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J. Boone Kauffman

In the tropics, widespread deforestation and conversion of primary forests to agricultural and pasture lands has resulted in losses of composition, structure, and functions of forest landscapes. Deforestation in the tropics is typically preformed via slash-and-burn practices; the byproducts from combustion have been identified as the second-highest form of anthropogenically derived 'greenhouse-gases' (such as carbon dioxide) to the atmosphere, and have been linked to the warming of the earth. Landscape-scale measures of species composition and biomass structure of primary forests are important for two reasons: (i) they provide accurate, land-based measures to predict what has been lost due to land-uses, and (ii) they aid in the discovery of key factors which explain patterns in compositional and structural diversity that are useful for defining conservation objectives. In this thesis, I enumerate the landscape-level patterns in species composition and biomass and C structure for 20-0.79 ha primary tropical forest stands within the region of "Los Tuxtlas", Veracruz, Mexico. These 20 sites were selected to capture the variability in composition and structure with respect to an array of environmental variables. These variables included a wide elevational range (15 – 1280 m.a.s.l.), variable slopes (Range: 3 – 41% slope), 3 soil-types (ash derived, lava flows, and weathered soils), a gradient of mean annual temperatures (~19.5 – 25.7°C), a broad precipitation range (2500 – 4000 mm year^{-1}), a rainfall frequency range (i.e. max rainfall in 24 hours; ranged 30 - >100 mm day^{-1}), and 3 Holdridge Life Zones (Tropical Moist Forest, Subtropical Wet Forest, and Subtropical Lower Montane Rain Forest).

Species composition was highly correlated with the environmental variables, particularly elevation. In general for plants ≥10 cm dbh, site species richness declined at a rate of ~2 species per 100 m rise in elevation. Forest sites located at similar elevations were most similar in their species compositions as compared with sites separated by large elevational differences. Despite the gradual change in species richness and composition, four sub-regions, or forest environments, within Los Tuxtlas were identified that had different species compositions and distinct combinations of elevation, soil-types, and climates. These four sub-regions were described as community-types according to their geographic location: Lowland-Reserve (LR), La Perla Plateau (LP), Volcanic Upslope (VU), and Cloud Forests (CF). The LR, LP, and VU community-types were coarsely described as Tropical Evergreen Forests (TEF's; INEGI 2001). All community-types corresponded with classifications within the Holdridge Life Zone System; the LR community-type was classified as Tropical (transition to Subtropical) Moist Forest; LP and VU community-types were classified as Subtropical Wet Forest, and the Cloud Forest community-type was classified as Subtropical Lower Montane Rain Forest. These community-types and Life Zones are useful tools for conservation, as they represent unique forests that collectively capture much of the variation in the species richness and compositional diversity of the Los Tuxtlas region.

Unlike species composition, the variability in forest structure among the 18 TEF sites was not associated with the environmental variables of the Los Tuxtlas landscape. On average, TEF's had a total aboveground biomass (TAGB) of 422 ± 17 Mg ha^{-1} and 205 ± 8 Mg ha^{-1} total aboveground carbon (C). The TAGB and C pools for Cloud Forests was ~18% lower than TEF's, and averaged 346 ± 1 and 168 ± 1 Mg ha^{-1}, respectively. The majority of this biomass difference was due to large trees within the forest structure. Cloud Forests had generally fewer trees ≥70 cm dbh, and a more even distribution of trees 30-70 cm dbh than TEF's. The biomass contribution of large trees (≥70 cm dbh) accounted for most, if not all, of the variation in TAGB and C for these tropical forests. The relatively high TAGB and C pools implicates Los Tuxtlas forests as a significant pool of aboveground biomass and C within the Neotropics.

Landscape Level Patterns in Biodiversity: Plant Species and Biomass Structure

by

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I understand that my thesis will become part of the permanent collection of Oregon State University Libraries. My signature below authorizes release of my thesis to any reader upon request.

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Christopher Heider, Author

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I wish to thank all the people who have supported, encouraged, and challenged me throughout all phases of this project. This has been a very rewarding experience for me personally, it has enhanced my understanding of ecology, and more importantly, has deepened my respect and awe for the mysteries of the rainforest.

Before I continue, I insist upon offering a quick but very important disclaimer: Throughout this thesis, you will read sentences constructed in the First Person (i.e. I, Me, My). This was a recommendation by my wise committee, but I register my protest here, in writing, that I do not find First Person to be completely appropriate. While it is true that I wrote this work, many people, especially the following individuals, contributed greatly to the success of this project.

Foremost, I would like to thank my major professor, Dr. Boone Kauffman, as his enjoyment and love of ecology has made me appreciate the forest for the trees. He provided me with a great opportunity and framework to learn and discover, and the freedom and encouragement to succeed. I thank Dr. Víctor Jaramillo for his tremendous help in Mexico, which seemed to appear at precisely the moment that I realized I needed it. To my committee members, I thank Dr. Mark Harmon for his advice and insight into ecology, and for the enlightening opportunity to help him in Los Tuxtlas on his wood decomposition study; it was an experience that helped me to recognize the importance of life and death in tropical forests. I thank Dr. Bruce Coblentz because he always left his door open to me, and he could ask me the right questions. I am grateful to the U.S. Environmental Protection Agency and the OSU Fisheries and Wildlife Mastin Fund for monetary support for this project.

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And finally I ask you, Dear Reader, for a moment of solemn reflection for the only casualty from this great expedition: the tan, 1985 Chevrolet Suburban that was resurrected from Motor Pool surplus and rechristened "*Guadelupe*". Instead of living out her golden years with all the other mechanically-challenged SUV's in the OSU scrap yard, she came back for one last shot at glory and survived two engine fires, three flat tires, a "cleaning" by the *brujos* of Catemaco, sheared alignment pins, an arc-welded frame, a ruptured gas tank, two "U"-joint welds, and countless dislodged shock absorbers. In all, she gave us 10,000 more miles and took us to the ends of the razor-sharp lava "roads" and high-elevation cattle pastures so Miguel, Santiago, Braulio, Prax and I could walk to where No Ecologist Has Gone Before. I don't know how, but it worked, and I'm here to tell you what we found. May you rest in pieces, *Guadelupe*.

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CHAPTER 1

INTRODUCTION

Deforestation and land-use conversion from forests to agricultural lands and pastures has dramatically changed the structure, composition, and function of forest landscapes. In the tropics, land-use conversion is often accomplished by slash-and-burn practices, which result in fluxes of terrestrial carbon (C) and nutrient pools to the atmosphere in the form of radiatively-active gases. These 'greenhouse' gases are primarily carbon dioxide (CO_2), carbon monoxide (CO), methane (CH_4), and nitrous oxide (N_2O) (Houghton 1994; Cairns et al. 1995), and have been directly linked to warming of the earth's atmosphere (IPCC 2001). Of all vegetation, tropical evergreen forests (TEF's) store nearly 30% of the world's terrestrial aboveground C and are second only to wetlands in net primary production (Houghton and Skole 1990); yet these forests are experiencing the highest rate of deforestation than any other forest type (IPCC 2001).

TEF's have long been recognized as areas of high biological diversity. They are estimated to contain approximately half of the world's species although they only occupy ~11% of the Earth's total land surface (Wilson 1988, Dixon et al. 1994). TEF's of Mexico are of particular importance as they represent the northernmost forests of their type and the most biologically diverse forest type in North America (Dirzo and Garcia 1992). Approximately 10% of the world's biodiversity is concentrated in Mexico (Flores and Gerez, 1988), and Mexico has been recognized as one of the most biologically diverse countries in the world (Dirzo and Raven 1991; MacNeely et al. 1990). The TEF landscape of the Los Tuxtlas region of Southeast Veracruz has experienced extraordinary rates of deforestation. From 1967 to 1986, ~84% of the primary TEF's of the Los Tuxtlas region were converted to pastures and agricultural lands at a rate of approximately 4.2% $year^{-1}$, with an estimated total loss to date of 91% (Hughes et al. 2000, Dirzo and García 1992). For Los Tuxtlas, conversion of primary forest to non-forest (i.e. agricultural land-uses) through slash-and-burn practices was found to convert approximately 95% of C ha^{-1} to the atmosphere (Hughes et al. 2000). Based upon local-scale measurements, Hughes et al. (2000) estimated that burning due to land-uses could convert ~30 Tg of terrestrial biomass to the atmosphere, of which ~14 Tg is C. The high rate of deforestation within the Los Tuxtlas region has clear implications as a loss of terrestrial C related to climate change, but what is less known how the landscape-scale variability in the total aboveground biomass (TAGB) and C pools affects these TAGB and C estimates, and what losses to plant species accompanies this loss in forest structure.

Biological diversity has been described as having three complementary components: composition, structure, and function (Noss 1990; Perry 1994). Dramatic losses in species composition are often accompanied by a loss in structure (Terborgh 1992), and ultimately may result disruptions of ecosystem hydrology, and ecosystem nutrient and carbon cycles (Silver et al. 1996, Laurance et al. 1997). It has been demonstrated that land-uses, particularly the conversion of primary forests to agricultural and pasture lands, have resulted in habitat loss and the extirpation of native species (Rappole and Morton 1985; Dirzo and Miranda 1990; Dale et al. 1994). To better understand the site-specific consequences of land-use on biodiversity, it is important to explore the relationships among species composition, structure, and function within primary forests. Many have recognized this (Franklin 1988; Terborgh 1992; Perry 1994), and have stressed the importance of understanding structural and compositional diversity in order to quantify the functional roles of species within primary ecosystems.

In late 1998, Mexican President Ernesto Zedillo expanded the 640 ha Los Tuxtlas Biological Station Reserve (LTBS) to include an additional 155,122 hectares in a newly declared biosphere reserve within the Los Tuxtlas region (Vargas 1998). While much information about the composition, structure, and the ecology of forests and the biota within Los Tuxtlas has been described (Bongers et al. 1988, Hughes et al 2000; Álvarez-Buylla and Martínez-Ramos 1992, González-Soriano et al. 1997), little to no such data exist outside the boundaries of 640 ha LTBS reserve. To better understand the biodiversity of the remaining forest landscape of the Los Tuxtlas region, it is important to identify the differences in compositional and structural diversity on multiple spatial scales.

In this thesis, my global objectives were to identify and describe the patterns of compositional and structural diversity for the primary forests throughout the topographically diverse Los Tuxtlas region. The environmental variables that are characteristic of this region include a wide variation in elevation, slopes, soils, and climate. Specifically, I present results having had the following objectives: (Chapter 2) identify and describe the species richness and diversity among the dominant growth forms at local and regional scales; and (Chapter 3) to quantify and describe the total aboveground biomass (TAGB) and C pools for the Los Tuxtlas region, and how biomass and C varies within the forest structure, with respect to environmental variables and species composition.

CHAPTER 2

Landscape-Scale Patterns in Species Diversity for the Los Tuxtlas Region, Mexico

Christopher Heider

ABSTRACT

In the tropics, widespread deforestation and conversion of primary forest to agricultural and pasture lands has resulted in the loss of many species. Tropical rainforests are well-known for their high biological diversity, yet few studies have addressed the landscape-scale variation in plant species and structure within primary tropical forests, especially with respect to environmental attributes. In the topographically diverse landscape of the Los Tuxtlas region of SE Veracruz, Mexico, I sampled primary tropical forests with the objective to quantify and describe the variation in plant species richness and diversity as it relates to the environmental attributes of the landscape. Specifically, I identified plant species and measured for dbh (diameter at 1.3 m ht) rooted-plants ≥10 cm dbh within 20 – 0.79 ha primary forest stands; in 12 of these stands, all rooted-plants were identified and measured within all diameter classes (including <1.3 m in ht.). I did not consider epiphytes in my sampling. Forest stands were selected to incorporate the diverse environmental attributes of the forested landscape. These environmental attributes included a broad range of elevations, slopes, soil-types, and climate regimes. Each primary forest site was sampled using a nested plot design that was based on diameter-class; plots ranged from 0.79 ha to 0.25 m^2 in size. In the 20 forest stands, a total of 228 plant species (≥10 cm dbh) in 145 genera and 65 families were identified. For the 12 sites in which all rooted-plant species were identified, a total of 432 species within 270 genera and 110 families were encountered. These forests were predominately composed of rare species, or those species that occurred within only a few sites (i.e. low constancy). Of the 432 species in all diameter classes, 159 species (37% of all species) were only present within 1 of the 12 sites; 246 species (57% of all species) were present in two or fewer sites (i.e. <17% constancy). On the stand level (0.79 ha) for plants ≥10 cm dbh, the most abundant species represented a mean of 19% of the stem density; an average of 20 species, or 46% of the species richness (≥10 cm dbh) were represented by only one individual in that forest stand.

Species composition was highly correlated with the environmental attributes of the landscape. Along an elevational gradient for plants ≥10 cm dbh, species richness declined at a rate of ~2 species per 100 m rise in elevation. Forest sites located at similar elevations were most similar in their species compositions as compared with sites separated by large elevational differences. Incorporating soil-types and slopes with the gradual elevational

changes in species richness and composition, I identified four sub-regions, or forest environments, within Los Tuxtlas that had different species compositions and distinct combinations of elevational ranges, soil-types, and climates. These four sub-regions were described as community-types according to their geographic location: Lowland-Reserve (LR), La Perla Plateau (LP), Volcanic Upslope (VU), and Cloud Forests (CF). All community-types corresponded with classifications within the Holdridge Life Zone System; the LR community-type was classified as Tropical (transition to Subtropical) Moist Forest; LP and VU community-types were classified as Subtropical Wet Forest, and the Cloud Forest community-type was classified as Subtropical Lower Montane Rain Forest. These community-types and Life Zones are useful tools for conservation, as they represent unique forests that collectively capture much of the variability in species diversity within the Los Tuxtlas region.

INTRODUCTION

Biological diversity has been described as having three complementary components: composition, structure, and function (Noss 1990; Perry 1994). Dramatic losses in species composition are often accompanied by a loss in ecosystem structure (Terborgh 1992), and ultimately may result in disruptions of ecosystem hydrology, and ecosystem nutrient and carbon cycles (Silver et al. 1996, Laurance et al. 1997). It has been demonstrated that land-uses, particularly the conversion of primary forests to agricultural and pasture lands, have resulted in habitat loss and the extirpation of native species (Rappole and Morton 1985; Dirzo and Miranda 1990; Dale et al. 1994, Lugo 1988). To better understand the site-specific consequences of land-use on biodiversity, it is important to explore the relationships among species composition, structure, and function within primary forests. Many have recognized this (Franklin 1988; Terborgh 1992; Perry 1994), and have stressed the importance of understanding structural and compositional diversity in order to quantify the functional roles of species within primary ecosystems.

Tropical evergreen forests (TEF's) have long been recognized as areas of high biological diversity. They are estimated to contain approximately half of the world's species although they only occupy ~11% of the Earth's total land surface (Wilson 1988, Dixon et al.

1994). TEF's of Mexico are of particular importance as they represent the northernmost tropical forests of their type and the most biologically diverse forest type in North America. Approximately 10% of the world's biodiversity is concentrated in Mexico (Flores and Gerez, 1988), and Mexico has been recognized as one of the most biologically diverse countries in the world (Dirzo and Raven 1991; MacNeely et al. 1990). The TEF landscape of the Los Tuxtlas region of Southeast Veracruz has experienced extraordinary rates of deforestation. From 1967 to 1986, ≈84% of the primary TEF's of the Los Tuxtlas region were converted to pastures and agricultural lands at a rate of approximately 4.2% $year^{-1}$, with an estimated total loss to date of 91% (Hughes et al. 2000, Dirzo and García 1992). The high rate of deforestation within the Los Tuxtlas region poses a threat to biodiversity, and our capacity to conserve and to benefit from biodiversity is becoming more limited with persistent losses and fragmentation of the remaining primary forests.

In late 1998, Mexican President Ernesto Zedillo expanded the 640 ha Los Tuxtlas Biological Station Reserve (LTBS) to include an additional 155,122 hectares in a newly declared biosphere reserve within the Los Tuxtlas region (Vargas 1998). While much information about the composition, structure, and the ecology of forests and the biota within Los Tuxtlas has been described (Bongers et al. 1988, Hughes et al 2000; Álvarez-Buylla and Martínez-Ramos 1992, González-Soriano et al. 1997), little to no data exist about the compositional and structural diversity for the forest stands outside the boundaries of 640 ha LTBS reserve. To better understand the biodiversity of the remaining forest landscape of the Los Tuxtlas region, it is important to identify the differences in compositional diversity on multiple spatial scales. In this chapter, my objectives were to identify and describe the patterns of compositional and structural diversity for the primary forests of the Los Tuxtlas region. Specifically, I examined patterns in diversity as they related to a suite of environmental attributes. These attributes included a wide elevational range, variable slopes, three soil-types, and differences in climate (i.e. temperature and precipitation). My specific objectives were: (i) to describe the species richness and diversity among the dominant growth forms at community and landscape scales; (ii) to identify how species composition was related to the environmental attributes of the landscape; and (iii) to suggest specific sub-regions, or forest environments, in Los Tuxtlas that are in need of conservation and expanded study.

METHODS

Study Area

This study was conducted within the remaining primary forest fragments of the Los Tuxtlas region, located in Southeast Veracruz, Mexico (18° 30' N; 095° 06' W). The region consists of an isolated volcanic mountain range that parallels the Gulf Coast of Mexico (Figure 2.1) and provides a topographic barrier to weather systems entering the region from the Gulf of Mexico to the north. This area is approximately 90 x 50 km, and contains watersheds shaped by three volcanoes: Santa Marta, San Martín Pajapan, and San Martín de Los Tuxtlas (Dirzo and Garcia 1992). The study area was located along the slopes of San Martín de Los Tuxtlas, encompassing an altitudinal range from sea level to 1780 m at the summit of the Volcano. The dominant unaltered vegetation type is tall tropical evergreen forest (TEF, *selva alta perenifolia*, Ibarra-Manríquez et al 1997), and is considered the northernmost of its type in North America (Dirzo and Garcia 1992). Other vegetation types have been identified for this region, including mangroves, 'medium' evergreen forest (*selva mediana perenifolia*), tall *Liquidambar* forest, humid tropical oak (*Quercus*) forest (*selva con encinos*), cloud forest (*bosque tropical nuboso*), elfen forest (*bosque enano*), and many variations of perturbed vegetation types, including second growth forest (*acahuales*), croplands, and cattle pasture lands (Dirzo et al. 1997, Hughes et al. 2000). Within the region, the National University of Mexico (UNAM) maintains the Los Tuxtlas Biological Research Station (LTBS) and 640 ha biological reserve, containing mostly primary TEF vegetation.

Figure 2.1: The Los Tuxtlas region (*From*: Ibarra-Manríquez and Sinaca 1987), located in the southeastern portion of the state of Veracruz, Mexico. The Los Tuxtlas Biological Station Reserve (shaded area) is 640 ha in size. The region consists of variable slopes and an elevational gradient from sea level at the Gulf of Mexico extending to 1780 m at the summit of the Volcán San Martín de Los Tuxtlas.

Climate

Soto and Gama (1997) described four major climate zones within the Los Tuxtlas region that corresponded with elevation. Each climate zone was qualitatively described on the basis of mean annual temperature, mean annual precipitation, and rainfall intensity (i.e. average rainfall in a 24-hour period) (Soto and Gama 1997). Weather station data reported from five elevational transects revealed a general decline in mean annual temperature at a rate of ~0.5 °C for each 100 m rise in elevation above sea level (a.s.l.), beginning with a mean annual temperature of ~26 °C at sea level (Soto and Gama 1997, Appendix). Mean annual precipitation also increased with elevation, although rainfall intensity was higher at lower elevations (Soto and Gama 1997). These climate zones also corresponded to different Life Zones of the Holdridge System (Holdridge et al. 1971), using mean annual precipitation and mean annual temperature as explanatory variables. For Los Tuxtlas, these zones range from Tropical (transition to Subtropical) Moist Forest in the lower elevations to Subtropical Wet Forest in the mid-elevations to Subtropical Lower Montane Rain Forest in the upper elevations (Tosi and Watson personal communication, Holdridge et al. 1971) (Table 2.1).

Table 2.1: Climate zones within the Los Tuxtlas region, Veracruz, Mexico. Climate type is based upon mean annual temperature, mean annual rainfall, and rainfall intensity (Soto and Gama 1997).

Elevation Range (m.a.s.l.)	Temperature[*] (°C)	Rainfall[*] (mm/year)	Max. Rainfall in 24 H (mm)	Climate Type (Soto and Gama 1997)
<600	26 – 23	2500 – 3500	60 – >100	Hot, Monsoon
600 – 1000	23 – 21	3000 – 4000	40 – 50	Warm, Wet
1000 – 1600	21 – 18	3000 – 4000	30 – 40	Warm, Very Wet
>1600	<18	>4000	<30	Cool, Super Wet

[*]Mean annual temperature was modeled from data presented by Soto and Gama (Appendix A).

Geology and Soils

The topographically diverse landscape of the Los Tuxtlas region has been formed by an active volcanic history, involving more than 300 volcanic cones (Martin-Del Pozzo 1997). The most active and significant of these volcanoes has been the Volcán San Martín de Los Tuxtlas. The volcanic eruptions by the Volcán San Martín have contributed to the formation of three unique soil-types that appear to be correlated with elevation and age since formation. These soil-types are categorically described as ash-derived, lava flows, and weathered soils (i.e. weathered lava and ash) (Martin-Del Pozzo 1997). Ash deposits are located in the higher elevations and are the youngest of the three dominant soil-types. The most recent and noteworthy ash formation was caused by a major eruption by the Volcán San Martín in 1793. This eruption "completely destroyed all of the vegetation along the slopes of San Martín," and ash "continued to rain for a period of eight days" (Friedlaender and Sander 1923).

The majority of the lava flows within Los Tuxtlas were formed between 2.4 and 1.0 million years ago (Gonzáles-Caver and Nelson 1990). These lava flows are approximately 2 m thick and have similar characteristics in as pahoehoe lava of the Hawaiian archipelago (Martín-Del Pozzo 1997). Earlier volcanic activity (between 7 and 2 million years ago) had formed basalt deposits that were prone to erosion (Friedlaender and Sander 1923). These compose the weathered soils that are most commonly found in lowland areas, and due to their distance from the most active volcanoes, have not likely experienced the same intensity of disturbance related to recent volcanic activity.

Although no data are currently available for the Los Tuxtlas region on the soil chemistry and nutrient availability along the elevational gradient or for each of the three soil-types, studies from a similar volcanic region in Costa Rica indicated an increase in total N and C, soil organic matter, P, Ca, Mg, and ammonium with increasing elevation and decreasing soil age (Sollins et al. 1994). In addition, there was a decline in NO_3^{-1} and organic matter decomposition with increasing altitude (Sollins et al. 1994). In lower elevation forests over the weathered soils in Los Tuxtlas (ca. 150 – 350 m.a.s.l.), Hughes et al. (2000) reported total soil C ranged from 178 – 307 Mg ha^{-1} and total soil N ranged from 17 – 29 Mg ha^{-1} to a 1 m depth.

Data Collection

Twenty-0.79 ha sites (75 x 105 m) were selected to sample the species composition and structure of primary forest stands within the San Martín de Los Tuxtlas watershed of the Los Tuxtlas region. The presence of stumps or cut logs, livestock dung, or trails (by human, livestock, or timber exploitation) rendered a site unsuitable for this study. Site selection was limited due to the unavailability of recent aerial photographs, access difficulties, and the highly fragmented nature of the remaining forests. I selected sites without preconceived bias with the prime objective to capture the variability in primary stands with respect to the environmental attributes that were associated with the Los Tuxtlas landscape. Specifically, I selected sites throughout the elevational range (15 - 1280 m above sea level) and replicated sites on each of the 3 soil-types (henceforth described as 'ash-derived', 'lava flows', and 'weathered soils') (Martin-Del Pozzo 1997). All sites were located at least 150 m to several kilometers from a road or trail. I had no *a-priori* knowledge of forest structure or composition for any site. Elevation was measured using an altimeter that was calibrated daily to the elevation of the LTBS.

Each site was composed of a series of nested plots to sample rooted-plant species composition. Specifically, the aboveground components of the forest were divided into strata based on size – diameter at breast height (dbh, 1.3 m in height) — and growth form (Figure 2.2). The forest canopy (plants ≥10 cm dbh) was divided into three strata based on diameter class: tall-canopy (≥70 cm dbh), mid-canopy (30 - 70 cm dbh), and low-canopy (10 – 30 cm dbh) (Figure 2.2). The forest understory was categorized as plants at least 1.3 m in height and <10 cm dbh (i.e. 0 - 10 cm dbh). The forest floor strata was defined as all rooted plants <1.3 m in height. Species' growth forms included trees, palms, woody lianas, herbaceous vines, ferns, and free-standing herbaceous plants. Woody lianas and herbaceous vines were distinguished by the presence or absence of wood in mature stems. Palms were non-climbing members of ARECACEAE; the few climbing palm species of ARECACEAE were described as lianas, as their structural characteristics resembled lianas more than free-standing palms. I did not include epiphytes in my sampling.

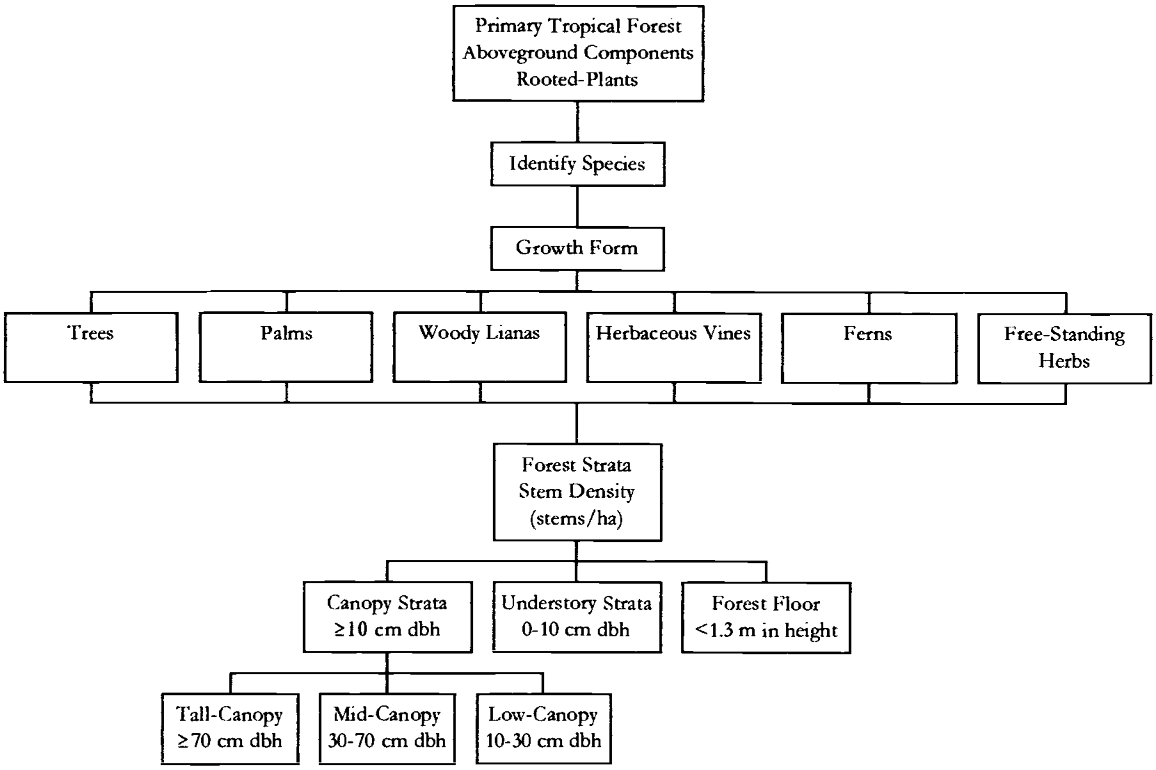

Figure 2.2: Diagram of sampling the aboveground components within a primary tropical forest. All rooted plants were identified to species and were assigned to one of six growth form categories. Each individual was classified according to its structural class within the forest strata, based on diameter at 1.3 m in height (dbh). Diameter classes were consolidated into three structural categories: the canopy strata (≥10 cm dbh), understory strata (0-10 cm dbh), and the forest floor (<1.3 m in height).

Tall- and mid-canopy composition and structure (≥30 cm dbh) were measured within the entire 0.79 ha plot (Figure 2.3, Table 2.2). All rooted plants ≥30 cm dbh were identified to species, assigned a growth form, and measured for dbh. In cases where buttress roots were present, dbh was measured above the buttress. I established a subplot (25 x 105 m) within the center of the larger plot to sample rooted plants ≥10 cm but <30 cm dbh (i.e. low-canopy strata). These individuals were also identified to species, assigned a growth form, and measured for dbh (Figure 2.3, Table 2.2).

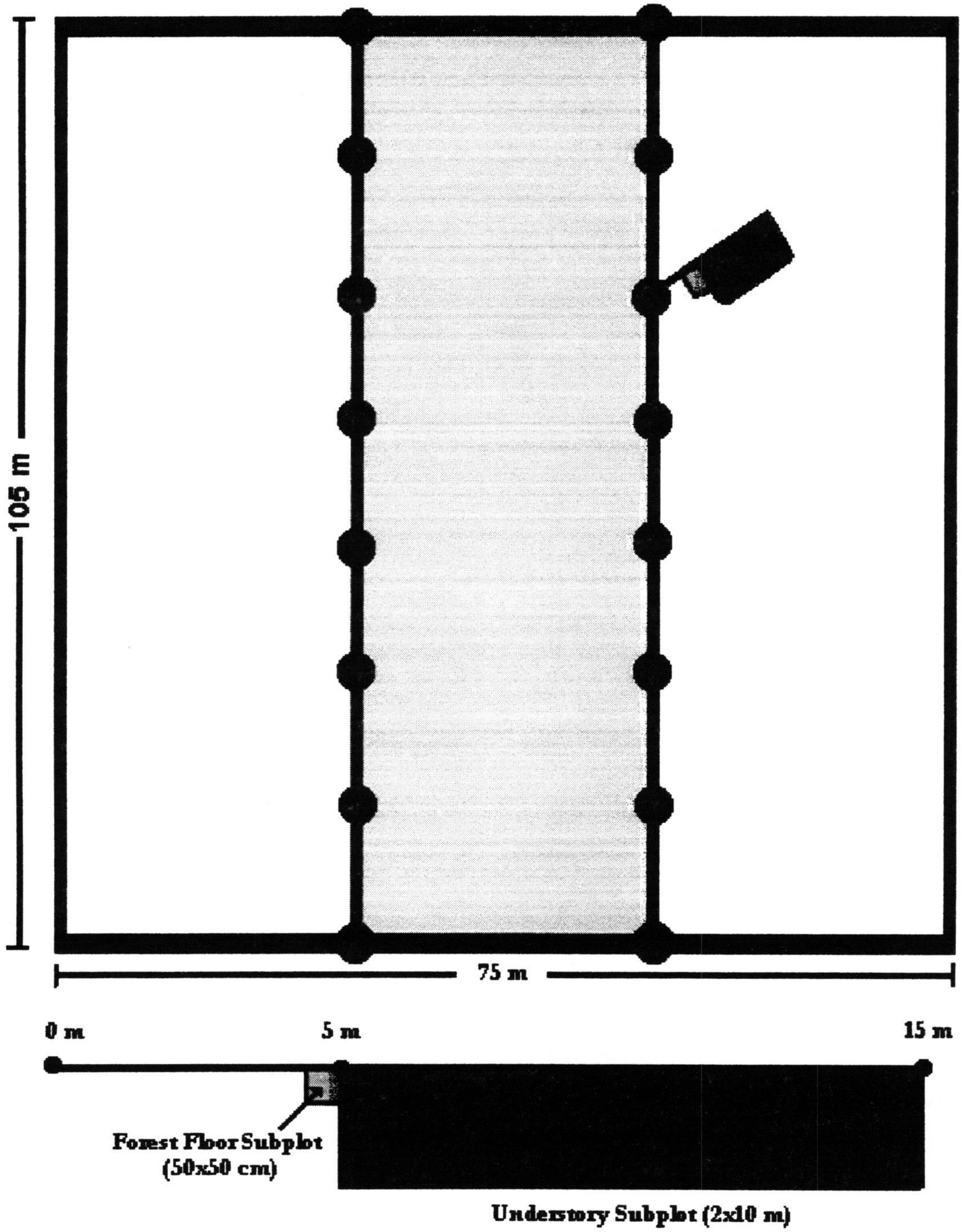

Figure 2.3: Nested-plot design for primary tropical forest sites. Tall and mid-canopy plants (≥30 cm dbh) were sampled in the entire site (75x105 m); low-canopy plants (10-30 cm dbh) were sampled in the center plot only (lightly shaded area, 25x105 m). Rooted understory plants (0-10 cm dbh) were sampled in 16 - 2x10 m belt transects (dark shaded area); forest floor plants (<1.3 m in height) were sampled in the 16 - 50x50 cm quadrats (medium shaded area). Species composition and structure for canopy plants (≥10 cm dbh) were quantified in 20 sites and understory and forest floor composition was included in 12 sites throughout the Los Tuxtlas region, Veracruz, Mexico.

I sampled the forest understory (0 – 10 cm dbh) along two parallel transects, originating at the 25 m and 50 m points along the 75 m edge of the site (Figure 2.3). Each transect line extended for the 105 m length of the plot. At equally spaced 15 m increments, 8 sample points were established for a total of 16 points per site. At each of these sample points, I established a 15 m transect in a random direction; parallel to this transect was a 2 x 10 m plot to sample understory species composition (Figure 2.3). All rooted stems were identified for species, growth form, and were measured for dbh.

Forest floor composition (plants <1.3 m in height) was sampled using a 50 x 50 cm plot, positioned at 4.5 m along each of the 15 m transects (16 plots per site) (Figure 2.3). In each of these plots, taxon, growth form and the abundance for each species was measured.

Table 2.2: Nested-sampling design for each 0.79 ha site sampled within the Los Tuxtlas region, Veracruz, Mexico. Forest strata were based upon diameter-classes of the forest, measured as diameter at 1.3 m in height (dbh). A total of 20-0.79 ha sites were selected for this study, 12 of which included understory and forest floor species composition.

Forest Strata	Diameter Class	Plot Dimensions	Plot Area (m^2)	No. of Plots $site^{-1}$	Total Area ($m^2 site^{-1}$)	No. of Sites Sampled
Tall Canopy	≥70 cm dbh	75 x 105 m	7875	1	7875	20
Mid Canopy	30-70 cm dbh	75 x 105 m	7875	1	7875	20
Low Canopy	10-30 cm dbh	25 x 105 m	2625	1	2625	20
Understory	0-10 cm dbh	2 x 10 m	20	16	320	12
Forest Floor	<1.3 m ht	50 x 50 cm	0.25	16	4	12

Canopy species, or those plants ≥10 cm dbh, were identified within all 20 sites (Table 2.2). At 12 of these sites, species in all forest strata were identified. Nomenclature followed that of Ibarra-Manríquez and Sinaca (1997), Sosa and Gomez-Pompa (1994), and Martinez et al. (1994). When possible, all individuals were identified to the species level.

Data Analysis

Species composition was based upon stem density (stems ha^{-1}). Species relative abundance (RA, %) within each site was calculated as the ratio of each species' stem density to the site total stem density. Because the overwhelming majority of stems were <1.3 m in height, relative abundance data were analyzed within the three dominant forest strata categories: canopy (≥10 cm dbh), understory (0-10 cm dbh), and forest floor (<1.3 m in height). Species richness of each site was defined as the total number of species occurring within all sample plots of that site (as in Table 2.2). Any species that could not be identified to even the family level was excluded from all compositional analyses.

Species constancy was defined as the percentage of all sites that contained a given species (Oosting 1956). For example, if a particular canopy species occurred at least once in 10 of the 20 sites, that species would have a constancy of 50%. Species constancy was calculated for canopy species (20 sites) and for species within all forest strata (12 sites). I identified 'rare' species as those with a low constancy (i.e. <20%) (Oosting 1956, Richards 1996).

The similarity in species composition between two sites was compared using the percentage similarity index (PS, %). If two sites were completely similar in their species composition and their relative abundance for each species, the percentage similarity index (PS) of the two sites would be 100%. This value was calculated as follows (Krebs 1985):

$$PS_{12} = \Sigma \text{ minimum } (p_{1i}, p_{2i})$$

Where, PS_{12} = Percentage Similarity between sites 1 and 2

p_{1i} = Relative abundance of species i in site 1

p_{2i} = Relative abundance of species i in site 2

minimum = whichever is lower, p_{1i} or p_{2i}

A similarity matrix was calculated for all combinations of sites for canopy species composition (20 sites, 190 comparisons) and for species composition in all forest strata (12 sites, 66 comparisons). The difference in elevation for all combinations of sites was calculated. I used regression analysis to determine if there was an association between similarities in species composition and elevation. Specifically, I tested if sites closer in proximity along the elevational gradient were more or less similar in their canopy species composition than sites separated by large elevational differences.

Species-area relationships were constructed to examine the rate at which new species were encountered with the addition of sampled sites (PC-ORD program; McCune and Mefford 1997). Species richness was plotted against an increasing number of sampled sites. Using this relationship, I examined the distribution of species within the entire sample range, and examined the effectiveness of my sampling of the species richness on the landscape-scale.

To determine the degree by which sites could be grouped based upon their species composition, I used a cluster analysis. The matrix contained the stem density (stems ha^{-1}) of 158 canopy species in all 20 sites. This matrix did not contain 70 species because they occurred in only one site (i.e. 70 species had a constancy of 5%). The exclusion of these rare species reduced noise that is associated with matrices containing a high proportion of zeros (i.e. 'the zero-truncation problem'; Beals 1984). By this method, sites were grouped into community-types based upon the species that were present, rather than having been grouped because of their common absence of species (i.e. common zeros in the species matrix). Following cluster analysis, an analysis by Multiple Response Permutation Procedure (MRPP, Milke 1984) was used to test if groups were significantly different in their environmental variables of elevation, slope, and soil-type. All multivariate statistics were performed using PC-ORD software package (McCune and Mefford 1997).

RESULTS

Species Richness

For the canopy strata (≥10 cm dbh), a total of 228 species within 145 genera and 65 families were identified within the 20 study sites (Appendix). All species of this size class were trees, with the exception of 2 liana species: *Abuta panamensis* (Standl.) Krukoff & Barneby (MENISPERMACEAE) and *Machaerium floribundum* Benth. (FABACEAE). Twenty of these taxa could be identified only to the genus or family level. In addition, five unknown individuals were found in two sites that could not be identified even to the family level (two trees and three lianas). For the 12 sites in which all forest strata were measured, 320 plant species within 209 genera and 92 families were identified within the understory (0 - 10 cm dbh), and 212 species within 146 genera and 78 families were identified within the forest floor strata (<1.3 m in height) (Table 2.3). For all forest strata, a total of 432 species within 270 genera and 110 plant families were identified within the 12 sites (Appendix). Thirty-one taxa could be identified only to the genus or family level. Seven unknown individuals within three sites (six trees and one liana) could not be identified even to the family level.

Table 2.3: The combined total species richness by growth form within each of the three main forest strata for the 12-0.79 ha tropical forest sites in the Los Tuxtlas region, Veracruz, Mexico.

Growth Form	Canopy ≥10 cm dbh	Understory 0-10 cm dbh	Forest Floor <1.3 m ht	All Forest Strata
Trees	193	184	102	263
Palms	0	7	6	8
Lianas	2	87	44	90
Herbaceous Vines	0	25	21	28
Ferns	0	7	12	14
Herbaceous Plants	0	10	27	29
Total Species Richness	**195**	**320**	**212**	**432**

On average (± SE, n=12 sites), each site contained a total of 105 ± 7 species within all forest strata (Median = 115; Range: 48 – 128 species). Of these species, a mean of 44 ± 3 species were within the canopy strata (Median = 44; Range: 20 – 60 species), 64 ± 6 species were within the understory (Median = 72; Range: 28 – 91 species), and 36 ± 3 species were within the forest floor strata (Median = 35; Range: 19 – 53 species) (Table 2.4). The average stem density (± SE, n=20 sites) of the canopy strata was 401 ± 18 stems ha^{-1}, yielding an average of 9.1 stems $species^{-1}$. Of these 401 stems, the most abundant canopy species of a site was represented by an average of 78 ± 8 stems ha^{-1}, or ~19% of the canopy abundance. A mean of 20 canopy species (46% of the canopy species richness) were represented by only one individual in a site.

The majority of the site species richness was in the tree and liana growth forms. Trees and lianas accounted for a mean of 64% and 18% of the total species richness encountered in sites, and an average of 29% and 12% of the site total stem density, respectively (Table 2.4). While the species richness of herbaceous vines was low (~10% of the species richness), they comprised a mean of 41% of the total stem density within a site. A mean of 94 plant species, or 89% of the site species richness, was encountered in plants ≥1.3 m in height (i.e. the canopy and understory strata only). Of all plants ≥1.3 m in height, a mean of 47% of the stem density was trees, 26% was herbaceous vines, 15% was lianas, 8% was palms, 2% was ferns, and 1% was free-standing herbaceous plants.

Rare Species in the Los Tuxtlas Region

The species composition of sites was predominately composed of rare species (i.e. species of low constancy) (Figure 2.4). Of the 432 species in all forest strata, 159 species (37% of all species) were present in only 1 of the 12 sites (8% constancy), and 246 species (57% of all species) occurred in two or fewer sites (<17% constancy; Figure 2.4). The pervasive herbaceous vine, *Monstera acuminata* C. Koch (ARACEAE), was the only species common to all 12 sites (100% constancy), had a maximum dbh of 1.9 cm, and comprised a mean of 10% and 7% of the understory and forest floor stem density of each site, respectively.

For the canopy strata (Figure 2.4), 70 species (31%) were encountered in only 1 of the 20 sites (5% constancy) and 109 species (48% of all canopy species) were encountered in two or fewer sites (≤10% constancy). No canopy species were common to all 20 sites. The most widely distributed canopy species was *Pseudolmedia oxyphyllaria* Donn. Sm. (MORACEAE). *P. oxyphyllaria* was found in 18 of the 20 sites (90% constancy), had a maximum dbh of 65 cm, and constituted an average of 8% of the abundance, 4% of the basal area, and 3% of the biomass of the canopy strata of each site (Chapter 3).

Table 2.4: The average partitioning of plant species richness (*S*) and relative abundance (*R.A.*, %) based upon rooted-plant density among the six growth forms within the three main forest strata—separated by diameter classes—for 12-0.79 ha tropical forest sites in the Los Tuxtlas region, Veracruz, Mexico. Actual stem densities are presented in Chapter 3 of this thesis.

Growth Form	**Canopy ≥10 cm dbh**		**Understory 0-10 cm dbh**		**Forest Floor <1.3 m ht**		**All Forest Strata**	
n = 12 sites	***S***	**R.A.**	***S***	**R.A.**	***S***	**R.A.**	***S***	**R.A.**
Trees	43	>99%	35	46%	15	28%	67	29%
Palms	0	0%	3	8%	2	7%	3	7%
Lianas	<1	<1%	16	16%	7	12%	19	12%
Herbaceous Vines	0	0%	9	27%	7	41%	10	41%
Ferns	0	0%	1	2%	2	4%	3	4%
Herbaceous Plants	0	0%	<1	1%	3	7%	4	7%
Mean Species Richness	44 ± 3		64 ± 6		36 ± 3		105 ± 7	

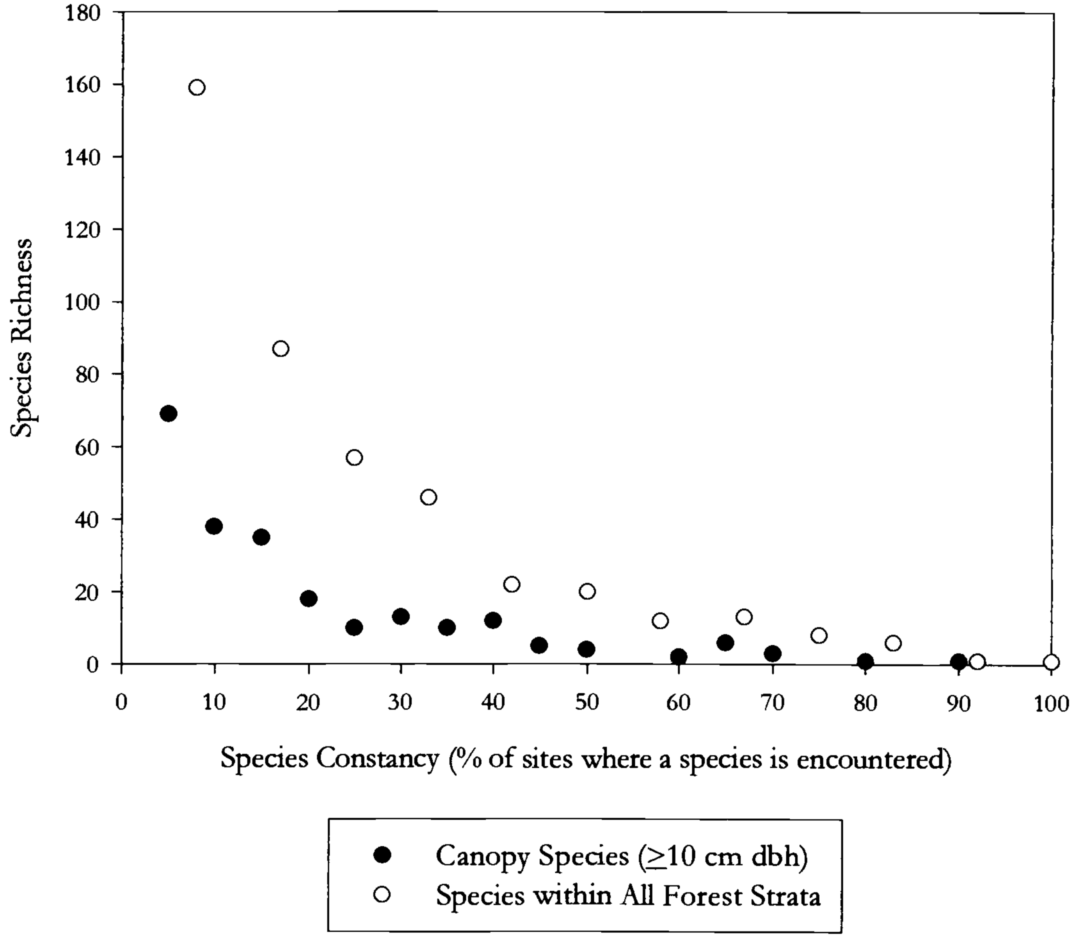

Figure 2.4: Species richness versus species constancy for canopy species (≥10 cm dbh, n=20 sites) and for species within all forest strata (n=12 sites). Species constancy was defined as the percentage of the total number of sampled sites in which a species was encountered. As evidenced from this graph, the majority of the species richness from the entire study was encountered in fewer than 20% of the sampled sites. Only one species, *Monstera acuminata*, was encountered in 100% of the sampled sites.

Differences in Species Composition

Overall, sites were markedly different in their species compositions. The average PS between any two sites was 22.3% for all forest strata (Range: 0.9 – 45.7%, n=12 sites), and 17.4% for canopy species (Range: 0.6 – 48.9%, n=20 sites) (Appendix). Species-area relationships indicated that on average, any two sites had 70 species that were not common to both sites (Figure 2.5). Thirty of these species were within the canopy, 46 were in the understory, and 27 species were within the forest floor strata. This difference between two 0.79 ha sites resulted in a 66% increase in total species richness (from 105 to 175 species), with a corresponding increase in species richness within the canopy, understory, and forest floor strata of 69%, 72%, and 76%, respectively. These results highlight how species diversity could be impacted with just one, 0.79 ha deforestation event within the Los Tuxtlas region.

Fewer new species were encountered with an increasing number of sampled sites, as evidenced by the 'flattening' of the species-area curve (Figure 2.5). An average of 13 new species were added with the addition of the 12th site, and this addition corresponded to a 3% increase in the total species richness (from 419 to 432 species). Of the 13 new species, 5 species were added to the canopy (3% increase), 12 species were added to the understory (4% increase), and 10 species were added to the forest floor strata (5% increase). While these results indicate that ≥95% of all species encountered in this study were detected within 11 of the 12 sampled sites, the species-area curves indicate that sampling greatly underestimated the species diversity of the Los Tuxtlas region.

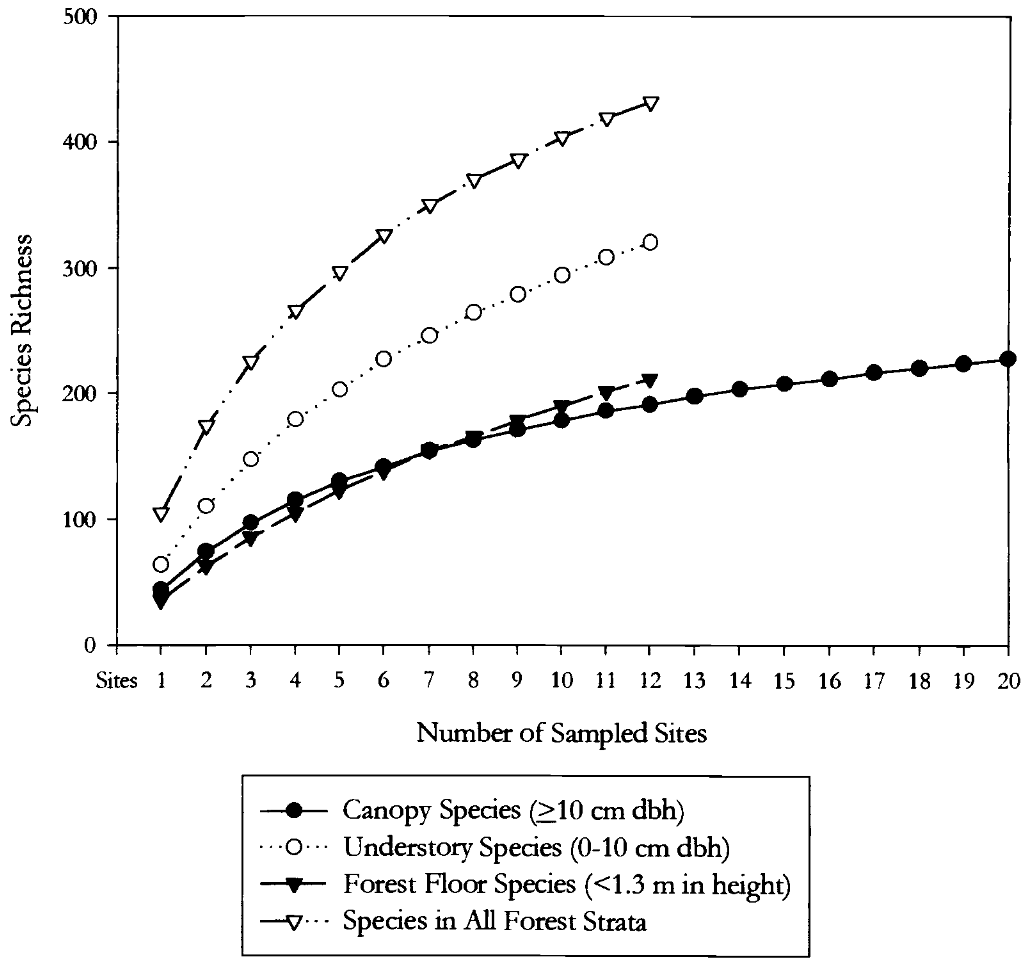

Figure 2.5: Species-area relationship for an increasing number of 0.79 ha primary forest sites within the Los Tuxtlas region, Veracruz, Mexico. This relationship is displayed for canopy species (≥10 cm dbh), understory plants (0-10 cm dbh), forest floor plants (<1.3 m in height), and for all forest strata combined. In all cases, ≥95% of the total species richness of this study was captured before the inclusion of the final (12th) site.

Environmental Factors That Influence Species Composition

Canopy species richness significantly declined with elevation (Adj. R^2=0.47, p<0.001, n=20 sites) at a rate of approximately 2 species per 100 m rise in elevation (Figure 2.6). The site at the lowest elevation (15 m.a.s.l.) had a total of 54 canopy species, while the two highest-elevation sites (1280 m.a.s.l.) had a mean richness of 24 canopy species.

In general, sites that were closest to one another along the elevational gradient were most similar in their canopy species compositions (Figure 2.7). The PS for canopy species between any two sites significantly declined with an increasing difference in elevation (Adj. R^2=0.49, p<0.001, n=190 comparisons). Pairs of sites at approximately the same elevation had a mean PS of 29%, regardless of whether each pair was situated in high or low elevation areas. In contrast, pairs of sites separated by at least 1,150 m in elevation had a mean PS of 2%.

Despite the importance of elevation in accounting for differences in species richness and composition among sites, I found uniformity in how species richness was partitioned among the forest strata within each site. Specifically, the proportion of the site species richness that was observed to be within each of the five forest strata appeared to remain constant among all sites, despite differences in soil-types (ANOVA, p>0.14 for 5 strata, n=12 sites) and elevation (p>0.26 for 5 strata, n=12 sites). For example, the mid-canopy strata (30 - 70 cm dbh) within each site contained a mean of 26% (± 2%) of that site's species richness, regardless of which species were present, the site's total species richness, soil-type, or the site's position along the elevational gradient (Table 2.5).

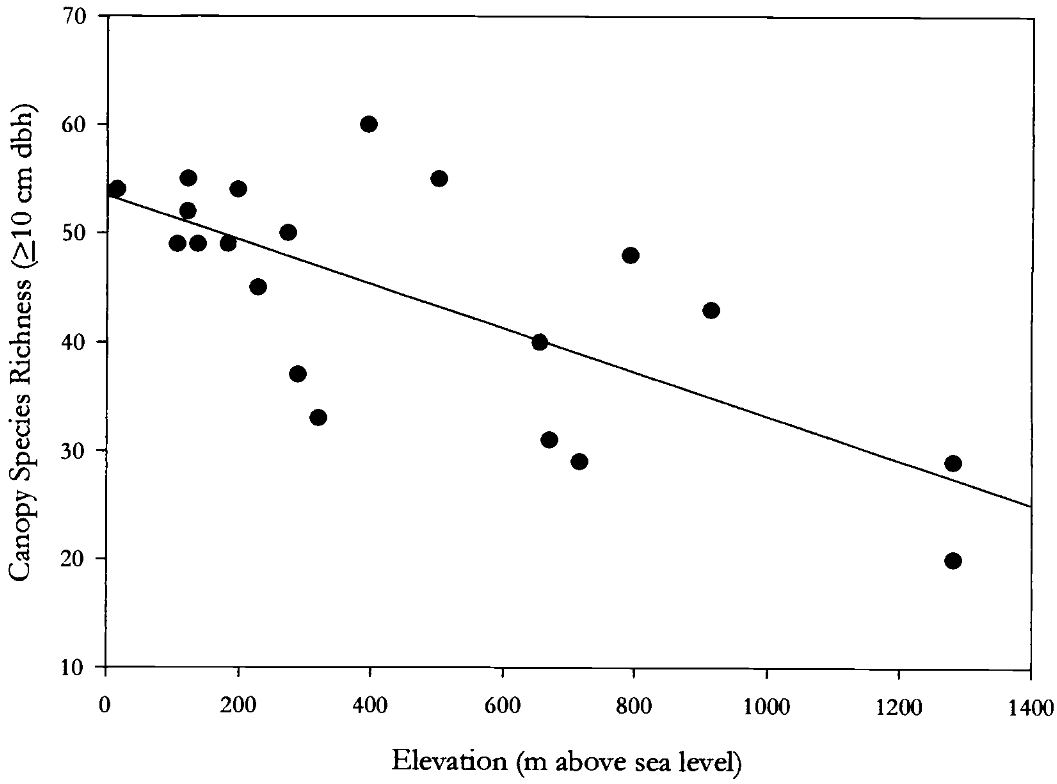

Figure 2.6: Canopy species richness (≥10 cm dbh) versus elevation for 20-0.79 ha primary forest sites within the Los Tuxtlas region, Veracruz, Mexico. In general, there was a decline in species richness with increasing elevation, at a rate of approximately 2 species per 100 m rise in elevation (Adj. R^2=0.47, p<0.001).

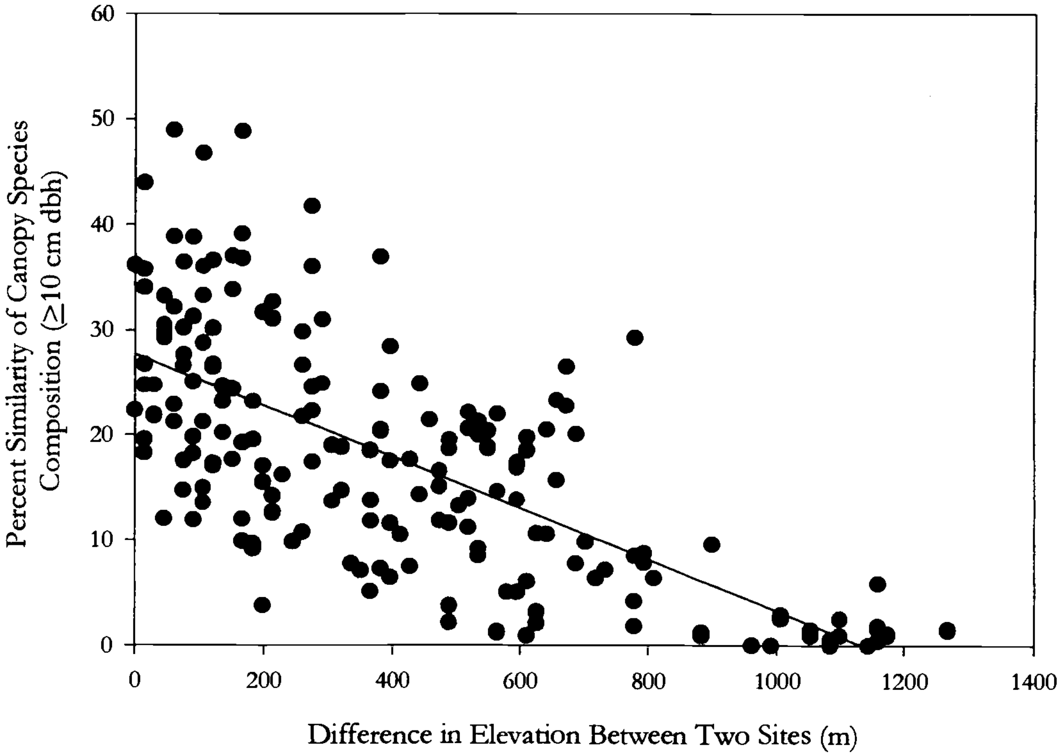

Figure 2.7: Percentage similarity (PS) in canopy species compositions (≥10 cm dbh) between two sites plotted against the difference in elevation (m) between those two sites. In general, sites that were closer together in elevation had a higher similarity in canopy species compositions than sites separated by large elevational differences (Adj. R^2=0.49, $p<0.001$, n=190 comparisons).

Table 2.5: The proportion of the plant species richness encountered in each site among the major forest strata—bound by diameter class—for 0.79 ha forest sites within the Los Tuxtlas region, Veracruz, Mexico (n=12 sites). The proportion of the species richness found within each diameter class of the forest remained constant, despite differences in a site's total species richness[¥], species composition, elevation (p>0.26), and soil-types (ANOVA, p>0.14).

Forest Strata	Diameter Class	Proportion of Total Species Richness Within Diameter Classes		*P*-value vs. Elevation	*P*-value vs. Soils
	n=12 sites	**Mean**	**SE**		
Tall Canopy	≥70 cm dbh	9%	1%	0.26	0.39
Mid Canopy	30-70 cm dbh	26%	2%	0.65	0.18
Low Canopy	10-30 cm dbh	24%	2%	0.66	0.34
Understory	0-10 cm dbh	61%	3%	0.52	0.15
Forest Floor	<1.3 m ht	34%	2%	0.86	0.14

[¥] The species richness for plants ≥10 cm dbh was shown to be associated with elevation (Figure 2.6). Canopy species richness declined at a rate of approximately 2 species per 100 m rise in elevation (Adj. $R^2=0.47$, $p<0.001$, n=20 sites).

Tropical Forest Community-Types and Life Zones

Four groups of sites were identified from cluster analysis (Figure 2.8). In addition to having different canopy species compositions (≥10 cm dbh), each group was found to have different environmental attributes. Although the high concentration of rare species accounted for low similarity in species composition among sites, the exclusion of rare species from cluster analysis (i.e. those species with a constancy ≤5%) clarified that sites could be grouped on the basis of their species compositions. The MRPP analysis indicated that the sites within each of the four groups had similar elevations, slopes, and soil-types ($R^*=0.40$), and that these environmental variables were significantly different among each of

[*] The "R" value within the MRPP analysis describes the homogeneity within groups as compared with that expected by chance. An R value of 1 indicates that all items are homogeneous within each group. Conversely, R=0 when the members of each group are as heterogeneous as expected by chance (McCune and Mefford 1997, Milke 1984).

the four groups (p=0.001) (Table 2.6). For canopy species composition (≥10 cm dbh), sites that were within the same group had an average PS of ~27%, which was ~10% higher than the average of ~17% between any two of the 20 sites. I named these groups as community-types, according to their dominant geographic location. These community-types were: Lowland-Reserve Forest (LR), La Perla Plateau Forest (LP), Volcanic-Upslope Forest (VU), and Cloud Forest (CF). I coarsely classified the LR, LP, and VU community-types as TEF's (INEGI 2001), although the presence of Mexican oak species (*Quercus* sp. and *Quercus skinneri* Benth. (FAGACEAE)) in one VU site (*CAMINO*) and one CF site (*BM1*) could indicate that the tropical oak forest type was also present (Dirzo et al. 1997). The Cloud Forest community-type was categorically described as *bosque tropical nuboso* (INEGI 2001). The four community-types also corresponded with the Holdridge Life Zone System, based on the range of elevations and mean annual temperatures estimated for each community-type (Table 2.6) (Holdridge et al. 1971). I report the LR community-type was Tropical (transition to Subtropical) Moist Forest, the LP and VU community-types were Subtropical Wet Forest, and the CF community-type was Subtropical Lower Montane Rain Forest (Tosi and Watson personal communication; Holdridge et al. 1971).

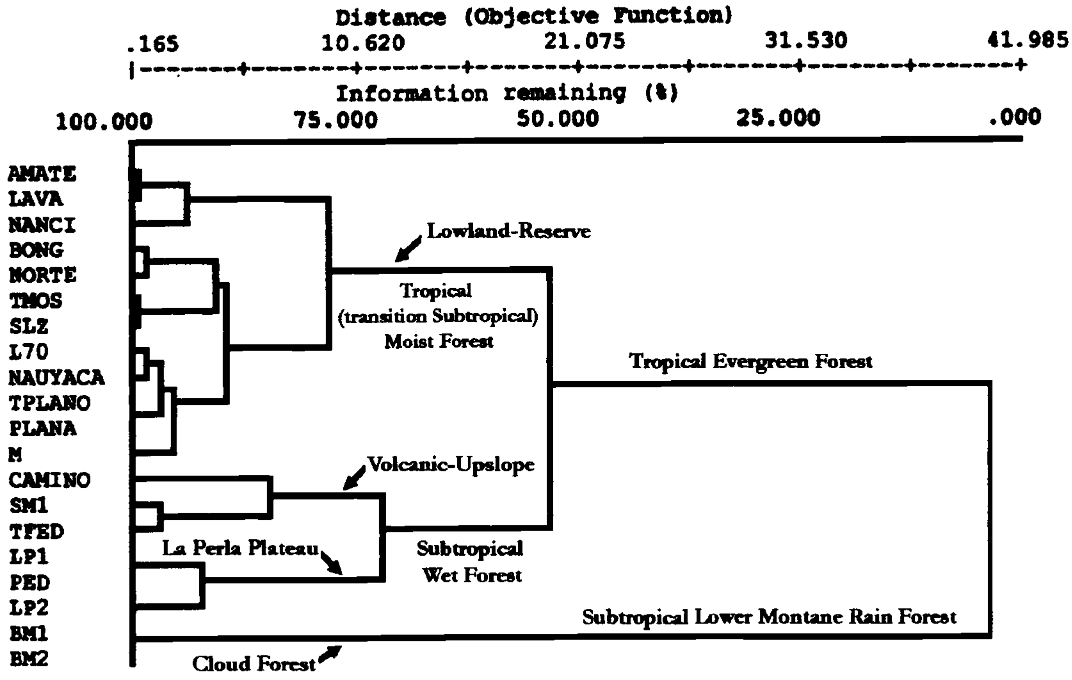

Figure 2.8: Cluster analysis of 20-0.79 ha forest sites, containing a total of 158 canopy species (≥10 cm dbh). Four community-types were identified by this analysis: Lowland-Reserve, Volcanic-Upslope, La Perla Plateau, and Cloud Forest. Each community-type had unique environmental variables of elevation, slope, and soil-type (MRPP, R=0.40, $p<0.001$). Differences in species compositions and environmental variables also corresponded with three Holdridge Life Zone classifications: Tropical (transition to Subtropical) Moist Forest in low elevations, Subtropical Wet Forest in the mid-elevations, and Subtropical Lower Montane Rain Forest in the upper elevations (Tosi and Watson personal communication; Holdridge et al. 1971). The most dissimilar groups of sites were coarsely categorized as Tropical Evergreen Forest (TEF) and Cloud Forest.

As their name suggests, the Lowland-Reserve forests were located within and around the boundaries of the LTBS. Eight of the 12 sites within the LR community-type were on weathered soils; the four sites on lava flows were: *Sitio Nauyacoso (NAUYACA)*, *Selva Lava (SL)*, *Sitio Amatal (AMATE)*, and *Nanciyaga (NANCI)* (Appendix). The LP sites were on lava flows located on the upper plateau (655 - 715 m.a.s.l.) above the boundaries of the LTBS. The three VU sites were on ash-derived soils on the lower slopes of the Volcán San Martín and a smaller, neighboring cinder cone (505 – 915 m.a.s.l.). Both Cloud Forest sites were positioned at 1280 m in elevation near the summit of the Volcán San Martín; both sites had ash-derived soils (Table 2.6).

Compared with one another, the four community-types had an average PS of 16% for canopy species (Table 2.7). The TEF community-types (i.e. LR, LP, and VU only) had a mean PS of 26% when compared with one another. The Cloud Forest was the most dissimilar in canopy species composition among community-types, as this community-type had a PS of 5% when compared with the three TEF community-types.

Out of all 228 canopy species (≥10 cm dbh) encountered in the 20 study sites, only one canopy species, *Nectandra salicifolia* (Kunth.) Nees (LAURACEAE), was present in all four community-types. Thirty-nine species in 32 genera and 25 families were common to 3 or more community-types. Thirty-two of these species (within 27 genera and 21 families) were found only in the TEF community-types (Appendix).

Table 2.6: Environmental features associated with each of the 4 community-types identified by cluster analysis, using the abundance (individuals ha^{-1}) of 158 canopy species (≥10 cm dbh) in 20-0.79 ha sites sampled within the Los Tuxtlas region, Veracruz, Mexico. Community-types had different environmental attributes (MRPP, R=0.40, p<0.001), and were named as sub-regions based on their topographic features and location within the Los Tuxtlas region.

	Lowland-Reserve (LR)	**La Perla Plateau (LP)**	**Volcanic-Upslope (VU)**	**Cloud Forest (CF)**
n of sites	**12**	**3**	**3**	**2**
Substrate	Weathered Soils, Lava Flows	Lava Flows	Ash Derived	Ash Derived
Elevation (m.a.s.l.)	15 – 395	655 – 715	505 – 915	1280
Slope (%)	3 – 36	13 – 19	17 – 41	14 – 29
Temperature (°C)*	23.9 – 25.7	22.3 – 22.6	21.3 – 23.3	19.5
Rainfall (mm)*	2500 – 3500	3000 – 3500	3000 – 3500	3500 – 4000
Holdridge Life Zone†	Tropical (transition to Subtropical) Moist Forest	Subtropical Wet Forest	Subtropical Wet Forest	Subtropical Lower Montane Rain Forest

*Mean annual temperature was modeled from data presented by Soto and Gama 1997 (Appendix A); Mean annual rainfall (Soto and Gama 1997); †Holdridge classification follows Tosi and Watson (personal communication) and Holdridge et al. (1971).

Table 2.7: Percentage Similarity (PS, %) in canopy species (≥10 cm dbh) composition (228 species total) among the four Los Tuxtlas forest community-types identified in this study. Tropical Evergreen Forest (TEF) represented all community-types other than Cloud Forest.

Community-Type (n of sites)	Lowland-Reserve (n=9)	La Perla Plateau (n=3)	Volcanic-Upslope (n=3)	Cloud Forest (n=2)	All TEF's (n=18)
Lowland-Reserve	—	28	27	2	—
La Perla Plateau	28	—	24	4	—
Volcanic Upslope	27	24	—	9	—
Cloud Forest	2	4	9	—	5

DISCUSSION

Species Diversity

The forest stands of Los Tuxtlas were largely composed of a diverse assemblage of rare species, where the majority of the species within a forest stand appeared to occur only within that stand, or within neighboring stands. I suggest the rooted-plant diversity within Los Tuxtlas is related to its diverse environmental features, namely the topography, edaphic conditions, wide elevational range, and climate. Based on the data, I have described sub-regions, or forest environments, each unique in their species compositions and in their physical attributes. These community-types are useful tools for conservation. Four clear, landscape-level patterns of species composition emerged from the data. These patterns were: (i) species richness declined with increasing elevation (Figure 2.6); (ii) sites that were closer in proximity along the elevational gradient were more similar in species composition than sites separated by large elevational differences (Figure 2.7); (iii) four community-types were identified based on species composition that corresponded with distinct combinations of elevation, slope, soil-types, and Holdridge Life Zones (Table 2.6, Figure 2.8); and, (iv) the proportion of the species richness found within each of the forest strata at each site was similar, regardless of the site species composition, species richness, position along the elevational gradient, or the environmental characteristics associated with each site (Table 2.5).

The TEF's of Los Tuxtlas have similar characteristics to other TEF's (Ibarra-Manríquez et al. 1997, Hughes et al. 2000), but on the stand level, Los Tuxtlas forests appear to be at the low end of rooted-plant species richness and diversity compared with other primary tropical forests. For canopy species richness (≥10 cm dbh), an average of 44 species were found for 0.79 ha plots (Range: 20 - 60 species), which contrasts with the more than 300 canopy tree species ha^{-1} for forests studied in northwestern Ecuador (Korning and Balslev 1994, Gentry and Dodson 1987). In terms of canopy tree species diversity (≥10 cm dbh), Richards (1996) reported an average of 6.2 ± 0.8 (Range: 2.0 – 14.1) stems $species^{-1}$ for 20 different studies having variable plot sizes (Range: 0.8 – 2 ha in size) for primary lowland forests within the tropical America, Africa, and the Asia-Pacific region. The corresponding average of 9.1 stems $species^{-1}$ from sites in this study would suggest Los Tuxtlas is within this range, but is more similar to African forests (average 8.5 ± 2.8 stems $species^{-1}$) than to other Neotropical forests (6.0 ± 1.1 stems $species^{-1}$) and Asian forests (5.5 ± 1.0 stems $species^{-1}$) (Richards 1996). This may be due to the northern latitudinal extreme of Los Tuxtlas within the Neotropics (i.e. 18 degrees N latitude). I acknowledge there are limitations in comparing data from this study with those from other studies, as the sample area of the nested plots were smaller than 0.79 ha (see Table 2.2).

The 'rare' species component of Los Tuxtlas forest stands is typical of that from other TEF's. In the species-rich forests of Malaysia, Cousens (1951) found that for one 0.61 ha plot, 56% of the canopy species (≥10 cm dbh) were represented by only one individual. Data from this study are consistent with this finding; a mean of 46% of the canopy species only occurred once within each 0.79 ha site. In addition, it has been observed that the most abundant species in the canopy strata rarely represents more than 15% of the stem density of a primary forest stand (≥10 cm dbh; Richards 1996). On average for Los Tuxtlas, the most abundant canopy species in each site was represented by 19% of the canopy strata stem density. Because of the rarity and limited distribution of most species, these data suggest that the widespread deforestation of the Los Tuxtlas region has likely resulted in the loss of many plant species.

The relationship between elevation and changes in species composition has been identified in other tropical regions (e.g. Holdridge et al. 1971). In the Volcán Barva region of Costa Rica, Lieberman et al. (1996) examined changes in the canopy species composition (≥10 cm dbh) along a 2,600 m elevational transect. They found changes in species composition were continuous throughout the elevational range, and found no evidence of discrete floristic zones. However, the authors acknowledged that due to their research objectives, they did not replicate samples at similar elevations, and hence their assessment of compositional changes did not take into account the significance of other environmental factors, including topographic position and soils. In the dry forests of Mexico, Vázquez and Givnish (1998) identified elevation as the dominant environmental factor correlated with species composition. Similar to the results of Lieberman et al. (1996), they found continuous shifts in species composition throughout a 1,000 m elevational transect and concluded discrete floristic zones did not exist in their region of study. They also reported within-elevation similarity was higher than across-elevation similarity for woody species (Vázquez and Givnish 1998), which supports the conclusion presented here that sites at similar elevations were more similar in species composition than sites separated by large elevational differences. Another similarity between the Los Tuxtlas region and other studies was the apparent limited range of most species. Lieberman et al. (1996) reported 36% of all species (≥10 cm dbh) were observed in only a single sample unit (i.e. 7% constancy). Similar values were observed from this study, with 31% of the total canopy species richness having had a 5% constancy.

Global models to classify vegetation have been made (Holdridge et al. 1971) that have involved precipitation, temperature, and evapotranspiration as variables to describe coarse changes in vegetation. On the Eastern slope of the South American Andes, large-scale classifications of vegetation have been made (such as Grubb and Whitmore 1966) that involved different moisture regimes and soil-types. Gentry (1982) found that species richness corresponded with precipitation. Using 0.1 ha plots in the Neotropics, species richness ranged from 50 plant species in dry forests, to 100 – 150 species for tropical moist forests, and >200 species for tropical wet forests (Gentry 1982). For Los Tuxtlas, changes in species richness and composition corresponded with changes in a multitude of environmental factors, particularly elevation, soil-type, topography, mean annual temperature, mean annual precipitation, and rainfall intensity (Soto and Gama 1997). For purposes of conservation and management, it is clear that the community-types identified here for the Los Tuxtlas region are biologically unique from one another, both in their species compositions and in their environmental attributes. Expanded study into habitat uses by other organisms to include the sub-regions other than the Lowland-Reserve community-type would greatly enhance our understanding and appreciation for the biodiversity of the Los Tuxtlas region.

The final conclusion involved forest structure and rooted-plant species richness. There was clear uniformity in how the plant species richness was partitioned within all strata of the primary forest. These patterns existed with all 12 sites, despite any changes in elevation, soil-type, topography, moisture regimes, or community-types. This conclusion, where species composition changed but forest structure remained relatively constant (see Chapter 3 for more discussion on forest structure), enhances our ability to investigate the functional roles of different groups of species which occupy similar niches within primary tropical forests.

Implications for Conservation

The high species richness and low species constancy of forest stands suggests the widespread deforestation in Los Tuxtlas has resulted in habitat loss and in the extirpation of many species. Continued pressures of deforestation underscore the need for a well-designed and large biological reserve that would maintain the remaining diversity of the native forests. This includes the preservation and conservation of forest stands along the broad topographic and edaphic gradients that are characteristic of the Los Tuxtlas region. The conservation objectives of the Los Tuxtlas Biosphere Reserve declared by former President Zedillo (Vargas 1998) would benefit from active involvement from the surrounding communities to conserve primary forest reserves within each of the four community-types identified in this study: the Lowland-Reserve, La Perla Plateau, Volcanic-Upslope, and the Cloud Forest community-types. These areas are unique from one another in their species diversity, and one can only assume the vegetation and climate differences among the community-types would promote equally unique assemblages of epiphytic plants, insects, and wildlife. While all of the factors that influence biodiversity are unknown, I submit that for the San Martín de Los Tuxtlas watershed, there is a clear relationship between the physical attributes of a site and its species composition. Using these key factors, I suggest these results are applicable to conservation efforts within the Santa Marta and San Martín Pajapan watersheds. Within these watersheds, contiguous areas of primary forest should be delineated for conservation values. By capturing the broadest possible range of at least elevation and soil-types, we may effectively conserve some of the remaining biological diversity of the most diverse forests of North America.

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CHAPTER 3

Landscape-Scale Patterns in Aboveground Biomass, Carbon, and Forest Structure For the Primary Tropical Forests of Los Tuxtlas, Mexico

Christopher Heider

ABSTRACT

Deforestation and land-use conversion of tropical forests to agricultural and pasture lands has been identified as a significant source of greenhouse gases to the atmosphere. While many estimates of total aboveground biomass (TAGB) and C have been made for tropical forests, a limited number of studies have addressed the variability of TAGB and C on landscape-scales, especially for topographically diverse environments. In this study, I quantified and described the variability in the TAGB, C pools, basal area, and stem density for 20-0.79 ha primary forest sites situated within a topographically diverse landscape of the Los Tuxtlas region, SE Veracruz, Mexico. The environmental variables that were associated with this landscape included an elevational range (15 – 1280 m.a.s.l.), variable slopes, three soil-types, and three Holdridge Life Zones. The primary forest vegetation was classified as 4 forest community-types, incorporating two coarse vegetation descriptions (Tropical Evergreen Forest and Cloud Forest). The results suggest that TAGB, C, and forest structure were not significantly different with respect to environmental variables for sites within the coarse Tropical Evergreen Forest (TEF) vegetation classification. Cloud Forests differed from TEF's in TAGB, C, and forest structure. For TEF's, TAGB and total aboveground C pools were 422 ± 17 Mg ha^{-1} and 205 ± 8 Mg ha^{-1}, respectively, which were ~22% higher than that of Cloud Forests (346 ± 1 and 168 Mg ha^{-1} for TAGB and C, respectively). Cloud Forests had generally fewer trees ≥70 cm dbh, and a more even distribution of trees 30-70 cm dbh than TEF's. A total of 25 trees representing 17 species, 15 genera, and 12 families exceeded the dbh range limit of the allometric biomass models I employed (i.e. >130 cm dbh; Brown et al. 1989). The biomass contribution of these individuals accounted for most, if not all, of the variation in TAGB and C for all TEF sites. Despite any limitations associated with biomass estimates, the Los Tuxtlas region represents a significant pool of aboveground biomass and C within the Neotropics.

INTRODUCTION

Deforestation and land-use conversion from forests to agricultural lands and pastures has dramatically changed the structure, composition, and function of forest landscapes. In the tropics, land-use conversion is often accomplished by slash-and-burn practices, which result in fluxes of terrestrial carbon (C) and nutrient pools (e.g. nitrogen, sulfur, and phosphorus) to the atmosphere in the form of radiatively-active gases. These 'greenhouse' gases are primarily carbon dioxide (CO_2), carbon monoxide (CO), methane (CH_4), and nitrous oxide (N_2O) (Houghton 1994; Cairns et al. 1995), and have been directly linked to warming of the earth's atmosphere (IPCC 2001). Tropical evergreen forests (TEF's) occupy only ~11% of the earth's land surface; they store nearly 30% of the world's terrestrial aboveground C and are second only to wetlands in net primary production (Houghton and Skole 1990). Due largely to socio-economic pressures, TEF's are experiencing the highest rates of deforestation on earth.

Tropical evergreen forests of Mexico represent the northernmost TEF's and the most biologically diverse forest type in North America (Dirzo 1992). The Los Tuxtlas region of Southeast Veracruz has experienced extraordinary rates of deforestation. From 1967 to 1986, approximately 84% of the primary TEF's of the Los Tuxtlas region were converted to agricultural lands and pastures at a rate of approximately 4.2% year^{-1}, with an approximate total conversion to date of 91% (Hughes et al. 2000, Dirzo and García, 1992). Hughes et al. (2000) found for the Los Tuxtlas region that the conversion from forest to non-forest (i.e. agricultural land-uses) results in a 95% loss of ecosystem C ha^{-1}. Based upon local-scale measurements, land-uses have removed as much as 30 Tg of biomass from Los Tuxtlas, of which approximately 14 Tg was C (Hughes et al. 2000). The high rate of deforestation and subsequent land-uses within Los Tuxtlas have clear implications of C inputs to the atmosphere, but what is less known is how the landscape-scale variability in total aboveground biomass (TAGB) and C pools affects these estimates.

Landscape-scale measures of forest structure are important for understanding how environmental factors explain the variation associated with measures of TAGB and C pools. To improve global estimates of biomass and C pools contained within specific forest types, it is necessary to first understand how forest structure varies within each forest type, then to identify the key factors which explain the majority of the variation in TAGB and C among forest types. Many have recognized this, and have highlighted individual environmental factors as key mechanisms to explain TAGB and C variation on landscape scales (Laurance et al. 1999, Brown 1997, Clark and Clark 2000, Korning and Balslev 1994). However, few have enumerated landscape-scale variation in TAGB, C, and forest structure across an topographically and floristically diverse region that incorporates many variables, including elevation, variable slopes, soil-types, climate, and plant species composition, especially for the high-latitudinal extremes of the tropics.

In this paper, I identify and describe the landscape-level patterns of TAGB, C, and the basal area and stem density (i.e. forest structure) with respect to a suite of environmental variables for the primary forests of the Los Tuxtlas region, Mexico. The environmental variables included elevation, slope, soil-types, Holdridge Life Zones (Holdridge et al. 1971), and Los Tuxtlas community-types (Chapter 2). My specific objectives were to (i) quantify the TAGB, C pools, basal area and stem density for the Los Tuxtlas region, (ii) enumerate patterns in how TAGB, C, basal area, and stem density varied with respect to the environmental variables, (iii) quantify and describe the variation in how biomass, C, basal area, and stem density were partitioned among diameter classes and growth forms on the landscape-scale, and (iv) identify key factors that explained the variability in landscape-level TAGB and C estimates.

METHODS

Study Area

This study was conducted within the remaining primary forest fragments of the Los Tuxtlas region, located in Southeast Veracruz, Mexico (18° 30' N; 095° 06' W). The region consists of an isolated volcanic mountain range that parallels the Gulf Coast of Mexico (Figure 3.1) and provides a topographic barrier to weather systems entering the region from the Gulf of Mexico to the north. This area is approximately 90 x 50 km, and contains watersheds shaped by three volcanoes: Santa Marta, San Martín Pajapan, and San Martín de Los Tuxtlas (Dirzo and Garcia 1992). The study area was located along the slopes of San

Martín de Los Tuxtlas, encompassing an altitudinal range from sea level to 1780 m at the summit of the Volcano. The dominant unaltered vegetation type is tall tropical evergreen forest (TEF, *selva alta perenifolia*, Ibarra-Manríquez et al 1997), and is considered the northernmost of its type in North America (Dirzo and Garcia 1992). Other vegetation types have been identified for this region, including mangroves, 'medium' evergreen forest (*selva mediana perenifolia*), tall *Liquidambar* forest, humid tropical oak (*Quercus*) forest (*selva con encinos*), cloud forest (*bosque tropical nuboso*), elfen forest (*bosque enano*), and many variations of perturbed vegetation types, including second growth forest (*acahuales*), croplands, and cattle pasture lands (Dirzo et al. 1997, Hughes et al. 2000). Within the region, the National University of Mexico (UNAM) maintains the Los Tuxtlas Biological Research Station (LTBS) and 640 ha biological reserve, containing mostly primary TEF vegetation.

Climate

Soto and Gama (1997) described four major climate zones within the Los Tuxtlas region that corresponded with elevation. Each climate zone was qualitatively described on the basis of mean annual temperature, mean annual precipitation, and rainfall intensity (i.e. average rainfall in a 24-hour period) (Soto and Gama 1997). Weather station data reported from five elevational transects revealed a general decline in mean annual temperature at a rate of ~0.5 °C for each 100 m rise in elevation above sea level (a.s.l.), beginning with a mean annual temperature of ~26 °C at sea level (Soto and Gama 1997, Appendix). Mean annual precipitation also increased with elevation, although rainfall intensity was higher at lower elevations (Soto and Gama 1997). These climate zones also corresponded to different Life Zones of the Holdridge System (Holdridge et al. 1971), using mean annual precipitation and mean annual temperature as explanatory variables (Chapter 2). For Los Tuxtlas, these zones range from Tropical (transition to Subtropical) Moist Forest in the lower elevations to Subtropical Wet Forest in the mid-elevations to Subtropical Lower Montane Rain Forest in the upper elevations (Tosi and Watson personal communication, Holdridge et al. 1971) (Table 3.1).

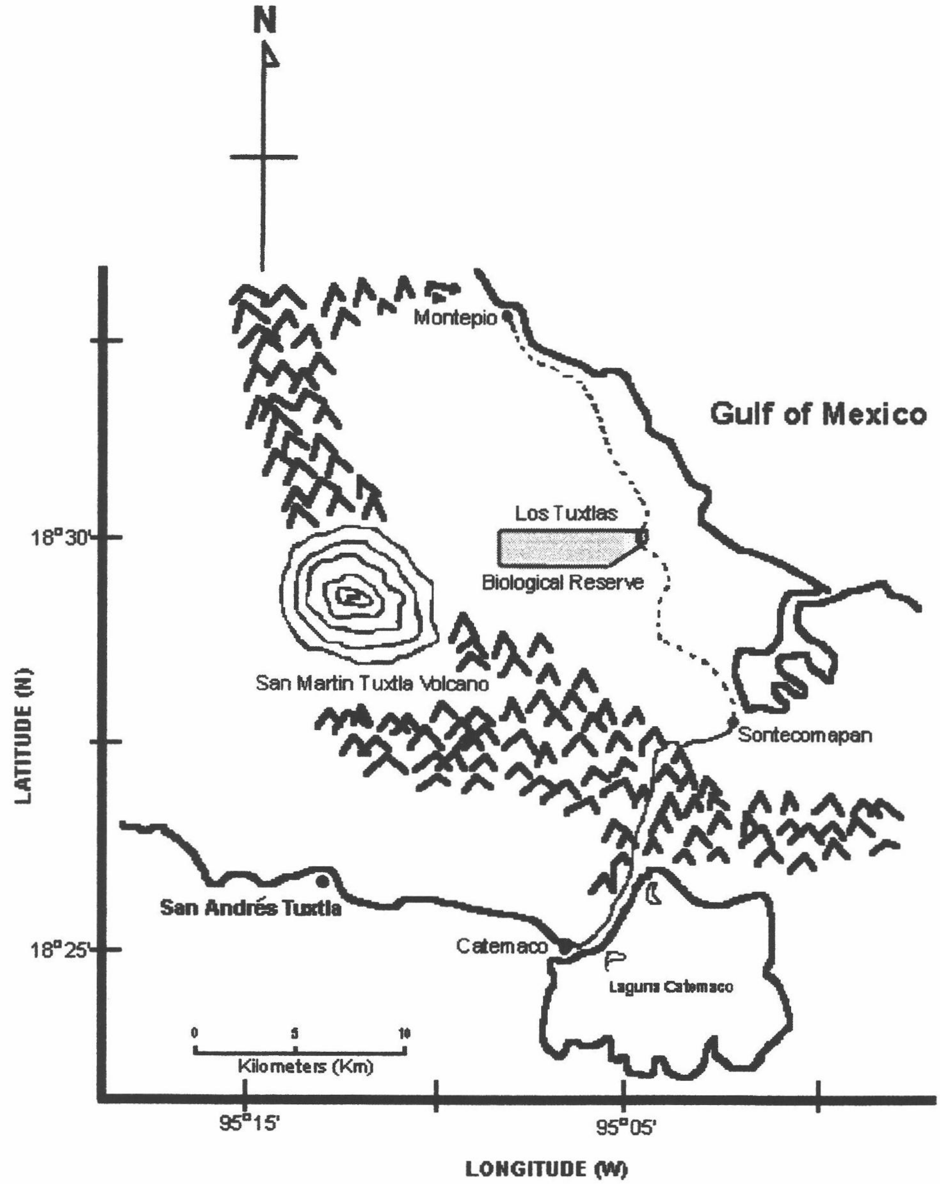

Figure 3.1: The Los Tuxtlas region (*From*: Ibarra-Manríquez and Sinaca 1987), located in the southeastern portion of the state of Veracruz, Mexico. The Los Tuxtlas Biological Station Reserve (shaded area) is 640 ha in size. The region consists of variable slopes and an elevational gradient from sea level at the Gulf of Mexico extending to 1780 m at the summit of the Volcán San Martín de Los Tuxtlas.

Geology and Soils

The topographically diverse landscape of the Los Tuxtlas region has been formed by an active volcanic history, involving more than 300 volcanic cones (Martin-Del Pozzo 1997). The most active and significant of these volcanoes has been the Volcán San Martín de Los Tuxtlas. The volcanic eruptions by the Volcán San Martín have contributed to the formation of three unique soil-types that appear to be correlated with elevation and age since formation. These soil-types are categorically described as ash-derived, lava flows, and weathered soils (i.e. weathered lava and ash) (Martin-Del Pozzo, 1997). Ash deposits are located in the higher elevations and are the youngest of the three dominant soil-types. The most recent and noteworthy ash formation was caused by a major eruption by the Volcán San Martín in 1793. This eruption "completely destroyed all of the vegetation along the slopes of San Martín," and ash "continued to rain for a period of eight days" (Friedlaender and Sander 1923).

The majority of the lava flows within Los Tuxtlas were formed between 2.4 and 1.0 million years ago (Gonzáles-Caver and Nelson 1990). These lava flows are approximately 2 m thick and have similar characteristics in as pahoehoe lava of the Hawaiian archipelago (Martin-Del Pozzo 1997). Earlier volcanic activity (between 7 and 2 million years ago) had formed basalt deposits that were prone to erosion (Friedlaender and Sander 1923). These compose the weathered soils that are most commonly found in lowland areas, and due to their distance from the most active volcanoes, have not likely experienced the same intensity of disturbance related to recent volcanic activity.

Although no data are currently available for the Los Tuxtlas region on the soil chemistry and nutrient availability along the elevational gradient or for each of the three soil-types, studies from a similar volcanic region in Costa Rica indicated an increase in total N and C, soil organic matter, P, Ca, Mg, and ammonium with increasing elevation and decreasing soil age (Sollins et al. 1994). In addition, there was a decline in NO_3^{-1} and organic matter decomposition with increasing altitude (Sollins et al. 1994). In lower-elevation forests over the weathered soils in Los Tuxtlas (ca. 150 – 350 m.a.s.l.), Hughes et al. (2000) reported total soil C ranged from 178 – 307 Mg ha^{-1} and total soil N ranged from 17 – 29 Mg ha^{-1} to a 1 m depth.

Vegetation

In Chapter 2 of this thesis, I reported the plant species richness, composition, and diversity of the Los Tuxtlas forests was correlated with the environmental attributes of the landscape. In general, species richness declined with increasing elevation, and forest sites at similar elevations were more similar in species composition than sites separated by large elevational differences (Chapter 2). In addition, there were four sub-regions within Los Tuxtlas, each with unique species compositions, elevational ranges, slopes, soil- and climate-types. These four sub-regions were appropriately named according to their geographic position: Lowland-Reserve forest (LR), La Perla Plateau forest (LP), Volcanic-Upslope forest (VU), and Cloud Forest (CF) (Table 3.1) (Chapter 2). The differences in climate among these community-types corresponded with Holdridge Life Zone classifications. These classifications were: Tropical (transition to Subtropical) Moist Forest (corresponding with LR), Subtropical Wet Forest (corresponding with LP and VU), and Subtropical Lower Montane Rain Forest Life Zones (corresponding with CF) (Tosi and Watson personal communication, Holdridge et al. 1971). For Los Tuxtlas, Tropical Moist Forest and Subtropical Wet Forest represent the northern extremes of TEF's in the Neotropics (INEGI 2001, Dirzo 1992).

Table 3.1: Environmental features associated with each of the 4 Los Tuxtlas community-types within the Los Tuxtlas region, Veracruz, Mexico (Chapter 2). Community-types had different environmental attributes, including Holdridge Life Zones (Holdridge et al. 1971), and were named as sub-regions based on their topographic features and location within the Los Tuxtlas region.

	Lowland-Reserve (LR)	**La Perla Plateau (LP)**	**Volcanic-Upslope (VU)**	**Cloud Forest (CF)**
n of sites	**12**	**3**	**3**	**2**
Substrate	Weathered Soils, Lava Flows	Lava Flows	Ash Derived	Ash Derived
Elevation (m.a.s.l.)	15 – 395	655 – 715	505 – 915	1280
Slope (%)	3 – 36	13 – 19	17 – 41	14 – 29
Temperature (°C)*	23.9 – 25.7	22.3 – 22.6	21.3 – 23.3	19.5
Rainfall (mm)*	2500 – 3500	3000 – 3500	3000 – 3500	3500 – 4000
Holdridge Life Zone†	Tropical (transition to Subtropical) Moist Forest	Subtropical Wet Forest	Subtropical Wet Forest	Subtropical Lower Montane Rain Forest

*Mean annual temperature was modeled from data presented by Soto and Gama 1997 (Appendix A); Mean annual rainfall (Soto and Gama 1997); †Holdridge classification follows Tosi and Watson (personal communication) and Holdridge et al. (1971).

Data Collection

Twenty-0.79 ha sites (75 x 105 m) were selected to sample the TAGB, C pools, basal area, and stem density of primary forest stands within the San Martín de Los Tuxtlas watershed of the Los Tuxtlas region. The presence of stumps or cut logs, livestock dung, or trails (by human, livestock, or timber exploitation) rendered a site unsuitable for this study. Site selection was limited due to access difficulties and the highly fragmented nature of the remaining forests. Sites were selected without preconceived bias with the objective to capture the variability of the primary forest with respect to the environmental characteristics of the region. Specifically, I selected sites throughout the elevational range (15 - 1280 m above sea level) and replicated sites on each of the 3 soil-types (henceforth described as 'ash-derived', 'lava flows', and 'weathered-soils') (Martin-Del Pozzo 1997). All sites were located at least 150 m to several kilometers from a road or trail. I had no *a-priori* knowledge of forest structure or composition for any site. Elevation was measured using an altimeter that was calibrated daily to the known elevation of the LTBS.

Each site was composed of a series of nested plots to sample primary forest structure. I defined forest structure as the partitioning of biomass, C, basal area, and stem density among the dominant strata of the forest. Specifically, the aboveground components of the forest were divided into strata based on individual plant size – diameter at breast height (dbh, 1.3 m in height) — and growth form (Figure 3.2). The forest canopy (plants ≥10 cm dbh) was divided into three strata based on diameter class: tall-canopy (≥70 cm dbh), mid-canopy (30 - 70 cm dbh), and low-canopy (10 – 30 cm dbh) (Figure 3.2). The forest understory was categorized as plants at least 1.3 m in height and <10 cm dbh (i.e. 0 - 10 cm dbh). The forest floor strata was defined as all live and dead plant material <1.3 m in height. Growth forms included trees, palms, woody lianas, herbaceous vines, and dead material. Woody lianas and herbaceous vines were distinguished by the presence or absence of wood in mature stems. Palms were non-climbing members of ARECACEAE; the few climbing palm species of ARECACEAE were described as lianas, as their structural characteristics resembled lianas more than freestanding palms. I did not include epiphytes in my sampling.

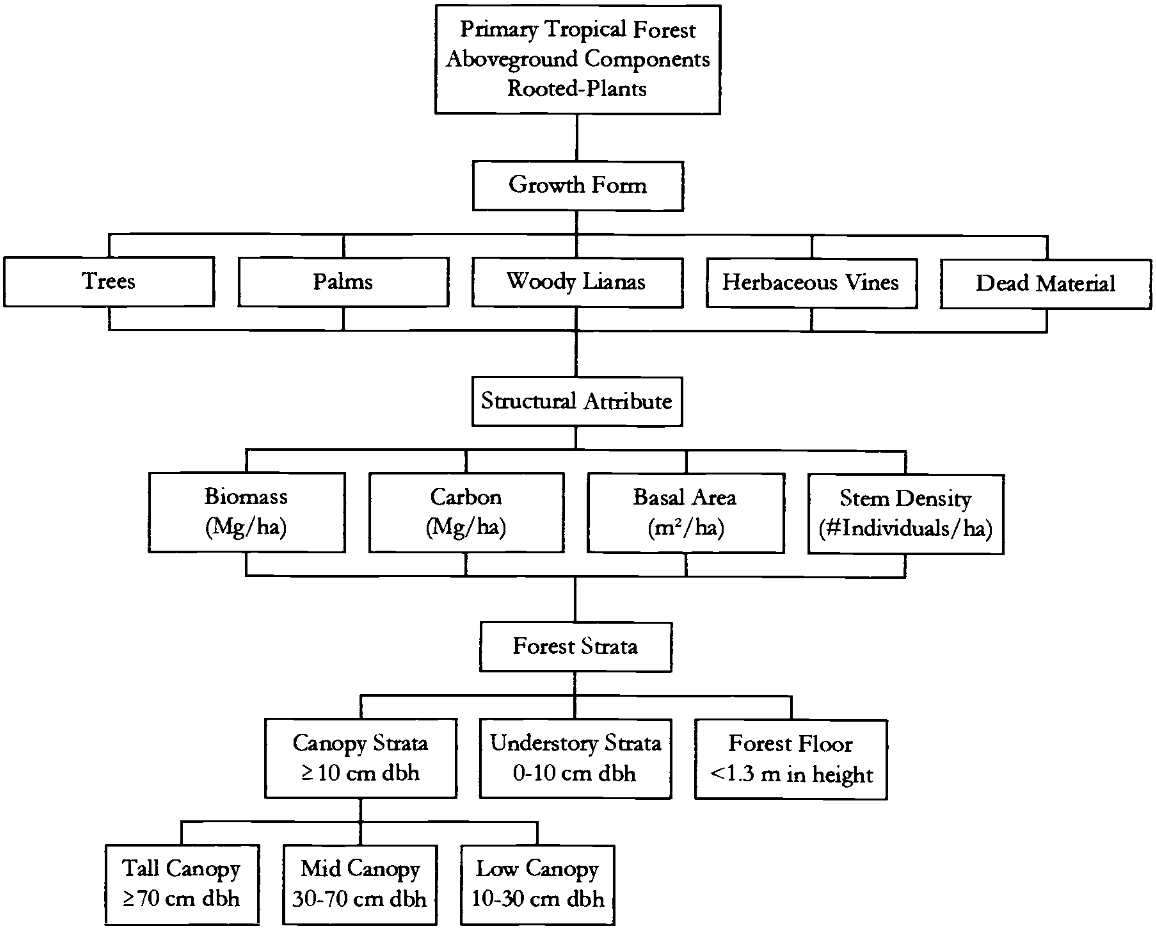

Figure 3.2: Sampling flow-diagram of the aboveground components within a primary tropical forest. All rooted-plants encountered within plots were assigned to one of five growth form categories, including dead material. Four structural attributes were measured and quantified: biomass, C, basal area, and stem density. Each individual plant was classified according to its structural class within the forest strata, based on size—diameter at 1.3 m in height (dbh). Diameter classes were consolidated into three major structural categories: the canopy strata (≥10 cm dbh), understory strata (0 - 10 cm dbh), and forest floor (<1.3 m in height). Plants ≥10 cm dbh were identified to species, when possible.

Tall- and mid-canopy composition and structure (all plants ≥30 cm dbh) were measured within the entire 0.79 ha plot (Figure 3.3). In the field, all individuals were identified to species, assigned a growth form, and carefully measured for dbh. In cases where buttress roots were present, dbh was measured above the buttress. I established a subplot (25 x 105 m) within the center of the larger plot to sample rooted plants ≥10 cm but <30 cm dbh (i.e. low-canopy strata). These individuals were also identified to species, assigned a growth form, and measured for dbh (Table 3.2). Nomenclature followed that of Ibarra-Manríquez and Sinaca (1997), Sosa and Gomez-Pompa (1994), and Martinez et al. (1994). In addition to dbh, height was measured for free-standing dead stems ≥10 cm dbh were <50% of the branch pattern was intact.

The forest understory strata (0 – 10 cm dbh) was sampled along two parallel transects, originating at the 25 m and 50 m points along the 75 m edge of the site (Figure 3.3). Each transect line extended for the 105 m length of the plot. At equally spaced 15 m increments, 8 sample points were established for a total of 16 points per site. A 15 m transect in a random direction was established at each sample point; parallel to this transect was a 2 x 10 m plot to sample understory forest structure (Figure 3.3). Slope was recorded using a clinometer along each 15 m transect line. All rooted stems within this plot were measured for dbh and growth form was identified.

I sampled the live and dead components of the forest floor strata (<1.3 m in height) using a 50 x 50 cm plot, positioned at 4.5 m along each of the 15 m transects (16 plots per site) (Figure 3.3). In each of these plots, live plants <1.3 m in height were destructively sampled at the ground level. Litter samples were collected to include all downed particles <2.54 cm in diameter, incorporating twigs, leaves, fruits, bark, and fallen flowers. Dry weight for both live and dead components in each 50 x 50 cm plot was recorded. Basal area and stem density were not measured for plants <1.3 in height (i.e. they were measured for the canopy understory strata only).

Biomass of coarse wood debris (≥7.6 cm in diam.) was calculated using the planar intercept technique (Van Wagner 1968). A total of 16-15 m transects were established at each site. Degree of decomposition of coarse wood debris was categorically evaluated as either sound or rotten based upon the integrity of each particle after the application of a swift force. Fine downed wood debris (2.54 – 7.6 cm in diam.) intersecting each 15 m transect line between meter 5 and 15 along were counted.

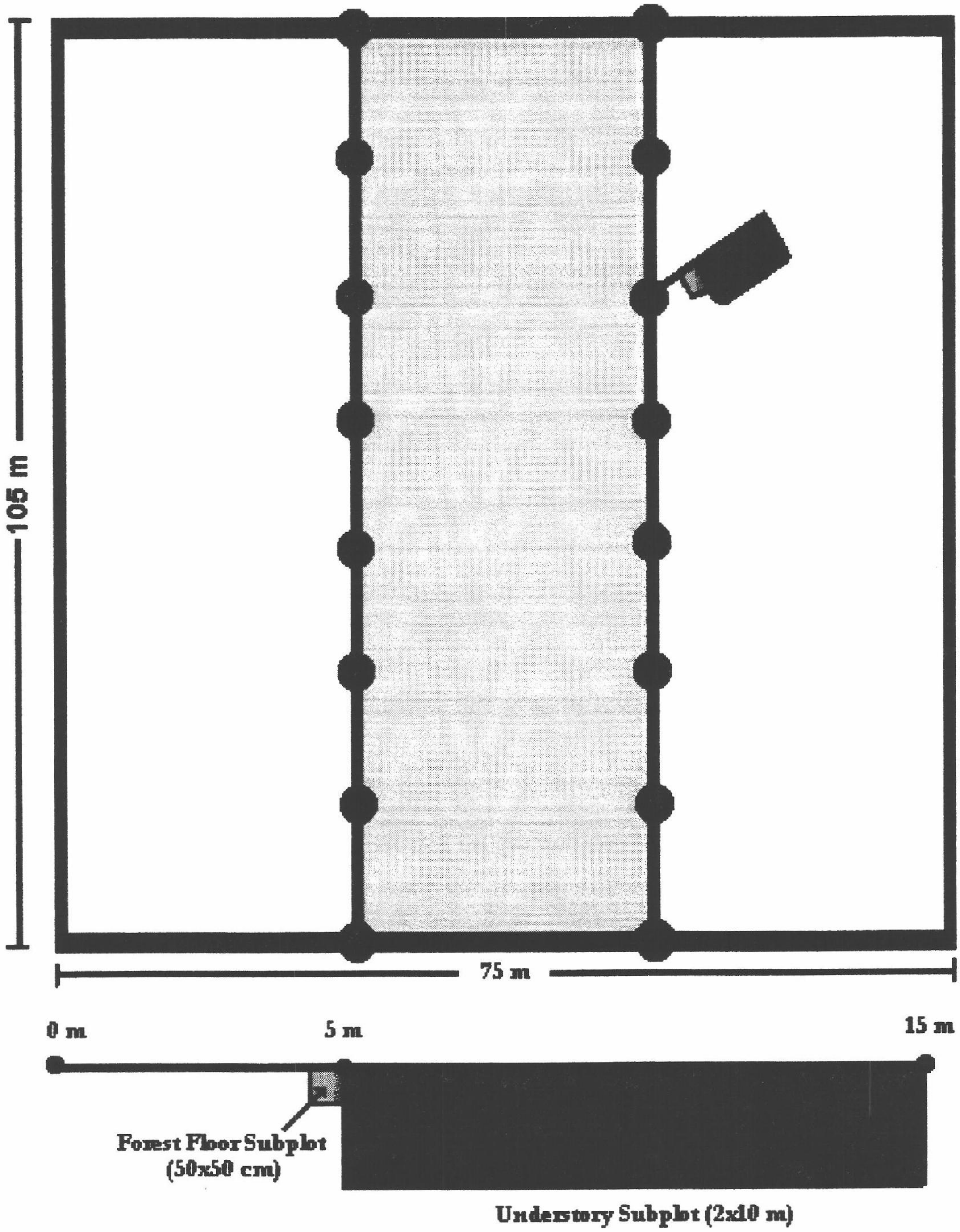

Figure 3.3: Nested-plot design for primary tropical forest sites. Tall- and mid-canopy plants (≥30 cm dbh) were sampled in the entire site (75x105 m); low-canopy plants (10-30 cm dbh) were sampled in the center plot only (lightly shaded area, 25x105 m). Rooted understory plants (0-10 cm dbh) were sampled in 16 - 2x10 m belt transects (dark shaded area); forest floor plants (<1.3 m in height) were sampled in the 16 - 50x50 cm quadrats (medium shaded area). Species composition and structure for canopy plants (≥10 cm dbh) were quantified in 20 sites throughout the Los Tuxtlas region, Veracruz, Mexico.

Table 3.2: Nested sampling design for primary forests within the Los Tuxtlas region, Veracruz, Mexico. Forest strata were based upon diameter-class, measured as diameter at 1.3 m in height (dbh). A total of 20-0.79 ha sites were sampled for forest structure to include biomass, C pools, basal area, and stem density. Basal area and stem density were not measured for the forest floor strata (<1.3 m in height).

Forest Strata	Diameter Class	Plot Dimensions	Plot Area (m^2)	No. of Plots $site^{-1}$	Total Area (m^2 $site^{-1}$)
Tall Canopy	≥70 cm dbh	75 x 105 m	7875	1	7875
Mid Canopy	30-70 cm dbh	75 x 105 m	7875	1	7875
Low Canopy	10-30 cm dbh	25 x 105 m	2625	1	2625
Understory	0-10 cm dbh	2 x 10 m	20	16	320
Forest Floor	<1.3 m ht	50 x 50 cm	0.25	16	4
Coarse Wood	≥7.6 cm	15 m	N/A	16	N/A
Fine Wood	2.54-7.6 cm	10 m	N/A	16	N/A
Litter	<2.54 cm	50 x 50 cm	0.25	16	4

Calculations

Tree biomass (≥10 cm dbh) was calculated using allometric equations for tropical moist forests presented by Brown et al. (1989) and Brown (1997). The equations utilized dbh, height, and specific gravity of wood (i.e. wood density) as parameters to estimate aboveground tree biomass (Table 3.3). Each individual tree measured in the field (≥10 cm dbh) was assigned a wood density value based on species. When possible, I utilized wood density values obtained from studies in Los Tuxtlas (Barajas-Morales 1987 and Carmona-Valdovinos unpublished data), followed by values from other Neotropical studies (Brown 1997) (Appendix). In cases where species could not be identified, I applied congener averages. In the few cases where genus could not be identified, or where wood density data were not available, the Los Tuxtlas wood density average of 0.58 g cm^{-3} was assigned (Barajas-Morales 1987, confirmed by this study). Canopy tree height was estimated using a predictive model based upon height and diameter relationships of >500 measured trees within the LTBS reserve (Hughes et al. 2000). Biomass for members of the genus *Cecropia* was calculated using models developed by Uhl et al. (1988), due to the unusual height-to-girth ratios of these individuals. I calculated canopy tree biomass (≥10 cm dbh) for the two sites within the Cloud Forest community-type using equations presented by Brown (1997) for tropical wet forests (Table 3.3). These equations utilized dbh and tree height as parameters and were selected because the climate conditions associated with the Subtropical Lower Montane Rain Forest classification (Holdridge et al. 1971) is characteristic of the climate parameters associated with the tropical wet forests used in the models to estimate biomass (Brown 1997, Brown et al. 1989). Biomass for dead standing trees (≥10 cm dbh) having ≥50% of their branch pattern intact was calculated in the same manner as for live trees, utilizing the value of 0.42 g cm^{-3} as the density for sound, dead wood (Hughes et al. 2000). For dead trees where <50% of the branch pattern remained, tree height was measured in the field, and biomass was calculated as the volume of a cylinder ($\pi r^2 h$) multiplied by the wood density value for sound, dead wood (0.42 g cm^{-3}).

Understory components were separated into the dominant growth forms: trees, woody lianas, palms, and herbaceous vines. Biomass equations for trees and palms (0 – 10 cm dbh) were obtained from studies in the Los Tuxtlas region (Hughes et al. 2000; Table 3.3). Biomass for woody lianas and herbaceous vines were estimated using equations developed by Putz (1983). In all cases, dbh was the model parameter used to estimate biomass; palms also incorporated height to the apical maristem as the predictive variable (Hughes et al. 2000).

Forest floor biomass was calculated as the mean oven-dry mass of live and dead material (16 plots $site^{-1}$). Biomass of downed and dead wood particles ≥2.54 cm was calculated based on equations developed by Van Wagner (1968). For all coarse wood particles (≥7.6 cm diameter), biomass was calculated using field diameter measures from each particle (Table 3.3). For fine wood (2.54 – 7.6 cm diameter), I applied the quadratic mean diameter (QMD) calculated for fine wood particles from Los Tuxtlas (QMD = 3.96 cm, Hughes et al. 2000) (Table 3.3).

Table 3.3: Models used to estimate aboveground biomass for each component within primary tropical forests for the Los Tuxtlas region, Veracruz, Mexico. Biomass is expressed is units of dry mass (Mg).

Paramater	Forest Component	Equation
Height[1]	Trees ≥10 cm dbh	$4.722 \ln (D^2) - 13.323$
Biomass (TEF's)[2]	Trees, TEF's only, ≥10 cm dbh	$\{\exp(-2.409 + 0.9522 \ln (D^2H\rho) + 0.0304)\}/1000$
Biomass (Cloud Forest)[2]	Trees, Cloud Forest, ≥10 cm dbh	$\{\exp(-3.3012 + 0.9439 \ln (D^2H) + 0.1055)\}/1000$
Leaf Biomass[3]	All Trees ≥10 cm dbh	$\{\exp(-1.897 + 0.836 \ln (D^2H))\}/1000$
Wood Biomass	All Trees ≥10 cm dbh	{Tree Biomass} – {Leaf Biomass} for All Trees
Wood Biomass[4]	*Cecropia spp.* ≥10 cm dbh	$\{\exp(-3.78 + 0.95 \ln (D^2) + \ln (H)\}/1000$
Leaf Biomass[4]	*Cecropia spp.* ≥10 cm dbh	$\{-0.56 + 0.02 (D^2) + 0.04 (H)\}/1000$
Biomass[4]	*Cecropia spp.* ≥10 cm dbh	{Wood Biomass} + {Leaf Biomass} for *Cecropia spp.*
Standing Dead Biomass[2]	Trees w/≥50% branches ≥10 cm dbh	{Tree Biomass ≥10 cm dbh}, where $\rho = 0.42$ g cm^{-3}
Standing Dead Biomass[1]	Trees w/<50% branches ≥10 cm dbh	$\pi(D/2)^2H\rho$, where $\rho = 0.42$ g cm^{-3}
Biomass[1]	Trees 0-10 cm dbh	$\{(\exp(1.123 \ln D^2 + 4.735)*1.107\}/10^6$
Wood Biomass[1]	Trees 0-10 cm dbh	$\{(\exp(4.747 + 1.092 \ln D^2))*1.132\}/10^6$
Leaf Biomass[1]	Trees 0-10 cm dbh	$\{(\exp(3.047 + 0.078 \ln D^2))*1.450\}/10^6$
Biomass[5]	Woody Lianas 0-10 cm dbh	$(10^{(0.12 + 0.91 \log(BA))})/1000$
Leaf Biomass[5]	Woody Lianas 0-10 cm dbh	$\{0.109 BA - 0.376\}/1000$
Wood Biomass	Woody Lianas 0-10 cm dbh	{Liana Biomass} – {Leaf Biomass}
Biomass[1]	Palms 0-10 cm dbh	$\{(\exp(3.627 + 0.577 \ln (D^2H)))*1.022\}/10^6$
Biomass[5]	Herbaceous Vines 0-10 cm dbh	{Woody Liana Biomass}
Standing Dead Biomass[1]	Trees 0-10 cm dbh	$\{(\exp(4.42 + 1.18 \ln D^2))*1.08\}/10^6$
Standing Dead Biomass[1]	Palms 0-10 cm dbh	$\{\exp(-0.53 + 0.99 \ln D^2H)\}/10^6$
Biomass	Live Plants and Litter <2.54 cm	Oven Dry Mass
Biomass Sound Dead Wood[6]	Coarse Wood (≥7.6 cm diam.)	$100\rho * \{(\pi^2 \Sigma D^2 S C d^2)/8L\}$, where $\rho = 0.42$ g cm^{-3}
Biomass Rotten Wood[6]	Coarse Wood (≥7.6 cm diam.)	$100\rho * \{(\pi^2 \Sigma D^2 S C d^2)/8L\}$, where $\rho = 0.23$ g cm^{-3}
Biomass[6]	Fine Wood (2.54 – 7.6 cm dia.)	$100\rho * \{(\pi^2 N S C QMD^2)/8L\}$

1=Hughes et al. 2000; 2=Brown 1997; 3=Crow 1978; 4=Uhl et al. 1988; 5=Putz 1983; 6=Van Wagner 1968;
D = diameter at 1.3 m ht (dbh, cm); H = height (m); ρ = wood density (g cm^{-3}); d = diameter at intercept (cm); QMD =Quadratic Mean Diameter = 3.96 cm; BA = Basal Area = πr^2; L=Length of transect (m); S=secant of wood debris tilt (= 1 if on forest floor); C=slope correction factor = $[1 + (\%\text{slope})/100)^2]^{1/2}$

Carbon pools were estimated using C concentrations as a percentage of biomass from vegetation located nearby the LTBS (Hughes et al. 2000; Table 3.4). In most cases, it was possible to estimate leaf and wood C separately for each growth form using allometric models for leaf and wood biomass (Table 3.3); total C for each individual was the sum of leaf C and wood C (Table 3.4). Carbon content was calculated by multiplying the biomass by the C concentration (%) for each individual (Table 3.4). Basal area and stem density were only calculated for stems ≥1.3 m in height. Basal area (m^2 ha^{-1}) was calculated as the cross-sectional area (πr^2) of each stem at 1.3 m in height (dbh) or if applicable, the diameter above the buttress roots. Stem density was calculated as the number of stems ha^{-1} within a sample plot at 1.3 m in height.

Data Analysis

The TAGB, C pools, basal area, and stem density for all individuals within each plot was calculated and reported on a hectare basis for all 20 sites. Regression analysis was used to determine if elevation was associated with TAGB, C, basal area, or stem density. One-way analysis of variance (ANOVA) was used to test if TAGB, C, basal area, or stem density differed among the 3 soil-types that are dominant to Los Tuxtlas (i.e. weathered soils, lava flows, and ash-derived). Comparisons with biomass, C, and structural partitioning among diameter classes of the forest among community-types and Holdridge Life Zones was conducted using a Mann-Whitney U, also known as the Wilcoxin rank-sum test. This test was chosen because of unequal variances in the data and small sample sizes (i.e. n=2 for Cloud Forest sites).

Table 3.4: Mean concentrations of carbon (%) within the aboveground components for primary forest within Los Tuxtlas region, Veracruz, Mexico (Hughes et al. 2000).

Forest Strata	Structural Component	Type of Plant Material	Carbon Content (%)	
	Live Material		**Mean**	**SE**
Canopy	Trees ≥10 cm dbh	Wood	48.58	0.13
Canopy	Trees ≥10 cm dbh	Leaf	46.25	0.51
Understory	Trees <10 cm dbh	Wood	45.82	0.25
Understory	Trees <10 cm dbh	Leaf	43.05	0.84
Understory	Palms 0-10 cm dbh	Wood	47.32	0.30
Understory	Herb. Vines 0-10 cm dbh	Live Stems	Use Canopy Tree Leaf	
Canopy/Understory	Lianas ≥0 cm dbh	Wood	Use Understory Tree Wood	
Canopy/Understory	Lianas ≥0 cm dbh	Leaf	Use Canopy Tree Leaf	
Forest Floor	<1.3 m ht	Live Stems	42.52	0.24
	Dead Material			
Coarse Debris	≥7.6 cm diam.	Sound Wood	50.12	0.33
Coarse Debris	≥7.6 cm diam.	Rotten Wood	49.29	0.63
Fine Debris	2.55-7.6 cm diam.	Wood	49.16	0.28
Litter	≤2.54 cm diam.	All Dead Mat.	46.15	0.88

Cluster analysis was used to determine if sites could be grouped on the basis of their forest structure. The data were arranged in a matrix of 20 sites by 32 structural components, and were analyzed using Euclidean Distance measures and Ward's Method (Beals 1984). The structural components used for this analysis included the biomass and C pools for all growth forms within all forest strata (18 variables total), and included the basal area and stem density for all growth forms in all strata ≥1.3 m in height (14 variables total). The specific objective of the cluster analysis was to group sites based on their combination of all 32 variables. Because all 32 structural variables were not expressed in the same units and their absolute values differed by orders of magnitude, it was necessary to express each structural variable on an equal footing. Hence, each structural component variable was independently relativized to the sum of squares of its variance among all 20 sites. This operation ensured no single structural variable was given more or less importance in the grouping of sites (Greig-Smith 1983). Following cluster analysis, an analysis by Multiple Response Permutation Procedure (MRPP, Milke 1984) was used to test group significance with environmental variables of elevation, slope, and soil-type. A final MRPP analysis was used to test group significance with the four Los Tuxtlas community-types (Chapter 2). I used both MRPP analyses as tools to test if forest stands that were different in their partitioning of biomass, C, basal area, and stem density within the forest strata (i.e. different structural configurations) could be explained by environmental variables alone, or if sub-regions having unique species compositions could account for structural differences. All multivariate statistics were performed using PC-ORD software package (McCune and Mefford 1997).

RESULTS

Total Aboveground Biomass, C, and Forest Structure

Mean (± 1 SE) TAGB was 414 ± 16 Mg ha^{-1} and varied between 309 and 550 Mg ha^{-1} for all 20-0.79 ha forest sites. The average total aboveground C pool was 201 ± 8 Mg ha^{-1} (Range: 149 – 267 Mg ha^{-1}), or 48.5 ± 0.0% of the TAGB (Range: 48.3 – 48.7%). For stems ≥1.3 m in height, an average of 12,600 ± 1,072 stems ha^{-1} (Range: 6055 – 25,023) had a mean basal area of 48 ± 2 m^2 ha^{-1} (Range: 33 – 66 m^2 ha^{-1}) (Table 3.5). These individuals ≥1.3 m in height contributed a mean of 382 ± 15 Mg ha^{-1} to the TAGB (Range: 274 - 482 Mg ha^{-1}) and 185 ± 7 Mg ha^{-1} to the aboveground C pools (Range: 133 – 233 Mg ha^{-1}). These plants (≥1.3 m in height) contributed 92.2 ± 1.1% to the TAGB and the total aboveground C (Range: 81.4 – 98.3%). For all stems ≥10 cm dbh, biomass averaged 363 ± 15 Mg ha^{-1} (Range: 257 – 470 Mg ha^{-1}) with a mean C pool of 177 ± 8 Mg ha^{-1} (Range: 125 – 228 Mg ha^{-1}). These canopy plants (≥10 cm dbh) contributed an average of 87.7 ± 1.1% (Range: 77.4 – 95.8%) to the TAGB and total C.

Despite the clear changes in species richness and composition that were associated with elevation, soil-types, and climate (Chapter 2), these tropical forests were noticeably similar to one another in their overall forest structure. For the 20 forest sites, there was no association with TAGB and total aboveground C with elevation (p=0.79 and 0.80, respectively), nor was there a relationship between elevation and total basal area (p=0.44) or total stem density (p=0.15). TAGB, total aboveground C, and total basal area did not vary according to soil-type (ANOVA, p=0.92, 0.91, and 0.52, respectively). Total stem density data were highly variable, although the data suggested sites on weathered soils had fewer stems ha^{-1} than did those on ash-derived soils and lava flows (ANOVA, p=0.09) (Table 3.5).

Table 3.5: The mean total aboveground biomass (TAGB), C pools, basal area, and stem density for 20-0.79 ha primary forest sites on the three dominant soil-types within the Los Tuxtlas region, Veracruz, Mexico. TAGB, C, and basal area did not vary according to soil-type (ANOVA, p>0.52); sites on weathered-soils appeared to have fewer stems ha^{-1} than did those on ash-derived soils and lava flows (ANOVA, p=0.09), although the data were highly variable.

Soil Type		**TAGB ($Mg\ ha^{-1}$)**		**C Pools ($Mg\ ha^{-1}$)**		**Basal Area ($m^2\ ha^{-1}$)**		**Stem Density (stems ha^{-1})**	
	n	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Ash Derived	4	410	39	199	19	50	1	14,992	826
Lava Flows	7	407	18	197	9	46	3	14,522	2,176
Weathered Soils	9	422	31	205	15	45	3	10,045	1,301
All Soils	**20**	**414**	**16**	**201**	**8**	**48**	**2**	**12,600**	**1,072**

With respect to species composition and climate, the Los Tuxtlas community-types were not different in TAGB, total C pools, basal area or stem density among the three TEF community-types (i.e. Lowland Reserve, La Perla Plateau, and Volcanic-Upslope) (p>0.28) (Table 3.6). On a hectare basis, the Cloud Forest sites had approximately 18% less TAGB and C than TEF's (p<0.001), with approximately 11% more basal area (p=0.02) and 19% more stems than TEF's (p=0.05). In terms of Holdridge Life Zones (Table 3.6), the Tropical Moist Forest type and the Subtropical Wet Forest classification were not significantly different in their overall TAGB, C ($p=0.22$) and forest structure ($p>0.10$). The Subtropical Lower Montane Rain Forest type (i.e. the Cloud Forest community-type) had ~20% less TAGB and C ha^{-1} ($p=0.04$) and approximately 16% more basal area ($p=0.07$) than the Subtropical Wet Forests; stem density data did not indicate any statistical differences ($p=0.21$) between the two Life Zones. I conclude that the community-types and Life Zones within the coarse TEF classification (Tropical Moist Forest and Subtropical Wet Forest) were not significantly different in their TAGB, total aboveground C, basal area, or stem density. This uniformity appeared despite changes in species composition, elevation, soils, and climate. In terms of TAGB, C, and forest structure for the San Martín Tuxtla watershed in the Los Tuxtlas region, I conclude there were two distinct forest types: TEF's and Cloud Forests.

Table 3.6: The mean total aboveground biomass (TAGB), C pools, basal area, and stem density for 20-0.79 ha primary forest sites located within different Community-Types (Chapter 2), Holdridge Life Zones (Holdridge et al. 1971), and the coarsely defined forest types (INEGI 2001) within the Los Tuxtlas region, Veracruz, Mexico. In terms of TAGB, C, and structure, the only significantly different forests were TEF's and Cloud Forests ($p<0.05$).

Forest Type		TAGB ($Mg\ ha^{-1}$)		C Pools ($Mg\ ha^{-1}$)		Basal Area ($m^2\ ha^{-1}$)		Stem Density (Stems ha^{-1})	
	n	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Community-Types									
Lowland-Reserve	12	416	24	202	12	46	3	11,602	1,711
La Perla Plateau	3	425	34	206	16	41	2	13,300	974
Volcanic Upslope	3	444	35	215	17	48	1	14,515	1,340
Cloud Forests	2	346	1	168	1	51	1	14,681	614
Holdridge Life Zones									
Tropical Moist	12	416	24	202	12	46	3	11,602	1,711
Subtropical Wet	6	434	22	211	11	44	2	13,907	789
Subtropical Lower Montane Rain	2	346	1	168	1	51	1	14,681	614
INEGI Classifications (Structurally Different Forests)									
TEF's	18	422	17	205	8	46	2	12,371	1,180
Cloud Forests	2	346	1	168	1	51	1	14,681	614
All Forest Types									
Landscape Total	**20**	**414**	**16**	**201**	**8**	**48**	**2**	**12,600**	**1,072**

Partitioning of Biomass Within The Forest Structure

As with total aboveground structure, environmental variables did not explain how biomass, C, and stems were partitioned among the forest strata. I selected three groups of sites based upon cluster analysis that were different in their partitioning of biomass, C, basal area, and stem density within all forest strata (32 variables total). The MRPP analysis identified that sites within these structural groups were randomly clustered (R*=0.001) and that elevation, slope, and soil-type were not significantly different among these structural groups (p=0.41). As expected from the differences in TAGB, C, basal area, and stem density with respect to species composition and climate (Table 3.6), there were differences in how these attributes were partitioned within the forest strata between TEF's and Cloud Forests. For the Los Tuxtlas community-types, the MRPP analysis demonstrated that although sites within each group were only loosely similar in structure (R=0.10), there was a significant difference among the four community-types in their partitioning of TAGB, C, basal area, and stem density within all the forest strata (p=0.008) (Tables 3.7 - 3.10). The majority of this difference in structural partitioning was found to be within the Cloud Forest community-type (i.e. the Subtropical Lower Montane Rain Forest Life Zone). As with the total aboveground structure, the data were in agreement that the three TEF community-types (i.e. LR, LP, and VU) were very similar in their partitioning of biomass, C, basal area, and stem density among all diameter classes (MRPP, R=0.04, p=0.08) (Tables 3.7 – 3.10). Any remaining differences among the three TEF community-types were due to high degrees of variability in stem density, as the Lowland-Reserve community-type (Tropical Moist Forest) appeared to have fewer stems than sites within the La Perla Plateau and the Volcanic-Upslope community-types (Subtropical Wet Forest), but no significant patterns were observed (p>0.19).

* The "R" value within the MRPP analysis describes the homogeneity within groups as compared with that expected by chance. An R value of 1 indicates that all items are homogeneous within each group. Conversely, R=0 when the members of each group are as heterogeneous as expected by chance (McCune and Mefford 1997, Milke 1984).

Table 3.7: Total aboveground biomass (TAGB, Mg ha^{-1}) partitioned within the forest structure for each of the Los Tuxtlas community-types, Veracruz, Mexico. The Lowland-Reserve, La Perla Plateau, and Volcanic-Upslope community-types are categorized as Tropical Moist Forest and Subtropical Wet Forest Life Zones (Holdridge et al. 1971); these three community-types are coarsely defined as Tropical Evergreen Forests (TEF's, INEGI 2001, Ibarra-Manríquez et al. 1997).

Diameter Class (cm dbh)	**Lowland Reserve**		**La Perla Plateau**		**Volcanic Upslope**		**TEF's**		**Cloud Forest**	
n of sites	**12**		**3**		**3**		**18**		**2**	
Live Biomass	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Trees ≥70	184	20	131	38	155	37	170	16	65	7
Trees 30-70	139	9	146	23	154	11	142	7	184	16
Trees 10-30	41	3	65	8	70	10	50	4	31	1
Trees 0-10	6	1	7	0	9	1	7	1	6	1
Palms 0-10	4	1	5	0	2	0	4	1	12	2
Lianas 0-10	6	1	5	2	5	3	6	1	1	1
Herb. Vines 0-10	2	1	2	0	1	0	2	0	1	0
Plants <1.3 m ht	1	0	1	0	0	0	1	0	2	0
Total Live Biomass	382	20	362	43	398	45	381	16	302	11
Dead Biomass										
Snags ≥70	5	2	11	7	3	3	6	2	3	2
Snags 30-70	2	1	4	0	4	2	2	1	6	0
Snags 10-30	0	0	2	1	1	1	1	0	1	0
Dead Plants 0-10	0	0	0	0	0	0	0	0	0	0
Sound Wood ≥7.6*	15	6	34	13	20	6	19	5	22	7
Rotten Wood ≥7.6*	4	1	4	2	7	2	4	1	5	2
Wood 2.54 - 7.6*	1	0	2	0	2	0	2	0	2	0
Litter <2.54	6	0	6	0	8	1	7	0	6	1
Total Dead Biomass	34	8	63	22	46	10	41	7	44	10
TAGB	**416**	**24**	**425**	**34**	**444**	**35**	**422**	**17**	**346**	**1**

*Dead wood was measured for diameter (cm) at intercept with transect line.

Table 3.8: Total aboveground carbon (C) pools (Mg ha^{-1}) partitioned within the forest structure for each of the Los Tuxtlas community-types, Veracruz, Mexico. The Lowland-Reserve, La Perla Plateau, and Volcanic-Upslope community-types are categorized as Tropical Moist Forest and Subtropical Wet Forest Life Zones (Holdridge et al. 1971); these three community-types are coarsely defined as Tropical Evergreen Forests (TEF's, INEGI 2001, Ibarra-Manríquez et al. 1997).

Diameter Class (cm dbh)	**Lowland Reserve**		**La Perla Plateau**		**Volcanic Upslope**		**TEF's**		**Cloud Forest**	
n of sites	**12**		**3**		**3**		**18**		**2**	
Live Plants	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Trees ≥70	89	10	64	18	75	18	83	8	32	3
Trees 30-70	67	5	71	11	75	5	69	4	89	8
Trees 10-30	20	1	32	4	34	5	24	2	15	1
Trees 0-10	3	0	3	0	4	0	3	0	3	0
Palms 0-10	2	0	3	0	1	0	2	0	5	1
Lianas 0-10	3	1	2	1	2	1	3	0	0	0
Herb. Vines 0-10	1	0	1	0	0	0	1	0	0	0
Plants <1.3 m ht	0	0	0	0	0	0	0	0	1	0
Total Live C Pools	185	10	175	21	192	22	185	8	146	6
Dead Plants										
Snags ≥70	2	1	5	3	2	2	3	1	2	1
Snags 30-70	1	0	2	0	2	1	1	0	3	0
Snags 10-30	0	0	1	0	1	0	0	0	0	0
Dead Plants 0-10	0	0	0	0	0	0	0	0	0	0
Sound Wood ≥7.6*	7	3	17	7	10	3	9	2	11	3
Rotten Wood ≥7.6*	2	1	2	1	3	1	2	0	2	1
Wood 2.54 - 7.6*	1	0	1	0	1	0	1	0	1	0
Litter <2.54	3	0	3	0	4	0	3	0	3	0
Total Dead C Pools	17	4	31	11	22	5	20	3	22	5
Aboveground C	**202**	**12**	**206**	**16**	**215**	**17**	**205**	**8**	**168**	**1**

*Dead wood was measured for diameter (cm) at intercept with transect line.

Table 3.9: Basal area (m^2 ha^{-1}) partitioned within the forest structure (>1.3 m in height) for each of the Los Tuxtlas community-types, Veracruz, Mexico. The Lowland-Reserve, La Perla Plateau, and Volcanic-Upslope community-types are categorized as Tropical Moist Forest and Subtropical Wet Forest Life Zones (Holdridge et al. 1971); these three community-types are coarsely defined as Tropical Evergreen Forests (TEF's, INEGI 2001, Ibarra-Manríquez et al. 1997).

Diameter Class (cm dbh)	**Lowland Reserve**		**La Perla Plateau**		**Volcanic Upslope**		**TEF's**		**Cloud Forest**	
n of sites	**12**		**3**		**3**		**18**		**2**	
Live Plants	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Trees ≥70	18	2	10	2	14	4	16	2	9	1
Trees 30-70	16	1	14	2	17	1	16	1	28	3
Trees 10-30	7	1	9	1	10	2	7	1	7	0
Trees 0-10	3	0	3	0	4	0	3	0	3	0
Palms 0-10	1	0	2	0	1	0	1	0	3	1
Lianas 0-10	1	0	0	0	0	0	1	0	0	0
Herb. Vines 0-10	0	0	0	0	0	0	0	0	0	0
Total Live Basal Area	45	3	38	2	46	3	44	2	49	2
Dead Plants										
Snags ≥70	1	0	1	1	1	1	1	0	1	0
Snags 30-70	0	0	1	0	1	0	1	0	1	0
Snags 10-30	0	0	1	0	0	0	0	0	0	0
Dead Plants 0-10	0	0	0	0	0	0	0	0	0	0
Total Dead Basal Area	1	0	3	1	2	1	2	0	2	0
Total Basal Area	**46**	**3**	**41**	**2**	**48**	**1**	**46**	**2**	**51**	**1**

Table 3.10: Stem Density (stems ha^{-1}) partitioned within the forest structure (>1.3 m in height) for each of the Los Tuxtlas community-types, Veracruz, Mexico. The Lowland-Reserve, La Perla Plateau, and Volcanic-Upslope community-types are categorized as Tropical Moist Forest and Subtropical Wet Forest Life Zones (Holdridge et al. 1971); these three community-types are coarsely defined as Tropical Evergreen Forests (TEF's, INEGI 2001, Ibarra-Manríquez et al. 1997).

Diameter Class (cm dbh)	**Lowland Reserve**		**La Perla Plateau**		**Volcanic Upslope**		**TEF's**		**Cloud Forest**	
n of sites	**12**		**3**		**3**		**18**		**2**	
Live Plants	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Trees ≥70	25	3	16	3	20	5	23	2	17	3
Trees 30-70	99	6	96	11	107	9	100	4	176	20
Trees 10-30	246	24	312	58	354	41	275	21	234	10
Trees 0-10	5,081	1,172	5,854	482	9,365	307	5,924	862	9,516	609
Palms 0-10	875	207	917	85	292	68	785	147	1,969	531
Lianas 0-10	2,107	316	2,969	841	1,854	807	2,208	277	688	219
Herb. Vines 0-10	2,768	686	2,677	590	2,208	754	2,660	473	1,844	313
Total Live Stems	11,202	1,621	12,841	915	14,200	1,327	11,975	1,124	14,443	616
Dead Plants										
Snags ≥70	1	0	1	0	1	1	1	0	2	1
Snags 30-70	3	1	5	2	4	2	3	1	10	2
Snags 10-30	6	2	15	8	8	4	8	2	8	0
Dead Trees 0-10	206	46	240	55	271	63	222	33	172	16
Dead Palms 0-10	23	15	94	18	0	0	31	13	31	31
Dead Lianas 0-10	91	36	94	94	21	21	80	28	16	16
Dead H. Vines 0-10	70	31	10	10	10	10	50	22	0	0
Total Dead Stems	400	108	459	109	315	81	396	74	616	3
Total Stems	**11,602**	**1,711**	**13,300**	**974**	**14,515**	**1340**	**12,371**	**1,180**	**14,681**	**614**

The Cloud Forest community-type differed from the TEF's in the partitioning of TAGB, C, basal area, and stem density within the canopy strata (≥10 cm dbh) (Tables 3.7 – 3.10). Biomass of trees ≥10 cm dbh was approximately 23% lower in Cloud Forests than TEF's ($p=0.04$), with 280 Mg ha^{-1} (81% of TAGB and C) for Cloud Forests and 362 Mg ha^{-1} (86% of TAGB and C) for TEF's (Tables 3.7 – 3.8). This biomass difference was apparent although stem density and basal area data were highly variable and were not significantly different between TEF's and Cloud Forests ($p=0.10$ and 0.22 for stem density and basal area, respectively). TEF's had an average of 398 stems ha^{-1} ≥10 cm dbh with 39 m^2 ha^{-1} of basal area; Cloud Forests averaged 427 stems ha^{-1} and 44 m^2 ha^{-1} of basal area (Tables 3.9 – 3.10).

Between TEF's and Cloud Forests, the clearest and most significant difference in TAGB and C was due to a shift in forest structure from very large-diameter trees (≥70 cm dbh) in TEF's that had substantial individual biomass, to a more evenly-distributed biomass structure that involved many medium-diameter trees (30 - 70 cm dbh) in the Cloud Forests (Tables 3.7 – 3.10). In TEF's, approximately 40% of the TAGB and total C were trees ≥70 cm dbh, compared with a corresponding mean of 19% for Cloud Forests ($p=0.005$). The concentration of TAGB and C in this size class involved only 23 trees ha^{-1} (Range: 11 – 48) in TEF's and 17 trees ha^{-1} (Range: 14 and 20) in Cloud Forest stands. These trees (≥70 cm dbh) had an average biomass of 7.5 ± 0.3 Mg for TEF's versus 3.9 ± 0.2 Mg for Cloud Forests. On a hectare basis, a single tree ≥70 cm dbh contributed an average of 2.2% to the TAGB and C for TEF's and an average of 1.4% for Cloud Forests. The difference in absolute value of these biomass measures may be related to the different biomass equations chosen for TEF's and Cloud Forests (Brown et al. 1989, Clark and Clark 2000), but their relative contribution to TAGB and C would not change with respect to which model was used.

Cloud Forest TAGB and C was more influenced by the medium-diameter trees (30 - 70 cm dbh) than were TEF's (Tables 3.7 – 3.10). Trees in this structural class accounted for 53% of the TAGB and C in Cloud Forests, compared with 34% in TEF's ($p=0.05$). An average of 100 stems ha^{-1} (Range: 66 – 126 stems ha^{-1}) occupied an average of 16 m^2 ha^{-1} (Range: 10 – 21 m^2 ha^{-1}) of basal area within the TEF sites. Cloud Forests had approximately 76% more stems and 88% more basal area in the mid-canopy strata than TEF's ($p<0.01$), or an average of 176 stems ha^{-1} (Range: 156 and 196 stems ha^{-1}) with a mean basal area of 30 m^2

ha^{-1} (Range: 27 and 32 m^2 ha^{-1}). A single tree in the mid-canopy strata of TEF sites had a mean dbh of 43.5 cm (Median: 40.8 cm) and a mean biomass of 1.4 Mg; individual Cloud Forest trees in this size class averaged 43.8 cm dbh (Median: 41.2 cm dbh) and averaged 1.0 Mg in biomass. Single individuals 30 – 70 cm dbh represented less-than one-half of one percent of the TAGB and total C for both TEF's and Cloud Forests. These data clarify the Cloud Forests are composed of many medium-diameter trees with generally less individual biomass, while TEF's are composed of more very large trees and generally fewer medium-sized trees; implicating the large trees in TEF's as important loci for tropical forest biomass and C.

Large Trees and Variability in TAGB

For all TEF's, the largest-diameter individual was *Jacaratia dolichaula* (Donn. Sm.) Woodson (CARICACEAE). This tree measured 195.8 cm dbh, and was estimated to weigh ~12 Mg and store ~6 Mg of C (Table 3.11). The second-largest individual by dbh was the most influential in terms of biomass and carbon storage. This individual, *Coccoloba montana* Standl. (POLYGONACEAE), was carefully measured to have a dbh of 183.0 cm, and was estimated to have ~43 Mg of biomass and ~21 Mg of C (or, ~250% more biomass and C than *J. dolichaula*). On a hectare basis, this single large tree contained approximately 10% of the TAGB and C for the forest stand in which it was encountered. The discrepancy in the biomass and carbon estimates from these 2 trees was primarily due to the wood density for each species (0.16 versus 0.74 g cm^{-3}, respectively) (Barajas-Morales 1987) (Figure 3.4), although tree height may also have had an influence had I measured it directly.

Table 3.11: The 17 plant species represented by the 25 trees that exceeded the 130 cm dbh range limit for the allometric model used to estimate biomass (Brown et al. 1989). These trees were encountered in 13 of 18 0.79 ha Tropical Evergreen Forests (TEF's) in the Los Tuxtlas region, Veracruz, Mexico. On a hectare basis, an average of 2 of these trees contributed a combined average of 50 ± 8 Mg ha^{-1}, or 11% to the TAGB.

Plant Species	Family	Wood Density (g cm^{-3})	DBH Range (cm)	n of sites	Comm. Type[7]	Mean Biomass (Mg tree^{-1})
Brosimum alicastrum	MORACEAE	0.44[1]	145	1	LR	15.8
Coccoloba montana	POLYGONACEAE	0.74[2]	183	1	LR	42.5
Dalbergia glomerata	FABACEAE	0.80[3]	145	1	VU	27.6
Diospyros digyna	EBENACEAE	0.79[1]	162	1	LR	34.8
Dussia mexicana	FABACEAE	0.51[1]	151-154	3	LR, VU	20.2
Ficus colubrinae	MORACEAE	0.42[4]	182	1	LR	24.5
Ficus petenensis	MORACEAE	0.48[5]	137-157	2	LR	17.6
Ficus yoponensis	MORACEAE	0.44[5]	141-149	2	LR	15.8
Jacaratia dolichaula	CARICACEAE	0.16[2]	196	1	LR	11.5
Mortoniodendron guatemalense	TILIACEAE	0.51[1]	141	1	LR	17.2
Ocotea uxpanapana	LAURACEAE	0.61[4]	170	1	LR	30.4
Pterocarpus rohrii	FABACEAE	0.52[1]	137-160	2	LR	19.6
Quercus skinneri	FAGACEAE	0.67[3]	141	1	VU	22.1
Sambucus mexicana	CAPRIFOLIACEAE	0.58[6]	139	1	VU	18.8
Sideroxylon portoricense	SAPOTACEAE	0.93[1]	139	1	VU	3.2
Ulmus mexicana	ULMACEAE	0.58[6]	132-140	2	LP, VU	17.8
Wimmeria bartlettii	CELASTRACEAE	0.58[6]	136-162	3	LP	19.1

[1] Barajas-Morales (1987); [2]Congener average, Barajas-Morales (1987); [3]Congener average, Brown (1997); [4]Congener average, Barajas-Morales (1987), Carmona-Valdovinos (unpublished data), and Brown (1997); [5]Carmona-Valdovinos (unpublished data); [6]Los Tuxtlas average specific gravity measure, 0.58 g cm^{-3}, Barajas-Morales (1987); [7]The TEF community types for Los Tuxtlas are Lowland Reserve (LR), La Perla Plateau (LP), Volcanic-Upslope (VU) (Chapter 2). See Appendix for more information about each species.

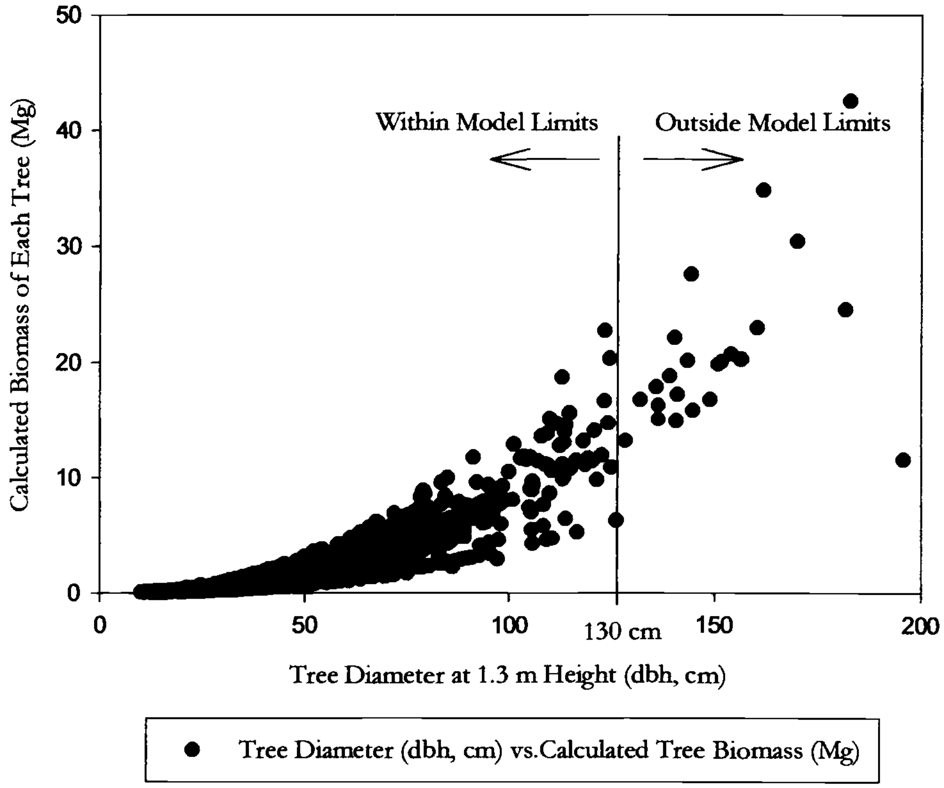

Figure 3.4: Biomass (Mg) plotted as a function of diameter at 1.3 m in height (dbh, cm). Biomass was calculated using an allometric equation presented by Brown et al. (1989) for tropical moist forests, using tree diameter (at dbh), tree height, and the specific gravity of wood (i.e. wood density) as parameters. This graph includes the 2,978 trees ≥10 cm dbh that were found within all 18-0.79 ha tropical evergreen forests (TEF's) presented in this study. All members of the genus *Cecropia* were excluded from this graph. At large diameters, the specific gravity of wood becomes the factor that most influences overall tree biomass and, ultimately, the total aboveground biomass (TAGB) of a forest stand. A total of 25 trees >130 cm were encountered that are outside the largest diameter trees destructively sampled to create this biomass model (Brown et al. 1989). These 25 trees contributed a mean of 50 ± 8 Mg ha^{-1}, or 11% (Range: 4 – 23%) of the TAGB and C of the forest stands in which they were found.

A total of 25 trees representing 17 plant species, 15 genera, and 12 families were found to exceed the dbh range limit of the 94 trees that were destructively sampled to create the allometric models used to estimate biomass (Range Limit: 10 - 130 cm dbh, Brown et al. 1989) (Table 3.11). These trees were located in 13 of the 18 TEF sites (72% of the TEF sites), and included all sites in the La Perla Plateau and Volcanic Upslope community-types (Subtropical Wet Forest Life Zone), and 7 of the 12 (58%) of the Lowland-Reserve sites (Tropical Moist Forest Life Zone). On average for the 13 TEF sites, a mean of 1.9 trees (Range: 1 – 4 trees) were >130 cm dbh (Table 3.12). Combined, these large trees contributed an average of 50 ± 8 Mg ha^{-1} (Range: 19 – 126 Mg ha^{-1}) to the TAGB of the TEF stand in which they were found. This quantity of biomass corresponded to a mean of 11% of the TAGB and C, with a highly variable range from 4% to 23%. On average for TEF's, the biomass and C in these few, large trees contributed as much to the TAGB and C as did all of the ~275 plants 10 – 30 cm dbh combined (50 ± 4 Mg ha^{-1}, Tables 3.7 – 3.10). The 25 trees >130 cm dbh encountered in this study were very influential to TAGB and C and yet were well outside the original dbh parameters of the allometric biomass model utilized (Brown et al. 1989). In addition, sources of error associated with accurate measures of specific gravity of wood, tree height (which I did not directly measure), and diameter had an amplified effect on TAGB and C measures with increasing diameter (Figure 3.4). These limitations underscore the need for expansion of allometric biomass models to include trees >130 cm dbh, including accurate field measures of diameter, height, wood specific gravity for each individual encountered.

Table 3.12: Data from the 25 trees >130 cm dbh where biomass was calculated using allometric equations developed by Brown et al. (1989). These 25 trees (17 species) were encountered in 13 of the 18 (72%) Tropical Evergreen Forest sites (TEF's) in the Los Tuxtlas region, Veracruz, Mexico. The biomass model was created using 94 destructively-sampled trees from tropical American TEF's (dbh range: 10 – 130 cm) (Brown et al. 1989). The authors cautioned against extrapolation of biomass estimates outside the dbh range. For the TEF's in Los Tuxtlas, trees >130 cm contributed an average of 11% (Range: 4 – 23%) to the total aboveground biomass (TAGB) and carbon (C) pools.

	Tropical Evergreen Forests				
Number of Trees >130 cm dbh	25				
Number of Plant Species >130 cm dbh	17				
Number of Sites Having Trees >130 cm dbh	13				
	Mean	**SE**	**Median**	**Range**	
Diameter at 1.3 m height (dbh, cm)	151.6	3.3	145.0	132.0	195.8
Wood Specific Gravity ($g\ cm^{-3}$)*	0.57	0.04	0.58	0.16	0.93
Species Biomass ($Mg\ ha^{-1}\ species^{-1}$)	38	5	39	4	77
Species Carbon Content ($Mg\ ha^{-1}\ species^{-1}$)	18	2	19	2	37
Number of Trees >130 cm dbh $site^{-1}$	1.9	0.2	2.0	1	4
Biomass Contribution to TAGB ($Mg\ ha^{-1}$)	50	8	46	19	126
Carbon Contribution to TAGC ($Mg\ ha^{-1}$)	24	4	22	9	61
Total Contribution to TAGB and C (ha^{-1})	**11%**	**1%**	**11%**	**4%**	**23%**

*Specific gravity measures follow Barajas-Morales (1987), Carmona-Valdovinos (unpublished data), and Brown (1997) (Appendix).

For the Cloud Forest sites, where the equations for Tropical Wet Forests were used to estimate biomass (Brown et al. 1989), the largest individual tree was *Turpinia occidentalis* (S.W.) G. Don subsp. *breviflora* Croat (STAPHYLEACEAE). This tree had a dbh of 100 cm, and was estimated to have ~6 Mg of biomass and ~3 Mg of C. No trees were found in the Cloud Forest community-type that exceeded the dbh limits for these equations (Range limit: 4 – 112 cm dbh; Brown 1997). However, the model utilized tree height as a parameter, and the height-diameter relationship presented by Hughes et al. (2000) was based upon trees found within the Lowland-Reserve community-type, where forest stands were found to be only 2% similar in species composition (≥10 cm dbh) as compared with Cloud Forests

(Chapter 2). It is likely there was a height discrepancy between Cloud Forest and Lowland-Reserve trees, and I suggest my estimates of Cloud Forest tree biomass were an overestimate of tree biomass and ultimately, the TAGB and aboveground C.

DISCUSSION

The variability in TAGB and C for the TEF's of Los Tuxtlas was chiefly due to the size, species' specific gravity, and frequency of the large diameter trees (≥70 cm dbh). In calculating TAGB, it is important to recognize the sources of potential error in the allometric equations, especially when field data exceed the parameters by which the original biomass equations were conceived (Brown 1997, Brown et al. 1989). In this study, I presented TAGB measures with 1 SE associated with sampled sites; I did not present confidence intervals on each tree that were associated with the allometric models (Brown 1997, Brown et al. 1989). The model I chose to estimate biomass of trees ≥10 cm dbh (Brown et al. 1989) utilized dbh, height, and specific gravity of wood as parameters, and was shown to have good fit (adjusted $R^2 = 0.99$). Understandably due to the difficulty in the destructive sampling of trees ≥70 cm dbh, only 3 individuals of this size class were incorporated into the model (Range: 127 – 133 cm dbh; Brown et al. 1989, Brown 1997). Baker (2000) found that wood specific gravity values for tropical forest trees were highly variable, from 4% to 73% of their mean value, depending on where the wood sample was taken from in an individual tree. In addition, specific gravity values have been shown to vary up to 33% among trees of the same species within a single forest stand (Baker 2000). This variability in wood specific gravity affects accurate estimates of large tree biomass, and ultimately affects the accuracy of TAGB and C estimates. Another source of error in my TAGB estimates involved the models for estimating tree height. I estimated height from a diameter-height model created from >500 trees located in the Lowland-Reserve community-type (Hughes et al. 2000). Lieberman et al. (1997) reported variation in tree height along a 2,000 m elevational gradient in Costa Rica, with tree height decreasing above and below 300 m.a.s.l. Assuming our values of dbh, specific gravity, and height were accurate, individual trees ≥70 cm dbh significantly diverged in their overall contribution to TAGB, by a factor of approximately 3 at ~130 cm dbh (Table 3.12, Figure 3.4). The sources of error associated with accurate measures of specific gravity of wood, tree height, and diameter had an amplified affect on TAGB and C measures for trees ≥70 cm dbh (Figure 3.4). In order to improve the accuracy of C estimates, it is at least necessary to obtain accurate field measures of dbh, specific gravity, and tree height for large trees, especially >130 cm dbh.

Despite the variability and model limitations associated with large trees, I found no differences in TAGB, C, and forest structure among TEF's on the landscape-scale. These similarities in aboveground structure existed although elevation, soil-types, slopes, climate, and species compositions varied among forest stands. The Los Tuxtlas community-types (Chapter 2) corresponded with the vegetation classifications in the Holdridge Life Zones, and no statistical differences were observed in TAGB, C, basal area or stem density across three community-types (LR, LP, and VU) and two Holdridge Life Zones (Tropical Moist Forest and Subtropical Wet Forest) (Table 3.6). In terms of how biomass and C were partitioned among diameter classes and growth forms, the TEF's all appeared to be structurally equivalent to one another (Tables 3.7 – 3.10), despite any differences in the environmental variables or species composition.

Above ~1100 m, where TEF's transitioned into Cloud Forests (i.e. Subtropical Lower Montane Forest Life Zone), TAGB and C were more dependent upon the medium-diameter trees (30 – 70 cm dbh) than the large trees (≥70 cm dbh). In these forests, the majority of the TAGB and C (53%) were trees 30 - 70 cm dbh compared with 34% in TEF's. In contrast, an average of only 19% of the TAGB and C were trees ≥70 cm dbh in Cloud Forests, and these large trees accounted for a mean of 40% of the TAGB and C in TEF's. On a hectare basis, stands within the Cloud Forest community-type had 18% less TAGB and C than TEF's, and had 11% more basal area and 19% more stems than TEF's. These results are typical of forests within the Subtropical Lower Montane Rain Forest Life Zone, where vegetation has been observed to have more stems, often greater abundances of epiphytes, and lower tree heights than lowland Life Zones (Holdridge et al. 1971, Tosi and Watson personal communication). The Los Tuxtlas Cloud Forests likely are the northernmost extreme of their type in America, yet little is known about these unique forests, outside of their structure (this study) and the rooted-plant species composition and diversity (Chapter 2).

Although a minor contingent in land area, the Los Tuxtlas region is an important locale in global TAGB and C relative to many other Neotropical forests. For Amazonian

TEF's, Laurance et al. (1999) reported a mean TAGB of 356 Mg ha^{-1} (Range: 231 – 492 Mg ha^{-1}) for 65 - 1 ha plots in the central Amazon. Cummings et al. (in press) reported a similar value of 345 Mg ha^{-1} (Range: 287 – 534) for 20 primary TEF's in Rondônia, Brazil. Compared with Los Tuxtlas, these measures of TAGB were more similar to the TAGB reported here for Cloud Forests (346 Mg ha^{-1}), and were approximately 16% lower than our measures for TEF's (422 Mg ha^{-1}). Clark and Clark (2000) reported a range in aboveground biomass for plants ≥10 cm dbh to be 161 - 186 Mg ha^{-1} for forests in the Tropical Wet Forest Life Zone of Costa Rica. I reported higher biomass values for all Life Zone classifications for plants ≥10 cm dbh (Range: 290 – 374 Mg ha^{-1}) as did Laurance et al. (1999; 318 Mg ha^{-1}) and Cummings et al. (in press; 269 Mg ha^{-1}) in the Amazon. The authors thought it likely they underestimated aboveground biomass due to the use of the Tropical Wet Forest allometric equation presented by Brown (1997), which involved dbh as the only parameter (Clark and Clark 2000). However, their data also suggest the number of large trees ≥70 dbh encountered in sample plots (0.01 ha, 0.5 ha, 4 ha, and 4.4 ha) was much lower on a hectare basis (Range: 4.7 – 10.1 trees ha^{-1}) compared to what was reported for Los Tuxtlas (Range: 11.4 – 49.5 trees ha^{-1}; this study) and for Southwestern Brazil (Mean: 12.6 trees ha^{-1}; Cummings et al. in press). These findings underscore that the presence or absence of trees ≥70 may account for most, if not all, of the variability in tropical forest TAGB and C (Tables 3.7 – 3.10).

On a more global perspective, Brown (1997) utilized existing forest inventory data (trees ≥10 cm dbh) and estimated aboveground biomass for moist TEF's of Africa and Asia to be approximately 218 Mg ha^{-1} and 334 Mg ha^{-1}, respectively, versus a mean of 354 Mg ha^{-1} for trees ≥10 dbh for TEF's in Los Tuxtlas (This study). I conclude the TAGB and C results presented by Hughes et al. (2000) based upon local-scale measures (i.e. the LR community-type) were within the mean, range, and variability of the landscape-scale measures presented here. These data suggest that on a hectare basis, Los Tuxtlas forests are important in global TAGB and C, and the high rate of localized deforestation and fragmentation within Los Tuxtlas has resulted in a significant flux of radiatively-active gases to the atmosphere (Hughes et al. 2000).

Variability in TAGB has been linked to environmental variables, particularly soils. In the Brazilian Amazon, where soils are known to be nutrient-poor (Sanchez et al. 1983), Laurance et al. (1999) found that soil fertility could explain almost one-third of the variability in TAGB for primary TEF's on heavily weathered soils (Oxisols). The authors observed the gradient was due to the capacity of soils to retain higher or lower levels of N and other cations (Laurance et al. 1999). For the young Los Tuxtlas soils (Andosols), Hughes et al. (2000) found total C to be 210 Mg ha^{-1}, which contrasts with reported values that ranged from 64 to 113 Mg ha^{-1} for soils typical of those found in the Brazilian Amazon (Sanchez et al. 1983). It is important to note the total aboveground C reported in this study (201 Mg ha^{-1}) and by Hughes et al. (2000) (196 Mg ha^{-1}) was approximately equal to the total soil C pools for Los Tuxtlas primary forests (210 Mg ha^{-1}, Hughes et al. 2000). In terms of soil nitrogen (N), Los Tuxtlas was found to have more than twice the concentration of total soil N as compared with other tropical soils (Hughes et al. 2000; Sanchez et al. 1983). The capacity for both soil C and soil N has been attributed to the high affinity of soil organic matter to Andosols (Hughes et al. 2000, Sollins et al. 1988). On similarly nutrient-rich soils in Costa Rica, Clark and Clark (2000) found differences in aboveground biomass (≥10 cm dbh) to be related to soil type for 0.01 and 0.5 ha plots. For TEF's within Los Tuxtlas, the contribution of large trees, especially trees >130 cm dbh (Table 3.12) to TAGB and C in 0.79 ha plots explained more of the variability in TAGB and C than any other environmental variable, including soils.

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CHAPTER 4

Conclusions and Recommendations for Future Work

The forest stands of Los Tuxtlas were composed of a diverse assemblage of rare species, where the majority of the species within a forest stand appeared to occur only within that stand, or within neighboring stands. I have suggested the rooted-plant diversity within Los Tuxtlas was related to its diverse environmental features, namely the topography, edaphic conditions, wide elevational range, and climate. Based on the data, I defined the presence of sub-regions, or forest environments, each unique in their species compositions and in their environmental attributes. These community-types are useful tools for conservation, as each represent an area within Los Tuxtlas where focused conservation efforts could minimize the losses to the species richness and biodiversity within the region.

Another significant finding was the relationship between the Los Tuxtlas community-types and the Holdridge Life Zones. While it is expected that different Life Zones would have different species compositions (Holdridge et al. 1971), their correspondence with the different Los Tuxtlas community-types suggests that most of the ecological studies in the Los Tuxtlas region have been done in a maximum of one-fourth of the unique forests, and in only one of the three Life Zones (i.e. the Lowland-Reserve community-type and Tropical Moist Forest only) (Gonzales-Soriano et al. 1997). The Los Tuxtlas region is diverse in its environment, and the forests have reflected this with different assemblages of plant species that were localized to elevational, edaphic, and climatic bands. In all hopes, scientists will recognize the different climatic zones and the forest environments to expand their current research questions to include all Life Zones and forest community-types.

In terms of forest structure and species composition, the three TEF community-types that spanned two Life Zones were only ~26% similar, but were not statistically different in their TAGB, C, stem density, or basal area; nor were they different in how biomass and C was partitioned within the diameter classes of the forests. In addition, the data indicated a pattern of species richness, where the proportion of the total species richness partitioned within the diameter classes a forest stand was similar despite any other changes in environmental characteristics. These findings highlight that groups of species occupied similar structural niches, as each group of species had similar amounts of biomass and C. Hence, I suggest there are opportunities to investigate the functional roles of species within forest environments, where groups of species appear to function similarly in the forest structure (in terms of biomass and C) over changing environmental and climatic regimes.

The presence of the large trees (i.e. >130 cm dbh) within forest stands greatly influenced the estimates of TAGB and C. Their overall contribution to TAGB and C (~11%) underscores that the sources of error associated with the measurement of a single tree can greatly affect the variability in TAGB and C estimates on local, landscape, and global scales. To improve estimates of TAGB and C pools, it is necessary to expand these models to include more, large-diameter trees and obtain accurate field measures of diameter, height, and the specific gravity of wood for each large tree encountered.

The Los Tuxtlas region has been a C source to the atmosphere through land-use and biomass burning, and should be considered an important species, biomass, and C reserve for the Neotropics and for North America. The high proportions of rare species within these forests coupled with the high rates of deforestation have likely resulted in the losses of many endemic species. However, Los Tuxtlas represents an area of tremendous potential for conservation, particularly through C offsets. It is not uncommon to observe pastures that have been in active use for as much as 30 years (Hughes et al. 1999); their proximity to primary forest fragments and the young, productive soils allow for an ideal opportunity to expand existing forest into adjacent pastures. For this to be effective, the socio-economic challenges associated with subsistence agriculture need to be better resolved. One way to resolve such issues is to provide economic incentives for *Ejido* farmers to (i) conserve the remaining forests, and (ii) to retire active pastures and promote forest regrowth. Focused attention in providing these economic incentives could yield a winning solution that improves the socio-economic conditions of the *Ejidos*, preserves and promotes biodiversity, and transforms Los Tuxtlas into a C sink rather than a source of C to the atmosphere.

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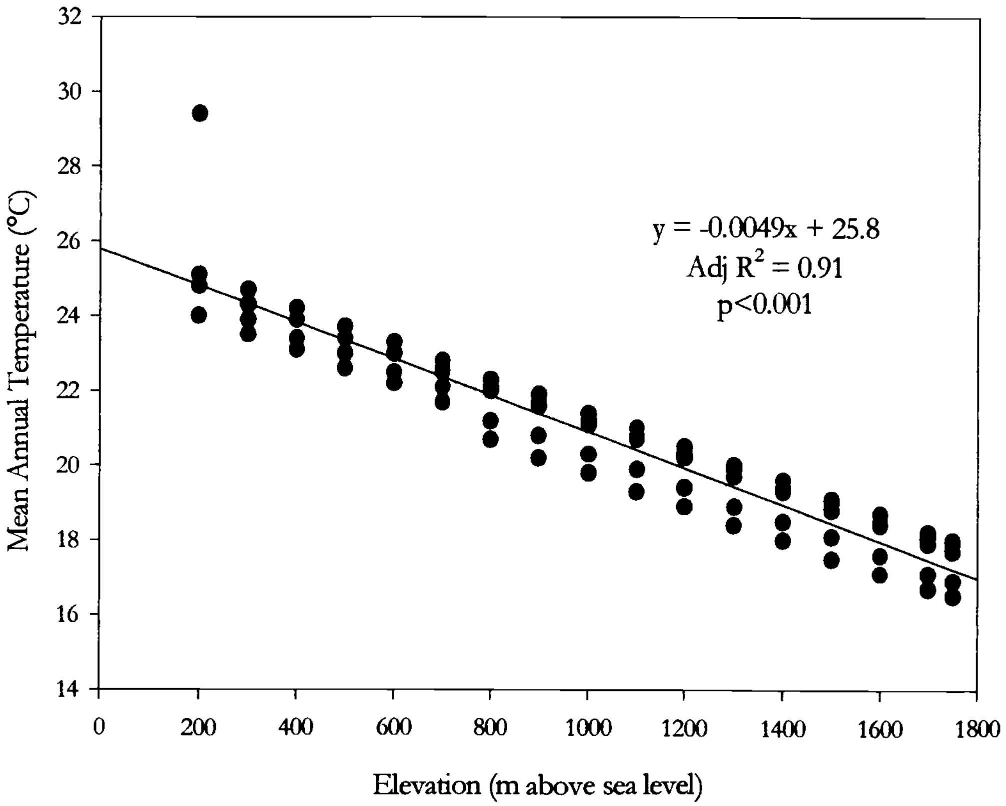
APPENDICES



Appendix A: Mean annual temperature for 5 weather station transects within the Los Tuxtlas region, Veracruz, Mexico (Soto and Gama 1997). Mean annual temperature declined at a rate of ~5°C per 100 m in elevation, beginning at a mean temperature of ~26°C at sea level (Adj. R^2=0.91, $p<0.001$).

Appendix B: The 456 species identified within the 20-0.79 ha sites within the Los Tuxtlas region, Veracruz, Mexico. Species growth form was identified as one of six categories: trees (T), woody lianas (L), palms (P), herbaceous vines (HV), herbaceous plants (H), and ferns (F). Maximum Strata indicates the diameter class of the largest individual encountered for the entire study, measured in dbh (diameter at 1.3 m height): ≥70 cm dbh (A), 30-70 cm dbh (B), 10-30 cm dbh (C), 0-10 cm dbh (D), and <1.3 m in height (E). Species constancy was calculated as the percentage of 0.79 ha sites in which a particular species was encountered: Canopy strata (A-C) were based on all 20 sites; Understory and Forest Floor species (strata D & E) were calculated on basis of 12 sites. Species were identified to their presence in each of the four community-types identified in this study: Lowland Reserve forest (LR), La Perla Plateau (LP), Volcanic Upslope forests (VU), and Cloud Forest (CF). Wood density values were obtained from Barajas-Morales (1987), Carmona-Valdovinos (unpublished data), and Brown (1997). Species nomenclature followed that of Ibarra-Manríquez and Sinaca (1997), Sosa and Gomez-Pompa (1994), and Martinez et al. (1994).

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Constancy (%)	Community-types where species was present: LR	LP	VU	CF
ACANTHACEAE									
	Aphelandra aurantiaca (Scheidw.) Lindl.	H	E		58	X			
	Justicia comata (L.) Lam.	H	E		17	X			
	Mendoncia retusa Turrill	HV	D		17	X			
	Odontonema cuspidatum (Nees) Kuntze	T	D	0.58	25	X			
	Ruellia tuxtlensis Ramamoorthy & Hornelas	T	D	0.58	8	X			
	Schaueria parviflora (Leonard) T.F. Daniel	F	D		25	X			
ACTINIDIACEAE									
	Saurauia belizensis Lundell	T	B	0.40	8		X		
	Saurauia scabrida Hemsl.	T	A	0.44	10		X		X
	Saurauia yasicae Loes.	T	A	0.40	50	X	X	X	X
ADIANTACEAE									
	Adiantopsis radiata (L.) Fee.	H	D		17	X			
	Adiantum sp.	F	E		8	X			
	Adiantum trapeziforme L.	F	E		8	X			
AMARANTHACEAE									
	Chamissoa altissima (Jacq.) Kunth.	L	D		17	X			
	Iresine arbuscula Uline & W.L. Bray	T	B	0.48	33	X			X
	Iresine celosia L.	H	D		17				X
ANACARDIACEAE									
	Mosquitoxylum jamaicense Krug & Urb.	T	A	0.58	15		X		
	Spondias radlkoferi Donn. Sm.	T	A	0.56	65	X		X	
	Tapirira mexicana Marchand	T	A	0.67	50	X	X	X	X
ANNONACEAE									
	Cymbopetalum baillonii R.E. Fr.	T	A	0.48	75	X	X	X	

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Constancy (%)	Community-types where species was present: LR	LP	VU	CF
	Desmopsis trunciflora (Schltdl. & Cham.) G.E. Schatz var glabra G.F. Schatz	T	D	0.58	25	X			
	Guamia sp.	T	C	0.75	50	X		X	
	Malmea depressa (Baill.) R.E. Fr.	T	C	0.71	17	X			
	Rollinia mucosa (Jacq.) Baill.	T	A	0.30	40	X		X	
	Tridimeris hahniana Baill.	T	C	0.58	30	X	X	X	
APOCYNACEAE									
	Apocynaceae sp.	T	B	0.58	8	X			
	Aspidosperma Mull. Arg. *megalocarpon*	T	B	0.75	20	X			
	Fornsteronia viridescens S.F. Blake	L	D		83	X	X	X	
	Prestonia guatemalensis Woodson	HV	D		17	X	X		
	Prestonia mexicana C. D.C.	L	D		25	X	X		X
	Stemmadenia donnell-smithii (Rose) Woodson	T	B	0.53	40	X			
	Stemmadenia galeottiana (A. Rich.) Miers	T	A	0.78	15	X	X		
	Tabernaemontana alba Mill.	T	C	0.66	25	X			
	Tabernaemontana arborea Rose ex. Donn. Sm.	T	B	0.66	8	X			
	Thevetia ahouai (L.) D.C.	T	D	0.72	8	X			
AQUIFOLIACEAE									
	Ilex aff. quercetorum I.M. Johnst.	T	A	0.63	35	X		X	X
	Ilex aff. valeri Standl.	T	A	0.63	35	X	X	X	

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present LR	LP	VU	CF
ARACEAE									
	Anthurium flexile Schott subsp. *flexile*	HV	D		67	X	X	X	X
	Anthurium (Aubl.) G.Don. var. bom. *pentaphyllum* (Schott) M. Madison	HV	D		67	X			
	Anthurium schlechtendalii Kunth subsp. *schlechtendalii*	HV	E		8	X			
	Dieffenbachia seguine (L.) Schott	H	E		33	X			
	Monstera acuminata C. Koch	HV	D		100	X	X	X	X
	Monstera tuberculata Lundell	HV	D		67	X			
	Philodendron escuintlense Matuda E.M.	HV	D		8	X			
	Philodendron guttiferum Kunth.	HV	D		67	X		X	
	Philodendron hederaceum (Willd.) Schott & Endl.	HV	D		17	X			X
	Philodendron inaequilaterum Liebm.	HV	D		42	X			
	Philodendron radiatum Schott	HV	E		8	X			
	Philodendron saggitifolium Liebm.	HV	D		33	X			
	Philodendron scandens K. Koch & Sell	HV	D		33	X			
	Philodendron tripartitum (Jacq.) Schott	HV	D		33	X	X		
	Rhodospatha aff. wendlandii Schott	HV	D		42	X			
	Spathiphyllum cochlearispathum (Liebm.) Engl.	HV	E		25	X			
	Syngonium chiapense Standl.	HV	D		75	X	X		X
	Syngonium podophyllum Schott	HV	D		92	X	X	X	X
ARALIACEAE									
	Dendropanax arboreus (L.) Decne & Planch.	T	A	0.41	75	X	X	X	
	Dendropanax schippii A.C. Smith	T	D	0.41	8			X	
	Oreopanax xalapensis (Kunth.) Decne. & Planchon	T	B	0.53	17				X

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Constancy (%)	Community-types where species was present: LR	LP	VU	CF
ARECACEAE									
	Astrocaryum mexicanum Liebm. ex Mart.	P	D		67	X	X	X	
	Bactris mexicana Mart.	P	D		33	X			
	Chamaedorea alternans H. Wendl.	P	D		75	X		X	
	Chamaedorea elatior Mart.	"L" (P)	D		8		X		
	Chamaedorea ernesti-augusti H. Wendl.	P	D		8	X			
	Chamaedorea oblongata Mart.	P	D		8	X			
	Chamaedorea pinnatefrons (Jacq.) Oerst.	P	D		67	X	X		
	Chamaedorea woodsoniana L.H. Bailey	P	D		42	X	X	X	X
	Desmoncus orthacanthus Mart.	"L" (P)	D		8	X			
	Reinhardtia gracilis (H. Wendl.) Drude ex. Dammer var. gracilior (Burnet) H.E. Moore	P	E		25	X			
ARISTOLOCHIACEAE									
	Aristolochia ovalifolia Duch.	L	D		17	X			
ASCLEPIADIACEAE									
	Gonolobus sp.	H	D		17	X			
ASPLENIACEAE									
	Asplenium laetum Swartz	H	E		8		X		
	Asplenium pteropus Kaulf	H	E		8	X			
	Asplenium sp.	H	D		17	X		X	
ASTERACEAE									
	Asteraceae sp.	T	C	0.58	8	X			
	Eupatorium daleoides (DC.) Hemsl.	T	D	0.58	8	X			
	Eupatorium galeotii B.L. Rob.	T	C	0.58	15	X		X	

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present LR	LP	VU	CF
	Hidalgoa ternata La Llave	L	D		8			X	
	Mikania cordifolia (L.F.) Willd.	HV	D		8	X			
	Mikania tonduzii B.L. Rob.	L	D		25	X	X		
	Piptocarpha chontalensis Baker	L	D		8	X			
	Senecio arborescens Steetz	T	C	0.58	8				X
	Tuxtla pittieri (Greenm.) Villasenor & Strother	L	D		17	X			
ATHYRIACEAE									
	Diplazium lonchophyllum Kunze	F	E		17	X			
BETULACEAE									
	Carpinus caroliniana Walter	T	A	0.58	8				X
BIGNONIACEAE									
	Amphilophium paniculatum (L.) Kunth var. paniculatum	L	D		17	X		X	
	Amphitecna tuxtlensis A.H. Gentry	T	C	0.46	33	X	X		
	Anemopaegma chrysanthum Dugand	L	D		8	X			
	Arrabidaea chica (Humb. & Bonpl.) Verl.	L	D		8	X			
	Arrabidaea florida DC.	L	D		17	X			
	Arrabidaea verrucosa (Standl.) A.H. Gentry	L	D		33	X			
	Callichlamys latifolia (Rich.) Schum.	L	D		17	X			
	Cydista potosina (Schum & Loes.) Loes.	L	D		42	X			
	Mansoa hymenaea (D.C.) A.H. Gentry	L	D		8	X			
	Macfadyena uncata (Andr.) Sprague & Sandw.	L	E		8	X			
	Macfadyena unguis-cati (L.) A.H. Gentry	L	D		17	X			
	Mansoa verrucifera (Schltdl.) A.H. Gentry	L	D		17	X			
	Mussatia hyacinthina (Standl.) Sandwith	L	D		8	X			

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
	Paragonia pyramidata (Rich.) Bur.	L	D		25	X		X	
	Schlegelia nicaraguensis Standl.	L	D		17		X	X	
	Stizophyllum riparium (Kunth) Sandwith	L	D		33	X			
BLECHNACEAE									
	Blechnum fraxineum Willd.	F	D		8	X			
BOMBACACEAE									
	Bernoullia flammea Olivier	T	A	0.25	15	X			
	Ceiba pentandra (L.) Gaertn.	T	A	0.38	10	X			
	Quararibea funebris (La Llave) Vischer	T	B	0.35	25	X			
	Quararibea yunckeri Standl. subsp. *sessiliflora* Miranda ex. W.S. Alverson	T	B	0.60	20	X		X	
BORAGINACEAE									
	Cordia alliodora (Ruiz & Pav.) Oken	T	B	0.48	17	X			
	Cordia megalantha S.F. Blake	T	A	0.39	35	X			
	Cordia sp.	T	B	0.50	8			X	
	Cordia stellifera I.M. Johnst.	T	A	0.65	45	X		X	
BURSERACEAE									
	Bursera simaruba (L.) Sarg.	T	A	0.59	60	X	X		
CAESALPINIACEAE									
	Cynometra retusa Britton & Rose	T	A	0.80	33	X			
	Dialium guianense (Aubl.) Sandw.	T	A	0.93	30	X			
	Senna multijuga (Rich.) Irwin & Barneby subsp. *doylei* (Britton & Rose) Irwin & Barneby	T	B	0.81	10	X			

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
CAPPARIDACEAE									
	Capparis baducca L.	T	C	0.48	17	X			
	Capparis mollicella Standl.	T	B	0.48	40	X	X		
	Cleome sp.	L	D		8			X	
	Crataeva tapia L.	T	B	0.55	35	X			
CAPRIFOLIACEAE									
	Sambucus mexicana C. Presl. [S. nigra L. subsp. *canadensis* (L.) R. Boll]	T	A	0.58	8			X	
CARICACEAE									
	Carica cauliflora Jacq.	T	D	0.58	17			X	X
	Jacaratia dolichaula (Donn. Sm.) Woodson	T	A	0.16	25	X			
CECROPIACEAE									
	Cecropia obtusifolia Bertol.	T	B	0.43	65	X	X	X	
	Cecropia sp.	T	B	0.35	17		X	X	
CELASTRACEAE									
	Celastrus vulcanicolus Donn. Sm.	L	D		33	X		X	X
	Crossopetalum (Hemsl.) Lundell *parviflorum*	T	C	0.58	25	X	X		
	Maytenus schippii Lundell	T	B	0.82	45	X	X	X	
	Rhacoma eucymosa Lundell	T	D	0.58	8	X			
	Wimmeria bartlettii Lundell	T	A	0.58	25	X	X		X
CHLORANTHACEAE									
	Hedyosmum mexicanum Cordem.	T	C	0.58	8				X
CHRYSOBALANACEAE									
	Couepia polyandra (Kunth) Rose	T	B	0.74	10	X			

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
CLETHRACEAE									
	Clethra aff. macrophylla M. Martens & Galeotti	T	A	0.58	25		X		X
CLUSIACEAE									
	Calophyllum brasiliense Cambess.	T	B	0.55	17	X	X		
	Rheedia edulis (Seem.) Triana & Planch.	T	B	0.70	65	X	X	X	
COMBRETACEAE									
	Combretum laxum Jacq.	L	D		33	X	X	X	
COMMELINACEAE									
	Commelina diffusa Burm. F.	H	E		8	X			
	Tradescantia zanonia (L.) S.W.	H	D		17		X		X
CONNARACEAE									
	Connarus schultesii Standl. ex R.E. Schult.	L	D		25	X			
	Rourea glabra Kunth.	L	D		8	X			
	Rourea schippii Standley	L	D		17	X		X	
CONVOLVULACEAE									
	Ipomoea batatas (L.) Poir.	HV	D		8	X			
	Ipomoea phillomega (Vell.) House	HV	D		67	X			
	Ipomoea reticulata O'Donnell	HV	D		8	X			
	Itzaea sericea (Standl.) Standl. & Steyerm.	L	D		8	X			
	Merremia tuberosa (L.) Rendle	HV	D		8	X			
COSTACEAE									
	Costus dirzoi Garcia-Medoza & Ibarra-Manriquez Manrrique	H	E		8	X			
	Costus laevis Ruiz & Pavon	H	E		8	X			
	Costus scaber Ruiz & Pav.	H	D		17	X	X		

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present LR	LP	VU	CF
CUCURBITACEAE									
	Cionosicyos sp.	HV	D		25	X	X		
	Melothria pendula L.	HV	D		8	X			
	Psiguria triphylla (Miq.) C. Jeffrey	HV	D		58	X	X	X	
CYCLANTHACEAE									
	Dichranopygium gracile (Matuda) Harling	HV	D		8		X		
DICHAPETALACEAE									
	Dichapetalum donnell- Engl. var. chiapasense *smithii* (Standl.) Prance	L	D		8	X			
DILLENIACEAE									
	Tetracera volubilis L.	L	D		25	X	X		
DIOSCOREACEAE									
	Dioscorea compositae Hemsl.	L	D		25	X			
EBENACEAE									
	Diospyros digyna Jacq.	T	A	0.79	25	X			
	Diospyros nicaraguensis (Standley) Standley	T	D	0.79	8				X
	Diospyros campechiana Lundell	T	C	0.79	8				X
ELAEOCARPACEAE									
	Sloanea medusula Schum & Pittier	T	A	0.67	25	X	X	X	
	Sloanea petenensis Standl. & Steyerm.	T	A	0.67	15	X	X		
ERYTHROXYLACEAE									
	Erythroxylum havanense Jacq.	T	D	0.98	8	X			
	Erythroxylum panamanense Turcz.	T	C	0.99	25	X	X		

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
EUPHORBIACEAE									
	Acalypha diversifolia Jacq.	T	D	0.58	17	X			
	Acalypha skutchii I.M. Johnst.	T	D	0.58	17	X			
	Adelia barbinervis (Schltdl.) A. Muell.	T	B	0.87	8	X			
	Alchornea latifolia S.W.	T	A	0.39	55	X	X	X	
	Cnidoscoulus multilobus (Pax) I.M. Johnst.	T	C	0.29	17	X			
	Croton lobatus L.	T	C	0.36	8	X			
	Croton pyramidalis Donn. Sm.	T	B	0.35	8			X	
	Croton schiedeanus Schltdl.	T	B	0.36	65	X	X	X	
	Croton sp.	T	C	0.40	8	X			
	Dalechampia magnistipulata G.L. Webster	L	D		8	X			
	Drypetes brownii Standley	T	B	0.69	25			X	X
	Omphalea oleifera Hemsl.	T	B	0.44	40	X			
	Plukenetia stipellata L.J. Gillespie	L	D		25	X			
	Sapium lateriflorum Hemsley	T	B	0.47	8			X	
	Sapium nitidum (Monach.) Lundell	T	A	0.48	35	X		X	X
	Tetrorchidium rotundatum Standl.	T	A	0.47	40	X		X	
	Tragia bailloniana Mull. Arg.	L	D		25	X			
FABACEAE									
	Dalbergia glomerata Hemsl.	T	A	0.80	20	X	X	X	
	Dussia mexicana (Standl.) Harms.	T	A	0.51	35	X		X	
	Erythrina folkersii Krukoff & Moldenke	T	C	0.38	25	X			
	Erythrina mexicana Miller	T	B	0.29	17			X	X
	Lonchocarpus cruentus Lundell	T	B	0.46	15	X		X	
	Lonchocarpus guatemalensis Benth.	T	A	0.73	40	X		X	

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
	Lonchocarpus unifoliolatus Benth.	T	B	0.86	8			X	
	Machaerium cobanense Donn. Sm.	L	D		25	X	X		
	Machaerium floribundum Benth.	L	B		25	X			
	Machaerium sp.	L	D		8	X			
	Platymiscium pinnatum (Jacq.) Dugand	T	B	0.76	20	X			
	Pterocarpus rohrii Vahl.	T	A	0.52	50	X		X	
	Swartzia guatemalensis (Donn. Sm.) Pittier	T	B	0.89	10	X		X	
	Vatairea lundellii (Standl.) Killip ex. Record	T	A	0.69	15	X			
FAGACEAE									
	Quercus skinneri Benth.	T	A	0.67	8			X	
	Quercus sp.	T	A	0.67	17			X	X
FLACOURTIACEAE									
	Casearia corymbosa Kunth	T	D	0.66	17	X			
	Casearia sylvestris SW. subsp. *sylvestris* SW.	T	B	0.64	20	X	X		
	Casearia tacanensis Lundell	T	B	0.64	17	X	X		
	Lunania mexicana Brandegee	T	B	0.58	40	X	X	X	
	Pleuranthodendron lindenii (Turcz.) Sleumer	T	B	0.68	75	X	X	X	
	Xylosma velutinium (Tul.) Triana & Planchon	T	B	0.76	17				X
GESNERIACEAE									
	Drymonia sp.	L	D		8		X		
	Gesneriaceae sp.	L	D		8		X		
GRAMINEAE									
	Lasiacis nigra Davidse.	H	E		8		X		
	Lasiacis sp.	H	E		8				X

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present LR	LP	VU	CF
GUTTIFERAE									
	Clusia lundellii Standl.	T	D	0.67	8		X		
HERNANDIACEAE									
	Sparatthanthelium amazonum Mart.	L	D		25	X			
HIPPOCRATEACEAE									
	Hippocratea celastroides Kunth	L	D		17	X			
	Hippocratea excelsa Kunth	L	D		8	X			
	Hippocratea volubilis L.	L	D		8	X			
	Salacia belizensis Standley	L	D		8			X	
	Salacia megistophylla Standl.	L	D		50	X	X		
HYMENOPHYLLACEAE									
	Trichomanes collariatum Bosch.	F	E		8				X
ICACINACEAE									
	Calatola mollis Standl. *[C. costaricensis* Standl.]	T	C	0.76	25		X	X	X
	Icacinaceae sp.	T	C	0.71	8				X
	Mappia racemosa Jacq.	T	B	0.65	20	X		X	
JUGLANDACEAE									
	Alfaroa mexicana Stone	T	A	0.58	25			X	X
	Juglans olanchana D.E. Stone E.V.	T	A	0.63	8		X		
LACISTEMATACEAE									
	Lacistema aggrega (Berg) Rusby	T	C	0.58	8	X			
LAURACEAE									
	Licaria velutina Van der Werff	T	B	1.02	20	X		X	
	Nectandra ambigens (S.F. Blake) C.K. Allen	T	A	0.57	70	X	X	X	

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density ($g\ cm^{-3}$)	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
	Nectandra cuspidata Nees	T	B	0.58	15			X	X
	Nectandra hihua (Ruiz & Pav.) Mez	T	A	0.60	20	X			
	Nectandra lundellii C.K. Allen	T	B	0.58	15	X		X	
	Nectandra reticulata (Ruiz & Pav.) Mez	T	B	0.65	40	X	X	X	
	Nectandra salicifolia (Kunth.) Nees	T	B	0.46	40	X	X	X	X
	Nectandra sp.	T	A	0.58	8				X
	Ocotea dendrodaphne Mez	T	B	0.57	50	X	X	X	
	Ocotea heydeana (Mez ex. J.D. Sm.) Bernardi	T	B	0.61	8	X			
	Ocotea rubiflora Mez	T	B	0.55	25	X	X	X	X
	Ocotea uxpanapana T. Wendt & Van der Werff	T	A	0.61	30	X	X	X	
	Persea schiedeana Nees	T	A	0.47	15	X		X	
LEGUMINOSAE									
	Bauhinia sp.	T	C	0.58	8	X			
LOGANIACEAE									
	Spigelia humboldtiana Cham. & Schltdl.	H	E		8	X			
	Strychnos tabascana Sprague & Sandwith	L	D		42	X			
LOMARIOPSIDACEAE									
	Bolbitis bernoullii (Kuhn y Christ) Ching	F	D		42	X			
	Bolbitis pergamentacea (Maxon) Ching	F	E		8	X			
MAGNOLIACEAE									
	Talauma mexicana (D.C.) Don	T	B	0.58	10			X	
MALPIGHIACEAE									
	Bunchosia lindeniana A. Juss	T	D	0.74	50	X		X	
	Heteropterys laurifolia (L.) A. Juss.	L	D		25	X	X		
	Hiraea fagifolia (DC.) A. Juss.	L	D		25	X	X		

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density ($g\ cm^{-3}$)	Con-stancy (%)	Community-types where species was present LR	LP	VU	CF
	Mascagnia rivularis C.V. Morton & Standl.	L	D		33	X	X	X	
	Malpighia romeroana Cuatrec. var. romeroana	T	D	0.58	8				X
	Mascagnia vacciniifolia Nied.	L	D		8	X			
	Stigmaphyllon lindenianum A. Juss	L	D		17	X			
	Tetrapterys donnell-smithii Small	L	D		8	X			
	Tetrapteris schiedeana Cham & Schltdl.	L	D		25	X	X	X	
MALVACEAE									
	Hampea nutricia Fryxell	T	C	0.39	40	X			
	Robinsonella mirandae Gomez-Pompa	T	A	0.50	40	X		X	
MARANTACEAE									
	Calathea macrochlamys Woodson & Standl.	F	E		17	X			
MARATTIACEAE									
	Danaea nodosa (L.) Smith	F	E		8	X			
MARCGRAVIACEAE									
	Marcgravia mexicana gilg.	L	D		17	X		X	
	Ruyschia enerva Lundell	L	D		17		X	X	
MELASTOMATACEAE									
	Miconia fulvostellata L.O. Williams	T	D	0.59	8		X		
	Miconia sp.	T	C	0.51	8				X
	Mouriri gleasoniana Standl.	T	C	0.77	8			X	
MELIACEAE									
	Guarea glabra Vahl	T	A	0.51	90	X	X	X	
	Guarea grandifolia A. DC.	T	A	0.57	50	X		X	
	Guarea sp.	T	C	0.54	8	X			
	Melia azedarach L.C.	T	B	0.58	8		X		

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
	Trichilia breviflora S.F. Blake & Standl.	T	D	0.72	42	X			
	Trichilia cuneata Radlk.	T	A	0.72	17			X	X
	Trichilia havanensis Jacq.	T	C	0.72	15		X	X	
	Trichilia martiana C. D.C.	T	B	0.47	40	X	X	X	
	Trichilia moschata S.W. subsp. *moschata*	T	B	0.88	40	X	X	X	
MENISPERMACEAE									
	Abuta panamensis (Standl.) Krukoff & Barneby	L	C		42	X	X		
	Disciphania calocarpa Standl.	L	D		33	X		X	X
MIMOSACEAE									
	Acacia hayesii Benth.	L	D		8	X			
	Albizia purpusii Britton & Rose	T	B	0.64	10	X			
	Cojoba arborea (L.) Britton & Rose	T	A	0.74	40	X	X		
	Inga acrocephala Steud.	T	B	0.58	30	X		X	
	Inga aestuariorum Pittier	T	B	0.60	17		X	X	
	Inga flexuosa Schltr.	T	B	0.60	8				X
	Inga paterno Harms.	T	B	0.60	25	X			
	Inga pavoniana Don.	T	B	0.61	33	X			
	Inga quaternata Poepp.	T	C	0.58	15	X			
	Inga sinacae M. Sousa & Ibarra-Manriquez	T	B	0.77	8	X			
	Inga vera Willd. subsp. *spuria* (Willd.) J. Leon	T	C	0.60	8				X
	Pithecellobium hymenaefolium (Kunth.) Benth.	T	E	0.52	8				X
	Pithecellobium volcanicola Sousa	T	A	0.52	17				X

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density ($g\ cm^{-3}$)	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
MONIMIACEAE									
	Mollinedia butleriana Standley	T	D	0.58	8				X
	Mollinedia viridiflora Tul.	T	D	0.58	8	X			
	Siparuna andina (Tul.) A. D.C.	T	D	0.49	25	X	X	X	
MORACEAE									
	Brosimum alicastrum SW. subsp. *alicastrum*	T	A	0.44	40	X			
	Clarisa biflora Ruiz&Pav.subsp.*mexicana*(Liebm.)W.C.Burger	T	A	0.52	55	X		X	
	Ficus colubrinae Standl.	T	A	0.42	15	X		X	
	Ficus cotinifolia Kunth	T	A	0.23	17	X			
	Ficus maxima Miller	T	A	0.54	15	X			
	Ficus petenensis Lundell	T	A	0.48	35	X	X	X	
	Ficus petiolaris (Watson) Carvajal subsp. *jaliscana*	T	A	0.42	8	X			
	Ficus sp.	T	B	0.51	8	X			
	Ficus sp.	T	C	0.42	8	X			
	Ficus teculotensis (Liebm.) Miq.	T	A	0.40	17	X			
	Ficus tuerckheimii Standl.	T	B	0.42	8	X			
	Ficus velutina Willd.	T	B	0.42	8			X	
	Ficus yoponensis Desv.	T	A	0.44	35	X	X		
	Poulsenia armata (Miq.) Standl.	T	A	0.30	50	X			
	Pseudolmedia oxyphyllaria Donn. Sm.	T	B	0.68	90	X	X	X	
	Trophis mexicana (Liebm.) Bureau	T	C	0.68	65	X	X	X	
MYRISTICACEAE									
	Virola guatemalensis (Hemsl.) Warb.	T	A	0.52	55	X	X	X	

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm⁻³)	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
MYRSINACEAE									
	Ardisia compressa Kunth	T	D	0.58	17	X			
	Ardisia sp.	T	D	0.58	8	X			
	Icacorea compressa (Kunth) Standl.	T	C	0.58	30	X	X	X	X
	Myrsinaceae sp.	T	B	0.58	8				X
	Oerstedianthus brevipes (Lundell) Lundell	T	D	0.58	8	X			
	Parathesis conzattii (S.F. Blake) Lundell	T	B	0.58	25	X	X		X
	Parathesis lenticellata Lundell	T	D	0.58	8				X
	Parathesis macronema Bullock	T	D	0.58	8			X	
	Parathesis psychotrioides Lundell	T	C	0.58	17			X	X
	Parathesis serrulata (S.W.) Mez	T	D	0.58	8				X
	Rapanea sp.	T	B	0.58	8				X
MYRTACEAE									
	Calyptranthes chiapensis Lundell	T	D	0.58	17	X		X	
	Calyptranthes chytraculia (L.) SW. var. americana McVaugh	T	C	0.58	17		X	X	
	Calyptranthes lindeniana O. Berg	T	D	0.58	25		X	X	X
	Eugenia acapulcensis Steud.	T	B	0.76	25	X		X	
	Eugenia aeruginea DC	T	B	0.73	33	X	X	X	X
	Eugenia capuli (Schltdl. & Cham.) O. Berg	T	B	0.73	33	X	X		X
	Eugenia colipensis O. Berg	T	D	0.74	17	X			X
	Eugenia inirebenis P.E. Sanchez	T	B	0.73	30	X	X		X
	Eugenia mexicana Steudel	T	B	0.73	75	X	X	X	X
	Eugenia oerstedeana O. Berg	T	B	0.73	17	X			X
	Pimenta dioica (L.) Merr.	T	B	0.96	25	X	X		

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density ($g\ cm^{-3}$)	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
NYCTAGINACEAE									
	Neea psychotroides Donn. Sm.	T	B	0.26	40	X	X	X	
	Pisonia aculeata L. var. aculeata	L	D		42	X	X		
OLEACEAE									
	Linociera dominguensis (Lam.) Krug & Urb.	T	A	0.81	15		X		
	Oleaceae sp.	T	A	0.81	8				X
ORCHIDACEAE									
	Orchidaceae sp.	H	E		8		X		
PASSIFLORACEAE									
	Passiflora cookii Killip	L	D		42	X			
	Passiflora helleri Peyr.	L	D		8				X
	Passiflora sp.	L	D		17		X		X
PHYTOLACCACEAE									
	Trichostigma octandrum (L.) H. Walter	L	D		17	X			
PIPERACEAE									
	Peperomia deppeana Schltdl. & Cham.	H	E		8		X		
	Peperomia obtusifolia (L.) O. Diertr.	H	D		8		X		
	Peperomia serpens (S.W.) Loud.	H	E		8		X		
	Peperomia sp.	H	E		8				X
	Piper aduncum L.	T	D	0.30	17	X			X
	Piper aequale Vahl.	T	D	0.30	83	X	X	X	X
	Piper amalago L.	T	B	0.31	55	X			X
	Piper auritum Kunth.	T	E	0.30	8	X			
	Piper hispidum S.W.	T	D	0.30	75	X	X	X	X
	Piper lapathifolium Steud.	T	D	0.30	42	X			

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density ($g\ cm^{-3}$)	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
	Piper nitidum Vahl.	T	D	0.30	17	X			
	Piper obliquum Ruiz & Pav.	T	D	0.30	17	X		X	
	Piper sanctum Schltdl. ex Miq.	T	C	0.29	33	X			
POLYGONACEAE									
	Coccoloba hondurensis Lundell	T	A	0.70	20	X		X	
	Coccoloba matudai Lundell	T	C	0.74	8			X	
	Coccoloba montana Standl.	T	A	0.74	25	X	X	X	
	Coccoloba schiediana Lindau	T	A	0.74	20	X		X	
POLYPODIACEAE									
	Campyloneurum angustifolium (SW.) Fee	F	D		8				X
	Polypodium polypodioides (L.) Watt var. *aciculare durlandii*	F	E		25	X	X		
PROTEACEAE									
	Roupala montana Aubl.	T	B	0.89	8			X	
PTERIDOPHYTA									
	Polypodium sp.	F	D		33	X			X
RHAMNACEAE									
	Colubrina heteroneura (Griseb.) Standley	T	A	0.97	8			X	
	Gouania lupuloides (L.) Urb.	L	D		25	X			
ROSACEAE									
	Prunus brachybotrya Zucc.	T	A	0.58	25		X	X	X
RUBIACEAE									
	Chiococca alba (L.) Hitchc.	L	D		8		X		
	Chione chiapasensis Standley	T	D	0.58	8	X			

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
	Coffea arabica L.C.	T	D	0.58	8	X			
	Coutarea hexandra (Jacq.) K. Schum.	T	D	0.58	8				X
	Faramea occidentalis (L.) A. Rich.	T	C	0.55	60	X	X	X	
	Hamelia longipes Standl.	T	C	0.50	33	X			
	Hamelia patens Jacq. var. patens	T	D	0.50	8	X			
	Hoffmannia bullata L.O. Williams	T	D	0.58	8			X	
	Hoffmannia aff. calycosa Donn. Sm.	T	D	0.58	17		X	X	
	Hoffmannia discolor (Lem.) Hemsl.	H	E		8		X		
	Psychotria chiapensis Standl.	T	C	0.65	55	X		X	
	Psychotria clivorum Standley & Steyerm.	T	C	0.65	17				X
	Psychotria faxlucens Lorence & Dwyer	T	C	0.62	17	X			
	Psychotria flava Oerst. ex. Standl.	T	D	0.65	33	X	X		
	Psychotria graciliflora Benth.	T	D	0.65	8		X		
	Psychotria limonensis Krause	T	D	0.65	17	X			
	Psychotria mexiae Standley	T	B	0.65	17			X	X
	Psychotria papantlensis (Oerst.) Hemsl.	T	D	0.65	8	X			
	Psychotria sarapiquensis Standl.	T	D	0.65	25		X		X
	Psychotria simiarum Standl.	T	B	0.62	40	X			
	Psychotria veracruzensis Lorence & Dwyer	T	D	0.65	8		X		
	Randia pterocarpa Lorence & Dwyer	T	D	0.78	25	X	X	X	
	Randia retroflexa Lorence & Nee	L	E	0.78	8	X			
	Randia xalapensis M. Martens & Galeotti	T	D	0.78	17	X			X
	Rondeletia buddleioides Benth.	T	C	0.56	8	X			
	Rondeletia galeotii Standl.	T	B	0.50	8			X	

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density ($g\ cm^{-3}$)	Constancy (%)	Community-types where species was present: LR	LP	VU	CF
RUTACEAE									
	Citrus reticulata Blanco C.	T	D	0.71	8	X			
	Esenbeckia sp.	T	C	1.19	8			X	
	Zanthoxylum kellermanii P.G. Wilson	T	B	0.69	30	X	X	X	
	Zanthoxylum procerum Donn. Sm.	T	B	0.91	10	X			
SAPINDACEAE									
	Allophylus campstachys Radlk.	T	C	0.77	40	X			
	Cupania dentata Mocino & Sesse ex DC.	T	B	0.66	17	X			
	Cupania glabra SW.	T	B	0.57	30	X	X	X	
	Cupania aff. macrophylla A. Rich.	T	A	0.94	25	X			
	Paullinia clavigera Schltdl.	L	D		50	X	X	X	
	Paullinia fuscescens Radlk.	L	D		25	X	X		
	Paullinia venosa Radlk.	L	D		58	X	X	X	
	Sapindus saponaria L.	T	B	0.83	15	X		X	
	Serjania goniocarpa Radlk.	L	D		8	X			
	Serjania mexicana (L.) Willd.	L	D		8	X			
	Thinouia myriantha Triana & Planchon	L	D		33	X			
SAPOTACEAE									
	Chrysophyllum venezuelanense (Pierre) T.D. Penn.	T	D	0.58	17	X			
	Manilkera chicle (Pittier) Gilly	T	B	0.85	8	X			
	Pouteria belizensis (Standley) Cronq.	T	B	0.79	8				X
	Pouteria campechiana (Kunth.) Baehni	T	B	0.79	35	X		X	
	Pouteria durlandii (Standl.) Baehni subsp. *durlandii*	T	B	0.80	55	X	X	X	
	Pouteria aff. reticulata (Engl.) Eyma subsp.	T	B	0.79	15	X	X	X	

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
	reticulata								
	Pouteria rhynchocarpa T.D. Penn	T	C	0.79	50	X	X		
	Pouteria sapota (Jacq.) H. Moore & Stearn.	T	A	0.81	8	X			
	Pouteria sp.	T	D	0.79	8			X	
	Pouteria sp.	T	C	0.79	8	X			
	Pouteria unilocularis (Donn. Sm.) Baehni	T	A	0.79	25	X			
	Sideroxylon persimile (Hemsl.) T.D. Penn. subsp. *persimile*	T	A	0.93	20	X	X	X	
	Sideroxylon portoricense Urb. subsp. *minutiflorum* (Pittier) T.D. Penn.	T	A	0.93	50	X	X	X	
	Sideroxylon sp.	T	A	0.93	10	X		X	
SIMAROUBACEAE									
	Picramnia hirsuta W. Thomas	T	D	0.58	17			X	X
	Picramnia teapensis Tul.	T	D	0.58	25	X			
SMILACACEAE									
	Smilax dominguensis Willd.	L	D		50	X	X	X	X
	Smilax regelii Killip & C.V. Morton	L	D		58	X	X	X	X
	Smilax spinosa Miller	L	D		8	X			
SOLANACEAE									
	Cestrum glanduliferum Francey	T	D	0.58	8	X			
	Cestrum luteovirescens Francey	H	D		8				X
	Lycianthes nitida Bitter	H	D		8				X
	Lycianthes purpusii (Brandegee) Bitter	L	D		8		X		
	Solanum diphyllum L.	L	D		8	X			
	Solanum schlechtendalianum Walp.	T	C	0.58	8	X			

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density (g cm^{-3})	Constancy (%)	Community-types where species was present: LR	LP	VU	CF
	Solanum tampicense Dunal	L	D		17	X			
STAPHYLEACEAE									
	Turpinia occidentalis (S.W.) G. Don subsp. *breviflora* Croat	T	A	0.33	70	X		X	X
STIRACACEAE									
	Stirax glabrescens Benth.	T	B	0.58	17				X
TECTARIACEAE									
	Ctenitis melanosticta (Kunze) Copeland	F	D		8	X			
	Tectaria heracleifolia (Willd.) Under.	F	D		8	X			
THELYPTERIDACEAE									
	Thelypteris blanda (Fee) Reed	F	E		8	X			
THEOPHRASTACEAE									
	Deherainia smaragdina (Plench. ex Linden) Decne. subsp. *occidentalis* Stahl	T	D	0.81	17	X			
TILIACEAE									
	Heliocarpus appendiculatus Jurez.	T	A	0.19	70	X	X	X	
	Mortoniodendron guatemalense Standl. & Steyerm.	T	A	0.51	35	X		X	
	Trichospermum galeottii (Turcz.) Kosterm.	T	B	0.41	10	X	X		
	Trichospermum mexicanum (D.C.) Baill.	T	A	0.41	10	X			
ULMACEAE									
	Ampelocera hottlei (Standl.) Standl.	T	A	0.83	20	X		X	
	Aphanante monoica (Hemsl.) Leroy	T	A	0.58	10	X		X	
	Celtis caudata Planchon	T	B	0.58	8	X			
	Celtis iguanaea (Jacq.) Sarg.	L	D		17	X			
	Trema micrantha (L.) Blume	T	B	0.45	15	X			

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density ($g\ cm^{-3}$)	Con-stancy (%)	Community-types where species was present: LR	LP	VU	CF
	Ulmus mexicana (Liebm.) Planch.	T	A	0.58	25		X	X	X
URTICACEAE									
	Myriocarpa longipes Liebm.	T	C	0.90	45	X		X	
	Urera caracasana (Jacq.) Griseb.	T	D	0.49	33	X			
	Urera eggersii Hieron.	L	D	0.49	8	X			
	Urera elata (S.W.) Griseb.	T	C	0.49	40	X	X	X	X
VERBENACEAE									
	Aegiphila costaricensis Moldenke	T	C	0.68	35	X			
	Citharexylum affine D. Don	T	B	0.65	15	X			
	Citharexylum hexangulare Greenm.	T	B	0.65	30	X	X	X	X
	Citharexylum sp.	T	B	0.65	10	X			X
	Lippia myriocephala Schltdl. & Cham.	T	C	0.88	8	X			
	Petrea volubilis L.	L	D		8	X			
VIOLACEAE									
	Orthion oblanceolatum Lundell	T	B	0.68	20	X			
	Rinorea guatemalensis (S. Watson) Bartlett	T	C	0.74	25	X			
	Rinorea hummelii Sprague	T	D	0.71	17	X			
VITACEAE									
	Cissus gossypifolia Standl.	L	D		58	X	X		
	Cissus microcarpa Vahl.	L	D		25	X	X		
	Cissus sicyoides L.	L	E		8	X			
	Parthenocissus sp.	L	D		25		X	X	X
	Vitis sp.	L	D		8				X
VITTARIACEAE									
	Antrophylum ensiforme Hook	H	E		8				X

Appendix B. continued.

Plant Family	Plant Species & Authority	Growth Form	Max. Strata	Wood Density	Con-stancy	Community-types where species was present			
				(g cm^{-3})	(%)	LR	LP	VU	CF
VOCHYSIACEAE									
	Vochysia guatemalensis Donn. Sm.	T	A	0.32	25	X	X	X	
ZINGIBERACEAE									
	Renealmia mexicana Klotzch ex Petersen	H	D		17		X		X

Appendix C: Percent Similarity (PS) matrix for the 20 sampled sites with the Los Tuxtlas region, Veracruz, Mexico. A total of 228 canopy species (≥10 cm dbh) were identified in the 20 sites. Values represent the percent similarity of the canopy species abundance between any two sites, and was calculated using the Renkonen (1938) equation for proportional abundances of species (Krebs 1985). For ease in interpretation, this matrix is symmetrical.

Appendix C. continued.

	AMATE	BM1	BM2	BONG	CAMINO	L70	LAVA	LP1	LP2	M	NANCI	NAUYACA	NORTE	PED	PLANA	SLZ	SM1	TFED	TMOS	TPLANO
AMATE	—	0	0	14	5	15	17	6	8	14	22	12	20	7	17	10	12	9	16	20
BM1	0	—	22	1	5	1	0	1	2	2	0	3	3	1	6	0	2	2	0	1
BM2	0	22	—	1	19	1	1	1	3	1	0	3	1	6	2	0	4	4	2	1
BONG	14	1	1	—	6	31	25	19	19	39	23	49	36	15	34	25	20	12	44	30
CAMINO	5	5	19	6	—	11	6	4	11	10	11	11	7	10	8	9	17	10	9	8
L70	15	1	1	31	11	—	32	19	27	37	14	37	33	25	36	22	28	21	42	39
LAVA	17	0	1	25	6	32	—	21	21	20	18	30	27	17	28	21	17	19	27	22
LP1	6	1	1	19	4	19	21	—	49	10	7	25	9	33	14	5	18	13	17	12
LP2	8	2	3	19	11	27	21	49	—	20	12	24	15	36	20	14	23	18	21	18
M	14	2	1	39	10	37	20	10	20	—	22	30	37	23	33	26	29	20	36	31
NANCI	22	0	0	23	11	14	18	7	12	22	—	20	15	7	19	24	13	13	10	23
NAUYACA	12	3	3	49	11	37	30	25	24	30	20	—	31	18	37	25	22	16	34	29
NORTE	20	3	1	36	7	33	27	9	15	37	15	31	—	19	32	30	20	15	39	30
PED	7	1	6	15	10	25	17	33	36	23	7	18	19	—	19	8	27	12	20	14
PLANA	17	6	2	34	8	36	28	14	20	33	19	37	32	19	—	18	23	20	36	47
SLZ	10	0	0	25	9	22	21	5	14	26	24	25	30	8	18	—	16	14	25	12
SM1	12	2	4	20	17	28	17	18	23	29	13	22	20	27	23	16	—	25	27	22
TFED	9	2	4	12	10	21	19	13	18	20	13	16	15	12	20	14	25	—	20	17
TMOS	16	0	2	44	9	42	27	17	21	36	10	34	39	20	36	25	27	20	—	29
TPLANO	20	1	1	30	8	39	22	12	18	31	23	29	30	14	47	12	22	17	29	—

Appendix D: Percent Similarity (PS) matrix for the 12 sites within the Los Tuxtlas region, Veracruz, Mexico in which all rooted plants in all forest starta were identified (432 species total). Values represent the percent similarity of the abundance and composition of all rooted species within 12-0.79 ha sites. For ease in interpretation, this matrix is symmetrically displayed.

	AMATE	BM1	BM2	CAMINO	L70	LP2	M	NANCI	NAUYACA	SLZ	TMOS	TPLANO
AMATE	—	9	8	12	21	21	28	33	25	33	22	27
BM1	9	—	31	23	6	13	9	6	16	12	1	6
BM2	8	31	—	31	6	19	9	6	23	13	2	13
CAMINO	12	23	31	—	17	38	17	13	31	23	12	18
L70	21	6	6	17	—	28	32	21	34	28	35	27
LP2	21	13	19	38	28	—	19	23	33	20	19	24
M	28	9	9	17	32	19	—	23	45	46	37	35
NANCI	33	6	6	13	21	23	23	—	24	22	24	19
NAUYACA	25	16	23	31	34	33	45	24	—	40	33	38
SLZ	33	12	13	23	28	20	46	22	40	—	32	35
TMOS	22	1	2	12	35	19	37	24	33	32	—	27
TPLANO	27	6	13	18	27	24	35	19	38	35	27	—

Appendix E: The 20-0.79 ha primary forest sites sampled in this study, with their environmental attributes and geographic position. For *CAMINO*, a precise geographic location was not obtained due to extensive cloud cover (uphill towards the top of San Martin from the Communidad Hidalgo, Los Tuxtlas—elevation ~915 m.a.s.l.). The three soil-types are ash-derived, lava flows, and weathered soils (Weath) (Martin-Del Pozzo 1997).

Site Name	Site Abbr.	Soil-Type	Elevation (m)	Slope (%)	Latitude (dec)	Longitude (dec)
Selva Pedregal	PED	Lava	671	19	18.56139	95.12667
San Martín	SM1	Ash	792	33	18.56639	95.23139
Selva Lava	LAVA	Lava	198	20	18.57722	95.09472
La Perla-1	LP1	Lava	716	14	18.56889	95.07972
Terreno Federal	TFED	Weath	503	41	18.48917	95.07722
Selva Bongers	BONG	Weath	107	12	18.27833	95.96056
Selva Plana	PLANA	Weath	122	10	18.63083	95.09000
Selva Norte	NORTE	Weath	183	36	18.58000	95.08944
Terreno Plano	TPLANO	Weath	230	4	18.56306	95.20944
Montepio	M	Weath	15	17	18.59283	95.08394
Selva L. Zacatal	SLZ	Weath	140	23	18.59711	95.09194
Bosque Mesofilo-1	BM1	Ash	1280	29	18.58767	95.07839
Nanciyaga	NANCI	Lava	290	5	18.44861	95.06750
Sitio Amatal	AMATE	Lava	320	3	18.45194	95.06761
La Perla-2	LP2	Lava	655	13	18.57528	95.13528
Lote 70	L70	Weath	400	15	18.57528	95.11444
Terreno Mosquito	TMOS	Weath	120	23	18.27833	95.96056
Termino del Camino	CAMINO	Ash	915	17	N/A	N/A
Sitio Nauyacoso	NAUYACA	Lava	275	14	18.58667	95.10083
Bosque Mesofilo-2	BM2	Ash	1280	14	18.57079	95.19155