct my field work. I greatly enjoyed my time at Caracol and I appreciate all that the Chases did to make it possible. A big thank you goes out to my field assistants in Belize, Don Goya and Don Victor, who shared with me their decades of knowledge on the forest of Belize. Without their assistance I would not have been able to identify the tree species of my study area.

I appreciate the support, both moral and intellectual, provided by the graduate students at UCF. Everyone was a great encouragement. I would like to thank the GAMES Lab for all the assistance and feedback over the course of my master program, specifically James Angelo for his assistance with FUSION and R. I would also like to thank Kim Medley for the brainstorming sessions and statistical assistance provided. My family and friends have been a great support during my time at UCF. Specifically, I would like to thank Tatum Branaman and Ashley Iketani for all of their support. I would also like to thank my mother, Coleene Hightower, for her support.

Finally, I would like to thank the organizations that funded this project and made this thesis possible. The NASA Grant #NNX08AM11G Space Archaeology program and a University of Central Florida – University of Florida - Space Research Initiative (UCF-UF-SRI) grant provided the funding for my research. I also thank NCALM (National Center of Airborne Laser mapping) for procuring and processing the LiDAR data. Thank you to the University of Central Florida for providing assistance in the form of teaching assistantships and travel funds to present my research at conferences. I would also like to thank the Belize Institute of Archaeology and the Drs. Arlen and Diane Chase, as the permit holders, for allowing me to conduct my research at Caracol.

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CHAPTER 1: GENERAL INTRODUCTION

Introduction

Understanding the consequences of human alteration of landscapes becomes increasingly important as human populations continue to expand and natural landscapes are continually transformed (Chazdon 2003, Foster et al. 2003). While deforestation is still occurring at an alarming rate throughout many parts of the world, afforestation is occurring in other regions as former agricultural fields are abandoned (Sponsel et al. 1996, Laurance 1999, Achard et al. 2002). By one estimate 50-80% of the forests in New England are on former agricultural fields (Bellamare et al. 2002). Human's extensive alteration of the landscape is not unique to the last century and the concept of "virgin" forests is now relatively obsolete (Clark 1996, Heckenberger et al. 2003). Locations that have traditionally been thought of as sparsely populated and fairly pristine prior to European colonization, such as the Americas, are now known to have been significantly altered by ancient humans (Sanford and Horn 2000, Gomez-Pompa et al. 2003). Evidence suggests that vast tracks of forest had been cleared for agriculture or burned by indigenous humans prior to western arrival in the new world (Delcourt 1987, Butzer 1996, Mann 2005). Given the current rate of land alteration and the extensiveness of past alteration by ancient man, understanding how long these land use legacies, particularly in forests, may persist and to what extent, are now important questions in ecology (Peterken and Game 1984, Motzkin 1996, Briggs et al. 2006).

Human land use legacies can vary according to type, intensity, extent, and the duration of the land use (Flinn and Vellend 2005). Land use legacies are commonly seen in the species composition, with the species found after abandonment of land use differing significantly from landscapes that had no former human disturbance (Motzkin et al. 2004, Flinn and Marks 2007). Even controlling for other environmental variables, such as soil and topography, land use legacies were still found to have had a significant effect on the plant species composition (Motzkin 1996, Flinn and Velland 2005). A similar pattern of altered species composition of the forest vegetation can be observed in tropical forests (Foster et al. 2003, Thompson et al. 2002, Grau et al. 2003).

Land use legacies may often be found in the structure of the forest, independent of species composition (Harper et al. 2005, Turner et al. 2010). Forests may take between 60-200 years to regenerate to previous canopy heights (Aide et al. 2000, Meuller et al. 2010). Forest structure has been shown to be influenced by topographic position (Clark and Clark 2000) and soil nutrients (Tateno and Takeda 2003). Beyond regeneration times, the soil and topography may have been irrevocably altered by past land use, making it impossible for forests to regenerate to pre-land alteration conditions (Motzkin et al. 1996, Foster et al. 2003). Forest structural complexity has been tied to increased biodiversity in other taxa (Ulishyn 2011, Verschuyt et al. 2008), as well as being used to estimate sources of carbon sequestration (Clark and Clark 2000). Therefore, understanding the processes that shape forest structure is important to our overall understanding of patterns and processes (Shugart et al. 2010).

The time since the land has been abandoned and allowed to revert back to a natural state can also be a determining factor in the legacies present and the extent to which they are present

(Chazdon et al. 2003, Foster et al. 2003, Heckenberger et al. 2003). In European forests, agricultural legacies have been shown to persist millennia after abandonment, with species composition in secondary forests that regenerated over former agricultural fields lacking native species found in ancient forests (Delcourt 1987, Dambrine et al. 2007). Another example of ancient land use legacies persisting today is found in Central America with the Maya civilization. A large percentage of forests in Central America are secondary forests that have regenerated after the collapse of the Maya civilization (Gomez-Pompa et al. 2003, Turner et al. 2003). There have been studies that have suggested these forests contain many species of trees that were of economic importance to the ancient Maya, which may remain as remnants of the Maya orchard-gardens (Gomez-Pompa et al. 1987). In addition to the introduction of species by the Maya, the disturbance introduced through agriculture and settlement constructions may have altered the landscape in a way that provided optimal habitat for specific, limestone loving species, such as the Ramon tree (*Brosimum alicastrum*) (Lambert and Arnason 1978, 1982).

The use of LiDAR (Light Detection and Ranging) can help address several problems associated with the study of ancient land use legacies. LiDAR is an active remote sensing system that sends down pulses of light in swaths, which are then reflected back to the device after hitting a reflective surface, such as the ground, building, leaves, etc. The LiDAR sensor is then able to record the level of return for the reflected light and, using GPS satellites and a georeferencing mechanism, record the reflected pulses in three dimensional space. These returns can be divided up into last return (usually your ground point), first return (such as tree top), and intermediate returns (leaves, branches, etc.). Using these point cloud data, we can create detailed topographic maps of an area, extract specific features, such as building and trees, and obtain structural

information on vegetation (Weishampel et al. 2000). With LiDAR we can look beneath the canopy to identify ancient archaeological features that would be indicative of ancient land uses, such as the terraces, structures, and causeways the ancient Maya left behind (Chase et al. 2011). These data provide accurate maps of ancient land uses that are typically unavailable (Dambrine et al. 2007). In addition to maps of ancient land uses, LiDAR provides a method to accurately measure canopy structure at a scale unavailable to traditional forestry measurements (Drake et al. 2007).

Understanding how forests are affected by different land use legacies is important to our overall knowledge of the consequences of anthropogenic disturbance and the factors impacting forest restoration (Foster et al. 2003). In this study, I investigate how the forest has changed in response to the massive landscape alteration performed by the ancient Maya at Caracol. At the meso-scale, topography and the related soils have been noted to have a sizable effect on forest structure and composition (Furley and Newey 1979, Clark et al. 1995, Clark et al. 1999, Thompson et al. 2003). By extensively altering their landscape, the Maya modified the topography and soil composition of the surrounding area (Beach et al. 2002, Gomez-Pompa et al. 2003). Terraces essentially create micro-valleys on hill slopes, changing soil composition, soil depth, and moisture content (Healy et al. 1983, Coultas et al. 1994, Beach et al. 2002). One study indicated that the terraces at Caracol had soils up to 2.5 times deeper than non-terraced slopes (Coultas et al. 1993). Structural mounds are the archaeological remnants of numerous building structures constructed by the ancient Maya (i.e. residential, palaces, temples). Structural mounds are found in the forest as small hills in a valley or on top of natural hills. These limestone structures are covered in a thin layer of soil and humus, with trees and sub-canopy vegetation

well established on the top. Causeways also represent a significant alteration of the landscape. These linear features, that are analogous to our modern roads, were built from the bed rock up and were often constructed with stone-lined sides. Today they can be found throughout the landscape at Caracol with a cover of thin soil, trees, and sub-canopy vegetation (Chase and Chase 2001). These large differences in soils and topography could result in differences in forest tree species composition (Penn et al. 2003). With variation in species composition among land use classes, we may also be able to detect corresponding variation in forest structural organization (Weishampel et al. 2007). Due to these persisting legacies, we would expect to find significantly different forest structure and composition among the ancient Maya land-use legacies: that is, terraces, non-terraced land, causeways, and structural mounds will differ in forest structure and composition. Legacies may be reflected in the vertical forest, such as canopy height, canopy openness, and vertical diversity. Tree species composition may differ in the species occurrence and abundance across different land use categories.

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CHAPTER 2: RELATING ANCIENT MAYA LAND USES TO TREE SPECIES COMPOSITION AT CARACOL, BELIZE.

Introduction

Human alteration of the landscape can have long lasting and complex impacts on the natural environment. Multiple factors can influence the legacies of past land use, including type, intensity, duration, and extent of the land use (Foster et al. 2003, Flinn and Vellend 2005). Land use legacies are commonly seen in the species composition, with the species found after abandonment of land use differing significantly from landscapes that had no former human disturbance (Motzkin et al. 2004, Flinn and Marks 2007). Even controlling for other environmental variables, such as soil and topography, land use legacies have been found to have a significant effect on the plant species composition of forests (Motzkin et al. 1996, Flinn and Vellend 2005). In studies investigating the floral species composition of former agricultural fields in temperate forests, the vegetation composition appears to be directly correlated to past land use type, with the presence and abundance of certain species determined by past land use history (Motzkin et al. 1996, Dyer 2010). A similar pattern of altered species composition of the forest vegetation in response to past land use has been observed in tropical forests (Foster et al. 1999, Thompson et al. 2002, Grau et al. 2003).

Legacies from past land uses have been documented to persist for centuries and even millennia post-abandonment in forested environments (Bellamare et al. 2003, Heckenberger et al. 2008). The time since the land has been abandoned and allowed to revert back to a natural state can be a determining factor in the legacies and the extent to which they are present

(Chazdon et al. 2003, Foster et al. 2003, Heckenberger et al. 2008, Ford and Nigh 2009, Lentz and Hockaday 2009). In European forests, agricultural legacies have been shown to persist for millennia after abandonment, with species composition in secondary forests that regenerated over former Roman agricultural fields lacking native species found in ancient forests (Delcourt 1987, Dambrine et al. 2007).

The majority of land use legacy studies have focused on the past 50-200 years in primarily temperate forest regions (Bellamare et al. 2003). However, there are few studies that investigate land use legacies dating back further than 200 years, particularly in tropical forests, which we now understand to have been heavily impacted during pre-Columbian times (Mann 2003, Heckenberger et al. 2008). This is largely due to the difficulty in recognizing regions with past human land use and our limited ability to accurately identify the land use. Previous studies have been restricted by the available methods to identify past land use, which include investigating historical records (i.e., written descriptions, old maps, or aerial photographs) or archaeological surveys, which can be spatially limited and are very time and labor intensive. These limitations have confined studies to areas such as North America and Europe, often overlooking the New World tropics. Given our current understanding of just how significant the density and extent of the human population in tropical South and Central American was prior to European colonization (Mann 2003), this represents a significant gap in our knowledge of human land use legacies in forest ecosystems.

Mesoamerica functions as an ideal region to investigate the role of ancient land use legacies in tropical forest environments. From 200 to 950 AD the Maya significantly altered their landscapes, deforesting large swaths of land (Binford et al. 1987, Turner et al. 2003, Oglesby et

al. 2010). In addition to building extensive urban centers with outlying hamlets and road systems (Chase and Chase 2001), the lowland Maya utilized a variety of agricultural techniques that were specifically adapted to their environment. Agricultural techniques include a combination of swidden farming, raised fields, intensive irrigation systems, home gardens, and orchards (Turner 1974, Ford and Emery 2008). In areas where the topography consisted primarily of hills and valleys, the Maya built extensive terrace systems along the hill slopes and throughout the valleys, enabling centuries of viable agricultural production (Wyatt 2008). At Caracol, the terraces are still in place 1,000 years after abandonment and are evident to archaeologists when conducting ground surveys (Healy et al. 1983, Chase and Chase 1998). After 900 AD Maya society was transformed and many Classic Period (250-900 AD) urban centers were abandoned. The abandonment of urban centers and agricultural resources in the Maya lowlands resulted in one of the most historically and ecologically significant post-human reforestation periods (Turner 1974).

Evidence suggests that a significant portion of the forests in Central America (Southern Mexico and the Yucatán peninsula, Belize, Guatemala, and northern Honduras) are secondary forests that have regenerated after the collapse of the Maya civilization (Gomez-Pompa et al. 2003, Turner 2003). Studies on the vegetation found around ancient Maya ruins have shown these forests to contain many species of trees that were of economic importance to the ancient Maya, and whose presence may be indicative of past cultivation of species selected by the Maya (Gomez-Pompa et al. 1987, Ford and Nigh 2009, Ross 2011). In addition to the introduction and cultivation of species by the Maya, the disturbance introduced through agriculture and the construction of limestone structures may have altered the landscape in a way that provided an

optimal environmental habitat for certain species, such as the “limestone loving” Ramon tree (*Brosimum alicastrum*), which appears to be found in higher density on the thin, calcareous soils of Maya ruins (Lambert and Arnason 1978, 1982, Puleston 1982). Previous studies on Maya land use legacies have focused on the tree species composition around areas with a high density of structural remains (Gomez-Pompa 1987, Lambert and Arnason 1982, Ross and Rangel 2011). The majority of studies have assumed differences in forest plant species due to prior human cultivation, dispersal pressures, or alteration of the soils due to land use. Few studies have investigated the effect of ancient agricultural legacies, such as terraces, on the contemporary forest directly, instead focusing on soil properties (Healy et al. 1983, Beach and Dunning 1995, Beach 1998).

This study takes advantage of the LiDAR (Light Detection and Ranging) data acquired in April 2009 for a 200 km² area around the epicenter of Caracol, Belize (Chase et al. 2010). LiDAR allows us to extract below canopy topographical features, in this case ancient Maya archaeological features, and to rapidly and efficiently identify past land use across a large region. Caracol, also known as the “Garden City”, is unusual in the known Maya landscape due to the extensive terraces the Maya built throughout the area (Chase and Chase 1998). By using the LiDAR to detail the topography and identify the terraced and non-terraced areas, as well as the structures and causeways throughout the landscape, I was able to investigate the extent to which the forest composition at Caracol is related to the past land use.

Study Area

Geography and Forest Characteristics of Caracol, Belize

Caracol is a Maya archaeological site located in western Belize near the Guatemala-Belize border. Situated on the Vaca Plateau, the Caracol Archaeological Reserve is surrounded by the extensive Chiquibul National Park and adjacent Chiquibul Forest Reserve, which together form part of one of the largest contiguous tracts of protected forest in Central America (Figure 1). The cone karst topography of Caracol consists of alternating hills and valleys, with elevations ranging between 450 to 600 m above sea level (Healy et al. 1983). The soils found within the reserve are predominantly calcareous, as is characteristic of karst landscapes (Lundell 1940, Coultas et al. 1994). Rainfall is moderate, with approximately 1500-2500 mm falling annually, and the majority of rainfall occurring during the wet season months of June and July (Healy et al. 1983). There are no major waterways within the 200 km² study area and any streams in the area are ephemeral in nature and likely to be present only during the rainy season.

With the exception of the epicenter (the central location with a high concentration of monumental structures from which causeways radiate outwards), the road leading to the main tourist area, and cleared areas near the Guatemala border (Weishampel et al. 2012), the entire study area is covered in a dense tropical forest. Brokaw (1992) classified the forest at Caracol as subtropical moist within the Holdridge System (Holdridge et al. 1971). Almost all tree species maintain leaves year-long, with leaf-off not exceeding 20% at any time of the year (Brokaw 1992). The average canopy height is ~20-25 m, with a few emergent trees reaching up to 35 m. The vertical forest structure is homogeneous, with no distinct layers.

Ancient and modern Land Use and Disturbance History

Around 650 AD Caracol was at its cultural and demographic peak with an estimated population of 100,000 people spanning over a 200 km² area (Chase and Chase 2003). As a result of such a dense population, the surrounding landscape was heavily developed. Development included hundreds of hectares of agricultural terraces, extensive causeways, and thousands of structures (Chase and Chase 1998, Chase and Chase 2001). These archaeological features are still visible today on the ground and through the use of LiDAR (Chase et al. 2010, Weishampel et al. 2010).

In an effort to adapt to their environment in the face of expanding populations, the Maya filled in their landscape with terraces at Caracol by the end of the Late Classic Period (550 to 900 AD). Construction of terraces entailed clearance of the slopes to bedrock, after which stone walls were built in intervals along the sides of the slopes, with soil added behind the walls to create even soil beds (Chase and Chase 1998). This method of agricultural land modification effectively increased soil depth and moisture along slopes, while drastically reducing soil erosion (Coultas et al. 1993, Beach et al. 2002). Terraces provided a highly productive environment for food crops, primarily maize, with other crops such as squash and beans grown (Murtha 2009, Chase et al. 2010). Today the terraces are still easily visible and continue to perform the function they were designed for in terms of soil conservation (Chase and Chase 1998).

In addition to extensive terracing, the site of Caracol also consists of causeways and a wide variety of structures, including residential and ceremonial buildings. Built of both rough and cut limestone, the causeways range in height from ground level to 2 m high, with causeway

widths varying from 2- 11 m wide (Chase and Chase 2001). The causeways at Caracol radiate out from the epicenter, extending throughout the 200 km² study area. The Maya also built extensive temples, palaces, and residential buildings out of limestone; these are found in high density throughout Caracol (Chase and Chase 2003, Chase et al. 2011). The structures range from the relatively small residential buildings (~0.1 m high) to the towering temple-palace, Caana, which is still considered one of the tallest man-made structures in Belize today at ~42.5 meters in height. Today, these structures can be seen as small mounds in valleys or on top of hills scattered throughout the forest. Most structures at Caracol remain unexcavated and are covered in a thin layer of soil, humus, and dense forest vegetation. These archaeological features represent significant alteration of the topography and landscape, which could lead to corresponding differences in tree species composition (Chase and Chase 2008, 2009, Chase et al. 2011).

Between 900 and 950 AD Caracol was abandoned (Chase and Chase 1996), yet the extensive terraces, causeways, and structural mounds remain. The forest eventually re-colonized the landscape, covering what was once a sprawling metropolis in a dense layer of vegetation, resulting in the tropical moist forest that we find today. The abandonment of Caracol was mirrored by the abandonment of Maya population centers throughout Mesoamerica.

Aside from land use by the ancient Maya, there has been disturbance to the area in the form of hurricanes, selective logging (legal and illegal), and chicle harvesting. Hurricane Hattie (1961) was the last hurricane to cause significant damage to the Caracol Archaeological Reserve (Friesner 1993). Selective logging targeted mahogany (*Swietenia macrophylla*) and cedar (*Cedrela odorata*) trees and, as a result, few individuals of these species remain in the area.

Caracol is now a protected area, with the only major threat being from the western border, where encroachment from Guatemala has led to an increased amount of illegal timber harvesting throughout the study area (Weishampel et al. 2012).

Methods

LiDAR Acquisition and Identification of Ancient Maya Land Use

Airborne LiDAR (Light Detection and Ranging) is an active remote sensing system mounted on a plane that sends down pulses of light in swaths, which are reflected back to the device after hitting a reflective surface, e.g., the ground, buildings, or leaves. The LiDAR sensor is able to measure the rate of return for the reflected light and record the location of each point of return. By using global positioning systems (GPS) on the ground and on the plane and an inertial measurement unit (IMU), which controls for the position of the aircraft, each point of return has precise coordinates in 3-dimensional space (x, y, z). These returns can be divided up into last return (usually your ground surface), first return (such as tree top), and intermediate returns (leaves, branches, etc.). Using these point cloud data, we can create detailed tomographic maps of an area, extract specific features, such as building and trees, and obtain structural information on the vegetation (Weishampel et al. 2010). With LiDAR, we can “look” beneath the canopy to identify archaeological features that could be indicative of ancient land uses, such as the terraces, structures, and causeways the ancient Maya left behind (Chase et al. 2011). The outputs derived from LiDAR data can provide detailed spatial information on ancient land uses that are typically unavailable to researchers.

In April 2009, airborne LiDAR was flown for a predetermined 200 km² area surrounding the epicenter of Caracol, Belize. The resulting output from the LiDAR yielded a high-resolution (1 m) digital elevation model (DEM), which revealed sub-canopy archaeological features, i.e., terraces, causeways, building structures, and reservoirs, as well as the natural topography of the region. Using this DEM I categorized land use as a) structure b) causeway c) terraced and d) non-terraced land (Figure 2). The archaeological features identified on the DEM corresponded accurately to prior archaeological surveys of Caracol and revealed thousands of new features (Weishampel et al. 2010, Chase et al. 2011).

Field Sampling

All sample plots were selected prior to field sampling, using a stratified random sampling procedure; random plot coordinates were generated using Hawth's tools in ArcGIS 9.3 (Beyer 2004). Using land use maps derived from the LiDAR, sample plots were stratified by land use (terraced, non-terraced, structure, causeway) and topography (slope vs. valley), for a total of 6 unique land use categories. For the purpose of this study, gradients $> 20^\circ$ were defined as slopes, while gradients $< 20^\circ$ were defined as valleys. Sampled plots consisted of terraced slopes (n=14), terraced valleys (n=10), non-terraced slopes (n=11), non-terraced valleys (n=9), structures (n=37), and causeways (n=25). Plots were visually confirmed in the field to be either terraced, non-terraced, structure, or causeway. A total of 106 plots were sampled throughout a sampling area that fell within a 1.5 km radius from the epicenter of Caracol. Sampling was restricted to fall within this radius due to the feasibility of accessing sample plots in a dense tropical forest.

Tree species with diameter at breast height (dbh) > 10 cm were identified to species within 400 m² circular plots (11.2 m radius) for terraced and non-terraced categories and 100 m²

circular plots (5.6 m radius) for structures and causeways (structure and causeway plot size was restricted by the size of the structure and width of the causeway). Plots of 100 m² were nested within the 400 m² terraced and non-terraced plots. Within the 100 m² terraced and non-terraced plots, all palms were identified to species and their approximate height was measured. The dbh of trees identified within all 100 m plots was measured. Tree species were identified with the assistance of a local expert and all species were keyed out using the *Trees of Guatemala* (Parker 2009) and a field report on the Caracol tree species (Brokaw 1992). Photographs of tree specimens were taken for future reference. On a few occasions trees could only be identified to genus (Appendix).

Standard soil samples were obtained from the 100 m² terraced (n=20) and non-terraced (n=20) plots sampled during the 2010 field season. Four core samples of the top 10 cm of soil (beneath the leaf layer) were extracted for each plot, processed together through a 2 mm sieve to homogenize the sample and subsequently air dried for one week. Samples were sent to the Brookfield Laboratory for standard soil analyses, which measured pH, organic matter, estimated nitrogen release, Bray II phosphorus, exchange capacity, % base saturation of cation, Mehlich III extractable P, Mn, Zn, B, Cu, Fe, Al, S, Ca Mg, K, and Na.

Statistical Analysis

Standard summary statistics were calculated for the tree and palm species data sets. Stem density/m², species richness, and diversity (Shannon Diversity Index) across all land use categories were measured and one-way ANOVAs were used to test for significant differences across land use categories. ANOVAs were followed by Tukey-Kramer HSD pairwise comparisons to determine significant differences between land use categories. One-way

ANOVAS were used to tests for significant differences in the soil parameters measured for terraced and non-terraced categories. After significant soil parameters were identified, Tukey-Kramer HSD was used to determine which land use categories were significantly different from the other categories.

Non-metric Multidimensional Scaling (NMS) was used to quantify patterns of tree species composition associated with land use and topography. NMS was chosen as the appropriate analysis to demonstrate the ecological relationship between tree species composition and land use, as the tree species data sets had a non-normal distribution and the data contained a large number of zeros, with many rare species and a few common species (McCune and Grace 2003). Because of the sensitivity to heterogeneous data sets, such as ecological community data, the Sørensen similarity index was used as the distance measure for all multivariate analyses performed in this study (McCune and Grace 2003). NMS analyses were run using the ‘slow and thorough’ autopilot method in PC-ORD (McCune and Mefford 1999), with a random starting configuration. Prior to analysis, species data sets were transformed using Beal’s smoothing function. Beal’s smoothing function is ideal for ecological community data sets that contain a large number of zeroes (McCune and Grace 2002). Beal’s smoothing calculates a probability of species occurrences in a plot based upon joint occurrences between species at other sites. The probabilities derived can then be used in combination with ordination procedures to highlight the dominant patterns in the data set (McCune 1994).

Using PC-ORD, Multi-response Permutation Procedure (MRPP) was run on the tree species data sets to test the hypothesis that tree species compositions were significantly different across land use categories and topography. MRPP is a non-parametric multivariate test of

significance that evaluates differences between groups of variables (Biondini et al. 1985, Mielke and Berry 2001). All groups were defined by land use category prior to running the analyses.

Lastly, indicator species analyses were performed for all tree species identified in the sample plots, using PC-ORD. Indicator species are commonly used as ecological indicators of the environmental conditions. Indicator values (IV) are assigned to each species to indicate the degree of correlation between species and land use category with higher values indicating a greater degree of correlation (McCune and Grace 2003). In our case, indicator species values (ISV) are used to further explain any differences in the groups that were used in the MRPP analyses with specific species potentially contributing more weight to the value of the differences between groups.

Results

A total of 75 tree species and 6 palm species were identified throughout the sampling area (Appendix). Average stem density (number of trees)/m², tree species richness, and tree species diversity were summarized for terraced and non-terraced plots (400 m²) (Table 2). One-way ANOVAs, with Tukey-Kramer HSD pair-wise comparisons, revealed significant difference between land use classes and tree species richness ($p < 0.05$) and stem density ($p < 0.005$) (Table 3). No significant differences were revealed in terms of tree species diversity. Non-terraced slopes differed significantly from non-terraced valleys and terraced valleys, but not terraced slopes in terms of stem density (Figure 3). Non-terraced slopes differed significantly from terraced slopes, non-terraced valleys, and terraced valleys in terms of species richness (Figure 4).

A one-way ANOVA of the macronutrient soil parameters revealed significant differences in the soil samples taken from different land uses and topographies, with most of the differences correlating to topography (slope vs. valley). A pairwise comparison using Tukey-Kramer HSD revealed significant difference between land use categories for pH, organic matter, % other bases, and Cu. Terraced valleys had a significantly lower pH than the other categories sampled. Organic matter was significantly higher on slopes compared to valleys. Percent of other bases was significantly higher in valleys versus slopes. Copper content was significantly higher in valleys compared to slopes (Table 4).

The data set for 100 m² plots, which contained sites across all land uses, consisted of 71 species across 105 sites. NMS yielded inconclusive patterns in the data, with the structure and causeway site roughly forming groups, but overlapping significantly with the other land use categories. The ordination for 100 m² data set stabilized at stress of 14.5, with a 3-D solution recommended (Figure 3). A closer examination of the terraced and non-terraced 400 m² data set yielded a more conclusive pattern in the data set.

The data set for 400 m² terraced and non-terraced sample plots consisted of 72 species (including palms) across 45 sites. The ordination for this data set stabilized at a final stress of 9 with a 3-dimensional solution, which allows for reliable inferences (McCune and Grace 2003). NMS ordination procedure was able to explain 71% of the variation in species composition, with the majority of variation accounted for in axis 1 at 43%, and the remaining variation accounted for in axis 2 at 18% and axis 3 at 10% (Figure 4). A clear pattern emerges along axis 3 as groups divide according to land use class and topography. In the ordination graph non-terraced valley

and non-terraced slope sites do not overlap, but form distinct groups, while the terraced valleys and terraced slopes both form distinct groups, but overlap with each other (Figure 4).

In the MRPP analyses chance-correlated within group agreement (A) is provided as a description of the effect size, with a p-value < 0.05 indicating a significant difference between groups. Results from the MRPP analyses for the 400 m² terraced and non-terraced plots indicated differences in species composition between the terraced and non-terraced land use categories (Table 1, Figure 5). For the 100 m² plots MRPP yielded the same results for terraced vs. non-terraced categories. Causeways differed significantly from all other land use categories aside from terraced valleys (p= 0.09, A= 0.02). Structures were also significantly different from all other land use categories, with the exception of non-terraced valleys, from which it did not differ significantly (p= 0.58, A= -0.004).

Indicator values (IV) were significant for a total of 11 species out of 75 species. *Bursera simaruba*, *Dendropanax arboreus*, *Pouterias* sp., and *Zuelania guidonia* were all strongly associated with non-terraced slope plots. *Psuedobombax Ellipticum* and *Sebastiana adenophora* were strongly associated with terraced slope plots. In the valley land use categories *Attalea cohune*, *Calophyllum brasiliense*, and *Dryeptes brownii* were strongly associated with non-terraced valleys, while *Sabal Mauritiformes* and *Cordia gerascanthus* were strongly associated with terraced valley plots. *Brosimum allicastrum* was the only species showing a strong association to structures and no species showed a strong association with causeways (Table 5).

Discussion

The remnants of the Maya civilization that persist at Caracol continue to impact the natural environment over 1,000 years after abandonment. Our analyses of the tree species and palm species composition over an array of ancient Maya land use classes has shown a strong relationship between past land use and species composition. The most compelling association was found in the forest vegetation over land that was terraced by the Maya. When separated by topography (i.e. slopes vs. valleys), NMS showed a pattern in tree species composition where non-terraced slopes and non-terraced valleys fell into separate clusters, with no overlap. This distinct community composition associated with topography is consistent with prior research in tropical forests that highlights the differences in vegetation composition associated with natural topography (Clark et al. 1999, Brewer et al. 2003). However, when terraced land uses are included in the analyses a different pattern emerges. While non-terraced slopes and non-terraced valleys were significantly different from each other, the addition of terraces to a slope or valley tended to blend those differences. Terraced slopes and valleys did not differ significantly from each other, indicating a compositional similarity. Terraces appear to provide a median environment between slopes and valleys.

Tree summary statistics revealed a similar pattern in differences between land use categories. Stem density was found to be significantly higher on non-terraced slopes compared to non-terraced valleys and terraced valleys, but this difference disappeared when the slopes were terraced. In terms of species richness, terraced slopes had significantly lower species richness than non-terraced slopes, indicating a closer similarity to non-terraced valley and terraced valley

plots. These patterns further reinforce the hypothesis that terraces blend the differences between slope and valleys.

The results from the ISV analyses further illuminate the relationship between trees species and land use. *Bursera simaruba* and *Dendropanax arboreus* are both species found on non-terraced slopes with high IVs; these trees are most commonly found growing in areas with rocky, well drained, calcareous soils (Decaisne and Planchon 1854, Parker 2008), which aptly describes non-terraced slopes. *Psuedobombax ellipticum*, a species with a high IV for terraced slopes, is also known to prefer open, rocky hillsides (Parker 2008). In our terraced valleys the species with the highest IV was *Attalea cohune*, which is a palm commonly found in high abundance in valleys (Brewer and Webb 2002). Palms are often an indicator species for valleys and lowland areas, as they require deep, wet soils (Clark et al. 1995). *Sabal maurtiformes*, another palm species, was a strong indicator species for terraced valleys. However, *Cordia gerascanthus* was also a strong indicator species for terraced valleys, but is commonly found in other regions on rocky hills with extremely dry slopes (Opler and Baker 1975, Parker 2008). These results begin to elucidate the unique environment created by terraces, which acts as a micro-environment with a combination of species usually found on either slopes or valleys.

While this study was unable to directly investigate the edaphic properties of the terraces, such as soil depth, grain size, and moisture content, there is a significant amount of research available on this subject. Research conducted by Beach and Dunning (2002) investigated the physical properties of terraces in Yucatán Mexico; their research indicated that by terracing, the Maya were effectively preventing soil erosion along hills, increasing the soil depth in the terraces, and increasing water retention. The terraces at Caracol, Belize have similar physical

characteristics to the terraces in this study. Caracol terraces were found to have soils up to 0.75 m deeper than adjacent, un-terraced land (Coultas et al. 1993). By creating garden beds along the hill, the Maya adapted to an environment with limited valleys for growing food by creating their own valleys on hills.

The standard macronutrient soil analysis revealed some significant differences between the land use categories sampled, but the differences appear to be associated more with topography than land use. Further quantification of edaphic properties on terraced and non-terraced land should include soil depth, substrate size, rockiness, and soil moisture. Field observations lead me to believe these properties would differ significantly across land use categories, but I was not able to measure them at the time. Correlations between these variables and species composition may yield more insight into the ecological relationship between the vegetation community and terraces.

In addition to the terraced land use, I investigated the relationship between tree species composition and structures and causeways. While the patterns to emerge from the NMS analyses were not as clear as the terrace versus non-terrace categories, there was some clustering between the two groups. According to the results from the MRPP analyses, structures and causeways are significantly different from the other land use categories, with the exception of terraced valleys and causeways and non-terraced valleys and structures, which were not found to be significantly different. In the case of structures and causeways, the variability of the two is very high with both archaeological features differing in size and architecture. They were not all created equally. To overcome this heterogeneity, we would need to increase the sample number of structures to account for variation in structure type or limit our sampling to specific types of structures in

order to relate tree species composition to structure type. With knowledge of structure size and possible type available through LiDAR at Caracol, this offers the unique opportunity to expand the study in the future.

In our ISV analysis for structures only one species was apparent as a strong indicator species, *Brosimum allicastrum*. This result is in concordance with other studies (Lambert and Arnason 1982, Puleston 1982, Ford 2008) on the documented relationship between *Brosimum allicastrum* and structures. It is thought that the presence of structures creates an ideal environment for *Brosimum allicastrum*, which does well in environments with highly calcareous soil. Structures often have a thin soil layer high in calcium, due to the limestone blocks the structures were constructed with. It is also thought that *Brosimum allicastrum* may take advantage of available space and resources by rooting deep into the bedrock water reserves, allowing them to grow in areas of thin soil and little available surface water, where many trees would find it difficult to establish (Querejeta et al. 2006).

The majority of studies to date on Maya land use legacies have focused on species composition found around high-density structural areas and small home gardens. The central hypothesis in these studies has been that many of the tree species found in high density housing areas are there due to the Maya, who cultivated economically important species around residential areas. These species are thought to be the legacy of the Maya home garden (Gomez-Pompa et al. 1987, Ford and Emery 2008). However, while forest gardens and Maya silviculture are the focus of many studies (Ford and Nigh 2009, Ross 2011), few investigate the forest legacies of larger scale or “intensive” agriculture. The terraces at Caracol have provided an opportunity to investigate the agricultural legacies of the terracing system the Maya built. This

study has shown that, through an alteration of the micro-topography and, subsequently, the physical environment, the tree species composition has been altered. When it is realized that in a 200 km² area, 80% of the landscape has been terraced, the scale of the resulting agricultural legacy represents a significant ecological factor (Figure 8).

Tables and Figures

Table 1: MRPP pairwise comparison for terraced and non-terraced land uses.

	Non-terraced Valley	Terraced Valley
Non-terraced Slope	p < 0.001, A = 0.16	p < 0.001, A=0.12
Terraced Slope	p < 0.05, A = 0.07	p = 0.19, A= 0.02

Table 2: Summary statistics for terraced vs. non-terraced land use categories.

	<u>Stem Density/m²</u>	<u>Species Richness</u>	<u>Species Diversity (H)</u>
	Mean (S.D.)	Mean (S.D.)	Mean (S.D.)
Non-Terraced Slope	0.079 (0.014)	15.5 (2.4)	2.5 (0.19)
Terraced Slope	0.071 (0.023)	11.8 (2.9)	2.1 (0.52)
Terraced Valley	0.051 (0.016)	11.6 (1.8)	2.3 (0.21)
Non-Terraced Valley	0.051 (0.011)	11.2 (2.3)	2.2 (0.25)

Table 3: Summary of Tukey-Kramer HSD pairwise comparison for stem density and species richness of terraced slope (TS), terraced valley (TV), non-terraced slope (NTS) and non-terraced valley (NTV) plots. Significant comparison denoted by * ($\alpha=0.05$).

	<u>Stem Diversity/m²</u> p-value	<u>Tree Species Richness</u> p-value
NTS vs. TV	0.0065*	0.0130*
NTS vs. NTV	0.0258*	0.0191*
NTS vs. TS	0.0760	0.0173*
TS vs. TV	0.2159	0.9824
TS vs. NTV	0.6269	0.9906
NTV vs. TV	0.9755	0.9999

Table 4: Significant results from ANOVA of standard soil macronutrients.

Soil Macronutrients	NTS(n=8)		NTV (n=10)		TS (n=13)		TV (n=13)		F-ratio	p-value
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.		
pH	7.75	0.12	7.4	0.11	7.52	0.09	7.27	0.09	3.6	0.021
Organic Matter	30.24	2.68	23.45	2.40	32.64	2.10	23.81	2.10	4.3	0.01
% Other Bases	3.65	0.12	4	0.11	3.88	0.09	4.13	0.09	3.6	0.0215
Cu	1.57	0.24	2.54	0.21	1.67	0.19	2.47	0.19	6.2	0.0015

Table 5: Summary of tree species that are a significant indicator for a specific land use category (non-terraced slope=NTS, terraced slope=TS, non-terraced valley=NTV, terraced valley=TV, structural mounds=STR, Causeways=CSW).

Land Use	Species	Family	Common Name	IV Observed	IV from Randomized Groups		p
					Mean	SD	
NTS	<i>Bursera simaruba</i>	Burseraceae	Chaca	51.1	18.4	6.91	.001
	<i>Dendropanax arboreus</i>	Araliaceae	Mano Leon	37.0	17.7	6.41	.015
	<i>Pouteria</i> sp.	Sapotaceae	Sapotillo	38.9	28.2	4.52	.025
	<i>Zuelania guidonia</i>	Flacourtiaceae	Tamay	29.0	16.6	6.14	.047
TS	<i>Pseudobombax ellipticum</i>	Bombacaceae	Mapola	37.4	13.8	6.6	.006
	<i>Sabastiana adenophora</i>	Euphorbiaceae	Chechem blanco	31.7	7.7	4.42	.001
NTV	<i>Attalea cohune</i>	Palmae	Cohune	54.6	25.4	6.53	.002
	<i>Calophyllum brasiliense</i>	Guttiferae	Barillo	22.2	8.5	5.18	.035
	<i>Dryeptes brownii</i>	Euphorbiaceae	Bullhoof	39.8	18.2	6.38	.008
TV	<i>Sabal</i>	Palmae	Botan	40.4	17.2	7.71	.009
	<i>Mauritiformes</i>	Boraginaceae	Bohon negro	29.5	16.1	6.26	.045
	<i>Cordia gerascanthus</i>						
STR	<i>Brosimum alicastrum</i>	Moraceae	Ramon	27.2	14.7	4.08	.001
CSW	None						

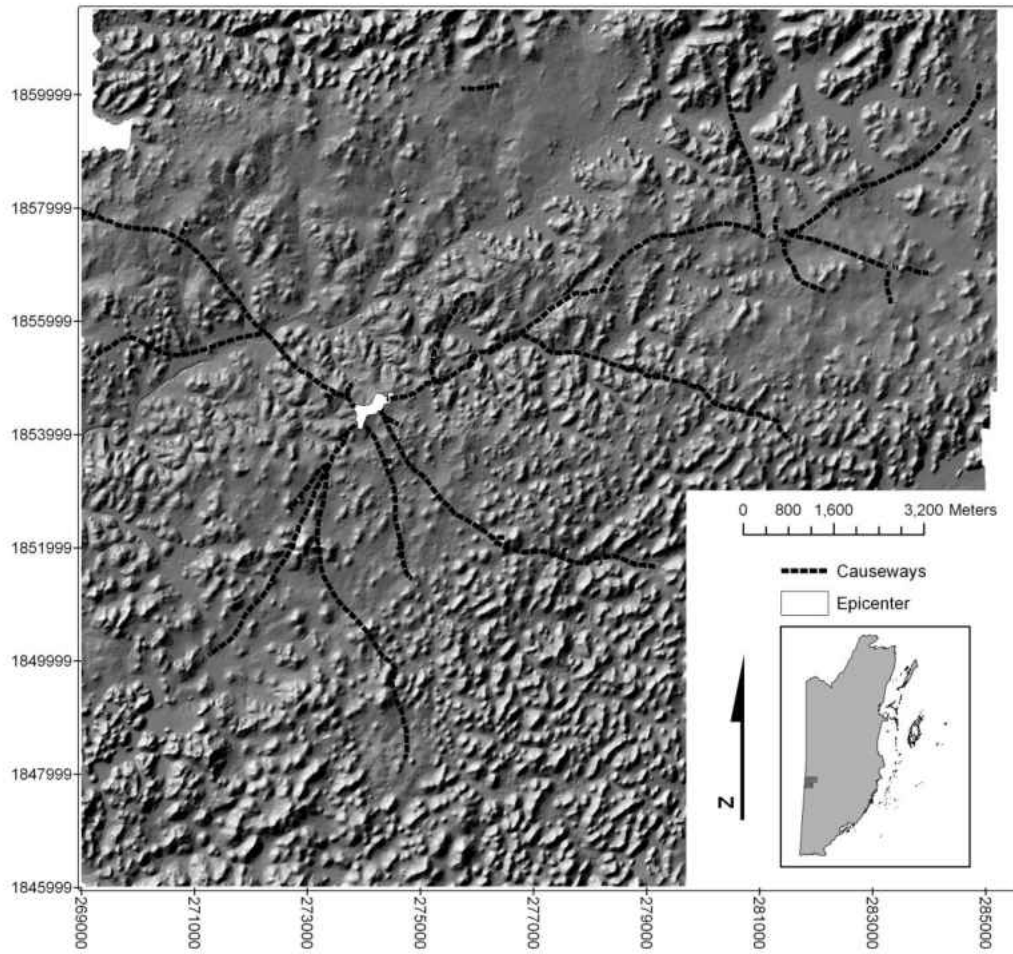
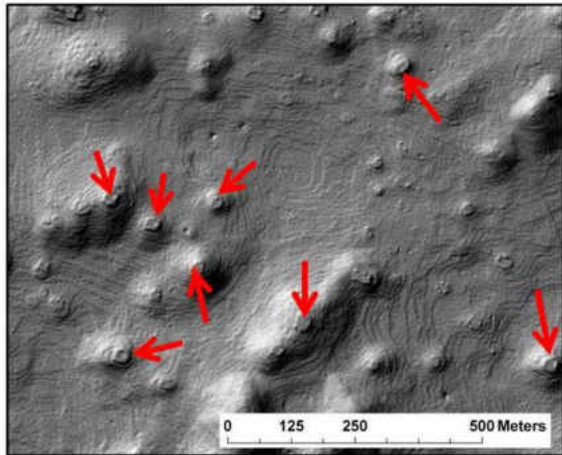
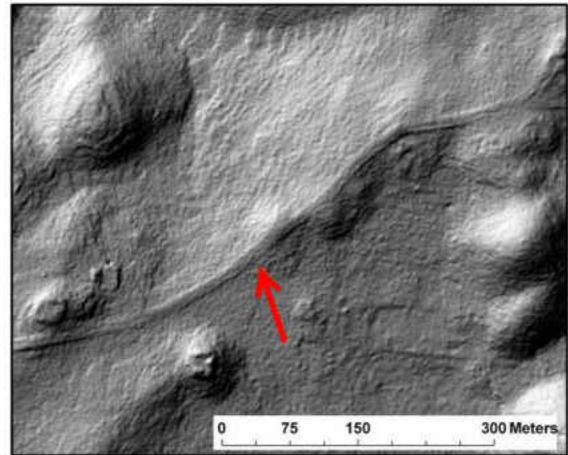


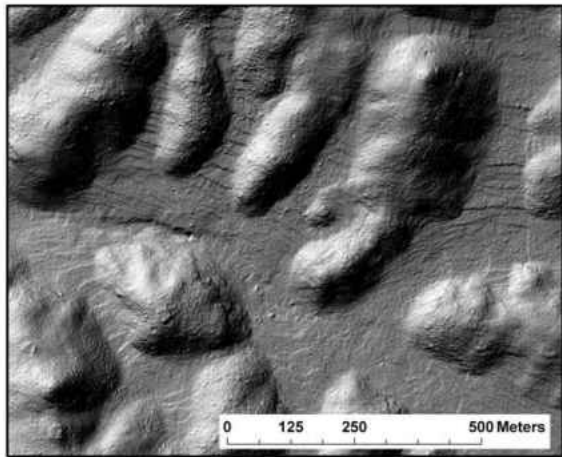
Figure 1: LiDAR derived hillshaded map of Caracol, Belize. The location of Caracol is shown as the gray polygon in the inset of Belize.



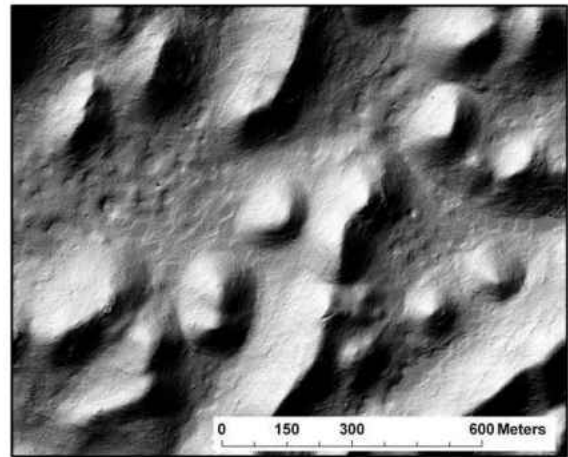
a. Structures



b. Causeway



c. Terraces



d. Non-terrace

Figure 2: Four ancient Maya land use classes: a. structures (red arrows point to structures) b. causeways (red arrow pointing to causeway) c. terraced slopes and valleys d. non-terraced slopes and valleys.

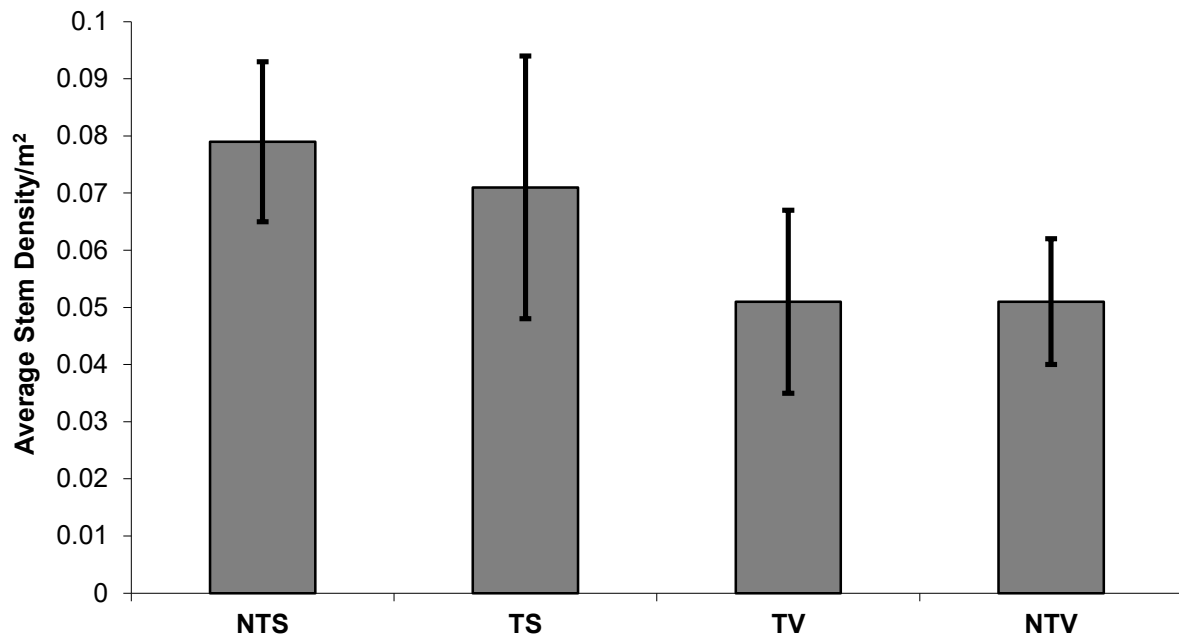


Figure 3: Average stem density/m² for non-terraced slope (NTS), terraced slope (TS), terraced valley (TV) and non-terraced valley (NTV) land use categories.

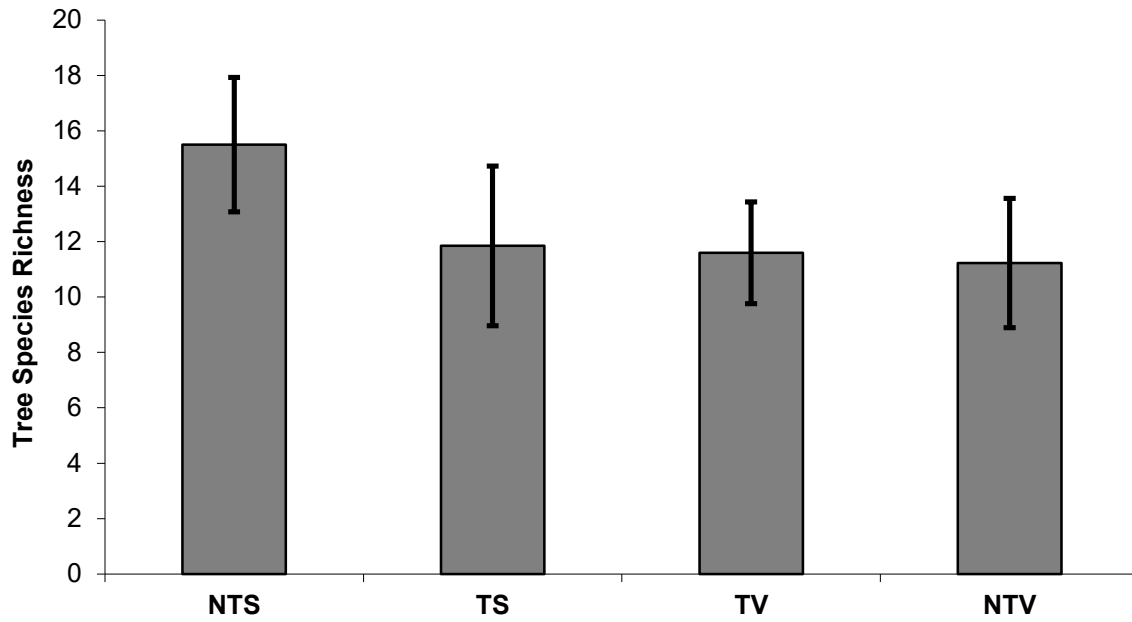


Figure 4: Average tree species richness for non-terraced slope (NTS), terraced slope (TS), terraced valley (TV) and non-terraced valley (NTV) land use categories.

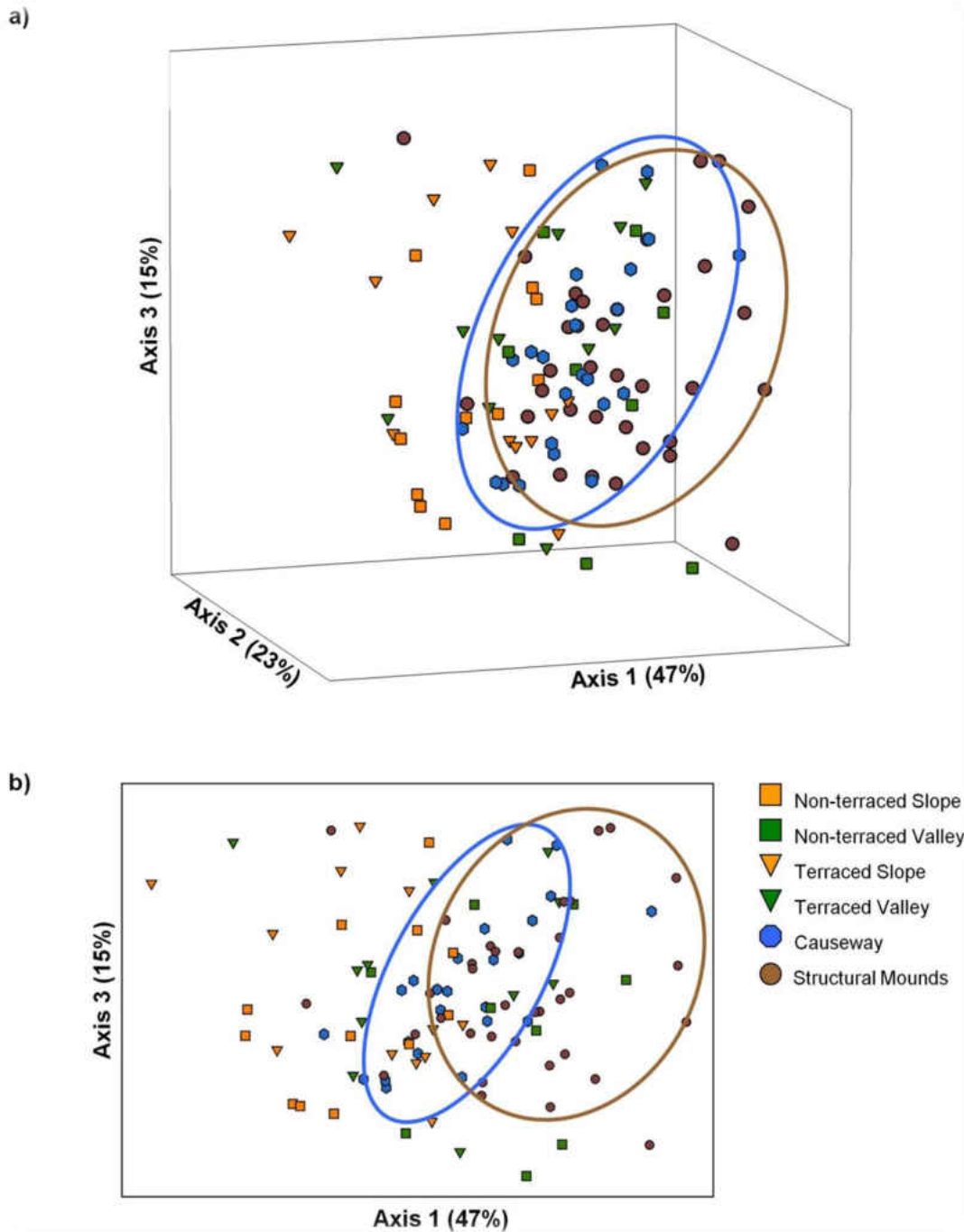


Figure 5: NMS ordination of 100 m² plot tree species data across all land uses. Results yielded a recommended 3-D solution (a) with a relatively low stress of 14.5. A 2-D graph (b) is included for comparison. Ellipses indicate groupings for specific land use categories. Amount of variation explained by each axis is included next to each axis as the percentage.

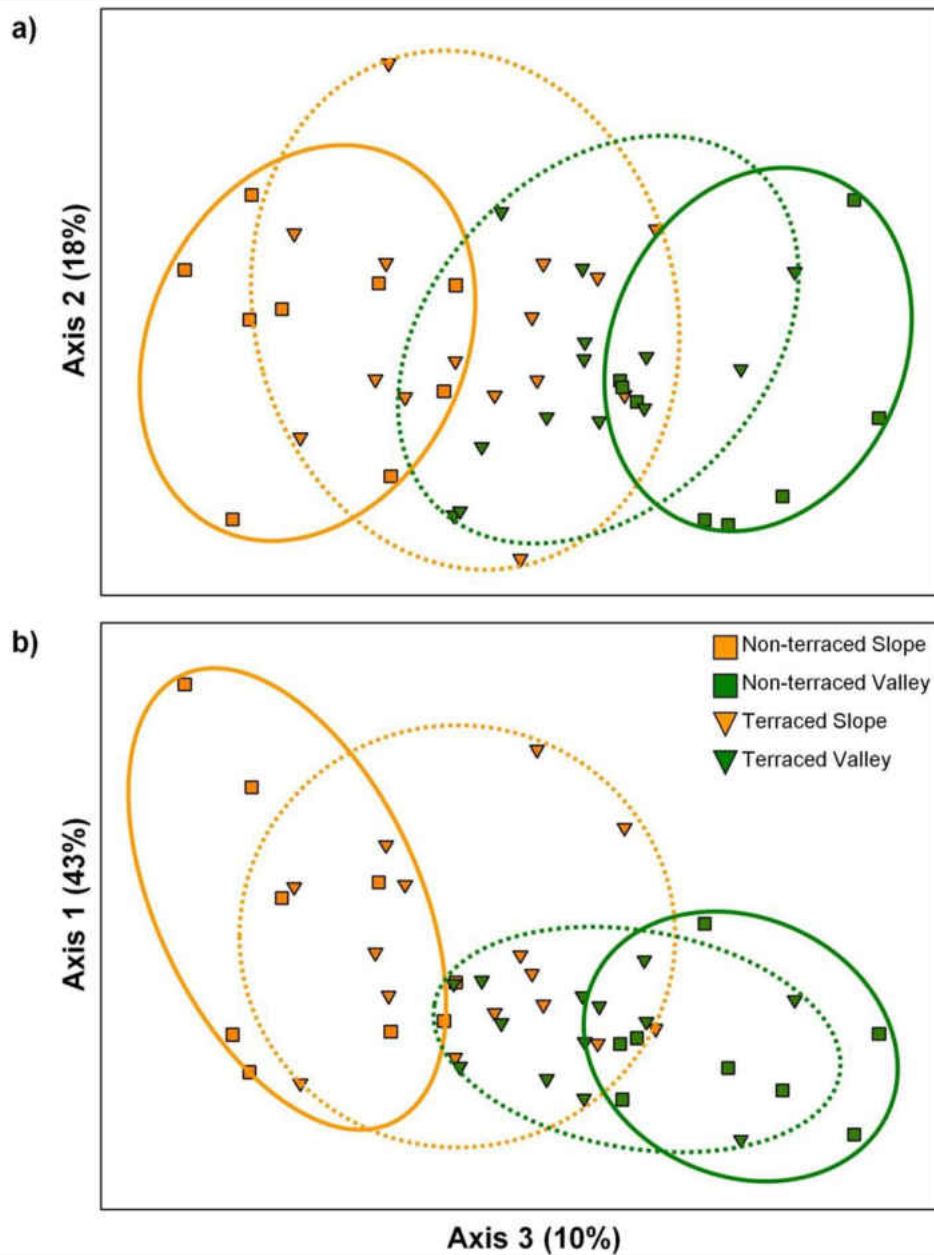


Figure 6: NMS ordination of 400 m² plot tree species data across terraced and non-terraced land (separated by slope vs. valley). Results yielded a recommended 3-D solution with a low stress of 9.8. Ellipses indicate grouping for specific land use categories. Amount of explained variation attributed to each axis is denoted as a percent next to the axis labels.

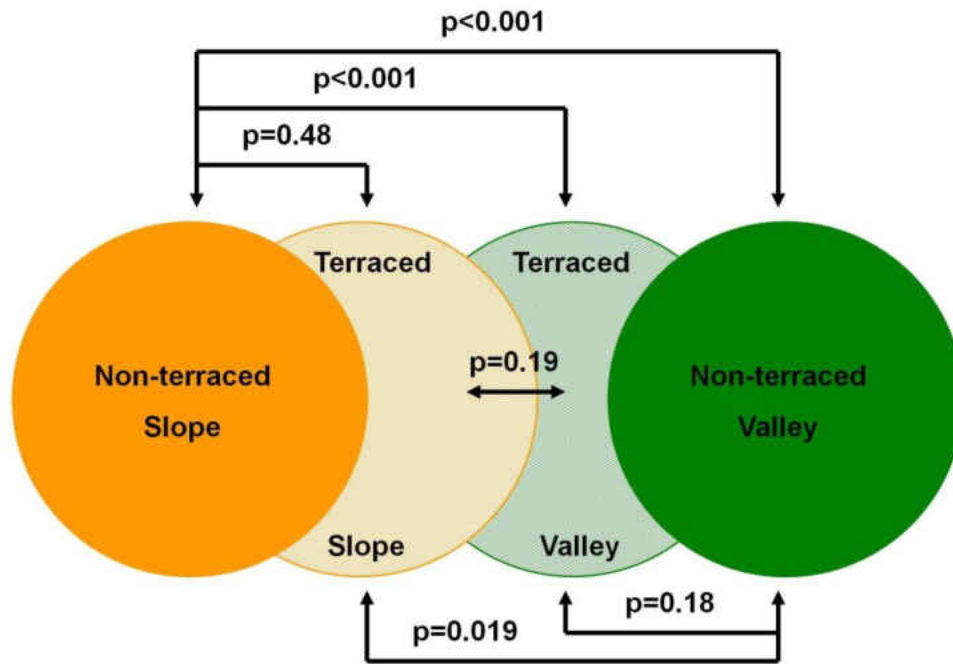


Figure 7: This diagram illustrates the relationship between the tree species composition across the terraced and non-terraced land use categories. P-values indicate significance from results of the MRPP test.

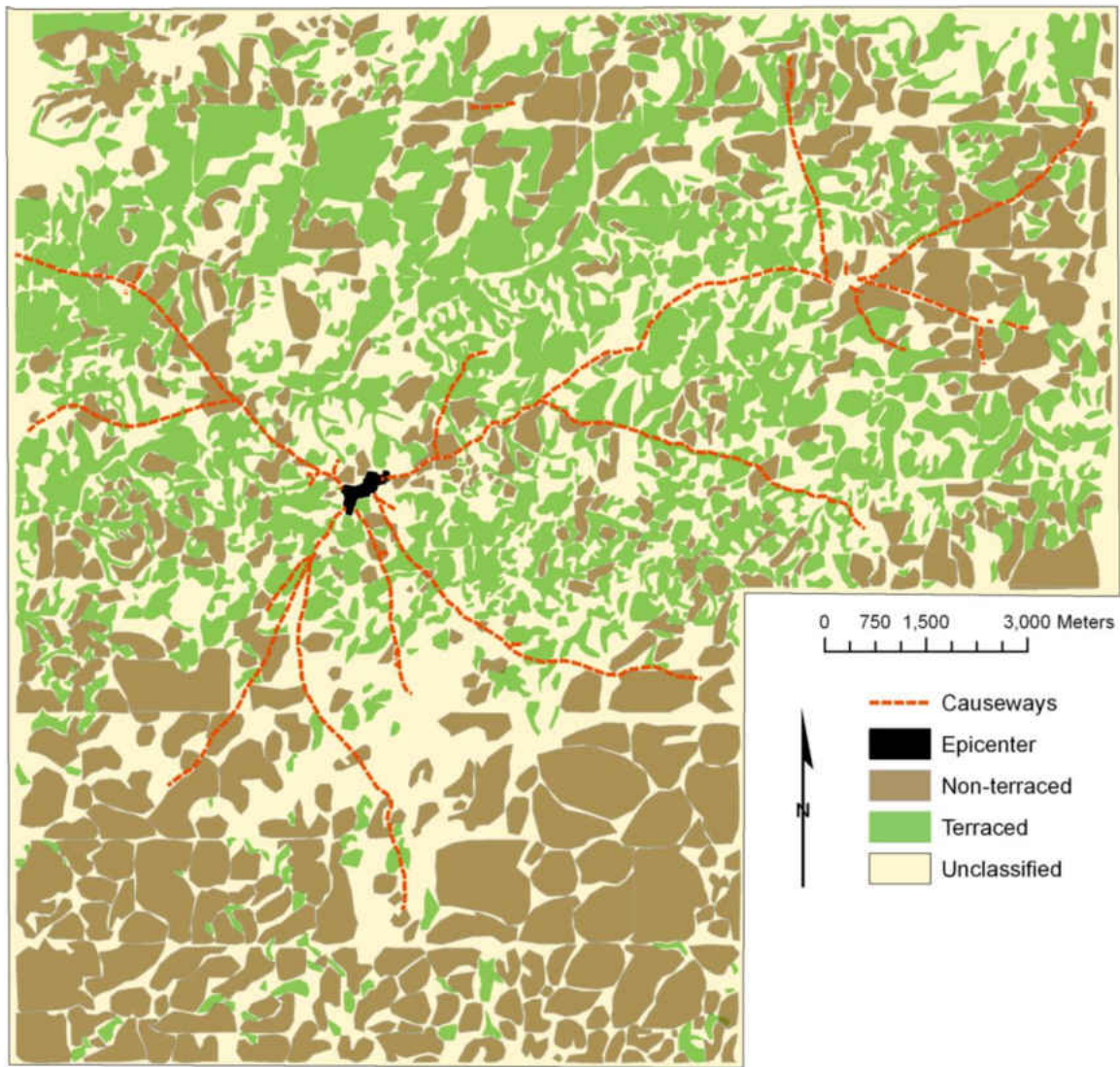


Figure 8: This map illustrates the extent of the terracing present at Caracol. Unclassified areas represent land that I was unable to classify as either terraced or non-terraced with absolute certainty.

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CHAPTER 3: EFFECTS OF ANCIENT MAYA TERRACING ON CONTEMPORARY VERTICAL FOREST STRUCTURE

Introduction

The structure of a forest offers key insights into ecosystem function and biodiversity. Structure (i.e. canopy height, basal area, canopy openness, etc.) has been directly correlated to a number of important ecological measures, such as biodiversity and above ground biomass (Spies 1998, Alves et al. 2010). By describing spatial patterns we can determine processes at work in a landscape (Turner 1989). Forest structure can be directly tied to species diversity, with a more heterogeneous structure often indicative of not only higher floral diversity, but high faunal diversity as well (MacArthur and MacArthur 1961, Verschuyt et al. 2008). The structure of forests is often used as a proxy for determining live above ground biomass, an important factor in identifying sources of carbon sequestration (Clark and Clark 2000, Alvares et al. 2012). Forest structure can be key to determining the health of an ecosystem, where a higher degree of heterogeneity is suggestive of a more dynamic forest (i.e. disturbance, gaps, recruitment) (Prentice and Leeman 1990, Brokaw 1992). Understanding the factors that drive forest structure can enable a better understanding of general ecosystem functions (Pacala and Deutschmann 1995, Philips et al. 2004, Shugart et al. 2010).

A number of factors are known to affect a forest's structure, among them natural and human disturbance (Urquiza-Haas et al. 2007), climate, soil type and available soil nutrients, and topographic position (Holdridge et al. 1971, Tateno and Takeda 2003). Topographic position, which include measures of relief (or slope) and elevation, have been shown to have a strong

effect on forest structure. Forest canopy height and above ground biomass (AGB) have been directly correlated to topographic relief, with high AGB and greater canopy heights in lower slopes and valleys compared to steeper slopes which are typically associated with lower AGB and lower canopy heights (Clark and Clark 2000). Canopy openness has also been shown to increase on steeper slopes compared to low slopes and valleys (Homeier et al. 2010). While topographic position appears to be a strong factor in influencing forest structure, another important, if indirect, factor to consider is disturbance.

While natural disturbances such as floods, fire, and wind damage can drastically alter the structure of a forest (Spies 1998), human disturbance can also have a significant impact (Laurence et al. 1998, Harper et al. 2005, Turner 2010). However, for many human land uses, forests that regenerate attain levels of vertical structure very close to original levels within 50 to 200 years (Aide et al. 2000, Mueller et al. 2010). Other forms of human land use may have longer lasting impacts, depending on the intensity of former land use (Foster et al. 2003). Land use that alters the topography of the landscape has the potential to permanently alter the structure of the forest that regenerates, so long as the change in topography remains. One such land use can be found at Caracol, Belize, where the Maya extensively terraced across the hilly landscape. The terraces were constructed over a millennium ago (A.D. 650-900) and are still in place today (Chase and Chase 1998). The terracing has essentially created fine-scale, level areas along hill slopes, effectively transforming the micro-topography of the region. Caracol provides the opportunity to investigate if and how human-altered topography continues to impact forests 1,000 years after forests reestablished.

In April 2009, LiDAR (Light Detection and Ranging) was flown over Caracol in an effort to detect sub-canopy archaeological features and quantify the tropical forest structure (Chase et al. 2011). The project allowed researchers to delineate the full extent of terracing throughout the ~200 km² study area. The resulting data set also allowed us to quantify vertical forest structure at a landscape scale. LiDAR has been used in past studies to quantify forest structure over a variety of land uses in a number of different forest types (Lim et al. 2003). LiDAR has been shown to effectively measure canopy height, canopy openness, vertical structure diversity, and above ground biomass (Drake et al. 2002, Dubayah et al. 2010, Asner et al. 2011). It is an ideal technique to provide a robust description of vertical forest structure.

Methods

Study Area

The Caracol Archaeological Reserve is located in central Belize along the Guatemalan border. The reserve us a karst landscape consisting of alternating hills and valleys, with elevation ranging between 450 to 500 m asl. The Caracol study site encompasses an area of ~200 km² and is surrounded by the Chiquibil National Park (Figure 9). The dense subtropical moist forest of Caracol reaches average heights of 22 m and leaf off never exceeds 20%, with maximum leaf off occurring during the end of the dry season (end of March- April) (Brokaw 1992). Recent human and natural disturbance of the forest has included hurricanes in 1968 and 1973 (Friesner 1993) and encroachment from Guatemala. Encroachment from Guatemala entails the clearing of large swaths of forest along the border and targeted removal of desirable tree species throughout the reserve, primarily *Swietenia macrophylla* (Mahogany) and *Cedrela odorata* (Cedar) (Weishampel et al. 2012).

Ancient Maya land use was ubiquitous throughout the study site. Thousands of residential and ceremonial structures are found throughout the ~200 km² area, as well as ~67 km of causeways radiating out from the epicenter (i.e., central metropolis area with a high density of temple, palace, and residential structures). The Maya built extensive limestone terraces throughout the landscape for agricultural purposes, growing maize and other crops, such as beans and squash (Chase and Chase 1998, Webb at al. 2004, Murtha 2009). These terraces cover as much as 80% of the study site and can be found along hill slopes and in valleys. Terraces at Caracol have been shown to increase soil depth along hill slope by up to 0.6 m (Coltas et al.

1994). Studies of other Maya terraces have shown that terraces effectively prevent soil erosion along slopes, increase soil depth, and increase moisture retention (Beach et al. 2002).

LiDAR Data Collection, Extraction, and Sampling

In April 2009, LiDAR was flown over the Caracol study site. The LiDAR survey used an Optech GEMINI Airborne Laser Terrain Mapper (ALTM) mounted on a twin-engine Cessna Skymaster. During the 9.5 hours of laser-on flight time a total of 122 flight lines were flown ~800 m above the ground surface, 66 in a North-South direction and 60 in an East-West direction, insuring optimal penetration through the dense canopy. The swath width was 520 m and flight lines were placed 260 m apart, insuring a 200% overlap. The survey yielded ~20 points per m², for a total of 4.28 billion measurements, of which, 295 million were classified as ground returns (1.35 ground return points per m² on average). The data were processed by NCALM (National Center for Airborne Laser Mapping); the final product included LiDAR point cloud files and a bare earth digital elevation model (DEM) with a 1 m horizontal resolution.

Three hundred 0.25 hectare circular plots were randomly placed across the Caracol DEM using Hawth's tools (Beyer 2004). Sample plots were stratified using terraced (n=150) and non-terraced (n=150) land use layers in ArcGIS that had been carefully digitized off the DEM (Figure 10). Samples were further stratified by low (0-10°; n=50), medium (10-20°; n=50), and high (20-40°; n=50) slopes to insure an even representation of slope classes in the sample. ArcGIS 9.3 spatial analyst was used to generate slope, aspect, and elevation layers for the Caracol DEM and slope, aspect, and elevation values were extracted for each sample plot. Using FUSION LiDAR analysis software (McGaughy 2009), LiDAR point returns were extracted for all plots (Figure 11). The Density Metrics function in FUSION allows users to sample LiDAR point clouds by

extracting slices associates with height ranges. Returns were sampled in 3 m height slices and sorted into a bin of height ranges (Angelo et al. 2010). The final FUSION product yielded a data set of vertically binned height returns for each plot. All plots were sampled using a fixed grid with 10 x 10 m cells and all cells were summed for each height class. The proportion of total points was calculated for all height bins within each plot for the final height bin data set.

Statistical Analysis

The following forest structural characteristics were calculated using the LiDAR point height bins for each sample plot: average canopy height, canopy openness, and a vertical diversity index (VDI) (Table 6). Average canopy height was calculated by taking the average of the maximum heights for each 10 x 10 m window in a plot. A measure for canopy openness was calculated by taking the ratio of ground returns divided by the sum of all other returns (ground returns/all non-ground returns) (Drake et al. 2002). Jost diversity index was calculated for the proportion of returns that had been binned into height classes for each plot and used as an approximation of vertical diversity (Jost 2006, Angelo et al. 2010).

Permutational multivariate analysis of variance (PerMANOVA) was used to test for significant differences in forest structure between non-terraced and terraced land. PerMANOVA allows for a non-parametric analysis of variance, which is ideal for non-normal data sets. PerMANOVA first calculates a distance matrix using a user selected distance measure. The test statistic (F-ratio) is calculated directly from the distance matrix. Permutations are then used to generate p-values to determine significance (Anderson 2001). The Adonis function in the vegan

package for R was used to perform the PerMANOVA analyses in our study (Oksanen et al. 2011).

For the first analysis, land use (terraced vs. non-terraced) was used as our factor, while slope, aspect, and elevation were held as covariates. A distance matrix (response variable) was calculated from the measured forest structural characteristics (average canopy height, canopy openness, and vertical diversity index) using `vegdist` in the R `vegan` package (Oksanen et al. 2011). `Vegdist` uses the Bray-Curtis (Sorensen) distance measure, which is appropriate for community ecology datasets (McCune and Grace 2002). In a second PerMANOVA, I used a distance matrix calculated directly from the point return height bin data set for each plot. For the second analysis, land use was retained as our factor, while slope, aspect, and elevation were held as covariates. A total of 9999 permutations were used for each analysis.

Results

PerMANOVA results from the LiDAR derived forest measurements indicated significant differences between terraced and non-terraced land uses ($p = 0.016$). Slope was also highly significant in explaining the variation between samples ($p=0.001$), as was elevation ($p=0.001$). The interaction of slope and aspect ($p = 0.026$), as well as the interaction of slope and elevation ($p = 0.001$), were also considered significant in explaining the variation seen between samples (Table 7).

Using the LiDAR height bin distance matrix, PerMANOVA revealed a significant proportion ($p = 0.005$) of the variation was explained by land use categories, i.e. terraced vs. un-terraced. Slope was again found to be significant in explaining the variation in the proportion of

points found in each height bin ($p=0.001$). In this analysis, aspect did not contribute significantly to the explanation of variation. Also elevation did not explain a significant proportion of the variation, but the interaction effects of slope:elevation and slope:land use were significant in explaining the variation of height bin distributions (Table 8).

When analyzed together as a distance matrix, the forest structure variables (canopy height, canopy openness, and vertical diversity index) were significantly impacted by the presence of terraces. When the individual trendlines of our three forest structural variables are graphed, a few patterns begin to emerge. On non-terraced plots you can see a trend of vertical diversity decreasing as the slope increases; however this decrease occurs at a slower rate for terraced land use. A similar pattern is observed with average canopy height, with canopy height decreasing as slope increases, but this decrease occurs at a slower rate on terraced land. Canopy openness increases as slope increase, with canopy openness on terraces increasing at a slower rate compared to non-terraced land (Figure 13).

Histograms generated from the LiDAR height bin data showed a similar trend, that is, non-terraced line showed a distinct gradient between low, medium, and high slopes, with medium slope point values falling between the low and high slope. However, on terraced land we can see a trend of decreased variation between slope categories. Slopes no longer illustrate a “stair step” pattern in terms of LiDAR point returns (Figure 12).

Discussion

These results indicate that the terraces constructed by the Maya over 1,000 years ago continue to influence the forest structure at Caracol. The terraces have significantly altered the

micro-topography of the terrain, resulting in a corresponding echo in forest structure. While topography (i.e., slope, elevation, and aspect) appears to act as the driving factor in forest structure variation, the addition of terraces dilutes the topographic gradient, reducing the variation in forest structure from low-lying valleys to highly-sloped hills.

Terraces are able to permanently transform hillside topography, as is evidenced by their continued persistence. While the Maya designed the terraces for the purpose of soil and water conservation related to food production, they have longer lasting impacts. The addition of terraces had a mediating effect on all variables examined. While average canopy height decreased with an increase in slope on non-terraced land, differences in average canopy height are blended with the addition of terraces. Canopy openness, a measurement to determine how much light penetrates to the ground, increased as the topographic gradient increased for both land uses; however, canopy closure varied less on terraced land. Vertical diversity, which provided an estimate for the vertical spatial heterogeneity, followed the same pattern as the average canopy height, exhibiting a decrease in variance along the topographic gradient when terraces were present. The analysis of the LiDAR height bins followed the same patterns, with the variation between low, medium, and high slopes decreasing with the addition of terraces (Figure 12). The terraces mediated the effect of slope of the proportion of returns, which indicates that when terraces were present, forest structure did not differ as much across the topographical gradient as when terraces are absent. This leads us to the conclusion that terraces, while not eliminating the influence of slope on forest structure, do effectively blend it.

The shaping of forest structure by topographic variables may be explained by two factors: differences in tree species and the effect of topographic position on tree growth. Observations

from previous studies have noted that terraces contain flora, such as palms, that are typically found in forest valleys (Healy et al. 1989). In chapter two, I was able to show how tree species composition varies across terraced and non-terraced areas, with terraces acting as a type of environmental “bridge” between slope and non-sloped areas (Hightower 2012: Chapter 2). Prior studies in the tropical forests of the Maya have shown how topography can strongly influence the composition of tree species, with forests in valleys, along slopes, and along ridges forming distinct tree communities (Brewer et al. 2003, White and Hood 2004). Tree species with specific topographic requirements can be expected to have a direct impact on forest structure as species can act as a driver of forest structure (Spies et al. 1998).

Variation in species composition alone may not explain the difference observed in forest structure. Edaphic factors related to topography, i.e. nutrient, water, and light availability, directly influence the growth of trees (Clark and Clark 2000, Tateno and Takeda 2003). The differences we see in forest structure over terraces can be explained by altered edaphic conditions (Coultas et al. 1994, Beach et al. 2002). Where slopes would typically have thin soils and limited water availability, terraces increase soil depth and water availability, which has been shown to impact forest structure (Furley and Newey 1979). One characteristic of slopes is the decrease in nutrients, specifically nitrogen, further upslope. However, terraces are able to contain nutrients that would otherwise be leached out of the soil (Coultas 1994, Healy et al. 1983). One interesting aspect of this study was the significant interaction of slope and elevation. Studies have shown that as position upslope increases, nitrogen decreases, which can have an effect on the growth of trees, resulting in reduced basal area and canopy cover (Tateno and Takeda 2003).

Outside of the implications for human land use legacies, this study illustrates how relatively small changes in topography can result in significant changes to forest structure.

One thousand years after abandonment, agricultural practices of the Maya continue to influence forest structure. . While this study looked at only the terraces at Caracol, they are found throughout the Maya region (Wyatt 2008), including the Petén forests (Beach and Dunning 1995), throughout Belize (Beach et al. 2002), and in the southern Yucatán peninsula (Turner et al. 2003). With the realization of the predominance of terraces throughout Mesoamerica comes the understanding of how ancient agriculture practices can leave a lasting legacy in the forest.

Tables and Figures

Table 6: Summary of environmental factors and forest structural measurements obtained.

Environmental Factors	Structural Measurements
Land Use Categories	Average Canopy Height
Slope	Standard Deviation Canopy Height
Elevation	Canopy Closure
Aspect	Forest Vertical Diversity Index (H)

Table 7: Results from the perMANOVA of the distance matrix constructed from LiDAR derived forest measurements.

Sources of Variation	df	Mean Square	F	r²	p
Land Use Type*	1	0.024	5.04	0.013	0.016
Slope	1	0.134	50.82	0.134	0.001
Elevation	1	0.028	10.74	0.028	0.001
Slope:Aspect	1	0.022	4.54	0.012	0.026
Slope:Elevation	1	0.042	15.78	0.041	0.001
Residuals	284	0.005		0.748	
Total	299	1.000			

*Factor, all other sources of variation calculated as covariates.

Table 8: Results from the perMANOVA of the distance matrix constructed from the height bin LiDAR data.

Sources of Variation	df	Mean Square	F	r²	p
Land Use Type*	1	0.227	5.02	0.015	0.005
Slope	1	1.048	23.21	0.068	0.001
Land Use Type: Slope	1	0.170	3.76	0.011	0.018
Slope:Elevation	1	0.482	10.68	0.031	0.001
Residuals	284	0.045		0.083	
Total	299			1.000	

*Factor, all other sources of variation calculated as covariates.

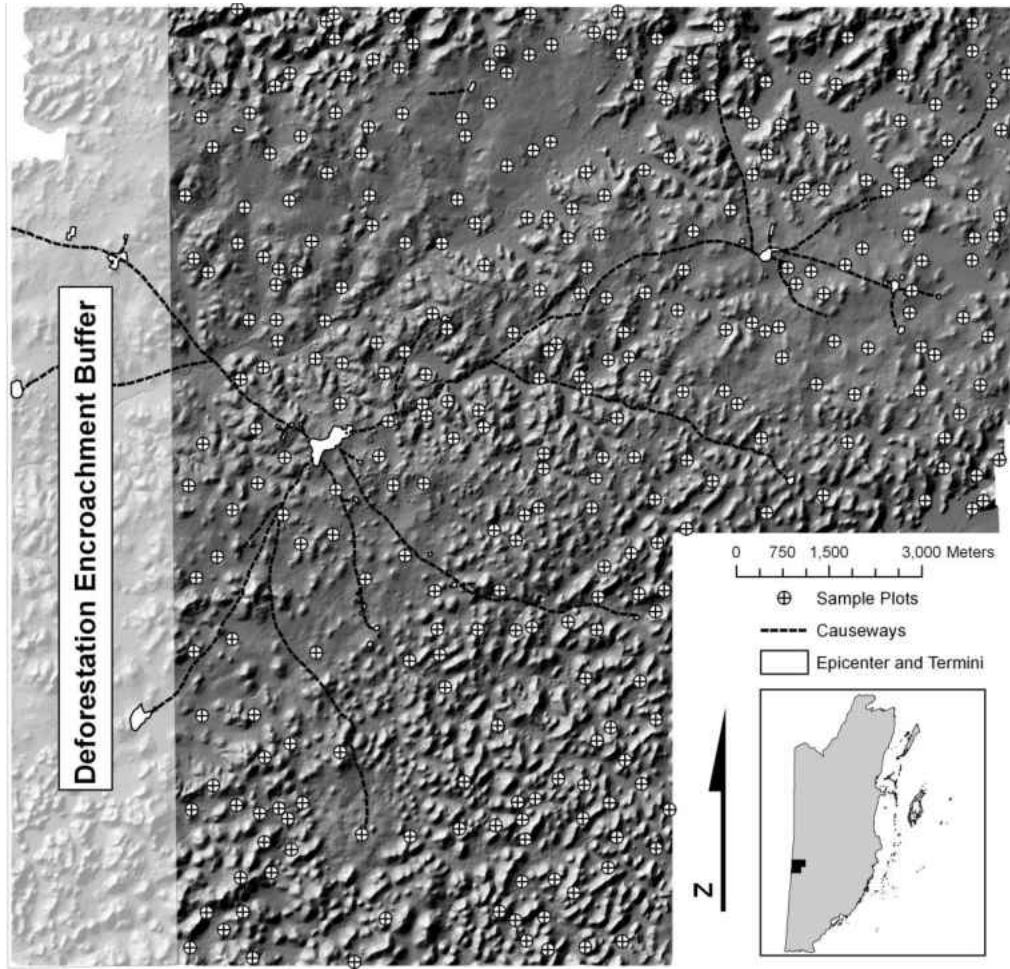


Figure 9: Map of the Caracol study site with sample plot locations.

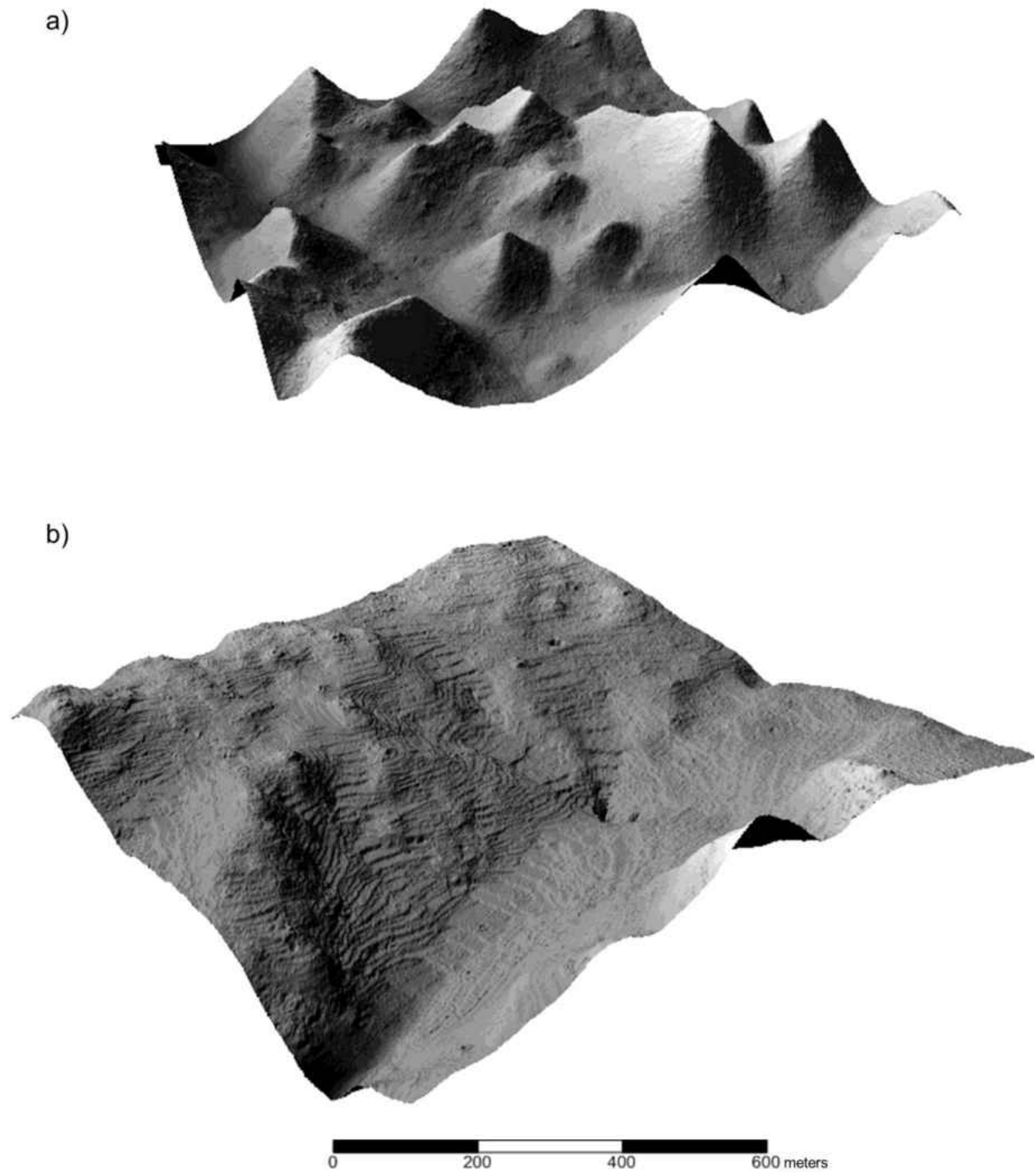


Figure 10: 2.5 dimensional representations of the a) non-terraced and b) terraced land types.

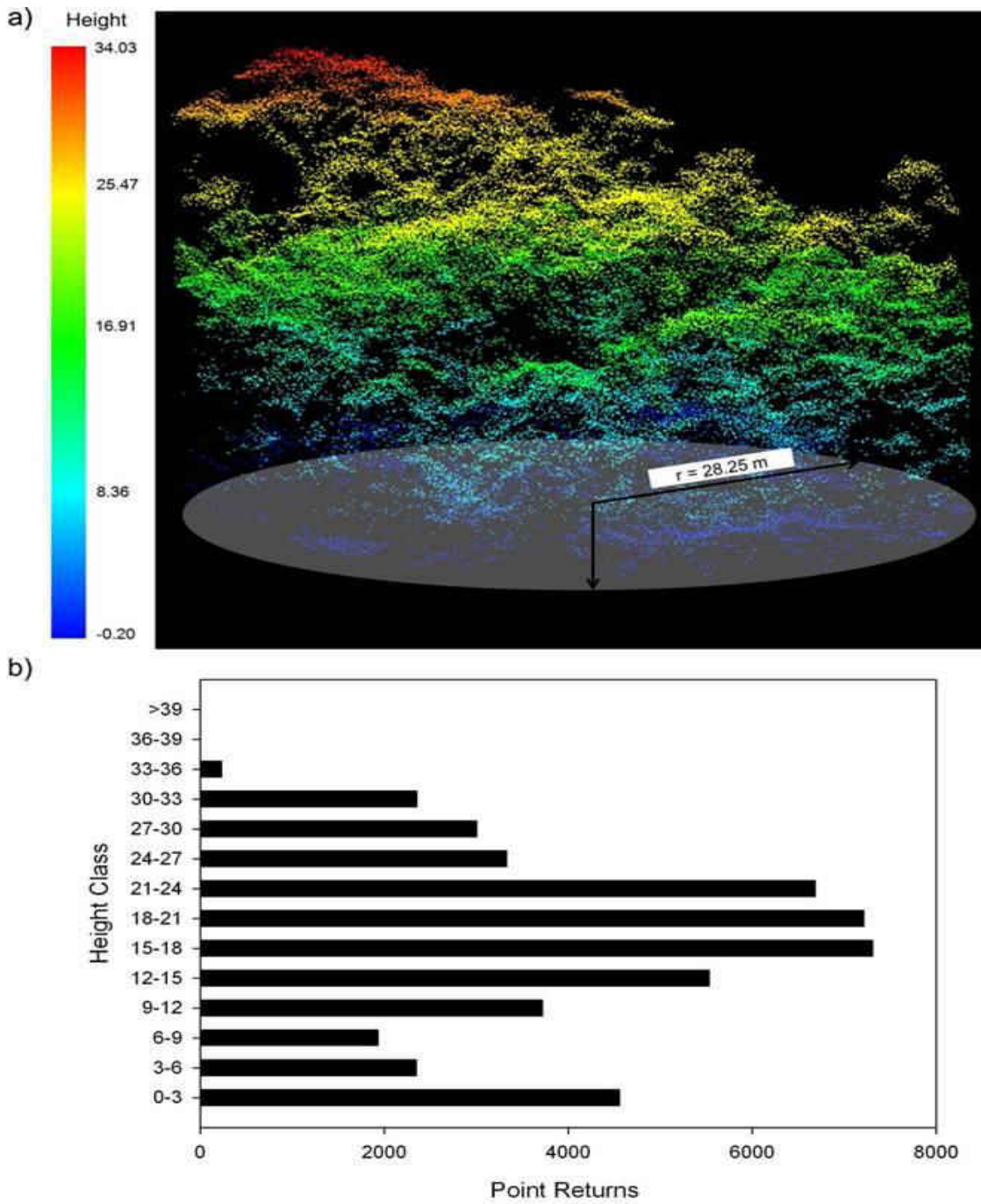


Figure 11: Terraced plot point cloud (a) sampled using FUSION and b) the associated histogram of points binned by height.

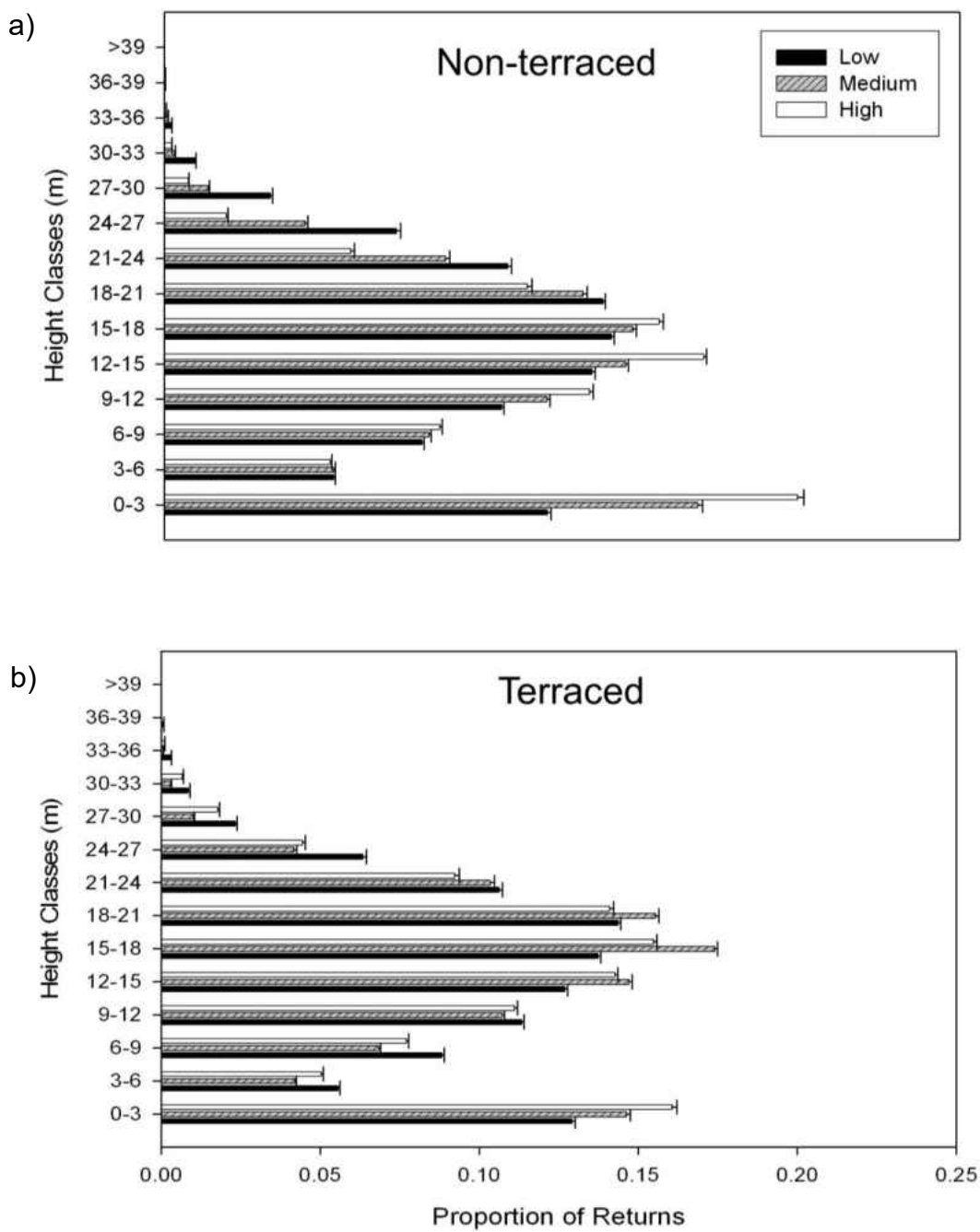


Figure 12: Histograms for average proportion of LiDAR point returns binned by height classes for a) non-terraced and b) terraced plots.

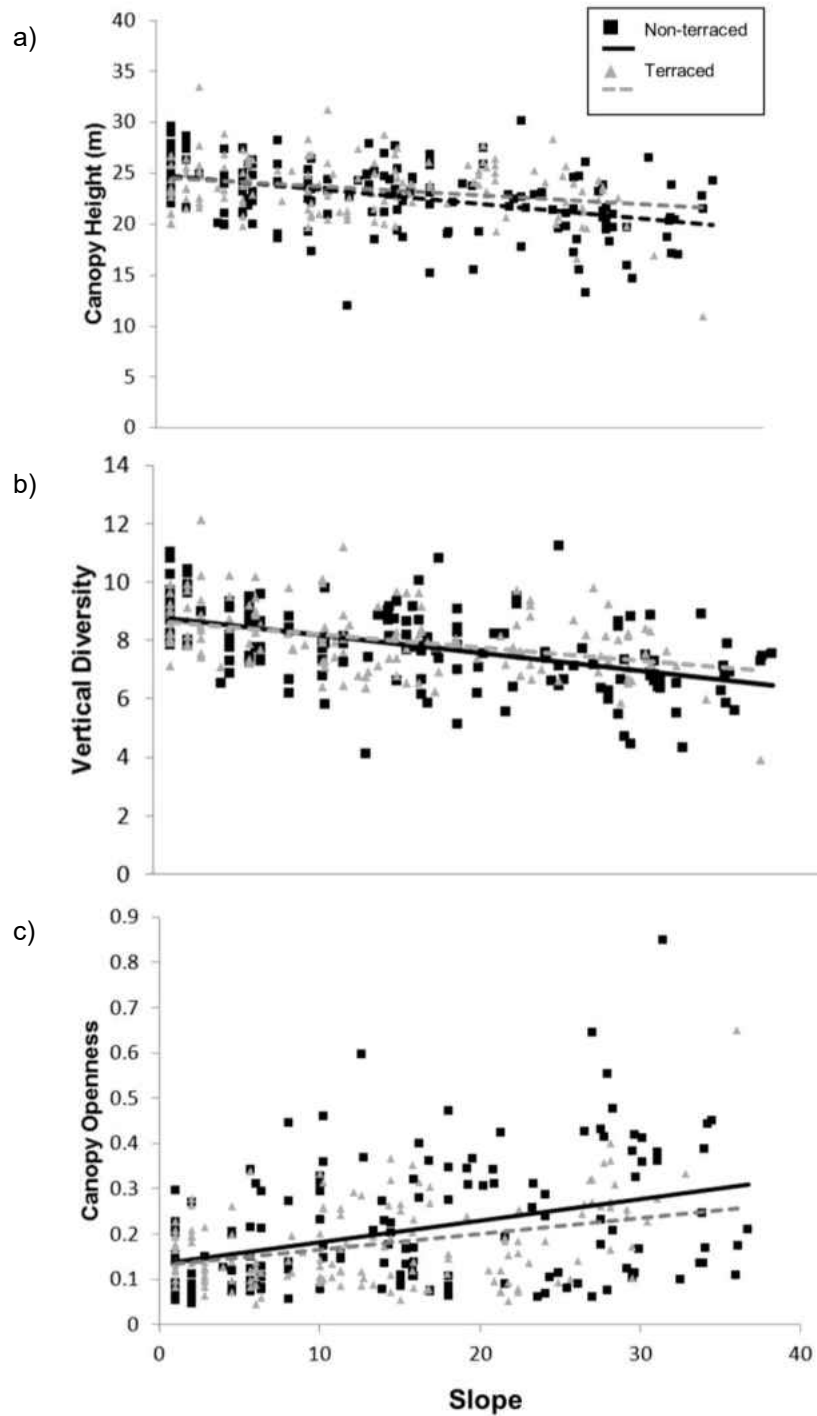


Figure 13: Patterns of increase and decrease between terraced and non-terraced land in a) canopy height b) vertical diversity and c) canopy openness as slope increases.

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APPENDIX: TREE SPECIES LIST OF CARACOL, BELIZE

Common Name	Scientific Name
Anona de monte	<i>Annona scleroderma</i>
Balsamo	<i>Myroxylon balsamum</i>
Barillo (Santa maria)	<i>Calophyllum brasiliense</i>
Bohon blanco	<i>Cordia sobestana</i>
Bohon negro	<i>Cordia gerascanthus</i>
Botan	<i>Sabal mauritiformes</i>
Bulhop	<i>Drypetes brownii</i>
Cacho venado	<i>Gymnanthes riparia</i>
Caoba	<i>Swientenia macrophylla</i>
Cedrillo	<i>Guarea glabra</i>
Cedro	<i>Cedrela odorata</i>
Chaca	<i>Bursera simaruba</i>
Chechem blanco	<i>Sebastiana adenophora</i>
Chico Sapote	<i>Manilkara zapota</i>
Chonte	<i>Zanthoxylum</i> species 1
Cinta caribe	Unknown
Cohune	<i>Attalea cohune</i>
Copal	<i>Protium copal</i>
Corcho	Unknown
Cuero de sapo	Unknown
Escoba	<i>Crysophila stauracantha</i>
Espinudo amarillo	<i>Zanthoxylum ekmanii</i>
Espinudo blanco	<i>Zanthoxylum</i> species 2
Espinudo colorado	<i>Zanthoxylum</i> species 3
Espinudo negro	<i>Caesalpinia</i> sp.
Faisan	<i>Sideroxylon stevensonii</i>
Guarumo	<i>Cecropia obtusifolia</i>
Guaya del monte	<i>Melicoccus oliviformis</i>
Guayabio	<i>Casearia commersoniana</i>
Habin	<i>Piscidia piscipula</i>
Hesmo	<i>Lysiloma acapulcense</i>
Huevo de Caballo	<i>Stemmadenia donnell-smithii</i>
Jaboncillo	<i>Sapindus saponaria</i>
Jobillo	<i>Astronium graveolens</i>
Jobo	<i>Spondias mombin</i>
Laurel	<i>Cordia alliodora</i>

Lengua de loro	<i>Myrcia leptoclada</i>
Limoncillo	<i>Citharexylum</i> sp.
Luin	<i>Ampelocera hottlei</i>
Madre de cacao	<i>Gliricidia sepium</i>
Malerio Blanco	<i>Aspidosperma megalocarpa</i>
Malerio colorado	<i>Aspidosperma</i> sp.
Manax	<i>Pseudolmedia oxyphyllaria</i>
Mancheche blanco	<i>Lonchocarpus</i> sp.
Mancheche negro	<i>Lonchocarpus castilloi</i>
Mano Leon	<i>Dendropanax arboreus</i>
Mapola	<i>Psuedobombax</i> sp.
Matapalo	<i>Ficus</i> sp.
Naranja	<i>Guarea grandifolia</i>
Nargusta	<i>Terminalia amazonia</i>
Palma de monte	<i>Euterpe pracatoria</i>
Palo danto	<i>Quercas</i> sp. (<i>Quercas acutifolia</i>)
Palo Quina	<i>Coutarea hexandra</i>
Pata vaca	<i>Bauhinia</i> sp.
Pimienta	<i>Pimienta dioica</i>
Pixoy	<i>Guazuma ulmifolia</i>
Quebraacha	<i>Pouteria</i> sp.
Ramon	<i>Brosimum alicastrum</i>
Sacoruch	Unknown
Sacuayun	<i>Pseudolmedia</i> sp.
Sacuche	<i>Casearia</i> sp.
Salem	<i>Albizia idiopoda</i>
Saltimuch colorado	Unknown
San Juan	<i>Vochysia guatemalensis</i>
Sapotillo Medium Leaf	<i>Pouteria</i> species 1
Sapotilo Small Leaf	<i>Pouteria</i> species 2
Sillion	<i>Sideroxylon hirtantherum</i>
Son	<i>Alseis yucatanensis</i>
Subin	<i>Acacia</i> sp.
Sufricaya	Unknown
Tamay	<i>Zuelania guidonia</i>
Yashnik blanco	<i>Vitex</i> species 1
Yashnik negro	<i>Vitex</i> species 2
Yaxox	<i>Trophis racemosa</i>
