

Primary Succession of Lianas in an Amazonian Floodplain Forest

By

Erin Michael McManus

A Thesis Submitted to the Graduate Faculty of

WAKE FOREST UNIVERSITY

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

in the Department of Biology

May 2003

Copyright by Erin McManus

Approved By:

Miles R. Silman, Ph.D., Advisor

Examining Committee:

Kathleen A. Kron, Ph.D.

Peter D. Weigl, Ph.D.

ACKNOWLEDGEMENTS

Foremost I thank my advisor, Dr. Miles Silman, whose enthusiasm and patience did not waiver as he consistently guided me to the final goal. And special thanks to my committee members; Dr. Peter Weigl and Dr. Kathy Kron; their encouragement and wisdom has been fundamental throughout my time at Wake Forest University.

Next, I owe an immense amount of gratitude to Robyn Burnham, Ph.D. Successful completion of this project would have not been possible without her assistance in the field and in the identification of voucher specimens. Her knowledge of tropical systems and her belief in this project have been an inspiration. Also, I thank Elizabeth Losos, Ph.D. for contribution of seral stage data and for her advice on this project.

My field season in Peru would have been both unproductive and unenjoyable without the comedic assistance and friendship of Camilla Hermana. Her contributions were essential to the completion of this project. And to Julian, who delivered me to far off field sites, despite the daily challenges of la selva. Much appreciation is due to Jim Brinson for his help on the surveys and Luis Imunda, for his contribution in cutting miles of trails. I would also like to thank the Ancaya family, for their photos, advice and most of all for making me comfortable in a place far away from home.

The encouragement and assistance of the graduate students at Wake Forest University has been quinessential to the completion of this thesis. Foremost, I want to express my deepest appreciation goes to Mary Beth Lovin, whose strength, support and friendship

(despite the exposure of her own backside) was, at times, the only thing that kept me going. Also, special thanks to the members of the Silman Lab: Julie Wyatt, Delphine Masse and Craig Moretz---whom always took time for my seemingly endless questions and whom have provided me with an excellent cheering section. And thanks to Ann Powell and numerous others for editing the many versions of this thesis.

Special thanks to my parents; Tom and MaryAnn McManus. They have have instilled in me the curiosity and adventure which inspired me to begin this project as well as the strength and confidence that allowed me to complete it. Thanks to all my friends and family that refused to give up on me, Greer, Christine and especially Finneus Cormac, who made me smile, even through moments of exhaustion, frustration and writers block.

Finally, I owe my greatest appreciation to Michael J. LaVoie. Though he did not begin this journey with me, he has taken on its successful completion as if it were his own. He has contributed to every page of this thesis and to every moment in which I wrote them. His efforts throughout this process have ultimately taught me the value of commitment, both to research and to each other. I am forever grateful.

Financial support for this research was provided by the Vecellio grant and Wake Forest University.

TABLE OF CONTENTS

	Page
List of Figures	6
List of Tables	7
List of Appendix	8
Abstract	9
Introduction	11
Overview	11
Literature Review	12
Primary Succession	12
Lianas	17
Methods and Materials	24
Field Sites	24
Data Collection	25
Data Analysis	26
Results	30
Individual Abundance	30
Species Richness	30
Diversity	31
Composition	32
Climbing Mechanism	33
Discussion	34
Individual Abundance and Species Richness	34
Diversity	38

Composition	43
Climbing Mechanism	44
Conclusion	46
Works Cited	48

LIST OF FIGURES

	Page
1. Study Site	52
2. Manu Chronosequence	54
3. Aerial Photos of Riverbends	56
4. Abundance, Species Richness, Shannon Weaver Diversity	58
5.1 Comparison of Liana Abundance	60
5.2 Comparison of Species Richness	62
6. Correlation of Light and Abundance	64
7. Correlation of Elevation and Abundance	66
8. Diversity measured by Rarefaction	68
9. Diversity measured by Fishers Alpha	70
10. NMS Ordination Results	72
11. Climbing Mechanism	75

TABLES

	Pages
1. Proportion of Species Dominance	77

Appendix

	Page
1. Survey of Beaches	79
2. Species List	81

ABSTRACT

PRIMARY SUCCESSION OF LIANAS IN AN AMAZONIAN FLOODPLAIN FOREST

Erin Michael McManus

Thesis under the direction of Miles R. Silman, Ph.D., Assistant Professor, Department of Biology.

Lianas (woody vines) are a major component of Neotropical forests. This investigation examined liana composition in a primary successional forest formed from bank erosion and main channel migration of the Manu River. Previous investigation of this system has shown that local tree species undergo a distinct pattern of succession (chronosequence) on each bend in the river. Four 100 x 4 m transects were established along the chronosequence in 4 distinct seral stages on 5 river bends. It was hypothesized that liana composition in the four seral stages would change over time and reflect that of the local trees.

Composition of lianas in seral stages was determined by abundance, species richness and diversity. Mean abundance and species richness increased throughout consecutively aged seral stages but these trends were highly variable on different beaches. Also, abundance and species richness in the 4 seral stages were much lower than abundance and species richness recorded in other studies of older seral stages within the same successional floodplain. No significant correlation was found between abundance and distinct environmental factors, including elevation in relation to the river and light levels. Additionally, to determine if mode of climbing influenced composition in seral stages, climbing guild was recorded for each of the species found in this study. Stem

twiners and tendrillate lianas were the most abundant climbers but these two modes of climbing were highly variable within beaches and across similar transects.

Diversity (as measured by Fishers Alpha) was low throughout the chronosequence and did not show a pattern of increase similar to the trees. Non-metric scale ordination of species presence/absence and quantitative data was conducted to determine similarity of community composition within beaches and across seral stages. Species presence/absence was grouped by seral stage, indicating that environmental components determine composition. Species quantitative data was also grouped by seral stage but revealed a loose grouping by beach implying that in addition to environmental components, species dominance is influenced by effects of independent beaches, such as source strength of dispersal.

I conclude that lianas do not exhibit a pattern of primary succession similar to that of the trees. High variability in abundance and diversity on independent beaches suggest that lianas are opportunistic structural parasites that show little preference of habitat in early seral stages. Furthermore, low diversity in early seral stages contrasted high diversity of older seral stages (> 250 years in age), implying that differences in internal dynamics of these forests change local liana habitat, ultimately changing liana composition.

INTRODUCTION

Primary succession is a fundamental force in the structure, composition and dynamics of many forest communities (Kalliola 1991; Lichter 2000; McCook 1994; Tilman 1988). This process occurs when newly formed substrate, that has never before been colonized, becomes inhabited by plant species (Cowles 1899, McCook 1994). Primary succession can take place along rivers, on newly formed dunes, following volcanic lava flows, or at the base of a retreating glacier (Kalliola 1991; Robertson and Augspurger 1999). In the tropics, primary succession occurs in river floodplains. The high site turnover, disturbance and variation of forest structure characteristic of colonization along rivers may be significant factors in the high species diversity of mature tropical floodplain forests (Salo et al. 1986). Successional floodplain forests are among the most diverse and abundant of remaining tropical communities. In Peruvian lowlands, 12% of forests are in successional stages along rivers (Kalliola 1991). Although primary succession of tropical floodplains is well documented, many components of these communities have remained unstudied. Investigations of tropical floodplain succession can provide insight into the diverse tropical floodplain communities that emerge from this process (Gentry 1991).

Lianas are a major component of all tropical communities, especially tropical floodplains (Putz 1982, 1984; Gentry and Dodson 1987; Putz and Chai 1987; Gentry 1991; Nabe-Nielson 2000; Kokou et al. 2002). In fact, lianas account for 25% of the overall phytomass in tropical communities (Foster et al. 1986; Burnham 2002). While the process and pattern of primary succession has been documented for the trees of the Rio

Manu floodplain community, lianas, or woody vines and climbers, remain virtually unstudied, in spite of their high abundance and fecundity. In addition, recent literature indicates that lianas significantly effect forest composition by directly impacting host species and acting as superior competitors for local resources (Laurence et al. 2001; Nabe-Nielson 2000; Putz 1984, 1990).

This thesis examines liana community structure within the Rio Manu tropical floodplain.

I begin with a literature review of previous analysis in the Manu River successional floodplain forest and similar riverine succession systems. These data describe environmental characteristics that distinguish the different seral stages including local light regime, inundation and soil macronutrients. Although liana dispersal is poorly understood, dispersal of tree/shrub species within the Manu chronosequence is well documented. A summary of this literature is provided below. In addition, the following literature review provides insight into liana diversity, climbing mechanics, geographic ditribution and community composition, of which little is understood.

Literature Review

Succession of the Manu River floodplain forest

Physical factors influencing riparian succession:

Primary succession within the Manu floodplain occurs on a dynamic and predictable series of substrates formed by the active migration of the river channel (Kalliola 1991; Losos 1993). Seasonal flooding, meandering and subsequent point bar formation typical

of the Manu River create an ideal environment to investigate primary succession in tropical floodplain communities (Foster et al. 1986; Salo et al. 1991). During periods of high water the outer river bends are eroded leaving point bar beaches, composed primarily of silt, on the inside of the advancing loop. Plants that colonize these beaches are often washed away in floods, or buried by sediment deposits (Kalliola 1991). However, over time (every 5-10 years), alluvial deposits and vegetation form levees, or ridges that block newly formed beaches from the river's inundation (Terborgh and Petren 1990). Plants eventually colonize this elevated substrate. This geomorphological process forms a distinct chronosequence, or successional order, with the oldest tree community members being located farthest away from the river (Kalliola 1991; Losos 1993; Salo et al. 1986). Over a 200year period, differential dispersal and survival of species within local niches transform these pioneer colonist assemblages into a diverse rain forest community, consisting of multiple layers, or strata (Losos 1993).

Vegetation Chronosequence

The successional chronosequence along the Manu River is separated into four distinct forest assemblages (Figure 2). These assemblages are defined by the tree, shrub or grass species that are most abundant within them. The grass, *Gynerium sagittatum* (*Poaceae*) and the tree *Tessaria integrifolia* (*Asteraceae*) dominate the early successional stages. Eventually, these are replaced by a second assemblage of *Cecropia membranacea* (*Cecropiaceae*), *Guazuma crinita* (*Malvaceae*) and *Ochroma pyramidale* (*Malvaceae*). The beginning of the third, mid-successional stage is marked by presence of *Sapium aereum* (*Euphorbiaceae*), *S. ixiamasense*, *Guarea guidonia* (*Meliaceae*), *Citharexylum*

popeppigee (*Lythraceae*), *Inga marginata* (*Fabaceae*), *Guatteria acutissima* (*Annonaceae*) and *Casearia decandra* (*Salicaceae*). The canopy within the 3rd seral-stage on beaches is dominated by *Ficus insipida* (*Moraceae*) and *Cedrela odorata* (*Meliaceae*). The oldest seral stage included in this study is referred to as the mature/transitional forest. This seral stage is marked by high diversity of large diameter trees and an abundance of palms (*Palmaceae*). Accumulation of biomass and turnover of tree species continues in the transitional forest. Though older seral forests (> 250 years) are still considered "successional systems" their stability and composition most resemble mature tropical forests. Turn over in composition within the chronosequence is marked by changes in dispersal mode of trees and the availability of environmental resources such as light, soil nutrients and flooding regime (Foster et al. 1986; Kalliola 1991; Losos 1993; Salo et al. 1986; Terborgh and Petren 1990).

Between seral stages of the Manu chronosequence heterogeneous environments are characterized by a combination of biotic and abiotic interactions, including soil macronutrients, sunlight variation, hydrologic regimes and seed dispersal characteristics (Losos 1993; Terborgh and Petren 1990). Losos (1993) found that soil acidity, potassium, magnesium, calcium and aluminum content did not differ between the seral stages of the Manu floodplain but inundation and light levels vary among each of the seral stages. These findings indicate that although soil nutrients can often contribute to the structuring of primary successional communities (Clinebell et al. 1995; Hall and Harcombe 1998; Tilman 1988), the composition of soil within the Rio Manu floodplain does not influence structure of tree seral stages (Losos 1993). Furthermore, Foster (1990)

hypothesized that floodplain soils along the Manu River are among the most fertile of all tropical forest soils and therefore availability of soil nutrients is not a determining factor in local community composition.

Differential light levels characteristic of successional forests may play a significant role in the composition of liana communities (Jarzomski 1998; Putz 1984). Light is a limiting resource in tropical forests and lianas are effective light competitors (Hall and Harcombe 1998; Nabe-Neilson 2000; Putz 1984, 1987). Light is most available in early successional areas. As the forest ages and the canopy closes, less light is available to the lower stratum (Lawton and Putz 1988; Losos 1993). Data from previous investigations confirm that more diffuse light enters the early and mid-seral forests than the late-seral forests (Losos 1993). However, both the *Cecropia/Gynerium* zones and the *Ficus/Cedrela* and transitional forests were not found to be significantly different in consideration of available light. Detailed description of diffuse light levels in the Manu chronosequence is provided in Losos (1993).

Differential dispersal of seeds may also be a significant factor in the succession of the Rio Manu floodplain (Clark et al. 1999). Although dispersal of liana species is not documented, much investigation has been devoted to the documentation of tree dispersal. The major dispersal agents within the seral stages are bats, birds, non-flying mammals and abiotic agents (Terborgh 1983). Losos (1993) documented that dispersal agents are specific to seral stages in the primary succession. There are seasonal differences in dispersal, however bat-dispersed species are abundant and evenly dispersed in early and

mid-successional seral zones during the wet and the dry season. Though *Gynerium* seeds are thought to be primarily wind dispersed, defecation of diurnally roosting frugivorous bats in *Gynerium* stands fosters bat dispersal within this stage (Foster et al. 1986; Losos 1993). According to Losos (1993), bats are responsible for most seeds dispersed to the *Cecropia* zone, where they eat and defecate while roosting. In addition, Foster et al. (1986) found that *Cecropia* trees and the other species found within this zone were primarily bat-dispersed. Abiotically dispersed seeds have an intermediate level of abundance and distribution in comparison to seeds dispersed by frugivores. Though it is possible that unusually high flooding could move seeds anywhere, abiotic seed dispersal do not vary due to changes in season or seral stage (Foster et al. 1986; Losos 1993). Dispersal of seeds by non-flying mammals and birds increases along the chronosequence. Although bat and wind dispersal remain as the most effective dispersal agents within the Manu floodplain, there is a significant representation of bird -dispersed seeds in *Ficus* and mature forests and an abundance of mammal-dispersed seeds in mature forests. See Foster et al. (1986) and Losos (1993) for further description of seed dispersal within this successional floodplain.

Elevation and Inundation

Duration and intensity of local flooding influence post dispersal survival of species (Foster et al. 1986; Hall and Harcombe 1998). In the Manu River floodplain the local elevational gradient determines intensity and length on inundation (Kalliola et al. 1991, 1992; Lamonette 1990;). Here, elevation varies with the presence of ridges and swales. Because ridges are formed at different times, elevation is distinct and therefore duration

and intensity of flooding varies throughout beaches (Kalliola 1992). During unusually high floods, low swales often act as secondary channels as the river exceeds its banks and enters the floodplain on the side of river meanders (Robertson and Augspurger 1999). Through this process, all seral stages of the succession are subject to floodwaters. Previous investigations provide that a greater elevational gradient decreases probability and length of flooding, therefore allowing higher survival rates of flood intolerant species (Kalliola et al. 1991 1992; Robertson and Augspurger 1999; Salo et al. 1986).

Lianas

Definition of a liana

Lianas are woody, climbing plants that rely on other plants for structural support (Putz 1982, 1984, 1985, 1990). However, this term is not always definitive. Many liana species will grow through a self-supporting stage until a trellis, such as a tree or shrub is available. Also, many non-dicotyledonous species exist as climbers, but do not produce a secondary xylem and therefore do not have woody stems (Putz 1984). Lianas can germinate in the canopy, as well as on the ground and, therefore, do not always come in contact with the forest floor (Jarzomski 1998; Nabe-Nielson 2001; Putz 1990). Climbers often produce vegetative offshoots making it difficult to distinguish between offshoots (ramets) and genets (Nabe-Nielson 2001; Schnitzer 2000). The present research considered a liana to be any climber that is rooted in the ground and currently supported by a host structure.

Liana-Host Relationships

Lianas typically grow on top of their hosts and are therefore often detrimental to host tree growth (Clark and Clark 1990; Gerwing and Vidal 2002; Mulkey et al. 1995, 1996; Roldan and Varela 1999; Putz 1984). They also may increase the probability of physical damage and tree fall due to mechanical abrasion and passive strangulation, or by increasing the weight of the tree canopy or by tying trees together, increasing the risks of multiple falls (Gerwing and Vidal 2002; Schnitzer 2000; Putz 1984). When lianas reach the forest canopy they most often extend horizontally across several trees. In this way, lianas increase the size of tree fall gaps by actively pulling down neighboring trees in the occurrence of local tree fall. Also, liana abundance increases in tree fall gaps due to increases growth rates and clonal reproduction experienced in these high light environments. Recent studies also indicate that abundance of lianas in tree fall gaps can stall tree regeneration and ultimately alter gap phase regeneration (Schnitzer 2000). In addition, certain liana species may increase the vulnerability of their hosts to herbivory and seed predation (Putz 1982, 1984, 1990, 1995). Jarzomski (1998) found that distribution of tropical lianas is not random, suggesting that availability of host tree surface area, current infestation of a host by other lianas, or bark type are also major factors influencing liana abundance.

Climbing mechanics

The ability to climb evolved numerous times in a wide diversity of independent plant lineages (Darwin 1867; Putz 1987; Schneck 1892). Approximately one half of all

vascular taxa contain woody climbers within communities ranging from moist tropical rainforests to semi-deserts (Putz 1984).

Without need for significant amount of support tissue, climbers may be able to allocate more growth resources to length extension (Roldan and Varela 1999). Lianas also have large diameter xylem vessel elements, which aid high flow rates and rapid growth in length. They can therefore support large leaf areas with relatively small stem diameters (Darwin 1867; Holbrook and Putz 1996; Putz 1984). Large bands of xylem, phloem and multiple vascular cambia and parenchyma allow liana stems to maintain the high degree of flexibility necessary for a climbing habit (Putz 1987).

Diversity in climbing mechanism makes lianas versatile in growth habit, enabling occupation of a wide range of habitat types over a broad distribution pattern (Jarzomski 1998; Nabe-Nielson 2001; Putz 1984, 1987). Phenotypic plasticity enables lianas to attach to different sized hosts in a number of ways. Tendril climbers employ modified leaves and inflorescence to encircle their hosts. They are often encountered in young forest stands due to their ability to attach to hosts with small stem diameters. In contrast, twiners are identified through characteristic wrapping of the main stem around the host structure. However in some species twining is accomplished using branches coming off the main stem to wrap around their host. Sprawlers are lianas that simply lean on a tree for structural support, not actually attaching themselves. Other species use adventitious roots to attach to their host (Putz 1984). Despite diversity in climbing technique, lianas have not been found to be specific to a host species, even though most liana species will

only use one climbing technique (Laurence et al. 2001; Putz 1982, 1984). Diversity in climbing mechanism makes lianas extremely versatile in growth habit, enabling occupation of a wide range of habitat types over a broad distribution patterns (Jarzomski 1998; Nabe-Nielson 2001; Putz 1985). The present investigation examined climbing type across this successional chronosequence. Mode of climbing was documented for each liana found within the study transects to determine if climber type influence the community composition and ultimately the distribution of liana species.

Geographic Distribution and Local Community Composition

Patterns of geographic liana distribution indicate that abundance and diversity are inversely related to increasing latitude (Gentry 1991). Over 25% of leaf primary productivity and approximately 10% of the flora in the Neotropics is attributed to lianas, as opposed to roughly 1% of the overall flora in the Carolinas and Southern Appalachians (Burnham 1996; Gentry 1991; Hubbell and Foster 1986; Jarzomski 1998; Nabe-Neilson 2000). Previous research has provided several possible explanations for the observed large-scale distribution patterns of lianas. For example, the complexity of host structure in tropical forest canopies is greater than those of temperate zones due in part to the multiple layering of a tropical forest and the greater diversity in structure among the species (Jarzomski 1998; Putz 1984). The multi-layered canopy typical of tropical forests provides a greater complexity of trellis support, as well as more available volume for plant growth (Roldan and Varela 1999). With a greater diversity of liana hosts than found in temperate forests, tropical forests can be inhabited by lianas of several climbing types while the decrease in competition for host space in the tropics may allow greater

diversification of structural parasites (Campbell and Newberry 1993; Nabe-Nielson 2001). In addition, the temperature and moisture conditions of tropical forests create a more suitable habitat for the wide vessel xylem anatomy typical of most lianas. Although wide vessels allow for more rapid xylem flow in long stems, it also makes climbers particularly vulnerable to desiccation and xylem embolisms due to cavitation (Jarzomski 1998; Putz 1987). Likewise, the narrow stem architecture found in lianas also makes them susceptible to cavitation in freezing or near-freezing temperatures (Jarzomski 1998).

Comparisons to other plant communities

The data collected in this investigation are compared with results taken from previous studies of lianas in older successional forests of the Manu floodplain. In addition, tree diversity in the Rio Manu chronosequence is compared to that of the lianas to determine if these two plant communities are similar in formation and ultimate composition. The knowledge gained by this investigation provides a greater understanding of the forces that shape liana communities, the processes of riverine succession and the formation, structure and ultimate diversity of tropical floodplain forests.

METHODS AND MATERIALS

Field Sites

Fieldwork was conducted along the Manu River, Manu National Park, Peru (11°54 S, 71°21 W). Manu National Park is a 2 million hectare protected area situated at the base of the Andes in the western section of the Amazon basin. The Manu River runs through the northern section of the park, creating a wide band of tropical floodplain forest along its banks. Mean annual temperature of this region is ~23.5° C (Silman 1996). Soil composition is typically clay and a silt/clay mixture in the uplands, but along the river it includes a mixture of clay, sand, silt and some gravel (Kalliola 1991, 1992). A majority of the 2400mm annual rainfall is received during a seven month wet season, beginning approximately in October (Silman 1996).

Rainfall contributes to water fluctuations of up to 13m in lowland rivers like the Manu (Salo et al. 1986). Flooding of the Rio Manu typically occurs in the wet season. During inundation this freely meandering river is subject to considerable bank erosion and main channel migration. Over time, erosion and movement of sediment along this river results in the formation of point bar beaches. As floodwaters recede, plants colonize the new beaches. These plant communities eventually form a successional chronosequence on many of the meander loops along the Manu River (Kalliola 1991, Losos 1993, Salo et al. 1986). Within each chronosequence four distinct successional stages can be distinguished by the dominant tree species within them (Losos 1993, Salo et al. 1986).

Data Collection

Initially a Landsat TM image was used to evaluate the overall shape of each point bar beach along the Manu River. Successional point bar beaches were selected for proximity to the Cocha Cashu Biological Station and point bar width, or distance across the river meander as viewed from the Landsat image. Using the Landsat image and a compass for direction, a meter wide trail was cut perpendicular to each ridge from the river to the mature floodplain forest. Dominant tree species were used to determine the four successional stages within each chronosequence (See Foster et al. 1986, Losos 1993 for detailed discussion of tree communities). A 100x4 meter transect was established on the first ridge encountered within each of the 4 stages of the chronosequence. A full inventory was taken of all lianas greater than 1cm diameter at breast height that rooted within the transect. Lianas were considered to be any plant that depended on other vegetation for structural support and actively climbed this structure towards the canopy (Putz 1985). Lianas were measured for diameter at breast height (DBH) and identified to species or morphospecies using vegetative characteristics (Gentry 1991). Voucher specimens and stem samples were collected for lianas not identified in the field. These specimens were later identified with the assistance of liana specialists or matched to known samples in American and Peruvian herbaria. Great care was taken to identify genetically different individuals from one another. However, these genets are often difficult to distinguish from vegetative offshoots (Putz and Chai 1986), particularly in riverine systems with rapid sediment accumulation. Therefore, each stem was considered an individual unless it could be determined otherwise (Jarzomski 1998). From these

collections stem (individual) abundance, species richness, diversity and climbing type were determined.

Data Analysis

Number of species within each transect was calculated to determine overall floristic composition of the local liana community. These data were combined for all *Gynerium*, *Cecropia*, *Ficus* and mature transects to determine total number of individuals and species per each seral stage (Figure 4.1 - 4.2). Species diversity was measured as species density (number of species/plot) and by Rarefaction to control for variation in stem number (Figure 4.3 and Figure 8). The rarefaction method allows the comparison of species abundance found in different transects when the sample size has differed.

Rarefaction produces a hyperbolic curve that represents the expected species diversity for a given sample size (Gotelli and Colewell 2001).

Diversity was also calculated using the Fishers Alpha Diversity Index (Figure 9). Similar to the Rarefaction Diversity Index, Fishers Alpha calculates diversity independent of stem number, allowing comparison of diversity for different sample sizes. This index only requires total number of individuals along with total species richness to calculate diversity and it was therefore used to compare liana diversity to that of older forests and to that of the local trees (Fisher 1943).

Composition

To examine composition changes through the succession, species data were analyzed using indirect Non-Metric Multidimensional Scaling ordination (NMS) (Noy-Meir et al. 1975). Ecological distances of species presence/absence (qualitative data) and dominance (quantitative data) were compared by seral stage and by beach to emphasize any underlying patterns in community composition (Figure 10 A – D) (Lefkowitz 1984).

Climbing Mechanism

Climbing mechanism, or the way in which a liana climbs a support structure is a unique characteristic that may influence local distribution of lianas. Availability of climbing substrate depends on the abilities of a liana to climb (Putz 1984). Previous investigations have found that following a forest disturbance tendrill climbers tend to dominate the young regenerating stands, followed by an increase in twining lianas as the forest ages (Putz 1985). In the successional floodplain of the Rio Manu, lianas appeared to be dominated by three types of climbers; tendrillate climbers, twiners and hook climbers. Tendrillate climbers are those lianas that use modified leaves to attach themselves to a host structure. Hook/ thorn climbers attach themselves to support structures with curved spines or hooks that grow around the stem of the host. Finally, twiners wrap around the branches or the stem of a host with circular movements originating from the shoot tip (Putz 1984). Successional trends in climbing type were expected to coincide with differences in available substrate throughout different aged forests. To answer the question, is there a pattern of climbing mechanism exhibited in the successional chronosequence of the Rio Manu floodplain, climbing technique was assigned to all

species collected during this investigation (Figure 11). Liana species were distinguished as tendrillate climbers, hook/thorn climbers or twiners. Although it is possible for a liana to utilize more than one mode of climbing, it was most often possible to distinguish the primary climbing mechanism (Putz 1985).

Topography

The five sampled beaches consisted of a series of ridges that were formed with alluvial deposits during inundation (Salo et al. 1986). Seasonal flooding continues to mold these ridges and the surrounding substrate as the river exceeds its banks and enters all stages of the successional forest through channels that are accessed at each meander in the river. Resident plant communities are susceptible to flooding dependent on the height of a ridge (Kalliola 1991). Though there is a lack of understanding of the influence of flooding on climbers (Putz and Windsor 1987), it is known that inundation limits diversity of several of their host species (Clinebell 1995). Therefore, it was hypothesized that elevational gradient may influence local distribution of lianas. To assess ridge height in relation to one another a trail profile was constructed on all beaches using a level and a level rod. Initially, a zero point was defined on the main trail within each mature floodplain at the farthest sampled point from the river. Measurements of vertical deviation, or elevational differences from the zero point were taken from the mature plot to the river. Horizontal distance along the main trail was recorded with a metric measuring tape. Trail profiles for each beach were constructed in Microsoft Excel using changes in elevation in relation to horizontal distance from the river.

RESULTS

Individual Abundance

Mean liana abundance increased in consecutively aged seral stages. However, abundance on individual beaches was highly variable and a pattern of increase over time was not consistent across transects or within beaches (Figure 4.1 B). Differences within beach and across transects was not statistically different (two way ANOVA, $p = 0.27$, $F=1.49$, $df=3$). Four out of five beaches had a decrease of lianas between the *Cecropia* and *Ficus/Cedrela* zone. The only trends of increased liana abundance seen on independent beaches were on Beaches 2 and 3 (Figure 4.1 A), where liana abundance was highest in the mature/transitional zone.

Liana abundance in young successional floodplain forests (< 100 years) were much lower than those of older successional forests (> 250 years) (Figure 5.1). The oldest transect (>500 years) had the highest level of abundance (data from this transect recorded by Robyn Burnham, Ph.D.)

Species Richness

Total species richness increased over time (Figure 4.2 B), however this trend was not consistent on all of the beaches (Figure 4.2 A). Additionally, a two-factor analysis of variance showed that differences in species richness within beaches and across transects was not statistically significant ($p = 0.096$, $F=2.6$, $df=3$). The lowest number of species per beach was found in the *Gynerium* zone on all beaches. Increase of species richness occurred in the *Cecropia* zone of Beaches 1, 2, 3 and 4. The number of species decreased

between the *Cecropia* and *Ficus/Cedrela* transects of Beaches 1, 2 and 4 and then increased in the mature seral stage on all of all beaches (Figure 4.2 B).

Comparison of liana species richness in young successional floodplain forests and older successional floodplain forests showed that younger forests are less species rich than older forests (Figure 5.2).

Diversity

The only consistent increase in diversity existed between the *Gynerium* and *Cecropia* transects on every beach (Figure 9). Diversity did not change between the *Cecropia* zone, the *Ficus/Cedrela* zone and mature zone on Beaches 1, 2 and 4. The only consistent increase of diversity was on Beach 3 and the highest overall transect diversity was found in the mature zone on this beach. Decrease of diversity in the third transect of Beach 5 correlates with the decrease in abundance found within the same transect on that beach. Beach 5 had the highest overall beach diversity.

The results of the Shannon-Weaver Index of diversity show that total liana diversity increased throughout consecutively aged seral stages (Figure 4.3 B). Diversity was lowest in the *Gynerium* zone on all beaches, except on Beach 2. Likewise an increase of diversity occurred in the *Cecropia* stand on all of the beaches. With the exception of Beach 2, each beach exhibited a decrease in diversity between the second and third transects. Beach 2 had the greatest overall diversity (Figure 4.3 B). This can be attributed to the high number of species recorded in the mature/transitional forest of that beach.

Diversity calculated with Fishers Alpha showed little change in liana diversity within the 4 seral stages of the early successional forest (Figure 9). In comparison, liana diversity increased in older successional forests (those > 250 years) and was greatest in the oldest transect which is thought to be approximately 500years old. Tree diversity increased consistently throughout the entire chronosequence. Similar to lianas, tree diversity was highest in the oldest forest (~500years) (Figure 9).

Composition

Non-metric multidimensional scaling (NMS) of community composition quantitative data resulted in the grouping of communities by seral stage (Figure 10 C). *Gynerium* transects were tightly grouped and distinct from *Cecropia*, *Ficus/Cedrela* or mature transects.

Grouping of the *Cecropia* plots occurred for all beaches, except for Beach 2. The *Ficus/Cedrela* and mature floodplain transects were marginally grouped but overlapping. Ordination of community composition presence/absence data by transect also resulted in grouping of communities by seral stage (Figure 10 A). *Gynerium* transects were tightly grouped and did not overlap with any of the other seral stages. However, *Cecropia*, *Ficus/Cedrela* and mature floodplain transects were not distinctly grouped together and showed a great deal of overlap in community composition (Figure 10 A).

NMS ordination of dominance data by beach showed loose groupings of community composition (Figure 10 D). These results contradict those of the ordination of species presence/absence by beach, which show a high degree of overlap for composition of all 5 study beaches (Figure 10 B).

Climbing Mechanism

Lianas of the Rio Manu floodplain were found to use tendrils, stem twining, branch twining and modified hooks and thorns to climb their hosts. Stem twining and use of tendrils were the most abundant mechanisms of climbing utilized in every stage of the successional floodplain (Figure 11.1 and 11.2). Branch twiners and hook/thorn climbers represented less than 1% of all the floodplain lianas and were not included in the results of this investigation.

Discussion

Individual Abundance and Species Richness

Though lianas are often associated with disturbed, high light environments, most similar to conditions found in the *Gynerium* zone, abundance and species richness was consistently lowest in this seral stage. These results suggest that lianas are limited by abiotic or biotic components of the first seral stage on all beaches; these components include frequent flooding, rapid sediment accumulation, availability and limitations of soil macronutrients and/or dispersal limitation. Due to a close proximity to the river, the first seral stage experiences a greater frequency of inundation than other seral stages (Losos 1993). Inability of root structure to endure flood events limits many liana species from persisting on the beach. Dominance of fast growing species such as Cucurbitaceae *Psiguria ternata* (Cucurbitaceae) and *Cissus sp.* (Vitaceae) indicate that rapid growth and reproduction rate, or rather the ability to reproduce between flood events is an important determinant of survival on the beach (Table 1). Abundance of *Psiguria ternata* may also indicate that many lianas are limited by the lack of soil macronutrients such as nitrogen available on the beach. Absence of organic material in the sandy soil may limit availability of nitrogen on the beach. Similar to most family members of Cucurbitaceae, the roots of *Psiguria ternata* are inhabited by nitrogen fixing bacteria or rhizomes and can therefore survive in nitrogen poor environments (Tilman and Wedin 1991).

Importance of soil factors on the abundance of lianas, including the occurrence of N, has been documented by Gentry (1991), who found that nutrient poor, white sand soils in the Amazon basin had a lower density of lianas than neighboring plots with less extreme soil

conditions. This also indicates that changing soil macronutrients in the seral stages may contribute to observed increases in average liana abundance. Though Losos (1993) did not find differences in seral stage soil content, she hypothesized that with larger sample sizes concentrations of soil macronutrients would change along the chronosequence. Finally, the low abundance of lianas in the *Gynerium* zone may be attributed to inability of many species to arrive on the beach. Though *Gynerium* is wind dispersed, Losos (1993) found that roosting bats were the primary dispersers of tree seeds in this zone. Absence of frugivorous birds and mammals can be attributed to the lack of suitable habitat offered by *Gynerium* grasses. Dispersal of liana species would therefore require assistance of wind, bats or through production of floating, flood tolerant seeds. A low number of liana species dispersed by water, wind and bats suggest dispersal limitation as an influence of liana composition. More investigation of liana seed dispersal is required to determine the influence of dispersal limitation in the Rio Manu chronosequence.

High liana abundance and species richness typical of many tropical floodplain forests was not found in any stage of the chronosequence, suggesting that liana habitat of successional floodplain forests differ from one another. Presence of lianas in mature forests has most often been associated with light, brought on by disturbance in the canopy, as well as an increase in abundance and diversity of substrate on which to climb. Though lianas of mature forests have been associated with light, liana composition could not be correlated to differences in specific environmental components of the successional forests suggesting that heterogeneity of early seral stages (< 250 yrs.) is not as important in the formation of liana communities as it was initially expected to be. Rather, internal

dynamics of older successional forests (those > 250 yrs.), such as increased light levels from the formation of tree fall gaps, enable the support of abundant, species rich liana communities. Lianas increase along tree fall gaps because several liana stems are often deposited on the forest floor when a tree falls. Also many liana species found only in mature tropical forests grow faster in high light, and can produce vegetative offshoots when stimulated by high light environments (Campbell and Newberry 1993; Putz 1985; Putz and Chai 1987). Likewise increase of lianas to establish on (Putz 1984) and may lower turnover rates by stalling tree regeneration (Ibarra-Manriquez and Marinez-Ramos 2002; Schnitzer 2000).

Average abundance and total species richness decreased in the *Ficus/Cedrela* zone on four of the five beaches (Figure 4.1 and 4.2). The establishment of these two tree species marks the first occurrence of large diameter trees typical of mature tropical forests and ultimately changes the liana habitat in two distinct ways. Foremost, Figure 6 indicates that percent of canopy openness decreases in the *Ficus* zone, thus decreasing below canopy light levels to all plants. The *Ficus/Cedrela* zone is the first stage of the succession with substantial light limitation. Previous investigations have shown that mature forest lianas are light limited and will increase in abundance when exposed to increased light (Putz 1984). Correlation of lianas and light are most evident in tree fall gaps, where disruption in forest canopy causes increased light levels (Ibarra-Manriquez and Marinez-Ramos 2002; Schnitzer 2000).

Increased tree diameter and biomass common in the *Ficus/Cedrela* zone may inhibit liana climbing ability thus leading to a decrease of abundance. Establishment of large diameter trees leads to an accumulation of biomass in the *Ficus/Cedrela* stage. Ibarra-Manriquez and Martinez-Ramos (2002) found a strong negative association between liana abundance and tree biomass. They offer three explanations for this trend. First, sites with increased biomass have most often experienced a low disturbance rate. Stability of tree communities would limit the opportunity for lianas to establish. Next, lianas and trees may be negatively correlated if lianas and trees respond in opposite ways to soils or other abiotic factors of forests. However, this proposal seems unlikely if considering that lianas and trees often respond positively to increased soil fertility (Laurence et al. 1999). Last, abundance of lianas may depress accumulation of tree biomass through increasing tree mortality and damage (Ibarra-Manriquez and Martinez-Ramos 2002; Putz 1983, 1984).

Trees and lianas of the Rio Manu floodplain experience two distinct types of succession resulting in different community structures. Once established on newly formed beaches, trees undergo species turnover through the dominance, sequential replacement and local extinction over time. Lianas do not turn over throughout seral stages instead, liana species accumulate over time. Inspection of abundance and species richness data show that all species found within *Gynerium* transects are also found in mature/transitional forests (Appendix B). As a result, early seral liana composition remains similar until older forests (> 250 years) (Figure 9), while tree abundance and diversity steadily increases over time. Review of existing data along with the results of this investigation reveal that 1) liana abundance, species richness and diversity in a beach chronosequence

are different than those of the trees and 2) differences exist between internal dynamics of floodplain habitats and these differences lead to major differences in liana community structure.

Diversity

In most successional systems, diversity increases as forests age (Whittaker 1975). While this pattern of succession is seen in the tree species of the beach chronosequence (Losos 1993), lianas do not increase in diversity until late in the succession (Figure 9). Liana diversity was low in all of the seral stages considered in this investigation. But previous studies in the Manu floodplain have shown that successional processes continue after the establishment of transitional forest and this continuation further changes environment and composition of the forest. It is not until we consider liana diversity in older mature forests (those exceeding 250years) that we find a high diversity typical of mature forests.

Consistency of changes in tree diversity have been attributed to local niche changes occurring in each seral stage, including decrease of local disturbance, especially flooding and an increase of soil macronutrients and dispersal agents. Differences in diversity accumulation of trees and lianas indicate that their communities are formed in different ways and moreover, late stages of the floodplain succession contain different abiotic and/or biotic components that enable them to support a higher diversity than early seral stages.

Figures 4.1 and 4.2 indicate that liana abundance and species richness was low in the 4 seral stages of the chronosequence. The low number of lianas in early stages may account for low diversity. However, Figures 6 and 7 indicate that no correlation was found between the number of lianas and changes in specific environmental components of seral stages, including decreased disturbance, especially flooding and increased dispersal agents and soil macronutrients. Increases in diversity and abundance found in later seral stages may be due to both the interactions of these components and other internal dynamics typical of older forests. One of the most significant changes between early and late seral stages is the occurrence of tree fall and the subsequent formation of gaps in the forest canopy.

Results of the Shannon Weaver and Fishers Alpha Index of Diversity indicate that liana diversity was increased with increasing sample size (Figure 4.3 and Figure 8). Previous investigations have provided two possible explanations for correlation between diversity and sample size. The first explanation for this trend is the positive spatial autocorrelation of liana species. This is attributed to either the ability of lianas to reproduce clonally or caused by species-specific niche requirements (Nabe-Nielson 2001; Putz 1984). Second, the observed correlation of species diversity and sample size may be due to the rarity of many liana species. In this case, increase of sample size would increase the probability of encountering a rare liana. Liana diversity of seral stages was (1) not expected to be similar to other seral stages and (2) not expected to have increased diversity with increased sample size in homogenous seral stages. Positive spatial autocorrelation or rarity of liana species may account for these unsuspected trends.

The only consistent change in liana diversity (as measured by Shannon Weaver Index of Diversity) found on all of the beaches was an increase of diversity that occurred between the *Gynerium* zone and *Cecropia* zone (Figure 4.3). Diversity in the *Cecropia* zone was variable on independent beaches but always higher than that of the beach. Low diversity in the *Gynerium* zone is attributed to species dominance brought on by flood frequency, low soil macronutrients and possible limitation of dispersal (See "Individual abundance and species richness" above).

The greatest overall diversity of lianas, as measured by Rarefaction index of diversity was seen on the second beach. Three distinct environmental characteristics of this beach may explain the increase of liana diversity on this beach. First, Beach 2 had a greater abundance of *Tessaria integrifolia* than any other beach in this study, indicating that it is undergoing a slower process of succession. On beaches that experience rapid cycle of succession, *Tessaria* shrubs are quickly replaced with *Gynerium* grasses (Losos 1993). A slowed process of tree succession, causes less disturbance through tree species turnover and allows the development of more host substrate, ultimately allowing slowly succeeding forests to support greater number of liana species unable to survive in highly disturbed, host limited environments. High liana diversity seen on Beach 2 may also be explained by the width of the point bar. Plant communities located in the center of wide point bars are more protected from sediment deposition and flooding caused by river migration than plant communities found on narrow point bars (Kalliola 1992). Finally, a distinct rise in elevation occurred before the fourth transect (Appendix A). This change in

elevation coupled with a change in tree composition indicated that this transect was not located on sandy alluvial deposits but rather this transect marked the beginning of the *terra-firme* uplands. *Terra firme* upland habitat occurs away from rivers and is never flooded (Burnham 2002). Though abundance was not influenced by these changes in habitat, a greater diversity of liana species was found in this transect.

The results of the Shannon-Weaver Index of diversity are different than those found by rarefaction (Figure 4.3B and Figure 8). The differences may be inherent in the structure of these tests. Because the Shannon-Weaver index of diversity is based solely on the proportion of individuals of a species, it does not account for the effects of sample size. Alternatively, rarefaction allows an investigator to determine diversity of a select sample size. Due to the varying sample sizes found in this investigation, rarefaction provides a more accurate index of diversity.

Species Dominance

Dominance of species, or those species representing the largest proportion of individuals within transects, varied within beaches and across seral stages, suggesting that species did not have habitat preference and instead were most influenced by chance arrival on beaches (Table 1). Species dominance can be attributed to clumped distribution of conspecifics which is most likely influenced by one of three factors, including competitive capability of species, source strength of dispersal or abundance of underground vegetative offshoots.

First, source strength for dispersal may be provided by the abundance of a species within the existing liana community. In this case, dispersal, or ability to arrive on a beach would most influence species presence and later, dominance would occur through availability of seeds produced by the local plant community (Hubbell 2001). Second, clonal reproduction or the production of vegetative offshoots may have led to the observed species dominance. Individuals counted as genetic individuals (genets) could be genetically similar vegetative offshoots of one individual (ramets). Lianas that were rooted in the ground were considered individuals, however Putz (1990) observed that lianas often produce ramets underground. Gentry (1991) observed that ramets might persist as individuals for several hundred years, only occasionally reproducing sexually (Burnham 2002; Gentry 1991). Ramets that emerged from the ground may have been counted as individuals, misrepresenting a pattern of true species occurrence within transects (Jarzomski 1998; Nabe-Nielson 2001; Putz 1990).

Last, differences in local niches may provide some species with advantages from specialized characteristics. A prime example of this is the observed dominance of *Psiguria ternata* Cucurbitaceae in the *Gynerium* zone. *Psiguria ternata* accounted for more than 40% of individuals found the first seral stage of two beaches and is represented in the *Gynerium* zone of all beaches (Table 1). Such abundance indicates that this species has characteristics that have allowed it to survive and reproduce in the dispersal limited, high light and flood frequent environment of the first seral stage. More specifically *Psiguria ternata* has nitrogen-fixing bacteria on its roots, along with floating seeds and rapid growth and reproduction rates, especially in high light environments (See

Individual abundance and species richness for greater details). These characteristics provide *Psiguria ternata* with a competitive advantage, which eventually allow it to dominate in the *Gynerium* zone.

While the beach was most often dominated by *Psiguria ternata*, mid and late successional seral stages show an abundance of lianas from the families *Bignoneaceae*, *Leguminosae*, *Sapindaceae* and *Urticaceae*. Similar results have been found in most investigations of Neotropical rainforests (Gentry 1991; Ibarra-Manriquez and Martinez-Ramos 2002; Nabe-Nielson 2001) In addition, the most abundant genera found in this study (*Sapindaceae Paullinia*) are among the most species rich lianas in other Neotropical rain forests (Gentry 1991; Ibarra-Manriquez and Martinez-Ramos 2002). Species dominance is attributed to clumping by conspecifics through strong dispersal source strength, advantage from specialized climbing structure evolved in certain families (e.g. tendrils in *Sapindaceae*) and ability of lianas to reproduce clonally (Ibarra-Manriquez and Martinez-Ramos 2002; Nabe-Nielson 2001).

Composition

NMS ordination of liana species presence/absence and quantitative data by transects showed that liana composition was more tightly grouped by successional effects of seral stages than by beach effects (Figure 10 A and 10 C). *Gynerium* zone was tightly grouped suggesting that liana composition in this seral stage is not similar to any of the other seral stages. Distinct composition in the *Gynerium* zone is most likely due to patterns of species dominance, brought on by distinct dynamics that occur in this stage. Though no

correlation was found between liana composition in the 1st seral stage and specific environmental components found there, formation of this community may be attributed to high disturbance rates, such as frequent flooding, low occurrence of soil macronutrients and/or dispersal limitation. Similarities in liana presence/absence and dominance caused overlap in the *Cecropia*, *Ficus/Cedrela* and mature transects. These results suggest that though the four seral stages are distinct in tree habitat, they share some similarities of liana habitat. Moreover, presence/absence and dominance of liana composition in later seral stages suggest that liana communities may grow to be more similar through time.

NMS ordination of liana presence/absence data by beach was highly overlapping, indicating that species pool is the same on all beaches (Figure 10 B and 10 C).

Alternatively, ordination of species dominance showed a loose grouping by beach. Beach species dominance is attributed to source strength of dispersal and production of vegetative offshoots.

Climbing Mechanism

Each climbing guild as defined by Putz (1984) was represented in the chronosequence. Stem twining and use of tendrils were the most common modes of climbing utilized by individuals (Figure 11.2). Similar to most climbing Angiosperms, the proportion of species that climb with the use of tendrils or by twining was greater than any other mode of climbing (Figure 11.1). Aside from an undisputed dominance of twiners and tendrillate lianas, no significant trend existed between beach, seral stage and occurrence of climbing

mode. Variation of climbing types may decrease in late successional stages but greater sample sizes are needed to distinguish if these trends are real.

CONCLUSION

Lianas of the Rio Manu beach chronosequence do not undergo a pattern of succession similar to that of the local tree species. Based on the results of the present study, lianas do not exhibit a pattern of increased abundance, species richness and diversity that is consistent across all of the beaches. Instead liana composition is highly variable on independent beaches. Furthermore, dominance of liana species appears to be influenced most by dispersal while tree dominance is most influenced by abiotic factors. The results of this investigation suggest that lianas are opportunistic and do not exhibit habitat preference.

Differences in liana composition of young and old forests is attributed to temporal and spatial heterogeneity of forest dynamics. Sudden increase of light levels caused by the formation of tree fall gaps may account for high abundance and diversity in older successional forests (those >250 years) while low abundance and diversity of younger successional forest suggest that lianas are limited by abiotic and biotic components within these stages. The results of species ordination show that liana presence is most influenced by seral stages but composition could not be linked to specific environmental components, such as elevation and light.

WORKS CITED

- Burnham, R.J. 2002. Dominance, diversity and distribution of lianas in Yasuni, Ecuador: who is on top?. *Journal of Tropical Ecology*. 18: 845-864.
- Burnham, R.J. Unpublished data from Manu National Park, Peru.
- Bush, M.B., R.J. Whittaker and T. Partomihardjo. 1995. Colonization and Succession on Krakatau: An Analysis of the Guild of Vining Plants. *Biotropica*. 27:355-372.
- Campbell, E.J.F and D. McC. Newbery. 1993. Ecological relationships between lianas and trees in lowland rain forest in Sabah, East Malaysia. *Journal of Tropical Ecology*. 9: 469-490.
- Clark, D.A. and D.B. Clark. 1984. Spacing Dynamics of a Tropical Rain Forest Tree: Evaluation of the Janzen-Connell Model. *American Naturalist*. 124: 769-788.
- Clinebell II, R.R., O.L. Phillips, A.H. Gentry, N. Starks and H. Zuuring. 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*. 4: 56-90.
- Cowles, Henry Chandler. 1899. The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan. *Botanical Gazette*. 27: 95-117.
- Darwin, C. 1867. On the movements and habits of climbing plants. *Journal of Linnean Society*. 9:1-118.
- Denslow, J.S. Tropical rain-forest gaps and tree species diversity. *Annual Review of Ecology and Systematics*. 18: 431-451.
- Fisher, R.A, A.S. Corbet, and C.B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Ecology*. 12: 42-58.
- Foster, R.B., Javier Arce B. and T. S. Wachter. 1986. Dispersal and the sequential plant communities in Amazonian Peru floodplain. ch 27 *In: Frugivores and seed dispersal*. Estrada, A. and T.H. Fleming (eds.). Dr W. Junk Publishers, Dordrecht.
- Foster, R.B. 1990. The floristic composition of the Rio Manu floodplain fores. Ch 7 *In: Four Neotropical Rainforests*. A.H. Gentry, eds. Yale University Press, New Haven.
- Gentry, A.H. 1991. Distribution and evolution of climbing plants. Pp. 3-52 in Putz, F.E. and Mooney, H.A. (eds). *The biology of vines*. Cambridge University Press, Cambridge.

- Gentry, A.H. and C. Dodson. 1987. Contribution of non-trees to species richness of a tropical forest. *Biotropica*. 19: 216-227.
- Gerwing, J.J. and E. Vidal. 2002. Changes in Liana Abundance and Species Diversity Eight Years after Liana Cutting and Logging in an Eastern Amazonian Forest. *Conservation Biology*. 16: 544-548.
- Gotelli, N.J. and R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*. 4: 379-391.
- Hall, R.B.W. and P.A. Harcombe. 1998. Flooding alters apparent position of floodplain saplings on a light gradient. *Ecology*. 79: 847-855.
- Hubbell, S.P. and R.B. Foster. 1986. Biology, Chance, and History and the Structure of Tropical Rain Forest Tree Communities. ch 19 *In: Community Ecology*. Diamond, J. and T.J. Case (eds.). Harper and Row, New York.
- Ibarra-Manriquez, G. and M. Martinez-Ramos. 2002. Landscape variation of liana communities in Neotropical rain forest. *Plant Ecology*. 160: 91-112.
- Jarzomski, C.M. 1998. Liana distribution and host relationships in some temperate versus tropical forest sites. M.S. Thesis.
- Kalliola, R., J. Salo, M. Puhakka and M. Rajasilta. 1991. New Site Formation and Colonizing Vegetation in Primary Succession on the Western Amazon Floodplains. *Journal of Ecology*. 79: 877-901.
- Kokou, K., P. Couteron, A. Martin and G. Caballe. 2002. Taxonomic Diversity of Lianas and Vines in Forest Fragments of Southern Togo. *Rev. Ecol.* 57: 3-18.
- Lamotte, S. 1990. Fluvial dynamics and succession in the Lower Ucayali River basin, Peruvian Amazonia. *Forest Ecology and Management*. 33: 141-156.
- Laurance, W.F., D. Perez-Salicrup, P. Delamonica, P.M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl and T.E. Lovejoy. 2001. Rain Forest Fragmentation and the Structure of Amazonian Liana Communities. *Ecology*. 82: 105-116.
- Lawton, R.O. and Putz, F.E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology*. 69: 764-777.
- Lefkovitch, L.P. 1984. A Nonparametric Method for Comparing Dissimilarity Matrices, a General Measure of Biogeographical Distance, and Their Application. *American Naturalist*. 123: 484-499.

- Lichter, J. 2000. Colonization constrains during primary succession on coastal Lake Michigan sand dunes. *Journal of Ecology*. 88:825-839.
- Losos, E.C. 1993. The influence of seed dispersal on primary forest succession in an Amazonian floodplain forest. Ph.D. thesis.
- McCook, L.J. 1994. Understanding ecological community succession: Causal models and theories, a review. *Vegetatio*. 110: 115-147.
- Mulkey S.S, K. Kitajima, and S. Wright. 1996 Seasonal leaf phenotypes in the canopy of a tropical dry forest: photosynthetic characteristics and associated traits. *Oecologia* 109: 490-498.
- Mulkey, S.S., K. Kitajima, and S.J. Wright. 1995. Photosynthetic capacity and leaf longevity in the canopy of a dry tropical forest. *Selbyana*. 16: 169-173.
- Nabe-Nielsen, J. 2001. Diversity and distribution of lianas in a neotropical rain forest, Yasuni National Park, Ecuador. *Journal of Tropical Ecology*. 17: 1-19.
- Noy-Meir, I., D. Walker and W.T. Williams. 1975. Data Transformations in Ecological Ordination: II. On the Meaning of Data Standardization. *Journal of Ecology*. 63: 779-800.
- Putz, F.E. 1982. Natural History of lianas and their influences on tropical forest dynamics. Ph.D. thesis, Cornell University.
- Putz, F.E. 1983. Liana Biomass and Leaf Area of a "Tierra Firme" Forest in the Rio Negro Basin, Venezuela. *Biotropica*. 15: 185-189.
- Putz, F.E. 1984. How Trees Avoid and Shed Lianas. *Biotropica*. 16: 19-23
- Putz, F.E. 1985. Woody vines and forest management in Malaysia. *Commonw. For. Rev.* 64: 359-365.
- Putz, F.E. and D.M. Windsor. 1987. Liana Phenology on Barro Colorado Island, Panama. *Biotropica*. 19: 334-341.
- Putz, F.E. 1990. Liana Stem Growth and Mortality Rates on Barro Colorado Island, Panama. *Biotropica*. 22: 103-105.
- Putz, F.E. and N. Holbrook. 1991. Biomechanical studies of vines. Pp. 73-97 in Putz, F.E. and Mooney, H.A. (eds.) *The biology of vines*. Cambridge University Press, Cambridge.

- Robertson, K.M. and C.K. Augspurger. 1999. Geomorphic processes and spatial patterns of primary forest succession on the Bogue Chitto River, USA. *Journal of Ecology*. 87:1052-1063.
- Roldan, A.I. and R.O. Varela. 1999. Seasonal Changes in Liana Cover in the Upper Canopy of a Neotropical Dry forest. *Biotropica*. 186-192.
- Salo, J., R. Kalliola, I. Hakkinen, Y. Makinen, P. Niemela, M. Puhakka and P.D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. *Nature*. 322: 254-258.
- Schenck, H. 1893. Beitrage zur Biologie und Anatomie der Lianen im Besonderen der in Brasilien einheimischen Arten. Botanische Mittheilungen aus den Tropen. Verlag von Gustav Fischer Jena. 253p.
- Schnitzer, S.A., J.W. Dalling and W.P. Carson. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*. 88: 655-666.
- Silman, M.R. 1996. Regeneration from seed in a neotropical rainforest. Ph.D thesis, Duke University, Durham, NC.
- Terborgh, J.W. 1985. Habitat selection in Amazonian birds. 311-338. In *Habitat selection in birds*. M.L. Cody, ed. Orlando, FL: Academic Press.
- Terborgh, J. and K. Petren. 1990. Development of habitat structure through the succession in an Amazonian floodplain forest. 28-46. In *Habitat structure: The physical arrangement of objects in space*. S.S Bell, E. McCoy, and H. Mushinsky, eds. London, Great Britain: Chapman and Hall.
- Tilman, D.W. 1988. Plant Strategies and the dynamics and structure of plant communities. Princeton, NJ: Princeton University Press.
- Tilman, D.W. and D. Wedin. 1991. Dynamics of Nitrogen competition between successional grasses. *Ecology*. 72: 1038-1049.
- Whitaker, R.H. 1975. Succession. Pp. 171-179. In: *Communities and Ecosystems Second Edition*. MacMillian Publishing Company, New York, NY.

Figure 1. Landsat TM image of the Manu River, Madre de Dios, Peru and the location of the five beaches investigated in this thesis.

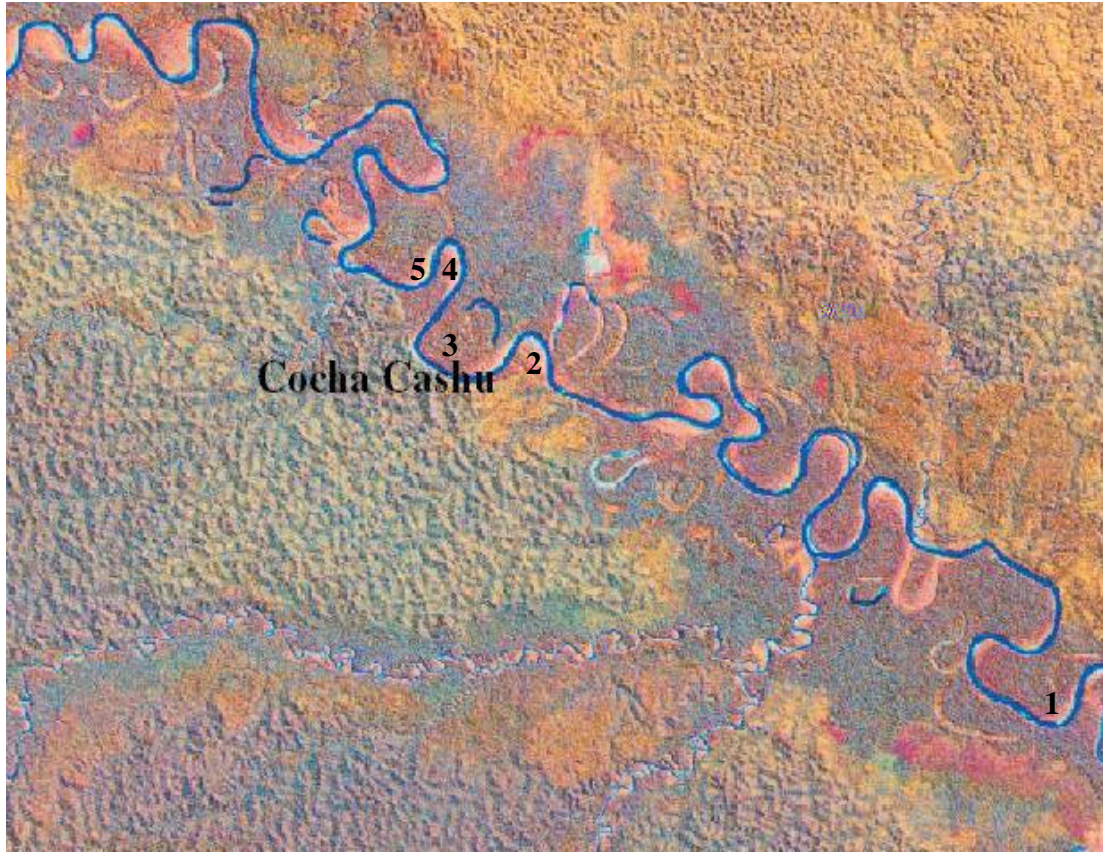


Figure 2. Schematic profile of the Manu chronosequence; portraying the successional progression from the river to the mature/transitional forest

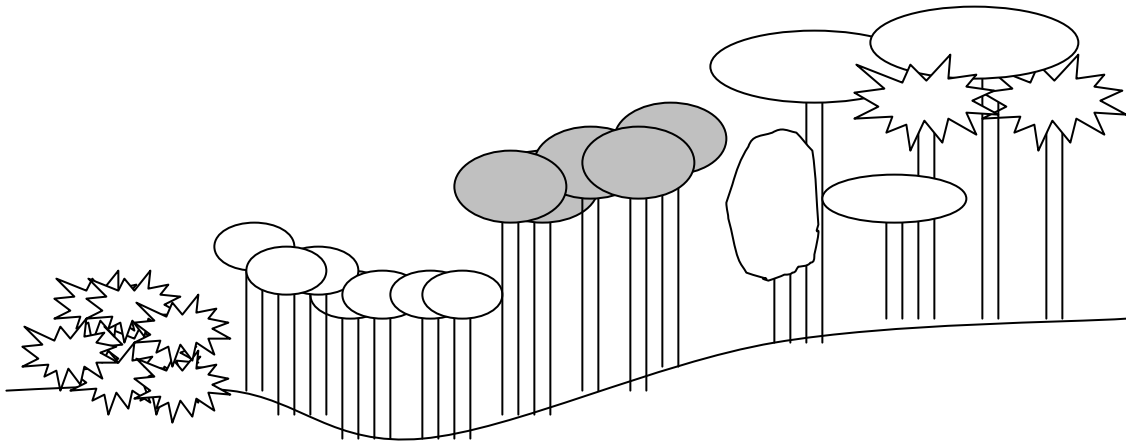
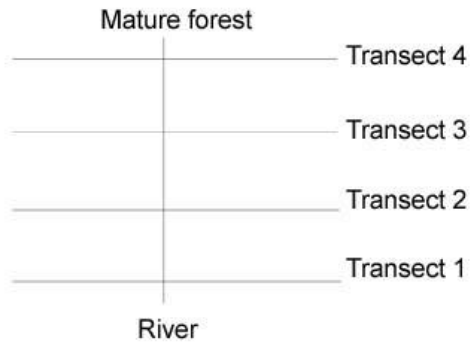
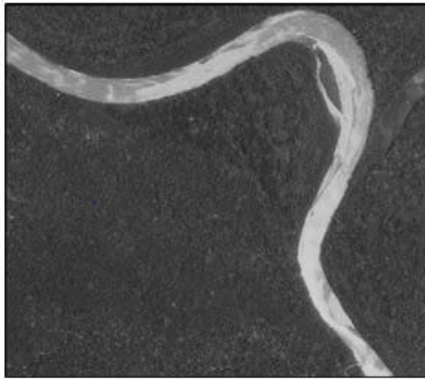


Figure 3. Aerial photos of the five point bar beaches investigated in this thesis. Photos orientated to river flow, northwest to southeast. Also included: schematic representation of transect layout applied to each of the beaches in this study, where Transect 1 is located in the *Gynerium* zone, Transect 2 is located in the *Cecropia* zone, Transect 3 is located in the *Ficus/Cedrela* zone and Transect 4 is located within the mature/transitional zone.



Beach 1



Beach 2



Beach 3



Beach 4



Beach 5

Figure 4.1(A) Number of individuals found on each the five study beaches

(B) Mean abundance and standard error of the four transects located in each stage of the chronosequence.

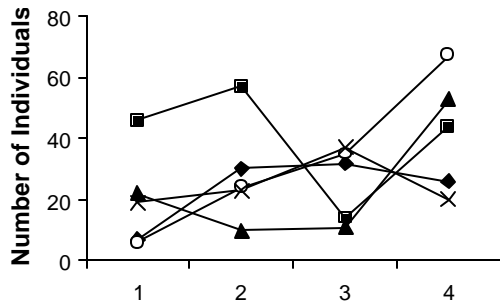
Figure 4.2(A) Number of liana species found on each of the five study beaches

(B) Total species richness calculated for the four transects located in each stage of the chronosequence.

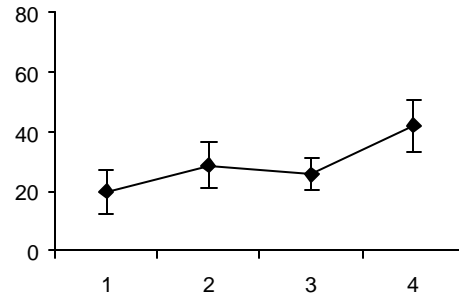
Figure 4.3 (A) Diversity of lianas measured by Shannon Weaver Index of Diversity for each of the five study beaches.

(B) Total Diversity as measured by Shannon Weaver Index of Diversity for the four transects located in each seral stage along the chronosequence.

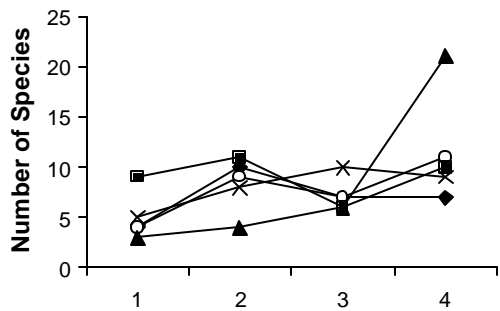
Abundance of Individuals



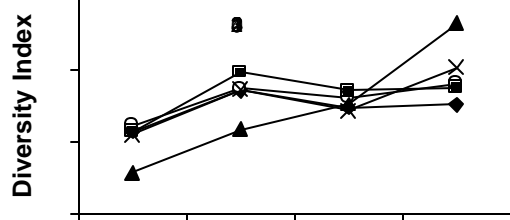
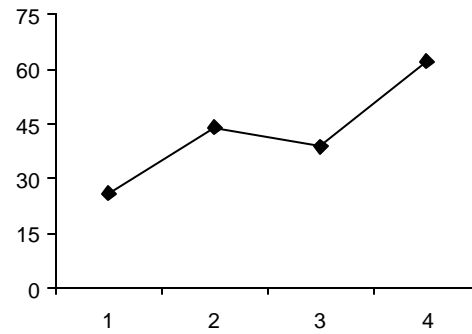
Average: Abundance of Individuals



Species Richness



Total: Species Richness



Total: Shannon Weaver Index

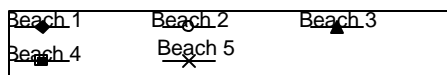
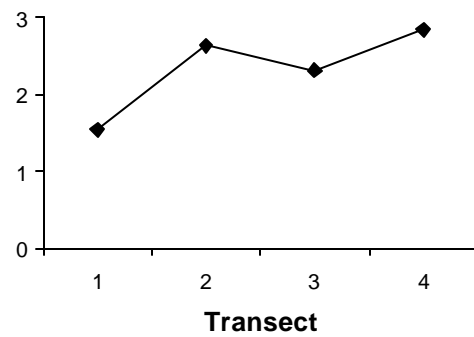


Figure 5.1. Liana abundance in young successional floodplain forests (recorded in the present study) compared to abundance of older successional forests (>250 years) also located in the Manu River floodplain (recorded by Robyn Burnham Ph.D.). Transect numbers represent seral stages where, 1=Gynerium zone, 2=Cecropia zone, 3=Ficus/Cedrela zone, 4=mature/transitional zone, M1=older successional forest (>250 years), M2=older successional plot (>500y years).

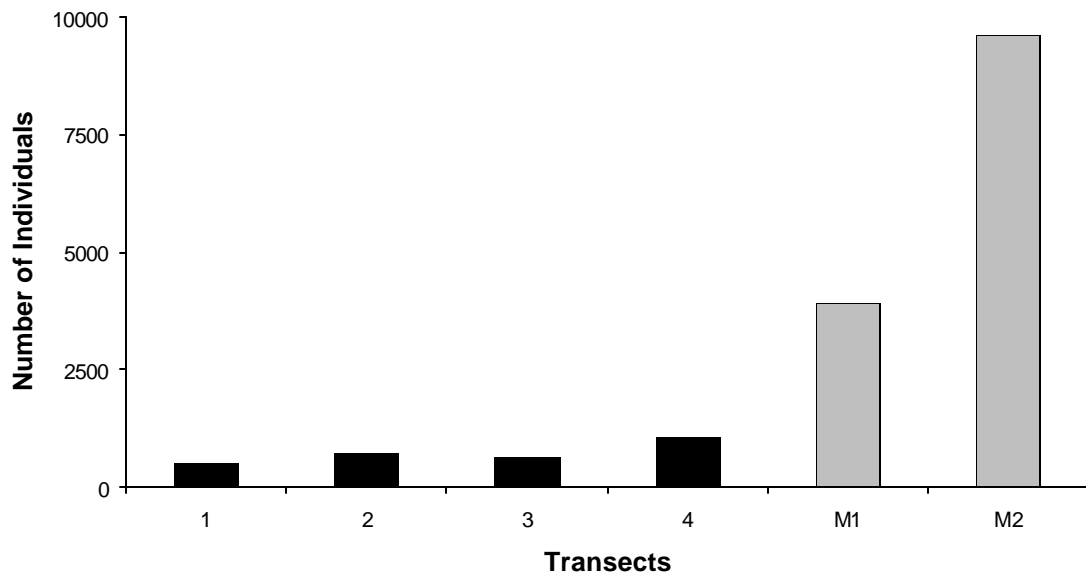


Figure 5.2 Liana species richness in young successional forests (recorded in the present study) and older successional forests (>250 years) also in the Manu River floodplain (recorded by Robyn Burnham, Ph.D). Transect numbers represent seral stages where, 1=*Gynerium* zone, 2=*Cecropia* zone, 3=*Ficus/Cedrela* zone, 4=mature/transitional zone, M1=older successional forest (>250 years), M2=older successional plot (>500y years).

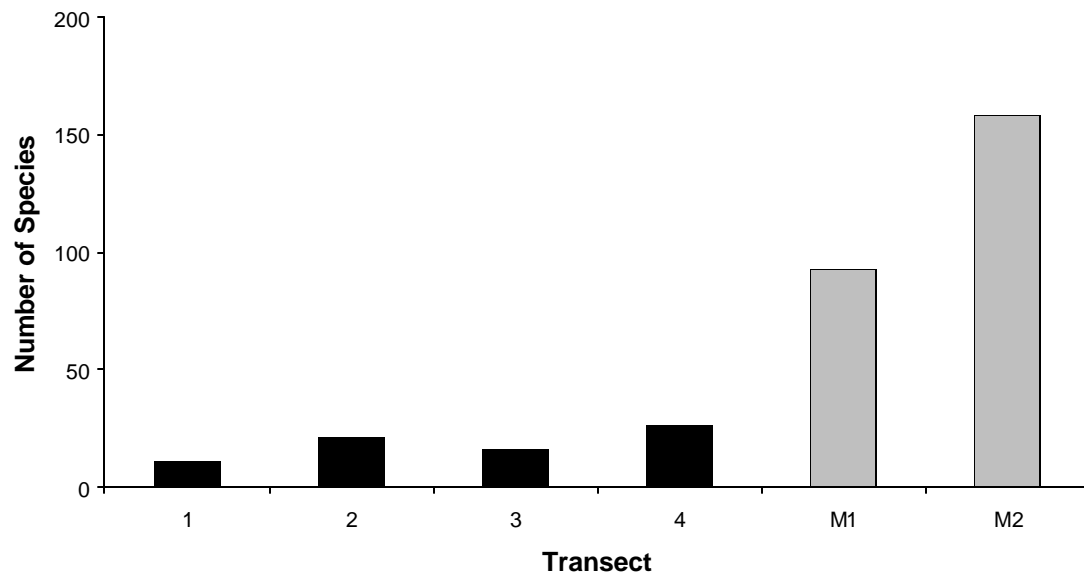


Figure 6. Correlation of mean liana abundance (recorded in the present study) and proportion of canopy openness (recorded in the doctoral thesis of Elizabeth Losos, Ph.D.). Triangles represent mean abundance of lianas found in *Gynerium*, *Cecropia*, *Ficus/Cedrela* and mature/transitional zones.

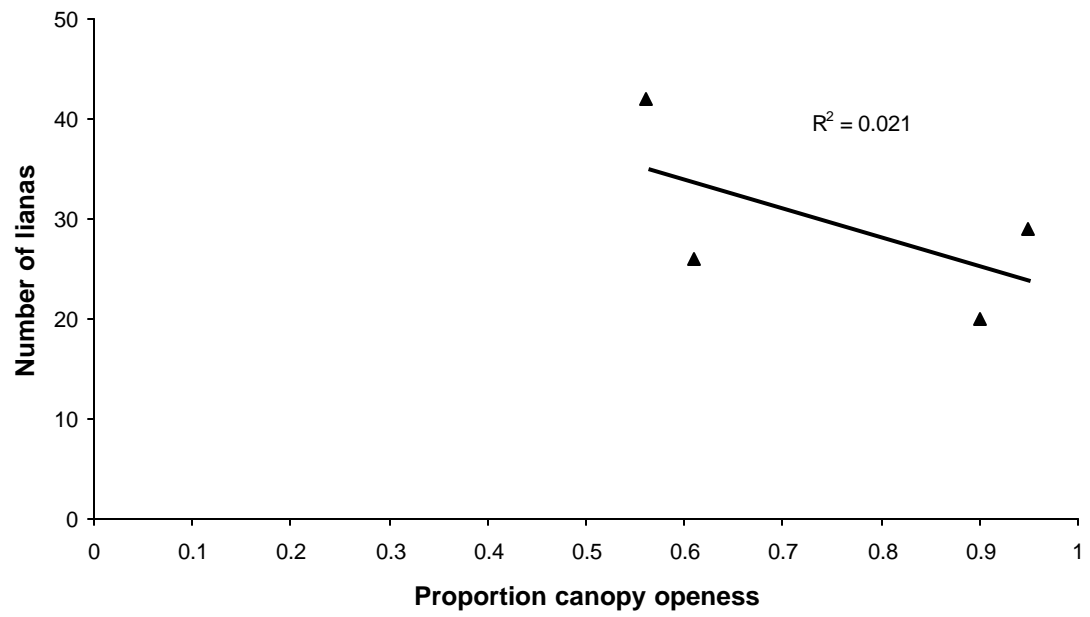


Figure 7. Correlation between elevation and abundance of lianas. Triangles represent mean abundance of lianas found in *Gynerium*, *Cecropia*, *Ficus/Cedrela* and mature/transitional zones.

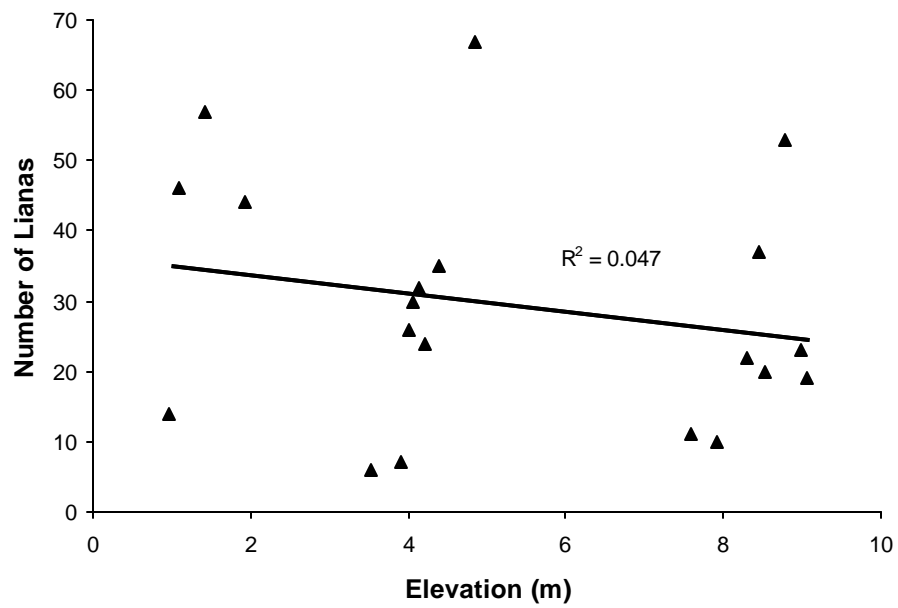
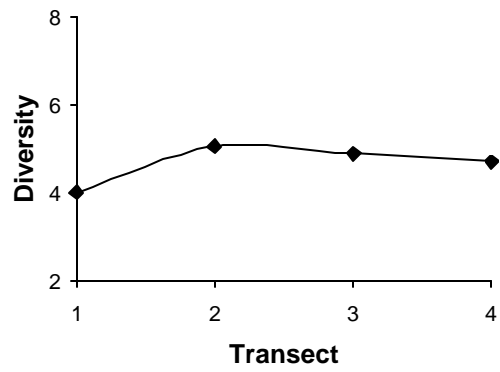
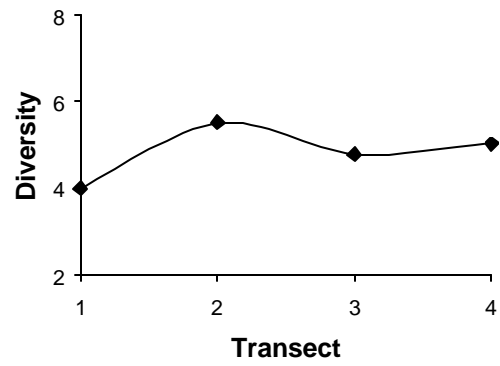


Figure 8. Beach diversity and total diversity of all beaches, as measured by Rarefaction Diversity Index. Rarified diversity represents subsample size of 10 individuals.

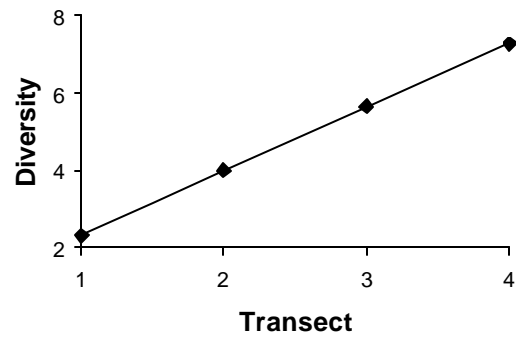
Beach 1



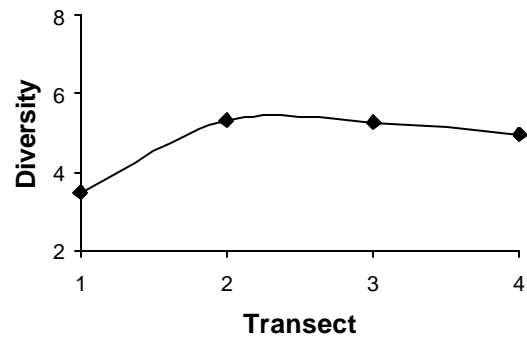
Beach 2



Beach 3



Beach 4



Beach 5

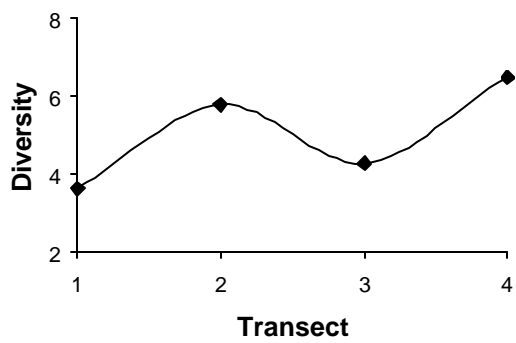


Figure 9. Diversity, as measured by Fishers Alpha for the trees (Losos 1993) and lianas in young (< 100 years)(recorded in present study) and older (> 250 years) successional forests (recorded by Robyn Burnham, Ph.D.). Transect numbers represent seral stages where 1=*Gynerium* zone, 2=*Cecropia* zone, 3=*Ficus/Cedrela* zone and 4=mature/transitional zone.

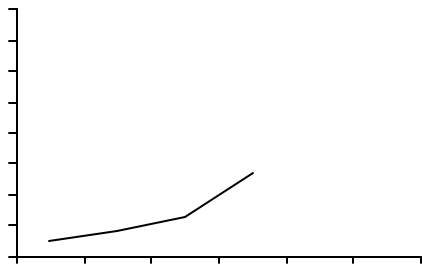
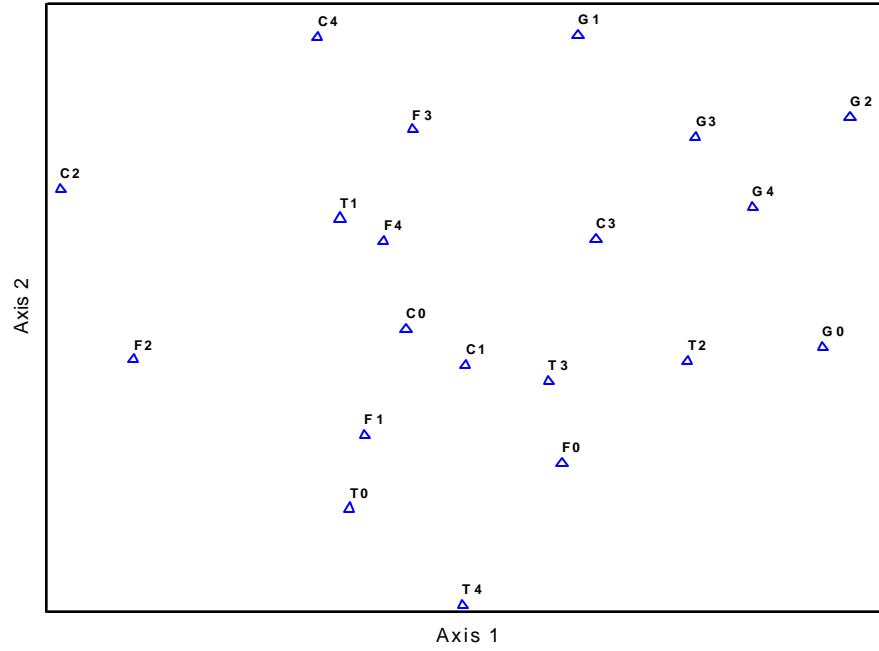


Figure 10. (A) Non-metric Multidimensional Scaling Ordination of species presence/absence (qualitative) data by seral stage and (B) by beach. Non-metric Multidimensional Scaling Ordination of dominance (quantitative) data by (C) seral stage and (D) by beach . Points are represented by seral stage or by beach number where, G = *Gynerium* zone, C = *Cecropia* zone, F = *Ficus/Cedrela* zone and T = mature/transitional zone. Numbers 1-5 represent community composition on the beach with the corresponding number.

A.



B.

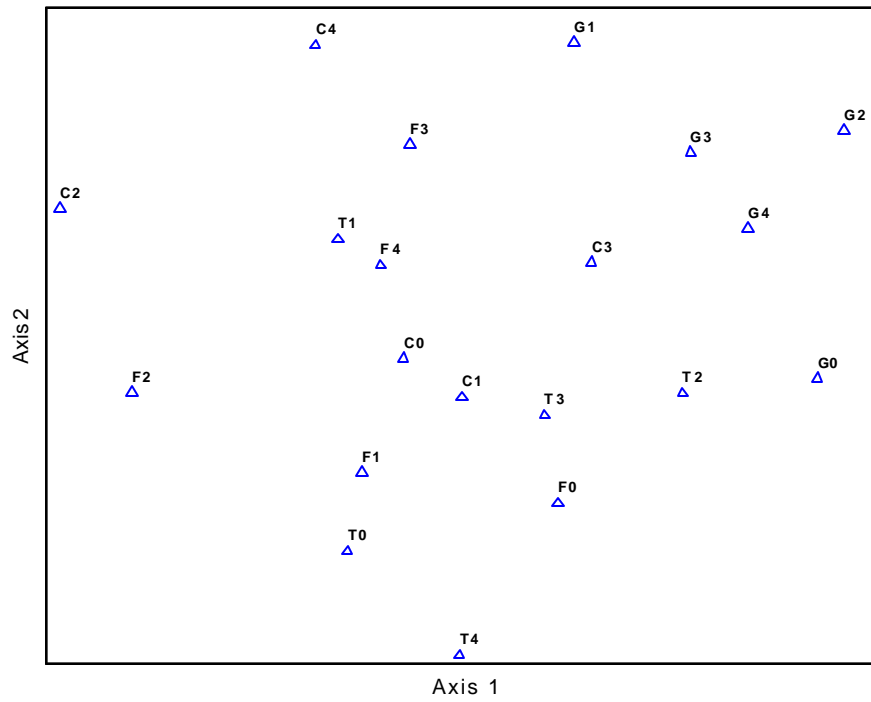


Figure 11. Proportion of climbing guilds represented in each transect of the 5 study beaches by (A) Proportion of species included in climbing guild sand (B) Proportion of individuals found within climbing guilds.

Species Climbing Guild Distributions

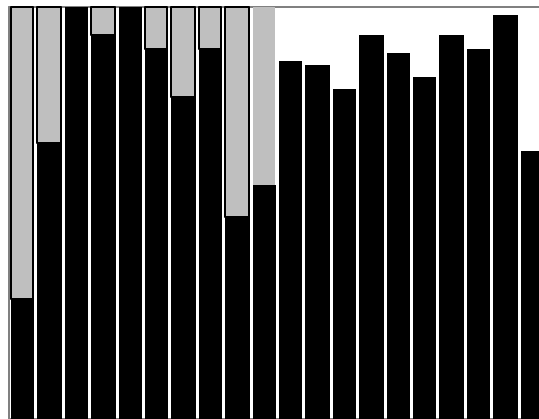
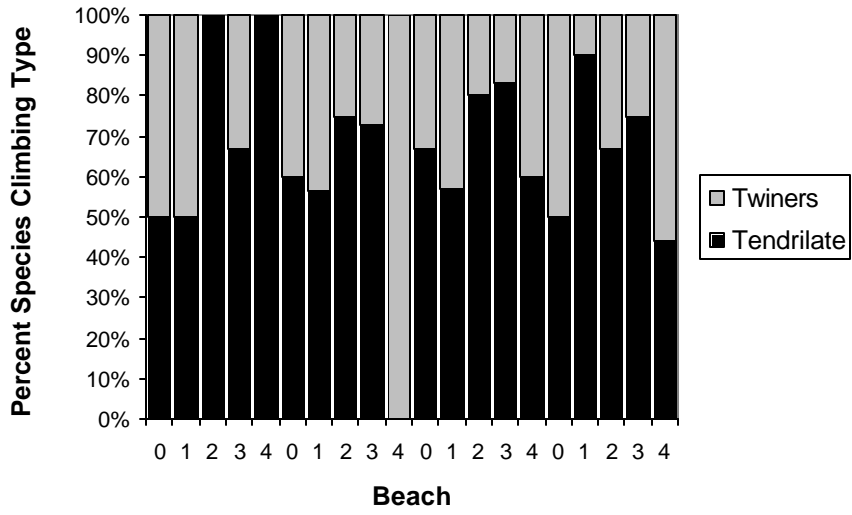
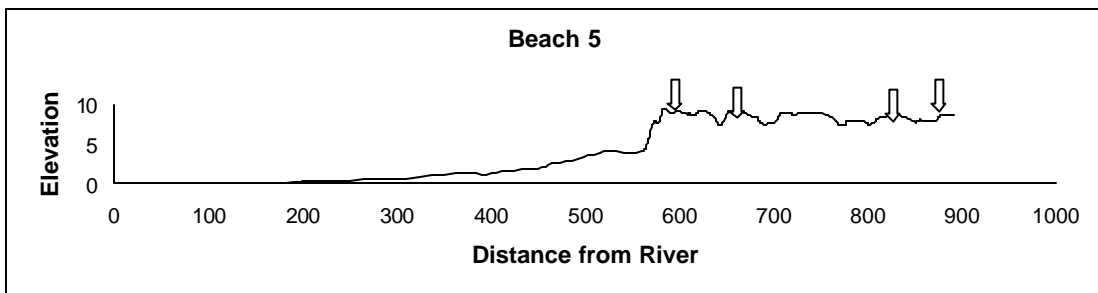
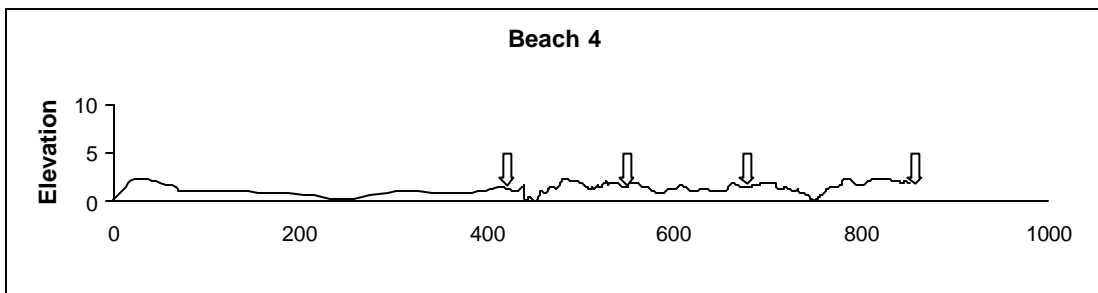
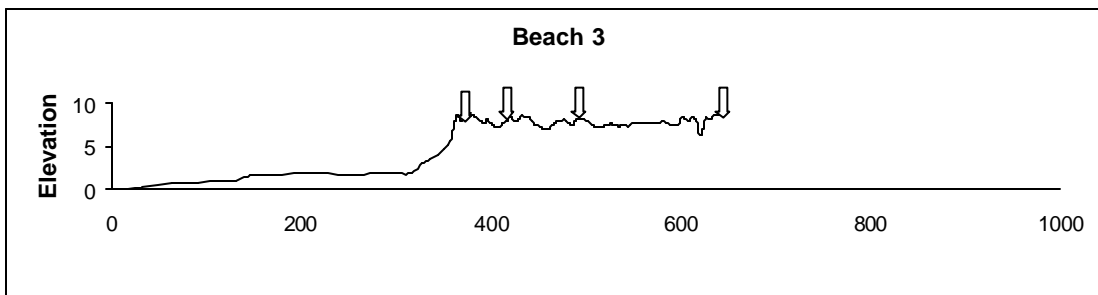
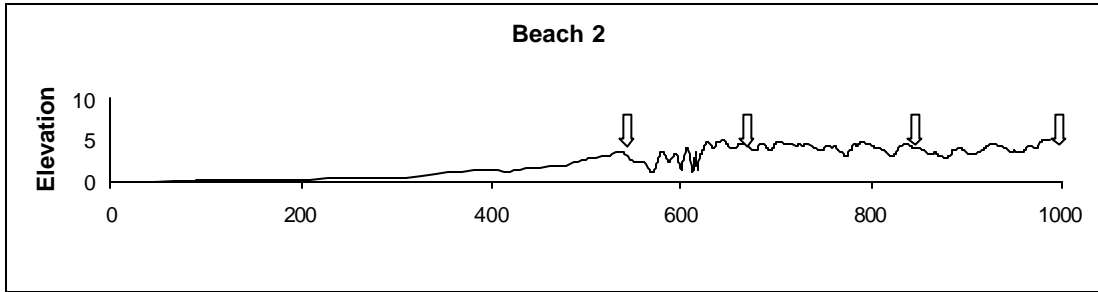
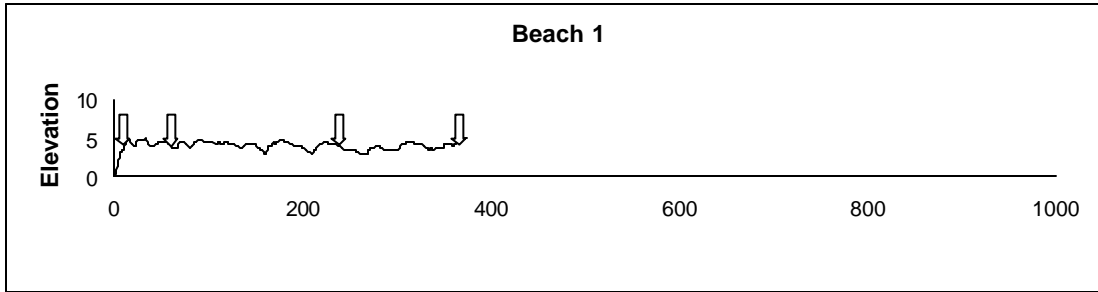


Table 1. Proportion of species dominance per transect.

TRANSECT	BEACH	FAMILY	GENUS SPECIES	COMPOSITION
Gynerium	Beach 1	Asteraceae	<i>Mikania sp.</i>	57.14%
		Vitaceae	<i>Cissus ulmifolia</i>	14.29%
	Beach 2	Convolvaceae	<i>Ipomea sp.</i>	16.67%
		Sapindaceae	<i>Paullinia sp.</i>	16.67%
	Beach 3	Cucurbitaceae	<i>Psiguria ternata</i>	81.82%
		Vitaceae	<i>Cissus ulmifolia</i>	13.64%
	Beach 4	Cucurbitaceae	<i>Psiguria ternata</i>	71.74%
		Vitaceae	<i>Cissus ulmifolia</i>	13.04%
Beach 5	Vitaceae	<i>Cissus ulmifolia</i>	57.89%	
	Cucurbitaceae	<i>Psiguria ternata</i>	21.05%	
Cecropia	Beach 1	Sapindaceae	<i>Paullinia sp. 6</i>	46.67%
		Cucurbitaceae	<i>Fevillea cordifolia</i>	16.67%
	Beach 2	Sapindaceae	<i>Paullinia sp. 6</i>	50.00%
		Sapindaceae	<i>Paullinia sp. 5</i>	8.33%
	Beach 3	Bignoniaceae	<i>Arrabidaea platyphylla</i>	40.00%
		Rhamnaceae	<i>Gouania sp.</i>	40.00%
	Beach 4	Urticaceae	<i>Urera baccifera</i>	38.60%
		Sapindaceae	<i>Paullinia sp. 6</i>	36.84%
Beach 5	Sapindaceae	<i>Paullinia sp. 10</i>	34.78%	
	Acanthaceae	<i>Mendoncia sp.</i>	30.43%	
Ficus / Cedrela	Beach 1	Cucurbitaceae	<i>Fevillea cordifolia</i>	37.50%
		Sapindaceae	<i>Paullinia sp. 6</i>	21.88%
	Beach 2	Sapindaceae	<i>Paullinia sp. 6</i>	45.71%
		Cucurbitaceae	<i>Fevillea cordifolia</i>	17.14%
	Beach 3	Bignoniaceae	<i>Paragonia pyramidata</i>	45.45%
		Amaranthaceae	<i>Pfaffia sp.</i>	18.18%
	Beach 4	Bignoniaceae	<i>Arrabidaea platyphylla</i>	50.00%
		Sapindaceae	<i>Paullinia sp.3</i>	35.71%
Beach 5	Sapindaceae	<i>Paullinia sp. 6</i>	64.86%	
	Bignoniaceae	<i>Arrabidaea platyphylla</i>	10.81%	
Mature / Transitional	Beach 1	Sapindaceae	<i>Paullinia sp. 6</i>	50.00%
		Cucurbitaceae	<i>Fevillea cordifolia</i>	15.38%
	Beach 2	Bignoniaceae	<i>Arrabidaea platyphylla</i>	41.79%
		Sapindaceae	<i>Paullinia sp. 6</i>	19.40%
	Beach 3	Sapindaceae	<i>Paullinia sp. 9</i>	22.64%
		Bignoniaceae	<i>Arrabidaea platyphylla</i>	11.32%
	Beach 4	Sapindaceae	<i>Paullinia sp. 6</i>	36.36%
		Bignoniaceae	<i>Arrabidaea platyphylla</i>	27.27%
Beach 5	Bignoniaceae	<i>Paragonia pyramidata</i>	25.00%	
	Sapindaceae	<i>Paullinia sp. 11</i>	25.00%	

Appendix A. Topography of beaches. Arrows represent transects from the river to mature/transitional forest.



Appendix B. List of liana species (> 1cm DBH) found on each transect

TRANSECT	BEACH	FAMILY	GENUS	SPECIES	# OF INDIVIDUALS
Gynerium	1	Aster	Mikania	sp.	4
		Cucu.	Fevillea	cordifolia	1
		Urtic.	Urera	baccifera	1
		Vita.	Cissus	ulmifolia	1
	2	Amar.	Chamisoa	sp.	1
		Conv.	Ipomea	sp.	1
		Sapi.	Paullinia	sp.	1
	3	Cucu.	Gurania	sp.	1
		Cucu.	Psiguria	ternata	18
		Vita.	Cissus	ulmifolia	3
	4	Bign.	Clytostoma	uleanum	1
		Cucu.	Gurania	sp.	1
		Cucu.	Psiguria	ternata	33
		Malp.	Stigmaphyllon	maynense	1
		Meni.	Chondrodendron	tomentosum	1
		Sapi.	Paullinia	sp. 6	1
		Sapi.	Serjania	glabrata	1
		Malv.	Byttneria	pescapraeifolia	1
		Vita.	Cissus	trifoliata	1
		Vita.	Cissus	ulmifolia	6
5	Bign.	Paragonia	pyramidata	1	
	Cucu.	Gurania	sp.	1	
	Cucu.	Psiguria	ternata	4	
	Sapi.	Paullinia	sp.3	1	
	Vita.	Cissus	ulmifolia	11	
Cecropia	1	Acan.	Medoncia	sp.	1
		Arac.	unidentified	sp.	1
		Aster.	Mikania	sp.	1
		Bign.	Arrabidaea	platyphylla	1
		Bign.	Paragonia	pyramidata	4
		Conv.	Ipomea	sp.	1
		Cucu.	Fevillea	cordifolia	5
		Icac.	Leretia	sp.	1
		Sapi.	Paullinia	sp. 6	14
		Vita.	Cissus	ulmifolia	1
		2	Arac.	unidentified	sp.
	Bign.		Arrabidaea	platyphylla	1
	Bign.		Paragonia	pyramidata	1
	Conv.		Ipomea	sp.	1
	Cucu.		Fevillea	cordifolia	2
	Cucu.		Psiguria	ternata	1
	Malp.	Stigmaphyllon	maynense	1	

TRANSECT	BEACH	FAMILY	GENUS	SPECIES	# OF INDIVIDUALS
Cecropia	2	Sapi.	Paullinia	sp.5	2
		Urtic.	Urera	baccifera	1
		Sapi.	Paullinia	sp. 6	12
	3	Aster.	Mikania	sp.	1
		Bign.	Arrabidaea	platyphylla	4
		Rham.	Gouania	sp.	4
		Vita.	Cissus	microcarpa	1
	4	Bign.	Arrabidaea	platyphylla	2
		Cucu.	Fevillea	cordifolia	1
		Cucu.	Gurania	sp.	1
		Cucu.	Psiguria	ternata	11
		Meni.	Chondrodendron	tomentocarpum	6
		Passi.	Passiflora	riparia	1
		Phyto.	Seguiera	sp.	1
		Rham.	Gouania	sp.	2
		Rham.	Gouania	sp.3	1
		Sapi.	Paullinia	sp. 6	21
		Sapi.	Paullinia	sp.8	1
		Sapi.	Paullinia	sp.9	3
		Urtic.	Urera	baccifera	22
		Vita.	Cissus	ulmifolia	3
	5	Acan.	Medoncia	sp.	7
		Aster.	Wulffia	sp.	1
		Bign.	Arrabidaea	platyphylla	2
		Conv.	Ipomea	sp.	1
		Cucu.	Fevillea	peruviana	1
		Legu.	Bauhinia	glabra	2
Legu.		Bauhinia	sp.5	1	
Legu.		Bauhinia	sp.10	8	
Legu.		Bauhinia	sp.12	2	
Vita.		Cissus	ulmifolia	1	
Ficus / Cedrela	1	Acan.	Mendoncia	sp.	1
		Aster.	Wulffia	sp.	3
		Bign.	Paragonia	pyramidata	5
		Cucu.	Fevillea	cordifolia	12
		Cucu.	Gurania	sp.	2
		Sapi.	Paullinia	sp. 6	7
		unid.744			2
	2	Apoc.	Aspidospermatinae	sp.	2
		Arac.	unidentified	sp.	1
		Bign.	Arrabidaea	platyphylla	1
		Bign.	Paragonia	pyramidata	5
		Cucu.	Fevillea	cordifolia	6

TRANSECT	BEACH	FAMILY	GENUS	SPECIES	# OF INDIVIDUALS	
Ficus / Cedrela	2	Meni.	Chondrodendron	tomentocarpum	2	
		Sapi.	Paullinia	sp.1	2	
		Sapi.	Paullinia	sp. 6	16	
	3	Amar.	Pfaffia	sp.	2	
		Bign.	Arrabidaea	platyphylla	1	
		Bign.	Paragonia	pyramidata	5	
		Rham.	Gouania	sp.	1	
		sapi	Paullinia	sp.14	1	
		unid. 812			1	
	4	Bign.	Arrabidaea	platyphylla	7	
		Bign.	Clyostoma	uleanum	2	
		Malp.	Mascagnia	sp.	1	
		Rham.	Gouania	sp.	1	
		Rham.	Gouania	sp.3	5	
		Sapi.	Paullinia	sp. 6	3	
		Vita.	Cissus	ulmifolia	2	
	5	-	-	-	-	-
		Apoc.	Aspidospermatinae	sp.	1	
		Bign.	Arrabidaea	platyphylla	4	
		Bign.	Paragonia	pyramidata	1	
		Conv.	Ipomea	sp.	1	
		Meni.	Chondrodendron	tomentocarpum	1	
		Meni.	Disciphania	ernstii	1	
		Piper.	Piper	sp.	1	
		Sapi.	Paullinia	sp. 6	24	
		Sapi.	Paullinia	sp.12	1	
	Sapi.	Serjania	glabrata	1		
Vita.	Cissus	ulmifolia	2			
Mature / Transitional	1	Amar.	Pfaffia	sp.	2	
		Arac.	unidentified	sp.	1	
		Bign.	Paragonia	pyramidata	2	
		Cucu.	Fevillea	cordifolia	4	
		Legu.	Pipiadenia	sp.	1	
		Sapi.	Paullinia	sp. 6	13	
		unid.680			3	
	2	Acan.	Medoncia	sp.	3	
		Amar.	Chamisoa	sp.	1	
		Amar.	Pfaffia	sp.	1	
		Aster.	Mikania	sp.	1	
		Bign.	Arrabidaea	platyphylla	28	
		Bign.	Clytostoma	uleanum	6	
		Bign.	Paragonia	pyramidata	1	
		Poly.	Moutabea	aculeata	1	
		Rham.	Gouania	sp.	2	

TRANSECT	BEACH	FAMILY	GENUS	SPECIES	# OF INDIVIDUALS		
Mature / Transitional	2	Sapi.	Paullinia	sp. 6	13		
		Sapi.	Paullinia	sp.7	3		
		Sapi.	Serjania	glabrata	1		
		Sapi.	Serjania	inflata	1		
		Vita.	Cissus	ulmifolia	1		
		unid.449				7	
	3	Bign.	Arrabidaea	platyphylla	6		
		Bign.	Clytostoma	uleanum	6		
		Bign.	Lundia	corymbifera	1		
		Bign.	Paragonia	pyramidata	3		
		Cucu.	Fevillea	cordifolia	1		
		Cucu.	Gurania	sp.	3		
		Cucu.	Psiguria	ternata	1		
		Legu.	Dioclea	ucayalina	1		
		Legu.	Bauhinia	sp.	1		
		Passi.	Passiflora	riparia	1		
		Passi.	Passiflora	sp.4	2		
		Passi.	Passiflora	sp.9	12		
		Passi.	Passiflora	sp.14	1		
		Smila. .	Smilax	sp.	1		
		Urtic.	Urera	baccifera	2		
		Ulma.	Celtis	iguanaeus	1		
		Vita.	Cissus	ulmifolia	7		
		unid.87				1	
		unid.90				1	
		Bign.	Arrabidaea	platyphylla	12		
		Bign.	Clytostoma	uleanum	1		
		Bign.	Paragonia	pyramidata	4		
		Cucu.	Fevillea	cordifolia	3		
		Cucu.	Gurania	sp.	1		
		Malp.	Stigmaphyllon	maynense	1		
		Sapi.	Paullinia	sp. 6	16		
		Urtic.	Urera	baccifera	4		
		Ulma.	Celtis	iguanaea	1		
		4	unid. 335				1
			Acan.	Medoncia	sp.	1	
	Apoc.		Aspidospermatinae	sp.	1		
	Apoc.		Forsteronia	amblybasis	1		
	Apoc.		Forsteronia	sp.	2		
	Bign.		Paragonia	pyramidata	5		
	Cucu.		Fevillea	cordifolia	1		
	Meni.		Chondrodendron	tomentocarpum	1		
	Meni.		Disiphania	ernstii	1		
	Meni.		Disiphania	sp.5	2		
	5		Meni.	Disiphania	sp.11	5	