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UNIVERSITY OF CALIFORNIA

Los Angeles

A Biogeography of Avian and Plant Communities in Tropical Dry Forest of Central America

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Geography

by

Thomas Welch Gillespie

1998

The dissertation of Thomas Welch Gillespie is approved.

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1998

Dedicated in the memory of Pat "Gigi" Deuel

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I owe my interest in natural history and tropical ecology to a Scarlet-rumped Tanager I spotted in Dominical, Costa Rica in the fall of 1990. After that encounter, I was hooked and decided to pursue a career in academia. Over the last eight years there are a number of people I would like to thank for helping me turn an idea into reality. First and foremost, I would like to thank Harmut Walter who got me into UCLA and guided me through graduate school. Nothing I have accomplished could have been done without his help. Melissa Savage, Glenn MacDonald, and Martin Cody helped me in numerous ways throughout all stages of my graduate career. Financial support from the Wildlife Conservation Society, Rainforest Action Network, Stephen T. Varva Plant Systematics Fellowship, Latin American Center, International Studies Overseas Program UCLA, and the Department of Geography at UCLA made this research possible. In the plant department, I owe everything to Al Gentry (who wrote a book on Neotropical plants and challenged a generation to follow his lead), Alfredo Grijalva (who taught me almost everything I know about Nicaraguan plants), Barry Prigge (who always took the time to help me with taxonomy) and Brian Enquist and Jon Sullivan (who helped me with plants in Santa Rosa). In the bird department, I would like to thank Bryan Bird and Murray Gel-Man for promoting early interest in bird-watching and Ole and Townson Peterson, who showed me what a professional ornithologist does. Juan Carlos Martinez-Sanchez provided all kinds of support and information on biodiversity in Nicaragua. Juan was always a friendly face in what at times seemed a sea of insanity. The Castillo's on the island of Ometepe were my Nicaraguan family and I thank them for

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ABSTRACT OF THE DISSERTATION

A Biogeography of
Avian and Plant Communities in Tropical Dry Forest
of Central America
By
Thomas Welch Gillespie
Doctor of Philosophy in Geography
University of California, Los Angeles, 1998
Professor Hartmut Walter, Chair

Tropical dry forests in Central America have been reduced to less than 0.1% of their original range on the Pacific side of Central America, and are considered by some to be the most endangered ecosystem in the lowland tropics. The objectives of this dissertation were to obtain data on plant and avian communities in remaining fragments of tropical dry forests in Costa Rica and Nicaragua. In particular, I identified biotic and abiotic variables associated with species richness and selective extinction.

A total of 204 plants were identified in seven 0.1 hectare plots. Anthropogenic disturbance was significantly correlated with total species richness, tree species richness, and liana abundance. The intensity and frequency of anthropogenic disturbances such as fire, wood collection, and grazing best predicted plant species richness in tropical dry forest. Reserve area, forest cover, and precipitation were not correlated with woody plant diversity. Certain breeding systems and dispersal mechanisms were rare in successively smaller forest fragments. Dioecious species and mammal-dispersed plants were correlated with forest cover within each reserve. Most plants in the tropical dry forest of Central America are not restricted to the dry forest life zone and have large geographic ranges. This forest may not deserve a high priority for conservation compared to other Neotropical forests.

A total of 240 point counts were undertaken in eight tropical dry forests. Seventy-two resident breeding birds were identified. Avian species richness was significantly correlated with forest cover within each reserve, tree diversity, and number of trees higher than 20 meters. Anthropogenic disturbance and precipitation were poor predictors of avian species richness. Biogeographic and natural history characteristics of extinction-prone resident forest birds in tropical dry forest were examined. Latitudinal extent and distance to edge of range are poor predictors of both local and regional extinction. Body mass, the carnivore guild, and forest dependence were important predictors of both local and regional extinction. Most resident birds restricted to tropical dry forest in Central America have healthy populations in remaining fragments of tropical dry forest.

CHAPTER 1. INTRODUCTION

1.1 Tropical Dry Forest

This dissertation examines tropical dry forest fragments of Central America. In particular, I inventory and test hypothesis related to plant and avian diversity and extinction. Research on plant diversity focuses on environmental variables correlated with diversity, while research on plant extinction focuses on life history characteristics associated with rarity. Research on avian diversity examines ecological and environmental variables associated with species richness, while research on avian extinction focuses on natural history variables correlated with rarity.

Tropical dry forest is loosely defined as forest in frost-free regions with 500-2000 mm of annual precipitation and a dry season of four to seven months with less than 50 mm of precipitation (Walter 1971). However, a number of different names (tropical deciduous forest, seasonally dry forest) and classification systems (Koppen system, Holdridge life zone system) exist (Holdridge et al. 1971; Bullock et al. 1995). Approximately 40% of the earth's tropical and subtropical land mass is dominated by open and closed forest. Forty-two percent of this forest are classified as dry forest according to Holdridge's life zone system (Murphy and Lugo 1986a).

The tropical dry forest life zone once covered 49% of the forested areas in Central America and the Caribbean (Holdridge et al. 1971). However, associated rich soils and amiable climates as well as agricultural expansion have resulted in a dramatic reduction in their original cover (Brown and Lugo 1980; Murphy and Lugo 1986a). This study focuses on tropical dry forest on the Pacific side of Central

America. Tropical dry forest in Central America once extended along the Pacific coast from sea level to 400 meters from Guatemala to Costa Rica with a disjunct patch in Panama (Sabogal 1992). Today, tropical dry forests have been reduced to less than 0.1% of their original expanse on the Pacific side of Central America, and are considered by some to be the most endangered ecosystems in the lowland tropics (Langley 1984; Janzen 1988a). All extant tropical dry forests in Central America exist as habitat fragments and degraded patches, all of which are still declining when not in protected areas (Janzen 1988b).

Costa Rica has led the way in the conservation of tropical dry forests by establishing the Guanacaste Conservation Area and Palo Verde National Park. These parks contain the largest patches of tropical dry forest in Central America (Gentry 1995). Nicaragua, which originally contained the largest expanse of tropical dry forest in Central America, has designated ten reserves with dry forest for a total of 74,307 hectares (Nietschmann 1990; IRENA 1991; Sabogal 1992). Nevertheless, lack of both human and financial resources have left most of these protected areas "paper parks" with no management plans or published information on their biological diversity (Gillespie 1994). There are few reserves that protect tropical dry forest in Central America outside of Costa Rica and Nicaragua. The Deininger Park in El Salvador and Sargua National Park in Panama both contain small patches of highly disturbed tropical dry forest (Janzen 1986b). There are no reserves that protect tropical dry forest in either Guatemala or Honduras.

1.2 Previous Research

Tropical Dry Forest Plant Diversity

Woody plant alpha diversity is lower in tropical dry forests than wet forests (Hartshorn 1983; Gentry 1995; Fensham 1995). Lower levels of plant species richness in dry forests are primarily attributed to less annual precipitation. Gentry (1982) and Clinebell et al. (1995) found that lowland plant diversity was tightly correlated with annual precipitation that reaches an asymptote at 4,000 mm. However, this pattern may not occur within tropical dry forests in the Neotropics. Gentry (1995) noted that once critical rainfall thresholds needed to maintain a closed canopy are achieved, increases in the amount of precipitation have only negligible effects on species richness until rainfall values are high enough to maintain a moist forest.

Plant alpha diversity in Central American tropical dry forests may be tightly correlated with area. Since tropical dry forests in Central America have been reduced and fragmented, reserve size and forest cover within each reserve may be important predictors of plant species richness. The species-area relationship is one of the best documented in ecology and biogeography (MacArthur and Wilson 1967; Brown 1995). However, the species-area relationship may not always apply to plants of oceanic islands or tropical habitat fragments (Sauer 1969; Carlquist 1974; Brown and Gibson 1983; Turner 1996; Whitmore 1997). There have been fewer recorded extinctions of plants in tropical rainforests than predicted from a species-area curve (Simberloff 1986; Brown and Brown 1992; Heywood et al. 1994). This anomaly in the species-area relationship is due to the fact that a number of small fragments of tropical forest can maintain significant levels of plant diversity even after being fragmented for over 400 years (Corlett 1992; Turner et al. 1994; Whitmore 1997). This species-area anomaly may also hold true for tropical dry forests of Central America. There have been no recorded plant extinctions in Central American tropical dry forest even though these forests have been reduced to less than 0.1% of their original range (Janzen 1988a; Janzen pers. comm.). There are little data on the relationship between plant species richness and area for habitat fragments in tropical dry forests.

A number of authors have noted the importance of natural and anthropogenic disturbance on plant diversity (Connell 1978; Pickett and White 1985; Foster 1990). Natural disturbances, such as hurricanes, landslides, and volcanic eruptions, all significantly affect levels of plant species richness (Watts 1954; Foster 1980; Pickett and White 1985). Anthropogenic disturbances, such as burning, grazing, and wood collection, may also affect plant species richness (Budowski 1966; Veblen 1982; Janzen 1986; Veblen et al. 1989; Sabogal 1992; Swaine 1992; Maass 1995). Yet, few researchers cite anthropogenic disturbance as a predictor of plant species richness because most research in tropical forest ecosystems focuses on undisturbed forest (Janzen 1983a; Gentry 1990; Primack 1993; McDade et al. 1994). There has been little quantitative research on the importance of anthropogenic disturbance as it relates to plant species richness in the tropical dry forests of Central America.

Gentry found that family richness is to a large extent deterministic and predictable in forests with a prolonged dry season (Gentry 1995). Fabaceae is always the most species rich tree family in Neotropical areas with a strong dry season and Bignoniaceae is always the most species rich liana family (Gentry 1988). The Fabaceae or Pea family is one of the largest plant families in the world with approximately 17,000 species (Heywood 1993). The Bignoniaceae or Trumpet flower family is relatively small with only 650 species worldwide. It is surprising that the Bignoniaceae family would "always" be the second most speciose family in tropical dry forests. Although family dominance may be predictable in tropical dry forest, Gentry found that species dominance in dry forest sites was never predictable, and not a single species was repeatably "most dominant" (Gentry 1988). This is in accordance with Hubbell's "random drift" hypothesis. Hubbell states that as species diversity increases in forest ecosystems, no species is able to dominate a stand of forest (Hubbell 1979; Hubbell and Foster 1986). This may also be the case for tropical dry forests, although they have significantly lower levels of diversity than lowland rainforest sites.

There is some dispute over the conservation value of Central American tropical dry forest. Some researchers have identified Central American tropical dry forest as a global "hotspot" which deserves a high priority for conservation (Janzen 1988a). Others believe that tropical dry forest in Central America deserve a low priority for conservation compared to other dry forest in other Neotropical regions (Myer 1980; Gentry 1995; Lott et al. 1987; Foster 1990). Gentry found that subtropical dry forests (along the Tropics of Cancer and Capricorn) of Mexico and Bolivia were richer in overall numbers of species and endemics than inter-tropical dry forests (closer to the equator). These conclusions were based on transect data from 28 tropical dry forest sites in the Neotropics. Unfortunately, due to the untimely death of Al Gentry, many of these plots contained only preliminary data. Although most sites were established and completed by Gentry, there were a number of incomplete data sets used in the analysis of tropical dry forests (Gentry 1995). For instance, Gentry's data on tropical dry forest of Central America came from only one dry forest sample. This sample was actually a conglomerate of two sites from Palo Verde and La Pacifica totaling only 700 m^2 and not the standard 0.1 hectare plot (Gentry 1982). This may not have been an adequate sample of Central American tropical dry forest.

Effects of Fragmentation on Plants

There are surprisingly few published studies on the effects of forest fragmentation on woody plant diversity in the tropics, but there are no shortages of theories for why certain plant species become extinct in habitat fragments (Howe and Smallwood 1982; Clark and Clark 1984; Janzen 1986a; Jordano 1995; Nason et al. 1997). Janzen (1986a) referred to severely fragmented tropical forests as the "living dead" because many large trees which have long generation times may respond slowly to forest fragmentation. This is because many trees may persist in a forest fragment for a number of years after fragmentation occurs. Many of these trees may eventually go extinct as co-evolved pollinators and seed dispersers go locally extinct (Janzen 1986a; Aizen and Feinsinger 1994; Murcia 1996; Nason et al 1997; Harrington et al. 1997; Laurance and Bierregaard 1997). More importantly, there has been little macroecological research on which plant species are vulnerable to extinction based on natural history characteristics. An empirical study by Meave and Kellman (1994) found that natural fragments of riparian forest in Belize appeared depauperate in dioecious and mammal-dispersed plants compared with continuous forest. The authors reported a 16.5% incidence of dioecy in natural riparian forest fragments compared with 24.7% in continuous forest (Bawa et al. 1985), suggesting that fragmentation may have a deleterious effect on dioecious plants. The pattern of selective extinction of dioecious plants is in agreement with the hypotheses of Ehrendorfer (1979) and Murcia (1996) that this sexual system is disadvantageous in isolated habitats. In theory, dioecious breeding systems promote cross-pollination and ensure genetic heterozygosity within a population (Endress 1994; Sakai et al. 1995). If there are a low number of dioecious individuals in a forest fragment and the species is absent from the surrounding landscape, there is a high probability that cross-pollination will not occur. Little empirical data exists to test this hypothesis.

Plant species exhibiting certain dispersal modes may also be more vulnerable to local extinction (Howe and Smallwood 1982; Howe 1984). Although tropical dry forests naturally have a higher percentage of wind-dispersed plants than wetter forest types, disturbance and fragmentation may lead to forests dominated by wind-dispersed plants with a notable lack of zoochoric or mammal-dispersed plants (Stiles 1983; Meave and Kellman 1994; Gentry 1995). Sabogal (1992) found that two plots of tropical dry forest in Central America were dominated by wind-dispersed tree species in both mature and regeneration stages. This pattern was linked to past disturbance in the stand and the removal of vertebrates (Sabogal 1992). Janzen (1988b) noted that regeneration of tropical dry forests in Costa Rica were dominated by wind-dispersed trees that would persist for hundreds of years and remain unattractive to vertebrate dispersers. Since there are nearly three times as many vertebrate-dispersed species as wind-dispersed species in Santa Rosa, vertebrate-dispersed plants may be the most extinction-prone after periodic disturbance in small habitat fragments (Janzen 1988).

Avian Diversity in Tropical Dry Forests

The total number of bird species from all Neotropical dry forests combined (635 spp.) barely exceeds the number found at a single site in Manu, Peru (Stotz et al. 1996). Nevertheless, no two tropical dry forest regions in the Neotropics share more than half of their species, while humid regions can share as much as 85% of their species (Stotz et al. 1996). This illustrates the unique assemblages of birds restricted to disjunct tropical dry forests in Latin America. There has been little biogeographical or ecological research on resident birds in tropical dry forest of Central America (Ceballos 1995). There are little quantitative community level data for birds in Central American tropical dry forest outside of a number of species lists for sites in Costa Rica (Stiles 1983).

A number of environmental and ecological variables have been identified to explain lower species diversity in tropical dry forests than wetter sites. These variables may also explain why different fragments of tropical dry forests have different levels of bird species richness. A number of studies use precipitation as an indicator of ecosystem productivity, which generally results in greater species richness (Rosenzweig and Abramsky 1993; Rosenzweig 1995). In theory, higher levels of annual precipitation within forest fragments of Central America may result in higher productivity and avian diversity. There has been no research on the role of annual precipitation on bird species richness in tropical dry forests.

Forest fragmentation has almost certainly caused a reduction in bird species richness. This pattern is particularly well documented in a number of studies of tropical bird communities and habitat fragments (Turner 1996 for review). Factors such as fragment size, degree of isolation, and time since isolation have significant effects on species richness (MacArthur and Wilson 1967; Willis 1974; Karr 1982; Diamond et al. 1987; Bierregaard and Lovejoy 1989; Kattan 1994). However, other factors such as habitat complexity within forest fragments may be of equal or greater importance (Wiens 1989; Simberloff and Martin 1991) Currently, data that examines bird species richness and area does not exist for tropical dry forests.

Vegetation structure can be correlated with lower species diversity, and tropical dry forests are less structurally complex than wetter forests (MacArthur 1964; MacArthur et al. 1966). The canopy in the tropical dry forest is generally about half as tall as the wet forest, which may account for lower species richness (Murphy and Lugo 1986). Other studies have concluded that vegetation structure (generally measured as foliage height diversity) is not the best predictor of avian diversity in wet forests (Orians 1969; Karr and Roth 1971; Howell 1971; Stiles 1982; Terborgh 1985).

Lower levels of bird species richness in tropical dry forests may also be associated with species guild and resource availability. A number of ecological guilds, such as frugivores and certain insectivores, may be unable to persist year round in tropical dry forests, due to a pronounced seasonal drought and lack of resources. Tropical dry forests have a higher percentage of wind-dispersed plants and fruit production is markedly seasonal, thus reducing the number of frugivores that can persist in these dry forests year round (Opler et al. 1980). Insect abundance and diversity is significantly decreased during the drought season in tropical dry forests, which may correlate with lower avian diversity (Janzen 1973).

Effects of Fragmentation on Birds

Birds have been the most researched taxonomic group with respect to the effects of tropical forest fragmentation (Turner 1996). Nevertheless, there is still no consensus as to which biogeographic and natural history characteristics can be used to predict extinction prone species. Empirical studies have identified a number of variables correlated with extinction prone birds, including: small geographic range, specialized guild, habitat specificity or forest preference, and large body size.

Geographic range has been cited as an important variable in determining extinction prone birds on islands and habitat fragments. Faaborg (1979) found that successful colonizers of islands tend to be species that are widespread on the continents, which may indicate that narrowly endemic species are more susceptible to extinction in habitat fragments (Turner 1996). Kattan et al. (1994) found that species at the edge of their geographic or altitudinal range were particularly susceptible to habitat fragmentation. Since Nicaragua in located at the crossroads between the Nearctic and Neotropic realms, there are a number of species at the edge of the geographic range in Central America which may be endangered with local extinction (Howell 1969). For Neotropical avifauna, a number of guilds have been identified as extinction prone. Leck (1979) and Kattan et al. (1994) identified raptors and large frugivores as especially extinction prone due to habitat fragmentation. Other authors have found that many suboscine insectivores appear to be the most susceptible to local extinction (Willis 1979; Stouffer and Bierregaard 1995). It is difficult to distinguish any clear trends based on ecological guild, possibly because these studies cover a wide range of forest types over different spatial scales (Turner 1996). Large body size has also been correlated with extinction prone species (Gaston and

Blackburn 1995). Willis (1974) noted that large bird species were among the first to drop out on a newly formed land-bridge island and other authors, focusing on mammals, have found that body size can be correlated with local extinction (Brown 1971; Robinson and Redford 1986). However, Gotelli and Graves (1990) found no evidence for greater extinction proneness among large-bodied bird species on islands. This may also be the case for large bodied birds in tropical dry forest fragments.

1.3 Research Objectives

The objectives of this dissertation are to obtain data on plant and avian communities in remaining fragments of tropical dry forests of Central America. In particular, I will identify biotic and abiotic variables associated with species richness and selective extinction. Answers to the following questions will be sought by testing a number of hypotheses and undertaking correlation analysis.

(I) Are tropical dry forest fragments of Central America similar in family and species composition?

H1-1 Plants with a dbh > 2.5 cm in tropical dry forests of Central America are dominated by Fabaceae with Bignoniaceae always the dominant liana family.

Ho All families are equally represented in tropical dry forests.

H1-2 Common plant species are never repeatably dominant in different patches of tropical dry forest.

Ho Common species are dominant at all tropical dry forest sites.

(II) Is plant species richness in tropical dry forest fragments significantly correlated with area, precipitation, or anthropogenic disturbance?

(III) Are tropical dry forests of Central America significantly different in structure and diversity compared to other Neotropical dry forests?

H3-1 Tropical forest fragments of Central America have a different forest structure compared to other Neotropical dry forests.

Ho Tropical dry forest fragments in Central America have forest structure similar to that of other Neotropical dry forests.

H3-2 Tropical forest fragments of Central America have a lower family and species richness than other Neotropical dry forests.

Ho Tropical forest fragments of Central America have similar family and species richness compared to other Neotropical dry forests.

(IV) Are the number and proportion of dioecious, zoochoric, and mammal-dispersed plants significantly correlated with area, precipitation, or anthropogenic disturbance in tropical dry forest fragments?

(V) Is bird species richness and abundance in fragments of tropical dry forest significantly correlated with area, precipitation, anthropogenic disturbance, vegetation structure, or plant diversity?

(VI) Are small geographic range, distance to edge of breeding range, body mass, and guild important macroecological predictors of selective local extinction of forest birds based on species incidence in eight fragments of tropical dry forest?

(VII) How important is range size, distance to edge of range, body mass, and species guild in identifying forest birds historically recorded in the tropical dry forest region of Nicaragua and Costa Rica but not encountered during point counts?

H7-1 Forest birds not found have smaller latitudinal extents than forest birds encountered during point counts.

Ho There is no difference between the latitudinal extent of forest birds not found and forest birds encountered during point counts.

H7-2 Forest birds not found are closer to the northern and/or southern edge(s) of their breeding ranges than forest birds encountered during point counts.

Ho There is no difference between the distance to the edge of breeding ranges for forest birds not found and forest birds encountered during point counts.

H7-3 Forest birds not found have larger body masses than forest birds encountered during point counts.

Ho There is no difference between the body masses of forest birds not found and forest birds encountered during point counts.

H7-4 Forest birds not found are in the carnivore and frugivore guild.

Ho There is no difference in guilds between forest birds not found and forest birds encountered during point counts.

The above hypotheses and associations will be tested and analyzed using a number of quantitative field methods. Results from this study will contribute to ongoing research in biogeography and conservation biology in tropical ecosystems. At a national level, this study will provide baseline data on the distribution of avian and plant diversity in the tropical dry forest of Central America. This information will aid in prioritizing conservation areas in Central America.

CHAPTER 2. STUDY SITES AND METHODS

2.1 Study Sites

Study sites were located in eight patches of tropical dry forests in Costa Rica and Nicaragua (Figure 1). These patches were all defined as Tropical Dry Forest according to the Holdridge classification life zone system (Holdridge et al. 1971). However, these tropical dry forests differ in annual precipitation, length of dry season, forest cover, soils, and disturbance history. The majority of these forests have some degree of protection and they are the best remaining patches of tropical dry forest in Central America. These sites include (1) Santa Rosa National Park, Costa Rica, (2) Palo Verde National Park, Costa Rica, (3) La Pacifica, Costa Rica, (4) La Flor Nature Reserve, Nicaragua, (5) Chacocente Wildlife Refuge, Nicaragua, (6) Reserve on the island of Ometepe, Nicaragua, (7) Masaya National Park, Nicaragua, and (8) Cosiguina Nature Reserve, Nicaragua.

Santa Rosa National Park

Santa Rosa National Park is located in the Guanacaste Conservation Area in northwestern Costa Rica (10° 50' N, 85° 40' W). The park covers 82,027 hectares and contains a diverse number of forest types and life-zones (Janzen 1983). The park was established in 1971 to protect some of the last remaining patches of tropical dry forest in Costa Rica. A majority of the park was originally dominated by African pasture grass and fire resistant trees with patches of tropical dry forest remaining in areas protected from fire. The forest regenerated quickly after ten years of intensive fire suppression and currently closed canopy forest covers a majority of the park

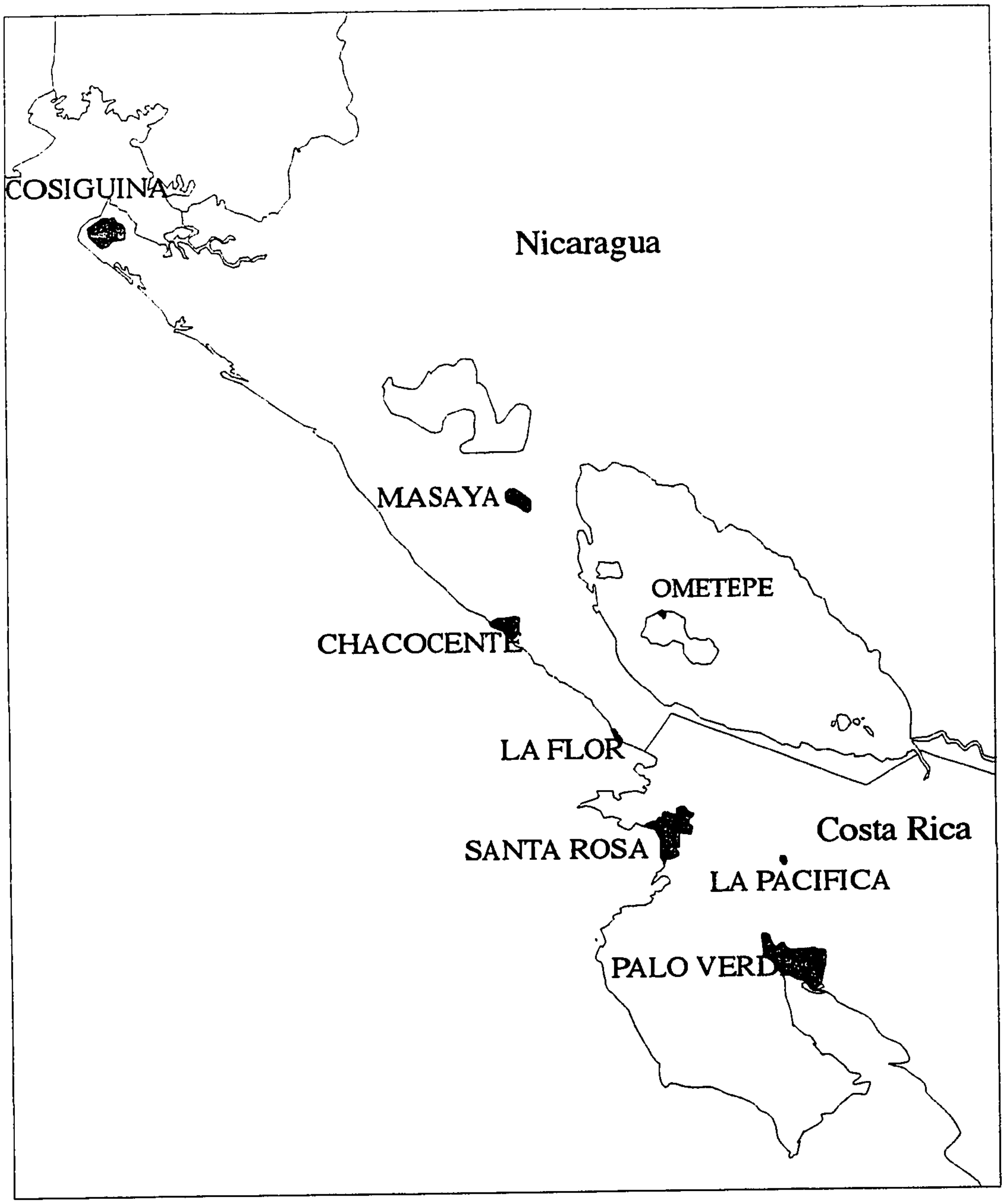


Figure 1. Eight tropical dry forest reserves in Central America

(Kramer 1997). Avian and floristic surveys were undertaken in upland dry forest near the Santa Rosa administration area. This study site is located at 300 meters in elevation in the forest behind La Casona. A majority of all research in Costa Rican tropical dry forest is performed in this area. Annual precipitation at the Santa Rosa Headquarters is 1,552 mm, and the soils are composed of Plio-Pleistocene aeolian ash from the Cordillera de Guanacaste (Hartshorn 1983). Most forms of anthropogenic disturbance have been suppressed and currently there are no fires, grazing, or wood cutting at the site.

Palo Verde National Park

Palo Verde National Park is located in the southern Guanacaste Province, Costa Rica (10° 20' N, 85° 20' W). The park contains 16,804 hectares and was originally established in 1977 to protect one of Costa Rica's largest wetlands, the Tempisque lowlands (Hartshorn 1983). Hills running east-west, composed of Eocene limestone, contain tropical dry forest (Hartshorn 1983). Floristic and avian surveys were undertaken on the lower slopes of limestone outcrops 500 meters from the Palo Verde administration office at approximately 50 meters in elevation. The annual precipitation at Palo Verde Headquarters is 1,717 mm. The soils at the floristic sites are derived from limestone, with a mixture of clay and silt sediments (Hartshorn 1983). Anthropogenic disturbance such as wood collection and grazing have been halted for approximately ten years; however, periodic burning still occurs due to the park's proximity to private agricultural land.

La Pacifica

The Hacienda La Pacifica is a private ranch located ten kilometers south of Bagaces (10° 26' N, 85° 08' W). The ranch consists of 1,980 hectares, with approximately 600 hectares of forest remaining in windbreak strips, on hill tops, and along rivers (Glander 1996). From 1984 to 1993, La Pacifica was considered a successful model of sustainable development, involving agricultural production in harmony with the environment and protection of tropical dry forest by promoting eco-tourism and research. However, the current owners are now in the process of extracting all valuable timber trees. Avian surveys were conducted in the largest fragment of tropical dry forest at La Pacifica at an elevation of 45 meters. Floristic surveys were not undertaken because the forests were actively being cut. The annual precipitation at La Pacifica is 1,440 mm. The soils are derived from volcanic ash on gently undulating terrain (Daubenmire 1972).

La Flor Nature Reserve

La Flor Nature Reserve is located in southern Nicaragua, 10 km from the Costa Rican border (11° 8' N, 85° 47' W). The park was established in 1991 to protect sea turtle nesting sites. This reserve is one of two nesting sites in Nicaragua where massive sea turtle "arrivada" still occurs. La Flor encompasses 1,800 hectares, 800 of which are tropical dry forest. Avian and floristic surveys were completed in the largest, most mature patch of tropical dry forest 100 meters from the beach at 41 meters in elevation. There is a high level of precipitation in this region as tropical westerly storms travel up the Rio San Juan unaffected by orographic processes associated with mountain ranges or volcanoes. Due to extensive fighting in the region during the Contra war, only five years of climate data are available; annual precipitation is approximately 1,805 mm. The soils are derived from marine sediment from the Rivas formation (Weyl 1980). There is a small population of farmers living around the reserve and fuel wood collection and grazing are minimal. Fires occur periodically in degraded patches of forest and are generally of low intensity due to a strong maritime influence and terrain.

Chacocente Wildlife Refuge

Chacocente is located in the Carazoa Department, Nicaragua (11° 32' N, 86° 12' W). This reserve contains the largest extent of tropical dry forest in Nicaragua. The reserve was established in 1983 and is privately owned by three landowners (IRENA 1990). The reserve covers 4,700 hectares, an estimated 1,500 of which is relatively undisturbed tropical dry forest (Sabogal 1992). Avian and floristic surveys were undertaken 500 meters from the Chacocente administration area at 30 meters in elevation. The annual precipitation at the reserve is approximately 1,362 mm. The soils are derived from marine sediments from the Brito formation (Weyl 1980). Due to the size of the reserve and the low population density around the reserve, there is little anthropogenic disturbance in the form of firewood or timber collection. Fires still occur periodically in the reserve, resulting in a patchy mosaic of tropical dry forest in different stages of succession.

Island of Ometepe

Lake Nicaragua contains over 400 islands, the largest of which is the island of Ometepe (11° 32' N, 85° 37' W), lying in the west side of the lake. Ometepe is dominated by the volcanoes Concepción and Madera, two strato–volcanoes whose bases have coalesced over time to cover 276 square kilometers. There are a number of lava flows around the Volcano Concepción that contain fragments of tropical dry forest. These forests occur on blocky lava flows which have not had adequate time for soil formation and are thus unsuitable for agriculture (Gillespie 1998). These tropical dry forests are the only lowland forests that remain on the island, and each has a unique composition and structure due to microclimate, age of substrate, and anthropogenic disturbance. Floristic and avian surveys were conducted in the largest tropical dry forest fragment on Ometepe, 500 meters from the town of Altagracia at an elevation of 49 meters. The fragment contains 420 hectares of tropical dry forest. The annual precipitation on the Altagracia side is approximately 1,650 mm. There has been minimal soil development on top of the *aa* lava flows, which date back approximately 500 years (Gillespie et al. 1996). Currently, wood collection is slowly eroding the biological integrity of these areas; many may not persist into the next century.

Masaya National Park

Masaya National Park is located 25 km south of Managua (11° 58' N, 86° 06' W). It is Nicaragua's first and only functioning National Park. The park was established in 1979 and covers an area of 5,100 hectares. Most of this park is dominated by the active volcanoes Masaya and Nindiri and the lagoon Masaya. The park contains a mosaic of plant communities in different stages of succession, including 1,300 hectares of tropical dry forest. Avian and floristic surveys were undertaken in the best patch of tropical dry forest 500 meters east of Park

Headquarters near the Sendero Coyote at appromiately 300 meters in elevation. The annual precipitation in the park is 1,251 mm. The soil is a mosaic of lava flows and quaternary ash. Although this area is a National Park, wood collection and hunting within park boundaries are very common. Natural fires from volcanic activity and anthropogenic fires also occur periodically within the park.

Cosiguina Nature Reserve, Nicaragua.

Cosiguina occupies the peninsula in the Gulf of Fonseca, Nicaragua (12° 54' N, 87° 32' W). The main crater was formed in 1835 during a Pelean-type eruption which was one of the largest volcanic events of the 19th century (McBirney and Williams 1965; Weyl 1980). The area was declared a nature reserve in 1958, and to this day no infrastructure exists. Floristic and avian surveys were undertaken at 300 meters in elevation on the southeast side of the volcano. The annual precipitation in the region is appromiately 1,827 mm. The soils are well-drained recent ash. The reserve is the most disturbed of all tropical dry forest sites, and fire, wood cutting, and cattle grazing presently continue. However, due to the size and isolation of the reserve, large expanses of tropical dry forest still remain on the upper slopes on the volcano.

2.2 Field Methods and Classification Systems

Plant Field Methods

Site selection for plots followed Gentry (1982, 1988), with an additional set of criteria established due to the inherent difficulty of identifying homogeneous and comparative patches of tropical dry forest. Extensive surveys of each site were undertaken to identify areas with low degrees of disturbance (based on liana size and evidence of cutting or fire) and appeared to be a representative sample of the site as a whole. Riparian or gallery forests were excluded from this study.

Ten sample plots totaling 0.1 hectares were established at each survey site. Each plot was a narrow rectangle of 100 m^2. All trees, shrubs, and lianas with a stem diameter of 2.5 cm or more were included (Gentry 1982, Gentry 1988). Trees, shrubs, and lianas were included if their base was rooted inside the plot. Each site was visited a minimum of three times to ensure the collection of fertile voucher specimens. All voucher specimens were deposited in the herbaria of the Universidad Centroamericana (UCA) in Managua and the University of California, Los Angeles. The height of all arborescent plants, excluding lianas, was determined for all individuals recorded in transects at all sites. A clinometer was used to calculate tree and shrub height. Final classification of all tree and shrub heights were given in two-meter size class increments.

Gentry's method was chosen because it offers a number of advantages over traditional techniques such as large permanent plots. Large one hectare plots generally focus on species with a dbh greater than 10 cm and significantly underestimate the species richness of woody shrubs and lianas. Furthermore, many of the remaining patches of tropical dry forest may be cut down over the next ten years, and resources required to establish one hectare plots in all sites may not be justified over the long term. Preliminary data and results from this method in other tropical dry forests around the world show that the species-area curve tended to level off in plots larger than 800 m^2; thus 0.1 ha is adequate for estimating species richness (Keel et al. 1993). Finally, this method has been applied in more sites in the Neotropics than any other, and a growing database is being created to compare patterns of species diversity (Phillips and Raven 1996). Disadvantages of Gentry's method are that it most certainly underestimates rare species and provides only relative density estimates. Nevertheless, since this study focuses on floristics and structure, and not on density and dispersion, the method is appropriate.

Four plots were established from June to September, 1996, and the final three were established in November and December of 1996. All sites were revisited from April to July, 1997. Voucher specimens were collected and identified in the Herbaria of the Universidad Centroamericana (UCA) in Managua and the Museo National in San Jose, Costa Rica.

Plant Taxonomy and Classification Systems

Species names are based on those recognized by the Missouri Botanical Garden. Family classification is purely a matter of personal preference, and I chose to recognize new familial names such as Fabaceae for Leguminosae and Asteraceae for Compositae. At the generic and species level, my taxonomic philosophy follows that of Al Gentry. My taxonomic premise is that the generic and species limits proposed by a particular monographer constitute a hypothesis, to be accepted or rejected like any other in science. Thus the generic and species concepts that seem to make the most sense to the taxonomic consumer is likely to be the best one (Gentry 1993).

Tropical dry forests contain a diverse and complex array of plant life-forms (Medina 1995). Two life form classes are used in this analysis of structure and diversity, following Gentry (1995). All species encountered in 0.1 hectare plots are classified as either trees/shrubs or lianas following Gentry (1988). The liana category is relatively straightforward and includes all woody vines with a diameter 2.5 cm or greater. The tree category contains all arborescent forms (trees and shrubs) with a dbh 2.5 cm or greater. Technically, this category clumps trees, shrubs, and even a number of herbs and succulents such as cactus and agaves. However, this method was chosen because the classification of life-forms such a shrubs, treelets, and canopy trees is subjective and this classification system can be compared to 18 other Neotropical dry forest sites (Gentry 1995).

Floristic data collected from 18 Neotropical dry forest sites were compared with data collected from seven Central American tropical dry forests (Table 1). Although Gentry's 1995 data set contained 28 sites, 10 were omitted because they were not complete. Only sites below 1000 meters that totaled 0.1 hectare and contained complete floristic and structural data were included. Sites that contain gallery forest were excluded.

Dispersal types were classified in five categories and one sub-category: anemochorous, zoochorous (sub-category: mammal-dispersed), autochorous, combination, and unknown (Van der Pijl 1982). Anemochoric dispersers are wind-dispersed plants that generally have winged seeds. Zoochoric dispersal are vertebrate-dispersed plants that have a fleshy exocarp. Mammal dispersal is a sub-category of zoochoric dispersal. The mammal-dispersed subcategory includes all plants with fleshy seeds greater than two cm and plants reported as mammal-dispersed in Gentry (1983) and Janzen & Martin (1982). Autochoric dispersers are plants that have explosive pods which usually disperses the seed. The combination

Table 1. Tropical dry forest sites in the Neotropics.

Sites	Data sources
West Indies	
Guanica, Puerto Rico	Murphy and Lugo 1986
Mogotes, Puerto Rico	Gentry 1995
Round Hill, Jamaica	Kapos 1982
Mexico	
Chamela (upland 1)	Lott et al. 1987
Chamela (upland 2)	Lott et al. 1987
Central America	
Chacocente, Nicaragua	Gillespie 1998
Cosiguina, Nicaragua	Gillespie 1998
La Flor, Nicaragua	Gillespie 1998
Masaya, Nicaragua	Gillespie 1998
Ometepe, Nicaragua	Gillespie 1998
Palo Verde, Costa Rica	Gillespie 1998
Santa Rosa, Costa Rica	Gillespie 1998
Southern subtropics	
Riachuelo, Argentina	Gentry 1995
Parque El Rey, Argentina	Brown et al. 1985
Chaquimayo, Bolivia	Gentry 1995
Northern South America	
Galerazamba, Colombia	Gentry 1995
Tayrona, Colombia	Heybrock 1984
Los Colorados, Colombia	Gentry 1995
Coloso, Colombia	Gentry 1995
Boca de Uchire, Venezuela	Gentry 1995
Blohm Ranch, Venezuela	Gentry 1995
Pacific coast of South America	
Capeira, Ecuador	Dodson and Gentry 1992
Perro Muerte, Ecuador	Gentry 1995
Cerros de Amotape, Peru	Gentry 1995
Tarapoto, Peru	Gentry 1995

category contains plants dispersed by two modes of dispersal, i.e. vertebrate-dispersed and autochorous. Unknown dispersal is for plants for which no reliable data exists to determine the dispersal mechanism.

Tropical breeding systems are diverse and extremely complex, especially for a number of species with small flowers (Endress 1994). All plants were classified into four breeding systems: hermaphroditic, monoecious, dioecious, and unknown, following Bawa (1974). Hermaphrodites are plants with male and female organs in the same flower. The hermaphrodite category includes all monostylous and heterostylous hermaphroditic species. Monoecious plants have male and female organs in different flowers on the same individual. The monoecious category includes all andromonoecious, gynomonoecious, polygamomonoecious, and monoecious species. Dioecious plants have male and female organs on different individuals. The dioecious category includes all androdioecious, gynodioecious, and dioecious species.

Avian Field Methods

All tropical dry forest sites were initially inventoried June-September and November-December 1996. I undertook these preliminary inventories to familiarize myself with songs and calls of resident birds and to create a preliminary checklist for each site. Final census fieldwork was carried out from April to July 1997, which coincides with the breeding season of a majority of species (Stiles & Skutch 1989). The single point survey method was used to determine presence-absence and relative abundance for resident breeding birds following Greenberg (1992, 1996). Each site contained a minimum of 30 survey stations or points, a minimum of 100 meters from the edge (when possible) and 100 meters apart. Each point was surveyed once for 10 minutes and all species detected within the fixed radius of 25 meters were tallied. Censuses were conducted from 5:30 AM to 8:00 AM and were not undertaken during rain or under high wind conditions. This method was chosen because it minimizes a number of shortcomings for estimating alpha diversity at different sites noted by Remsen (1994). This method focuses on "core" members in tropical dry forest, and quantity and quality of sampling effort are the same at all sites. Furthermore, it is undertaken in one habitat type only: tropical dry forest.

Biogeographic and Natural History Variables for Terrestrial Breeding Birds

Latitudinal extent, longitudinal extent, guild, forest preference, and weight were collected for all terrestrial breeding birds recorded in the tropical dry forest region of Nicaragua and Costa Rica. Only resident breeding birds were used in this study with migratory birds excluded. Resident birds were identified using a number of sources (Stiles 1982; Howell 1983; Howell & Webb 1995). The final list contains all birds recorded in the tropical dry forest region of Nicaragua and Costa Rica.

Biogeographic characteristics of latitudinal range, distance to edge of range, and longitudinal extent were collected for all recorded terrestrial breeding birds of this region. Latitudinal extent was calculated as the straight-line distance between the northern and southern extremes of a species breeding range with migratory ranges excluded (Brown 1995; Gaston 1996). It was expressed as the number of degrees within which a species is known to breed historically and determined using a number of range maps and breeding records. A complete list of 36 data sources for latitudinal extent is given in Gillespie & Nicholson (1997). The distance to the edge of a species northern and southern breeding range was calculated for all birds. Since the study sites in Nicaragua and Costa Rica are between 10 and 12 degrees north latitude, the number of degrees to the edge of northern ranges began from 12 degrees north and the number of degrees to the edge of southern ranges began from 10 degrees south. For instance, if a birds breeding range is between 25 degrees north and 6 degrees north, the distance to the edge of the species northern range is 13 degrees and the distance to the edge of the species southern range is 4 degrees.

Longitudinal extent identifies species presence in one or more of Nicaragua's three biogeographic regions: Pacific, Central, and Atlantic (Figure 2). The country can be divided into three general biogeographic regions based on physiography, climate, vegetation, and zoogeography (Taylor 1963, Incer 1975, Howell 1983). The Pacific region contains tropical dry forest and savanna below 400 meters on the western side of Nicaragua. The Central region contains upland pine forest and cloud forest on the tops of mountain ranges and volcanoes above 400 meters. The Atlantic region contains pine savanna and lowland rain forest in eastern Nicaragua below 400 meters. Terrestrial breeding birds were categorized as species recorded in only one biogeographic region, species recorded in only two biogeographic regions, or species recorded in all three biogeographic regions. The majority of this data comes from Howell (1983), personal field notes from nine months of field work in 1995, 1996, and 1997, and unpublished data kindly provided by professional ornithologists.

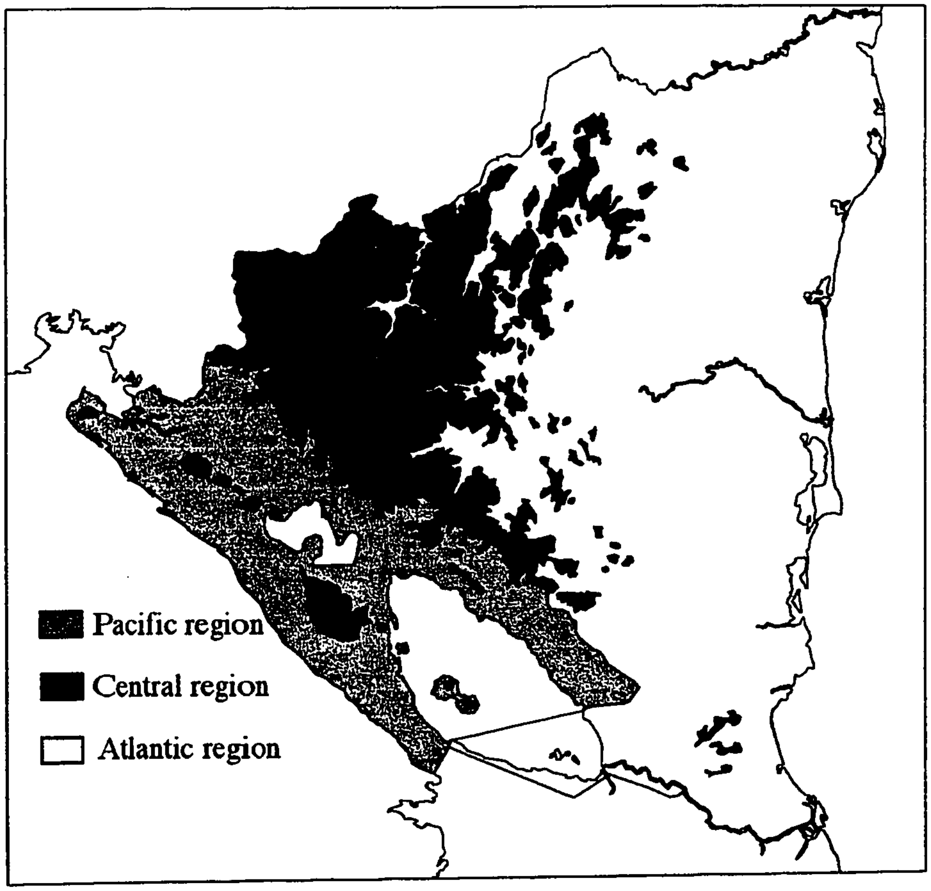


Figure 2. Three biogeographic regions in Nicaragua used to determine longitudinal extent.

Life history characteristics of body weight, forest preference, and guild were collected for all species recorded in the tropical dry forest region of Nicaragua and Costa Rica. Body weights were given in grams and were averages from mist net data from Stiles and Skutch (1989) and other sources (Dunning 1992). Habitat specificity followed the classification system of Stiles (1985), which is based on a species' dependence on forest. Species were classified as requiring almost solid forest, patchy forest, or not needing forest. A guild is a group of species that exploits a particular resource in a similar way (Root 1967). Guild classification was based on the resource which comprised over 50% of a species' diet (Stiles and Skutch 1989; Greenberg et al. 1997). All resident birds were classified into one of six guild categories: frugivore, granivore, insectivore, nectarivore, carnivore, or omnivore.

Classification of Extinction Prone Forest Birds

Studies on avian extinction in the tropics have been done using two approaches (Kattan et al. 1994). The first compares bird diversity in forest fragments of different size and identifies forest birds that go locally extinct from larger to smaller fragments (Willis 1979; Bierregaard & Lovejoy 1989; Newmark 1991). The second approach compares historical data of birds recorded in a region with recent surveys of birds to identify species that have disappeared in a reserve or in the region (Willis 1974; Leck 1979; Diamond et al. 1987; Kattan et al. 1994). This study employs both methods to assess local and regional extinction of forest birds in the tropical dry forest of Central America.

In order to assess local and regional extinction within forest fragments, resident birds recorded in the tropical dry forest region of Nicaragua and Costa Rica can be divided into two major groups: forest birds and non-forest birds. Only resident forest birds that require patchy or solid forest historically recorded in the tropical dry forest region are used to assess local extinction between forest fragments (Stiles 1985). Resident birds that required non-forest habitats were excluded because they are probably not threatened with extinction due to tropical dry forest fragmentation.

Forest birds historically recorded as permanent breeding residents can be subdivided into forest birds found and forest birds not found to assess regional extinction in tropical dry forest. Forest birds found include all species encountered during 240 point counts in eight fragments of tropical dry forest. Forest birds not found include all forest birds (excluding nocturnal species) historically recorded as permanent residents in the tropical dry forest of Nicaragua and Costa Rica, and not encountered during point counts. This classification was created due to a number of limitations presented by the method of conducting point counts in forest fragments for assessing extinction. There are a number of birds that occur at low densities that are missed by standard point counts. In particular, I saw the great curassow(Crax rubra), plain chachalaca, (Ortalis vetula), and crested guan (Penelope purpurascens) in the largest forest fragments but never during point counts or within the radius of the point count. These species are almost always underrepresented when undertaking point counts in tropical forest. Many studies that included over 100 points at a single site noted that many of the rarest species could only be recorded by incidence (Greenberg 1996; Estrada et al. 1997; Greenberg et al. 1997). These species are intuitively the most vulnerable to regional extinction in the tropical dry forest region of Central America.

Environmental Variables

Environmental variables of area, annual precipitation, and anthropogenic disturbance were collected for all eight study sites. Two types of aerial data were collected for all sites: the area of the decreed Nature Reserve and the area of forest canopy cover within each reserve. Data of reserve size is relatively straightforward and is available from a number of sources (Table 2). The area of tropical dry forest and semi-deciduous forest cover within each reserve for Costa Rica came from a variety of sources (Maldonado et al. 1995; Glander 1996; Kramer 1997). Forest cover for reserves in Nicaragua was calculated using vegetation maps and aerial photos of each reserve (IRENA 1990, IRENA 1994, MARENA 1997).

Climatic data on annual precipitation was collected for all sites from weather stations in or near each site (Table 3). There is extensive climate data for Costa Rica (Coen 1983). However, due to a civil war in Nicaragua only five years of climate data exist for La Flor and Ometepe. All other sites in Nicaragua have over 20 years of precipitation data.

Fire, wood collection, and grazing by livestock are the most important anthropogenic disturbances in tropical dry forest (Murphy & Lugo 1986). All sites were ranked based on the current intensity and frequency of anthropogenic disturbance following Veblen et al. (1992) (Table 4). Fire was scored as 1 for sites with active fire suppression programs and no signs of recent fires, 2 for sites with only periodic fires, and 3 for sites with annual fires. Grazing was scored as 1 for no evidence of any cattle, 2 for cattle seen in the reserve rarely, and 3 for cattle seen regularly in the reserve. Wood collection was scored as 1 for no current

Table 2. Central American reserve size and tropical dry forest cover within reserves.

Sites	**Reserve area in hectares**	**Forest cover in hectares**
Palo Verde	17,993	1,646
Cosiguina	12,420	5,100
Santa Rosa	10,700	3,556
Masaya	5,100	1,300
Chacocente	4,800	1,500
La Pacifica	1,980	600
La Flor	800	449
Ometepe	420	420

Table 3. Annual precipitation in tropical dry forest fragments in Central America.

Sites	**Precipitation in mm**
Palo Verde	1,717
Cosiguina	1,827
Santa Rosa	1,552
Masaya	1,251
Chacocente	1,362
La Pacific	1,440
La Flor	1,805
Ometepe	1,695

Table 4. Anthropogenic disturbance in tropical dry forest fragments in Central America.

Sites	Fire	Grazing	Wood collection	Anthropogenic disturbance
Palo Verde	2	1	1	4
Cosiguina	3	3	3	9
Santa Rosa	1	1	1	3
Masaya	2	2	3	8
Chacocente	2	1	2	5
La Pacifica	1	3	3	7
La Flor	2	1	2	5
Ometepe	2	1	3	6

evidence of wood collection, 2 for evidence of occasional wood collecting, and 3 for daily wood collection in the reserve.

2.3 Data Analysis and Evaluation

This research uses a number of simple statistical tests to accept or reject each hypothesis and non-parametric correlation analysis to examine associations between variables. The following is a list of research questions and summaries of data analysis methods used to test individual hypotheses and relationships between variables.

Plants

(I) Are tropical dry forest fragments of Central America similar in family and species composition?

H1-1 Plants with a dbh > 2.5 cm in tropical dry forests of Central America are dominated by Fabaceae with Bignoniaceae the dominant liana family.

Ho All families are equally or randomly represented in tropical dry forests.

Data on the number of trees and shrubs within each family from seven sites are compared in a table to identify if Fabaceae is always the dominant arborescent family in tropical dry forest. Data on the number of liana species within each family from seven sites are compared in another table to identify if Bignoniaceae is always the dominant liana family in tropical dry forest.

H1-2 Common plant species are never repeatably dominant in different patches of tropical dry forest.

Ho Common species are dominant at all tropical dry forest sites.

The frequency of plants encountered in 0.1 hectare plots from all sites are ranked. Plant species that repeatedly occur in the top five based on abundance were identified. Species are considered repeatably dominant if they are in the top five most abundant species at all sites following Gentry (1995).

(II) Is plant species richness in tropical dry forest fragments significantly correlated with area, precipitation, or anthropogenic disturbance?

Spearman's rank correlation was used to search for associations between environmental variables and plant species richness. Environmental variables include reserve size, area of forest cover within each reserve, precipitation, and anthropogenic disturbance at all seven tropical dry forest sites from which vegetation data was collected. Three categories of plant species richness were used, including total species richness, tree and shrub species richness, and liana species richness. Ecological variables of tree and shrub abundance and liana abundance were also included.

(III) Are tropical dry forests of Central America significantly different in structure and diversity compared to other Neotropical dry forests?

H3-1 Tropical forest fragments of Central America have different forest structure compared to other Neotropical dry forests.

Ho Tropical dry forest fragments in Central America have similar forest structure as other Neotropical dry forests.

H3-2 Tropical forest fragments of Central America have a lower family and species richness than other Neotropical dry forests.

Ho Tropical forest fragments of Central America have similar family and species richness compared to other Neotropical dry forests.

A two tailed Mann-Whitney *U* test was used to test for differences in forest structure and diversity between tropical dry forests in Central America and other Neotropical dry forests. Comparisons of forest structure include the number of lianas, trees, plants greater than 10 cm dbh, and basal area. Comparisons of diversity include family richness, total species richness, liana species richness and tree species richness.

(IV) Are the number and proportion of dioecious, zoochoric, or mammal-dispersed plants at each site significantly correlated with area, precipitation, or anthropogenic disturbance?

A Spearman's rank correlation was used to search for associations between dioecious richness, zoochoric richness, mammal-dispersed richness and environmental variables. Environmental variables including reserve size, forest cover within each reserve, annual precipitation, and anthropogenic disturbance were compared to breeding systems and dispersal mechanisms.

Birds

(V) Are bird species richness and abundance in fragments of tropical dry forests significantly correlated with area, precipitation, anthropogenic disturbance, vegetation structure, or plant diversity?

A Spearman's rank test is used to identify relationships between environmental and ecological variables and species richness in seven fragments of tropical dry forest. La Pacifica was excluded from this analysis because the site was actively being cut for timber which precluded the collection of floristic data. Environmental variables include reserve size, forest cover within reserve, precipitation, elevation, and anthropogenic disturbance. Ecological variables include plant species richness, tree diversity, tree abundance, number of trees > 10 cm dbh, number of trees > 20 m height, and zoochoric tree abundance.

(VI) Are small geographic range, distance to edge of breeding range, body mass, and guild significant macroecological predictors of selective local extinction of forest birds based on species incidence in eight fragments of tropical dry forest?

Only resident forest birds recorded during point counts at eight sites that require patchy or solid forest were used in this analysis (Stiles 1985). Resident birds encountered during point counts that required non-forest habitats were excluded from the final analysis. A Spearman's rank test identified biogeographic and life history variables correlated with forest bird incidence in eight fragments of tropical dry forest. Biogeographic variables included latitudinal extent, degrees to edge of northern range, degrees to edge of southern range, and longitudinal extent. Life history characteristics include data on body mass, cumulative abundance of species from all sites, forest preference, and guilds.

(VII) How important is range size, distance to edge of range, body mass, and guild in identifying forest birds historically recorded in the tropical dry forest region of Nicaragua and Costa Rica but not encountered during point counts?

H7-1 Forest birds not found have smaller latitudinal extents than forest birds encountered during point counts.

Ho There is no difference between the latitudinal extent of forest birds not found and forest birds encountered during point counts.

H7-2 Forest birds not found are closer to the northern and/or southern edge(s) of their breeding ranges than forest birds encountered during point counts.

Ho There is no difference between the distance to the edge of breeding ranges for forest birds not found and forest birds encountered during point counts.

H7-3 Forest birds not found have larger body masses than forest birds encountered during point counts.

Ho There is no difference between the body masses of forest birds not found and forest birds encountered during point counts.

A two-tailed Mann-Whitney *U*-test was used to test for differences between the latitudinal extent, distance to northern and southern edges of range, and body mass of found forest birds not found and forest birds found.

H7-4 Forest birds not found are in the carnivore or frugivore guilds.

Ho There is no difference between forest birds not found and guild.

A chi-square test was used to determine if forest birds not found in the carnivore and frugivore guild were more rare than other guilds. In particular, a chi-squared test will ascertain if certain guilds have a significantly low observed than expected value.

CHAPTER 3. TROPICAL DRY FOREST STRUCTURE AND DIVERSITY

3.1 Introduction

Tropical dry forest in Central America once extended along the Pacific coast from Guatemala to Costa Rica, with a disjunct patch in Panama (Brown and Lugo 1980; Murphy and Lugo 1986; Sabogal 1992). Today, tropical dry forests have been reduced to less than 0.1% of their original range on the Pacific side of Central America and are considered by some to be the most endangered ecosystems in the lowland tropics (Langley 1984; Janzen 1988a). The largest and best preserved fragments of tropical dry forest in Central America exist in Costa Rica and Nicaragua; however, relatively little quantitative data exists for these tropical dry forests (Janzen 1988b; Lerdau et al 1991; Gerhardt and Hytteborn 1992). Seven 0.1 hectare plots were established in fragments of tropical dry forest, two in Costa Rica and five in Nicaragua.

This analysis of tropical dry forest structure and composition has three primary objectives: 1) to summarize the structure, diversity, and floristic composition of seven tropical dry forest fragments, 2) to identify ecological and environmental variables correlated with plant richness and abundance, and 3) to discuss the similarities and differences between Central American dry forests and other Neotropical dry forests.

Results on forest structure include data on density, basal area, and height. Family and species richness of both trees and lianas at all sites are also summarized. Floristic composition is examined to determine if family and species dominance is predictable in different fragments of tropical dry forest. A Spearman's rank correlation is used to identify ecological and environmental variables correlated with species richness and abundance at all sites. In particular, I examine how species richness and abundance are associated with area, precipitation, and anthropogenic disturbance. The results from this study are compared to 18 other Neotropical dry forests sites in which 0.1 hectare plots were established (Gentry 1995).

3.2 Structure and Diversity of Tropical Dry Forests

Structure

A total of 1,484 individuals were encountered from seven sites with an average of 212 individuals per 0.1 hectare plot. La Flor, Santa Rosa, and Palo Verde had the most individuals per site (Table 5). Ometepe and Cosiguina had the lowest number of individuals per site. The average number of trees and shrubs encountered in 0.1 hectare plots in Central America was 169 individuals. Masaya and La Flor had the most tree and shrub individuals while Ometepe and Cosiguina had the lowest number of individuals. Lianas accounted for 20% of all stems (2.5 cm or greater) in the tropical dry forest with approximately 43 individuals per site. This high percentage underscores the importance of lianas in tropical dry forests. Santa Rosa had the highest number of lianas with 77 individuals. Cosiguina and Masaya had the lowest number of liana individuals.

The average basal area of tropical dry forest in Central America was 2,203m^2/0.1 hectare. Santa Rosa had the highest basal area (2,508.4m^2/0.1 ha.) of all sites. Chacocente, Cosiguina, La Flor, Masaya, and Palo Verde all had relatively

Table 5. Number of individuals and basal area in seven Central American tropical dry forests.

Forest structure	Cos.	S.R.	P.V.	Chac.	Mas.	L.F.	Ome
Total individuals	135	246	227	215	243	264	154
Number of tree individuals	118	169	185	177	223	202	107
Number of liana individuals	17	77	42	38	20	62	47
Total basal area	2331	2508.4	2284	2123.8	2118	2284	1777
Number of trees > 10 cm dbh	52	61	45	62	52	42	48
Number of liana > 10 cm	0	1	2	1	1	1	1

similar basal areas ranging from approximately 2,100 and 2,300m^2/0.1 ha. Ometepe had the lowest basal area at 1,777m^2/0.1 ha. Chacocente and Santa Rosa had the most trees with a dbh > 10 cm, while La Flor and Palo Verde had the least number of large tree individuals. There were few lianas with a stem diameter > 10 cm at all tropical dry forest sites. Palo Verde had only two species of liana > 10 cm, Cosiguina had none, and all other sites had one liana > 10 cm.

Most trees and shrubs with a dbh of 2.5 cm or greater in tropical dry forests were within the 4 to 6 meters size category (Table 6). In general, the number of individuals in each size class in Central American tropical dry forest decreases with height. Palo Verde and Santa Rosa had the most diverse forest structure. Both sites had the tallest canopy trees in size classes over 20 meters. Masaya had the lowest forest canopy with over half of all individuals under six meters.

Diversity

A total of 204 species and morphospecies were encountered in seven fragments of tropical dry forest (Appendix 1). Of these, 176 plants were identified to the species or sub-species, eight could only be identified to genus, and 14 could only be identified to family. Six plants were impossible to identify due to the inability to obtain an appropriate voucher specimen. Approximately 72% of these plants were classified as trees and shrubs (148 spp.) and 28 % were classified as lianas (56 spp.).

Family richness was relatively constant among all Central American dry forests sites with an average of 29 families per site (range 25 to 33) (Table 7). However, species richness varied between sites. The average species richness in Central American forests was approximately 56 species per site and the ranges varied

Table 6. Height of individuals, excluding lianas, in two meter size classes in tropical dry forest sites.

Height	Cos.	S.R.	P.V.	Chac.	Mas.	L.F.	Ome.	Total
0-2	2		3	5	1	2		13
2-4	25	26	31	37	71	41	25	256
4-6	27	45	51	33	75	61	21	313
6-8	10	28	33	29	34	37	19	190
8-10	17	17	20	22	27	26	15	144
10-12	10	12	7	10	8	7	6	60
12-14	6	11	10	13	5	7	7	59
14-16	8	12	6	14	-	13	6	59
16-18	4	8	3	5	1	5	5	31
18-20	5	2	5	4	-	-	2	18
20-22	2	2	4	2	-	3	-	13
22-24	1	1	4	-	1	-	-	7
24-26	-	4	3	1	-	-	1	9
26-28	-	1	1	2	-	-	-	4
28-30	-	-	4	-	-	-	-	4
30-32	1	-	-	-	-	-	-	1
32+	-	-	-	-	-	-	-	0
Total	118	169	185	177	223	202	107	1181

Table 7. Summary of floristic diversity of tropical dry forest by site.

Floristic composition	**Cos.**	**S. R.**	**P. V.**	**Chac**	**Mas.**	**L.F.**	**Ome.**
Number of families	27	33	29	28	28	25	31
Number of genera	42	69	55	47	41	52	42
Number of species	48	75	65	54	44	59	45
Number of tree species	38	54	48	43	33	45	27
Number of liana species	10	21	17	11	11	14	18

from a high of 75 species at Santa Rosa to a low of 44 species at Masaya. Tree and liana diversity also changed significantly between sites. Santa Rosa (54 spp.) and Palo Verde (48 spp.) had the highest tree species richness. Ometepe (27 spp.) and Masaya (33 spp.) had the lowest tree species richness. The proportion of tree species to liana species was remarkably constant between sites. Lianas accounted for approximately 20% to 26% of the total plant diversity at six sites. Ometepe was the only exception with liana species contributing to 40% of the total species diversity. Santa Rosa was the richest site with the highest family, genera, and species diversity of all sites. The forests on the island of Ometepe and Masaya had the lowest diversity with approximately half the number of species recorded at Santa Rosa.

3.3 Family and Species Composition

A total of 60 families were identified from all dry forest sites (Figure 3). A majority of these families were rare with approximately 65% of tropical dry forest families represented by two or less species. Fabaceae and Bignoniaceae were the most speciose families for all Central American sites followed by Sapindaceae, Rubiaceae, and Euphorbiaceae.

When tree family richness at all sites are compared, Fabaceae was the dominant tree or arborescent family at all sites except Ometepe (Table 8). Ometepe was dominated by species in the family Rubiaceae and Euphorbiaceae. Family abundance at each site was not always dominated by Fabaceae. When the number of tree and shrub individuals from seven tropical dry forest sites were combined, Fabaceae was dominant by abundance at only two sites (Cosiguina and Chacocente).

Figure 3. Plant family richness in tropical dry forests

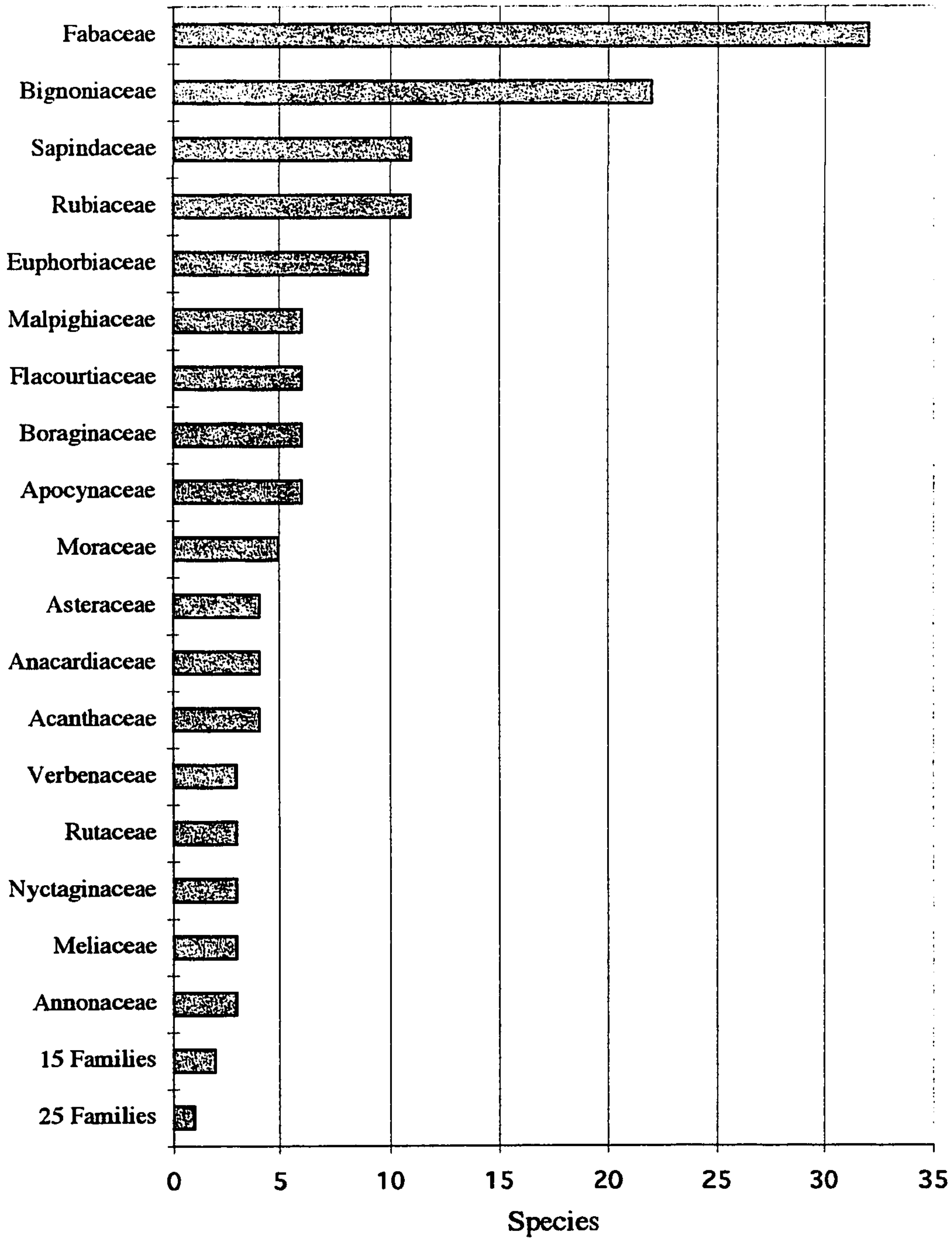


Table 8. The ten most species rich tree families and the ten most abundant tree families based on the number of individuals per site. (Most speciose and abundant families in bold).

Family richness	**Cos.**	**S.R.**	**P.V.**	**Chac.**	**Mas.**	**L.F.**	**Ome.**
Fabaceae	**6**	**10**	**9**	**9**	**3**	**13**	1
Rubiaceae	-	7	3	1	1	6	**3**
Euphorbiaceae	-	3	3	1	**3**	1	**3**
Anacardiaceae	2	3	4	-	1	2	1
Flacourtiaceae	2	1	3	2	1	1	1
Apocynaceae	1	1	1	1	**3**	2	1
Bignoniaceae	-	2	2	2	1	3	-
Boraginaceae	3	1	4	-	-	-	2
Annonaceae	2	1	1	1	1	1	1
Burseraceae	1	1	1	1	2	1	1

Family abundance	**Cos.**	**S.R.**	**P.V.**	**Chac.**	**Mas.**	**L.F.**	**Ome.**
Fabaceae	**14**	20	33	**34**	46	57	2
Rubiaceae	-	**32**	9	2	2	**63**	8
Burseraceae	6	10	6	4	**58**	3	14
Sapindaceae	7	1	**40**	19	-	2	-
Apocynaceae	4	7	6	22	16	3	5
Anacardiaceae	2	7	32	-	2	9	8
Euphorbiaceae	-	16	5	1	18	3	**15**
Bignoniaceae	-	7	14	16	2	18	-
Cochlospermaceae	2	2	2	-	15	17	2
Flacourtiaceae	2	4	3	7	3	1	10

Rubiaceae trees and shrubs were most abundant at Santa Rosa and La Flor. Sapindaceae was the dominant family by abundance at Palo Verde, and Burseraceae was the dominant family by abundance at Masaya.

When liana family richness at all sites are compared, Bignoniaceae was the dominant liana family in species richness at five sites (Table 9). Masaya and Cosiguina both had a higher number of Sapindaceae liana species. Bignoniaceae was the dominant liana family based on abundance only at Chacocente, La Flor, and Santa Rosa. Sapindaceae was more abundant than Bignoniaceae at Masaya, Cosiguina, and Ometepe.

Although floristic diversity changed significantly between sites, family richness of trees and shrubs was to a large extent predictable in different patches of tropical dry forest. Results from this research support Gentry's hypothesis that Fabaceae is the most speciose family in Neotropical areas with a strong dry season (Gentry 1986; Gentry 1996). However, Fabaceae family abundance was never predictable. Bignoniaceae was not always the richest liana family at all sites. Bignoniaceae species were rare in Masaya, Ometepe, and Cosiguina. All of these sites are on volcanic substrates and are relatively disturbed, which may account for the low incidence of Bignoniaceae species. Results from this research reject Gentry's hypothesis that Bignoniaceae is always the dominant liana family by species richness.

Bursera simaruba was encountered in all plots at each site (Appendix 2). However, it was not always the dominant species by frequency at all sites (Table 10). B. simaruba was the dominant species at Ometepe and Masaya and common at Santa Rosa and Cosiguina. B. simaruba occurred at low densities at Palo Verde, La Flor, and

Table 9. The ten most species rich liana families and ten most abundant liana families based on the number of individuals per site. (Most speciose and abundant families in bold).

Family richness	**Cos.**	**S.R.**	**P.V.**	**Chac.**	**Mas.**	**L.F.**	**Ome.**
Bignoniaceae	1	**12**	**9**	**7**	1	**9**	**3**
Sapindaceae	**2**	1	-	1	**3**	1	**3**
Vitaceae	**2**	-	1	1	-	1	1
Combretaceae	-	1	1	1	1	1	-
Fabaceae	**2**	1	1	-	-	-	1
Malpighiaceae	-	1	2	-	-	1	1
Apocynaceae	-	1	1	1	1	-	-
Trigoniaceae	-	1	1	-	1	-	1
Connaraceae	1	1	-	-	-	-	1
Dilleniaceae	1	1	-	-	-	-	1

Family abundance	**Cos.**	**S.R.**	**P.V.**	**Chac.**	**Mas.**	**L.F.**	**Ome.**
Bignoniaceae	1	**51**	12	**21**	4	**43**	9
Fabaceae	3	1	**18**	-	-	-	8
Sapindaceae	**6**	1	-	1	**6**	2	**11**
Combretaceae	-	2	3	11	2	8	-
Apocynaceae	-	9	1	3	1		-
Malpighiaceae	-	2	4	-	-	5	1
Dilleniaceae	2	8	-	-	-	-	1
Vitaceae	2	-	1	2	-	3	2
Trigoniaceae	-	1	2	-	2	-	4
Connaraceae	1	1	-	-	-	-	1

Table 10. The five most abundant species at seven tropical dry forest sites.

Site	Scientific name	Frequency
Masaya	Bursera simaruba	57
	Gliricidia sepium	34
	Diospyros nicaraguensis	15
	Cochlospermum vitifolium	15
	Myriocarpa bifurca	13
Cosiguina	Helianthinae sp. (G895)	10
	Cordia alliodora	9
	Guazuma ulmifolia	8
	Lippia cardiostegia	8
	Bursera simaruba	6
Ometepe	Bursera simaruba	14
	Cecropia peltata	12
	Casearia corymbosa	10
	Bombacopsis quinata	10
	Jatropha curcas	10
Chacocente	Stemmadenia obovata	22
	Tabebuia ochracea	15
	Thouinidium decandrum	12
	Combretum farinosum	11
	Gyrocarpus americanus	11
Palo Verde	Allophyllus occidentalis	38
	Astronium graveolens	25
	Bauhinia glabra	18
	Tabebuia ochracea	13
	Lonchocarpus phaseolifolius	12
La Flor	Calycophyllum candidissimum	53
	Acacia collinsii.	25
	Adenocalymma inundatum	18
	Cochlospermum vitifolium	17
	Tabebuia ochracea	16
Santa Rosa	Exostema mexicanum	15
	Hemiangium excelsum	14
	Arrabidaea mollissima	13
	Cydista diversifolia	13
	Bursera simaruba	10

Chacocente. Three other species, Spondias mombin, Cochlospermum vitifolium, and Simarouba amara, were recorded at six sites but none occurred in high frequency at all sites. Only Tabebuia ochracea could be considered repeatably dominant at Chacocente, Palo Verde, and La Flor. These finding supports Gentry's hypothesis that species dominance is never predictable in different tropical dry forests and is most likely determined by stochastic processes (Hubbell 1979; Gentry 1986).

3.4 Environmental Correlates of Plant Richness and Abundance

Environmental variables of area, precipitation, and anthropogenic disturbance were compared to plant species richness and abundance using a Spearman's rank correlation (Table 11). Although there was a significant correlation between reserve size and tropical dry forest cover within each reserve, neither was significantly correlated with plant species richness or abundance. Precipitation was also a poor predictor of species richness and abundance at all tropical dry forest sites. Anthropogenic disturbance was significantly correlated with total species richness, tree species richness, and liana abundance.

Anthropogenic disturbance was the only environmental variable significantly correlated with species richness, tree species richness, and liana abundance. Disturbance and liana species richness was marginally significant ($P = 0.059$). The degree of habitat disturbance has often been cited as a critical factor in determining tropical forest species diversity (Connell 1978). The decline of species richness with increasing anthropogenic disturbance stand has noted in a number of studies of tropical dry forest (Veblen 1982; Janzen 1986; Veblen et al. 1989; Sabogal 1992;

Table 11. Spearman's rank correlation coefficients between ecological and environmental variables.

	Reserve size	**Forest cover**	**Precip.**	**Disturb.**	**Species richness**	**Liana richness**	**Liana abundance**	**Tree richness**
Forest cover	.8571*							
Precipitation	.2143	.2500						
Disturbance	-.1622	-.1081	.1441					
Species richness	.3929	.4286	.2500	-.8829**				
Liana richness	-.1622	-.2342	-.1261	-.7364	.5225			
Liana abundance	-.3214	-.2857	.0000	-.7748*	.6429	.8829**		
Tree richness	.5000	.5000	.1429	-.8469*	.9643***	.3964	.5357	
Tree abundance	.1071	-.1786	-.3214	-.1801	.0000	-.2342	-.0714	.2143

*P<0.05; **P<0.01; *** P<0.001.

Swaine 1992; Maass 1995). These results suggest that a qualitative assessment of anthropogenic disturbances, such as the intensity and frequency of fire, grazing, and wood collection, is a better predictor of woody plant richness than reserve size, forest cover, or precipitation.

Fire frequency and intensity is often cited as an important predictor of forest structure and diversity (Hopkins 1983; Swaine 1992, White and Pickett 1985; Veblen and Lorenz 1986). Fire frequency and intensity also appears to be important predictors of forest structure and diversity in different tropical dry forest regions of the world (Janzen 1988; Rzedowski 1988; Sabogal 1992; Swaine 1992; Fensham 1995). The Cosiguina site is one of the largest fragments of tropical dry forest remaining in Central America; however, it is severely affected by annual burning. Human induced burning periodically breaks out in patches throughout the Cosiguina reserve during the dry season. Cosiguina had the lowest number of individuals at all sites but maintained relatively high basal area. This suggests that burning results in a forest dominated by widely dispersed large trees. This can be compared with sites like La Flor and Santa Rosa where there is a low incidence of fire and a high number of individuals in all dbh classes. Floristically, the most common woody plants at Cosiguina are early successional species that are resistant to fire such as Cordia alliodora, Guazuma ulmifolia, Lippia cardiostegia, Bursera simaruba, and Gliricidia sepium (Janzen and Liesner 1980; Hartshorn 1983, Janzen 1983). It would appear fire frequency and intensity reduce plant diversity by selecting for fire resistant species and a few early successional plants. Most importantly, fire destroys understory shrubs and lianas that make up a significant proportion of all woody plant diversity in tropical dry forests (Gentry 1982; Bullock 1985; Swaine et al. 1990;

Medina 1995). Most lianas have low wood densities in order to provide higher hydraulic conductivity in their stems (Gessner 1956). A high hydraulic conductivity in lianas is needed to transport water and nutrients from the soil through long meandering stems to the canopy. In essence, lianas invest resources in growth in length while trees allocate resources to supportive tissue (Putz 1984; Putz and Windor 1987). This low wood density may make a number of liana species extremely susceptible to burning, compared to a number of tropical dry forest trees which have a higher wood specific gravity that can resist burning (Daubenmire 1972). In particular, fire appears to destroy Bignoniaceae lianas, which is the second most speciose family in the Central American tropical dry forest. Bignoniaceae lianas are all but absent in areas where burning occurs. Generally, only lianas with high wood density, such as Combretum farinosum, and to a lesser extent lianas with milky latex, such as Serjania species, are able to persist in areas that are frequently burned.

Firewood is used by over 95% of Nicaraguans for cooking because alternatives such as natural gas stoves are expensive (Gillespie 1994). Wood collection also affects forest structure and diversity. Firewood collection is extremely common in sites such as Masaya and Ometepe because both sites are near towns with a high population density. Fuelwood collection significantly changes forest structure by lowering the density of fuelwood and timber species. This results in a mosaic of early and late successional tree species. Many tropical dry forest trees in Central America resprout from the base and trunk or from branches fortunate enough to stick into the ground after a tree falls (Sauer 1979). Since many trees resprout, cutting does not cause trees to become locally extinct in tropical dry forest but wood collection appears to lower tree basal area and biomass. Wood collection also affects liana and vine abundance. When low levels of wood collection occur, liana abundance appears to increase because most lianas vegetatively resprout after damage. This may result in a high abundance of liana individuals in sites where low to intermediate levels of fuelwood collection occur. However, in areas where wood collection is intense, lianas and vines tend to smother the forest (Savage 1992; Gentry 1995). In many tropical areas where fire is rare and wood collection intense, fast growing lianas and vines are able to out compete canopy trees for light. This type of intense fuelwood collection significantly affects both the diversity and structure of tropical dry forests.

Cattle ranching has long been a prestigious and profitable industry in Central America (Parsons 1983). Although cattle have been removed from National Parks in Costa Rica, cattle can still be found in almost all conservation areas in Nicaragua. The presence of cattle in remaining fragments of tropical dry forest in Nicaragua can significantly affect the forest composition and structure. Ungulates are infamous for compacting soils and destroying understory plants (Veblen 1982; Veblen et al. 1989). Compaction by cattle reduces the volume and continuity of larger pores in the soil, thus diminishing the movement of water and air through the soil profile (Maass 1995). This process reduces the ability of certain seeds to germinate and damages trees and shrubs with shallow root systems. Grazing also reduces the density of understory shrubs as saplings are consumed and foliage damaged (Dirzo and Miranda 1990). Intensive grazing by cattle can also result in an understory dominated by spiny or unpalatable shrubs which are unattractive to grazers. Even though grazing by cattle is not as deleterious to tropical dry forest ecosystems as fire and wood collection, the intensity and frequency of cattle grazing may significantly affect woody plant species richness with time.

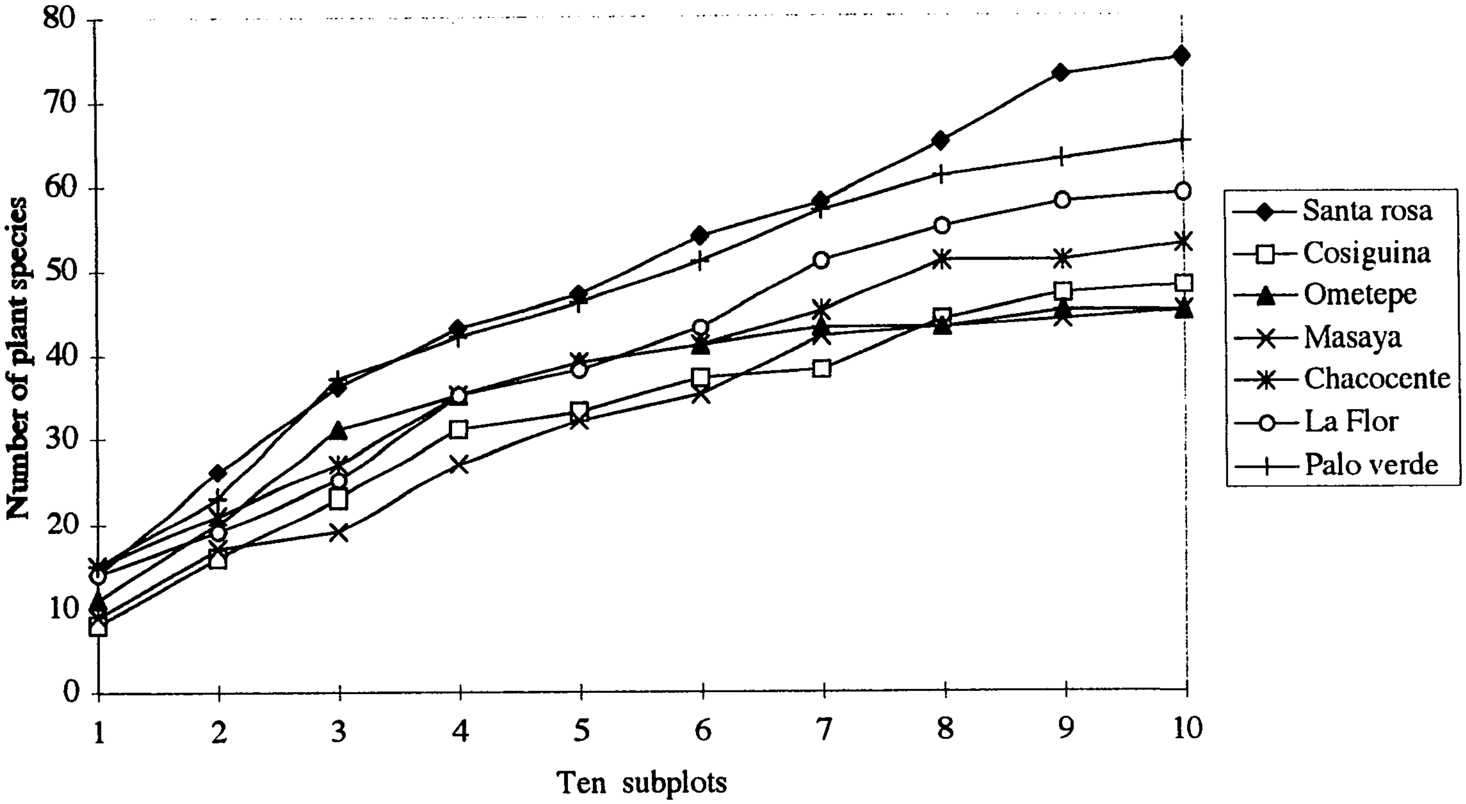
The species-area relationship is one of the best documented phenomena in ecology (Mac Arthur and Wilson 1967). However, there may not be a strong correlation for woody plants in tropical dry forest. This anomaly of the species-area curve is due to the fact that large reserves such as Cosiguina had a low plant species richness and small reserves such as La Flor had a relatively high plant species richness. If a complete flora was undertaken in each of the seven reserves, reserve area would most likely be correlated with total plant species richness. Nevertheless, it may not be correlated with overall woody plant richness in stands of tropical dry forest. Most importantly, the anomaly in the species-area phenomenon may provide insight into the value of small reserves in supporting significant levels of plant diversity (Turner and Corlett 1996). One possible explanation for this anomaly is the amount of species packing that occurs in tropical forest. For reasons not completely understood, a high diversity of tree species can coexist in a relatively small area. For instance, a 50 hectare plot at Pasoh in Malaysia contained 25% of the woody flora known from the Malay peninsula (Whittaker 1996). A 6.6 hectare plot in Sarawak contained over half of the trees with a dbh of 10 cm known for the whole country (Ashton 1969). The same pattern of species packing most certainly occurs in tropical dry forests of Central America. These results, however, should also be interpreted with caution for a number of reasons. First, it is not known if small forest fragments can retain a high level of genetic diversity to ensure the long-term success of tree populations. Second, there is no historical data by which to compare species richness before fragmentation. Since tropical dry forests have been reduced to less than 0.1 of their original range, a number of plant species may have already gone extinct over the last 400 years. Due to relatively little research in the region, the extinction process simply may not have been documented.

There can be little doubt that annual precipitation is directly correlated with plant species richness along a gradient from dry to wet tropical forests (Gentry 1988; Currie 1991; Clinebell et al. 1995). In general, water is one of the most important limiting factors in tropical dry forest (Murphy and Lugo 1986). However, within tropical dry forests, annual precipitation is a poor predictor of woody plant diversity. The wettest sites (Cosiguina, La Flor, and Ometepe) had significantly less woody plant diversity than some of the drier sites such as Santa Rosa and Chacocente. This is in accordance with Gentry's findings that annual precipitation is not significant in predicting plant richness within Neotropical dry forests (Gentry 1995).

3.5 Comparison to other Neotropical dry forests

Gentry's plot method appears to adequately sample floristic diversity of tropical dry forests in Central America. The number of new species identified in successive 100 m^2 plots tends to level off after the eighth or ninth plot at all sites (Figure 4). This method offers some advantages over traditional one hectare plots for undertaking biogeographic research in dry forests. First, this method required approximately 60 person hours to complete at each site, while a one hectare site in tropical dry forest generally requires 350 person hours (Inquist pers. comm.). Second, some of these sites will be degraded over the next five years precluding any useful long-term data on forest dynamics that is traditionally collected from one

Figure 4. Species-area curve for succesive subplots at seven sites



hectare plots. Third, in one hectare plots only trees with a dbh of 10 cm or greater are generally recorded (Dallmeier 1992; Parthasarathay and Karthikeyan 1997). This excludes a number of understory plants and lianas that have a dbh less than 10 cm. Since lianas account for approximately 25% of the plant diversity in the tropical dry forest, focusing on large trees ignores an important component of forest diversity. Finally, when data from my 0.1 plot in Santa Rosa is compared to a 20 hectare plot in the same site, Gentry's method included over 63% of all species encountered in the 20 hectare plot (Inquist pers. comm.). It should be noted that all sites were visited a minimum of three times to ensure positive identification of rare species and lianas.

Results from this study have a number of similarities and differences with Gentry's (1982) original data on tropical dry forests in Central America. Gentry's original data for tropical dry forests of Guanacaste came from two sites (200 m^2 La Pacifica, 500 m^2 COMELCO) that totaled just 0.07 hectares. Gentry used a regression analysis to estimate total data on structure and diversity. The number of individuals from Gentry's Central American plot was estimated at 437 total individuals, 81 liana individuals, and 356 tree individuals (Gentry 1982). These numbers are significantly higher than results from this study. The plots with the most individuals from this study were 264 total individuals at La Flor, 77 liana individuals at Santa Rosa, and 223 tree individuals at Masaya. However, Gentry's estimated basal area of 2,060m^2/0.1 ha and species diversity were within the range of this study. Floristically, Gentry estimated 22 families, 53 total species, six liana species, and 47 tree species within 1,000 m^2. With the exception of the number of liana species, Gentry's Central American data is within the range of this study.

These results suggest that Gentry's original data may have overestimated Central American forest structure but not floristic diversity.

Structurally, the seven remaining fragments of tropical dry forest in Central America have a significantly lower number of total individuals (Mann-Whitney U, *p* = 0.0004), tree individuals (Mann-Whitney U, *p* = 0.0006), trees and lianas > 10 cm dbh (Mann-Whitney U, *p* = 0. 02), and basal area (Mann-Whitney U, *p* = 0.005) than other Neotropical dry forests (Table 12). With the exception of one Neotropical site (Parque El Rey), all Central American tropical dry forests ranked last in total number of individuals within 1,000 m^2. Differences in density can most likely be explained by the current disturbance regime and extensive fragmentation of tropical dry forests in Central America. Large lianas are an important physiognomic indicator of mature forests, and the low number of any lianas with a dbh > 10 cm attests to the fact that there many be no undisturbed tropical dry forests in Central America (Budowski 1970; Gentry 1991; Janzen pers. comm.). Sites such as Cosiguina, Ometepe, and Masaya all showed clear signs of cutting, grazing, and fire which can significantly lower forest density (Veblen et al. 1989; Swaine 1992). Even Santa Rosa, which would appear to be the richest Central American site and most mature forest, has been significantly affected by anthropogenic disturbance over the last 500 years (Janzen pers. comm.). Lower densities in tropical dry forest of Central America did not, however, affect forest diversity.

Floristic diversity in Central American dry forests is still relatively high compared to a number of Neotropical forests (Table 13). Family richness (Mann-Whitney U, *p* = 0.46), total plant species richness (Mann-Whitney U, *p* = 0.18), liana richness (Mann-Whitney U, *p* = 0.71), and tree richness (Mann-Whitney U, *p*

Table 12. Number of individuals and basal area in 0.1 ha samples of lowland Neotropical dry forests.

Sites	**Total**	**Lianas**	**Trees**	**Trees & Lianas > 10 cm dbh**	**Basal area m^2 ha-1**
West Indies					
Guanica	1217	0	1217	32	17.8
Mogotes	455	37	418	119	48.1
Round Hill	566	9	557	132	36.7
Mexico					
Chamela (upland 1)	399	42	357	90	26.3
Chamela (upland 2)	506	55	451	97	21.8
Central America					
Chacocente	215	38	177	63	21.2
Cosiguina	135	17	118	52	23.3
La Flor	264	62	202	43	22.8
Masaya	243	20	223	53	21.1
Ometepe	154	47	107	49	17.7
Palo Verde	227	42	185	47	22.8
Santa Rosa	246	77	169	62	25.0
Southern subtropics					
Riachuelo	451	111	339	67	71.2
Parque El Rey	190	44	146	40	33.4
Chaquimayo	465	134	331	77	47.5
Northern South America					
Galerazamba	396	104	292	50	29.6
Tayrona	337	99	238	72	36.8
Los Colorados	534	151	383	69	36.7
Coloso	339	101	238	78	43.5
Boca de Uchire	297	75	222	31	13.1
Blohm Ranch	306	77	230	86	31.4
Pacific Coast of South America					
Capeira	304	61	243	69	57.2
Perro Muerte	325	53	272	56	36.4
Cerros de Amotape	401	37	377	66	35.8
Tarapoto	520	87	434	87	27.7

Table 13. Floristic summary in 0.1 ha samples of lowland Neotropical dry forest.

Sites	Families	Total species	Lianas	Trees
West Indies				
Guanica	19	34	0	34
Mogotes	28	49	12	37
Round Hill	32	58	4	54
Mexico				
Chamela (upland 1)	37	91	12	79
Chamela (upland 2)	34	89	8	80
Central America				
Chacocente	28	54	11	43
Cosiguina	27	48	10	38
La Flor	25	59	14	45
Masaya	28	44	11	33
Ometepe	31	45	18	27
Palo Verde	29	65	17	48
Santa Rosa	33	75	21	54
Southern subtropics				
Riachuelo	27	47	8	39
Parque El Rey	27	40	10	31
Chaquimayo	29	79	29	50
Northern South America				
Galerazamba	20	55	18	36
Tayrona	31	67	18	49
Los Colorados	41	121	40	81
Coloso	46	113	38	75
Boca de Uchire	20	69	16	53
Blohm Ranch	31	68	17	51
Pacific coast of South America				
Capeira	27	61	19	42
Perro Muerte	33	52	18	54
Cerros de Amotape	29	57	14	43
Tarapoto	38	102	27	75

= 0.12) are similar to other Neotropical forests. Santa Rosa was the sixth most diverse site based on family richness and in tree richness, seventh in total species richness, and the fifth richest site based on liana richness. However, tropical dry forests in northern South America and Mexico contain a higher species richness. Central American sites such as Masaya, Ometepe, and Cosiguina were still relatively depauperate compared to other Neotropical sites based on species richness.

Based on species richness sites such as Santa Rosa and Palo Verde deserve a high priority for conservation compared to other Neotropical sites. However, as noted by Gentry (1995) the tropical dry forests of Central America have low levels of endemism. There were only 17 species encountered in all seven plots that are restricted to Central America. The Santa Rosa site had the most plants endemic to Central America with 10 species (Appendix 1). A majority of the tropical dry forest plants in Central America are widespread from Mexico to northern South America. There are relatively few plants restricted to tropical dry forest. Most of the Central American tropical dry forest plants are generally weedy or early successional species in moist and even wet rainforests. These results support Gentry's finding that Central American tropical dry forests do not have a high priority for conservation based on endemism. Nevertheless, species richness in Central American dry forest is comparable to other Neotropical dry forests.

CHAPTER 4. EXTINCTION PRONE PLANTS

4.1 Introduction

Little empirical data exists on the effects of tropical forest fragmentation on plant species diversity (Turner 1997). Meave and Kellman (1994) found that natural fragments of riparian forest in Belize appeared depauperate in dioecious and mammal-dispersed species compared with continuous forest. This pattern of selective extinction of dioecious species is in agreement with the hypothesis of Ehrendorfer (1979) and Murcia (1996) that this sexual system is disadvantageous in isolated habitats. Janzen (1988b) noted that regeneration of tropical dry forest in Costa Rica was dominated by wind-dispersed trees that would persist for hundreds of years and remain unattractive to vertebrate dispersers. Since there are nearly three times as many vertebrate-dispersed species than wind-dispersed species in Santa Rosa, vertebrate-dispersed plants may be the most extinction-prone after periodic disturbance in small habitat fragments (Janzen 1988). Tropical dry forests in Central America are an ideal system in which to test these hypotheses of selective extinction of woody plants because all tropical dry forests have existed as habitat fragments for a number of years.

This analysis of tropical dry forest has two primary objectives: 1) to summarize richness and abundance of species breeding systems and dispersal mechanisms in Central American tropical dry forest 2) to identify ecological and environmental variables correlated with rarity in these breeding systems and dispersal mechanisms.

Species encountered in seven sites were classified by breeding system and dispersal mechanism. Plant breeding systems were classified as hermaphroditic, monoecious, and dioecious. Plant dispersal mechanisms were classified as anemochoric, autochoric, a combination of any two dispersal mechanisms, zoochoric, and the zoochoric sub-category of mammal-dispersed. A Spearman's rank correlation determined if richness and abundance of dioecious and vertebrate-dispersed plants can be correlated with area, precipitation, and disturbance. In particular, this study tests the hypotheses that dioecious species and zoochoric or mammal-dispersed plants are more extinction prone in successively smaller or more disturbed tropical dry forest fragments. The implications and applications of results are discussed.

4.2 Summary of Sexual Systems

Hermaphroditic plants were the most common breeding system in tropical dry forests with 131 species, accounting for approximately 64.2% of the flora (Table 14). There were 31 dioecious species (15.2%) and 30 monoecious species (14.7%) encountered from all seven sites. The breeding systems of twelve species could not be positively identified and were classified as unknown. Trees and shrubs had the highest incidence of dioecy (19.4%), while lianas had a relatively low percentage (3.6%). The percentage of monoecious lianas (14.5%) and trees and shrubs (14.7%) were relatively similar.

Hermaphrodites were the dominant liana breeding system by species richness at all Central American sites (Table 15). Hermaphrodites were also the dominant sexual system for lianas based on species abundance at all sites. There were only two species of dioecious liana (Pisonia aculeata and Tetracera volubilis) encountered

Table 14. Summary of breeding systems for Central American tropical dry forests. Percentages are in parenthesis.

Sexuality	**Total Species**	**Lianas**	**Trees**
Hermaphrodite	131 (64.2)	41 (74.5)	90 (60.4)
Monoecious	30 (14.7)	8 (14.5)	22 (14.7)
Dioecious	31 (15.2)	2 (3.6)	29 (19.4)
Unknown	12 (5.9)	4 (7.2)	8 (5.3)
Total	204	55	149

Table 15. Breeding system of lianas based on species richness and abundance by site.

Sexuality	Cos.	S.R.	P.V.	Chac.	Mas	L.F.	Ome.
Species richness							
Hermaphrodite	7	18	17	10	8	12	13
Monoecious	2	1	0	1	3	1	3
Dioecious	1	1	0	0	0	0	2
Unknown	0	1	1	0	0	1	1
Total species	10	21	18	11	11	14	19
Abundance							
Hermaphrodite	9	67	43	37	14	59	34
Monoecious	6	1	0	1	6	2	11
Dioecious	2	8	0	0	0	0	2
Unknown	0	1	1	0	0	1	1
Total individuals	17	77	44	38	20	62	48

in this study. Santa Rosa, Ometepe, and Cosiguina were the only sites with dioecious lianas.

Hermaphroditic plants were the most common tree and shrub breeding system encountered at all sites in Central America (Table 16). Dioecious plants were the second most common breeding system at all sites. There were 29 species of dioecious trees and shrubs encountered at all seven sites. Santa Rosa (14 spp.) and Palo Verde (13 spp.) had the highest number of dioecious trees and shrubs while La Flor (6 spp.), Ometepe (6 spp.), and Chacocente (6 spp.) had the lowest number. Only La Flor (14%) and Chacocente (14%) had a relatively low proportion of dioecious plants compared to other breeding systems. The proportion of dioecious plants at all other sites ranged from 23% to 28%. Hermaphroditic trees and shrubs were also the most dominant breeding system by abundance at all sites. Dioecious trees and shrubs were the second most abundant breeding system at five sites. Dioecious species were relatively abundant based on number of individuals at Masaya and Ometepe and again rare at Chacocente and La Flor.

Central American tropical dry forest does not appear to have a significantly lower proportion of dioecious plants when compared to other Neotropical sites (Table 17). Trees in the tropical dry forest of Chamela, Mexico contained approximately 23.9% dioecious species (Bullock 1996). Medium to large size trees from the moist forest of Barro Colorado, Panama had approximately 21.3% dioecious species (Croat 1979; Bullock 1996). Lowland rainforest at La Selva, Costa Rica contains approximately 23.1% dioecious species (Bawa et al. 1985). This suggests that tree breeding systems in lowland Neotropical forests all contain a

Table 16. Breeding system of tree and shrubs based on species richness and abundance by site.

Sexuality	**Cos.**	**S.R.**	**P.V.**	**Chac.**	**Mas.**	**L.F.**	**Ome.**
Species richness							
Hermaphrodite	22	32	25	30	22	31	15
Monoecious	5	7	7	6	3	4	5
Dioecious	11	14	13	6	8	6	6
Unknown	0	1	2	1	0	4	0
Total species	38	54	47	43	33	45	26
Abundance							
Hermaphrodite	82	105	72	122	113	173	49
Monoecious	10	18	61	36	16	9	24
Dioecious	26	44	48	16	94	14	33
Unknown	0	2	2	3	0	6	0
Total individuals	118	169	183	177	223	202	106

Table 17. Sexual systems by percent from other sites in the Central America.

Breeding System	This Study	Chamela, Mexico	Barro Colorado, Panama	La Selva, Costa Rica
Total species	141 spp.	188 spp.	211 spp.	333 spp.
Hermaphrodite	63.8%	57.9%	63.0%	65.5%
Monoecious	15.6%	18.0%	16.6%	11.4%
Dioecious	20.6%	23.9%	21.3%	23.1%

relatively similar proportion of dioecious species even as species diversity increases from dry to wet forest.

4.3 Summary of Dispersal Mechanism

Zoochoric dispersal was the most common dispersal type in Central American tropical dry forests, accounting for approximately 45% of all species encountered (Table 18). Anemochoric dispersal was the second most common dispersal mechanism, accounting for 38% of all species. Autochoric dispersal was relatively rare, accounting for only 2.9%. The combination of two dispersal mechanisms accounted for 6% of all species. Within the zoochoric category, there were 34 mammal-dispersed species, accounting for 5% of all species (Gentry 1982; Janzen and Martin 1982). The modes of dispersal were remarkably different for trees and lianas. A majority of all tropical dry forest lianas were wind-dispersed (67.2%) while vertebrate-dispersed species accounted for less than 20%. Zoochoric dispersal was the most common form of dispersal for trees and shrubs (55%), followed by anemochoric (27.5%).

Liana species richness by site was dominated by anemochoric dispersal, although there were an equal number of wind and vertebrate-dispersed liana species at Cosiguina (Table 19). Ometepe and Cosiguina both have a relatively high number of zoochoric-dispersed lianas. Anemochoric dispersal was always the most abundant mode of dispersal based on the number of individuals at all sites.

Zoochoric-dispersed trees and shrubs were dominated at all sites except for La Flor, which had a high number of wind-dispersed species (Table 20). Santa Rosa had the most zoochoric-dispersed trees and shrubs (34 spp.) with all other sites

Table 18. Summary of dispersal mechanism for tropical dry forest in Central America.

Dispersal type	Total	Percent	Lianas	Percent	Trees	Percent
Autochoric	6	2.9%	1	1.8%	5	3.3%
Anemochoric	78	38.2%	37	67.2%	41	27.5%
Zoochoric	92	45.0%	10	18.1%	82	55.0%
(Mammal dispersed)	(34)	(16.6%)	(0)	(0.0%)	(34)	(18.6%)
Combination	15	7.3%	2	3.6%	13	8.7%
Unknown	13	63.7%	5	9.0%	8	5.3%

Table 19. Dispersal mechanism by liana species richness and abundance.

Dispersal Type	**Cos.**	**S.R.**	**P.V.**	**Chac.**	**Mas.**	**L.F.**	**Ome.**
Species richness							
Autochoric	0	0	1	0	0	0	0
Zoochoric	5	3	1	1	2	1	6
Anemochoric	5	16	15	10	8	11	12
Combination	0	1	0	0	0	1	0
Unknown	0	1	1	0	1	1	1
Total	10	21	18	11	11	14	19
Abundance							
Autochoric	0	0	18	0	0	0	0
Zoochoric	7	10	1	2	2	3	11
Anemochoric	10	65	24	36	17	40	36
Combination	0	1	0	0	0	18	0
Unknown	0	1	1	0	1	1	1
Total	17	77	44	38	20	62	48

Table 20. Dispersal mechanism by tree species richness and abundance.

Dispersal type	Cos.	S.R.	P.V.	Chac.	Mas.	L.F	Ome.
Species richness							
Autochoric	0	2	2	1	1	0	1
Zoochoric	23	34	24	24	19	17	17
(Mammal)	(12)	(17)	(10)	(9)	(6)	(10)	(3)
Anemochoric	7	13	15	11	9	20	6
Combination	7	4	4	6	4	5	2
Unknown	1	1	2	1	0	3	0
Total	38	54	47	43	33	45	26
Abundance							
Autochoric	0	14	4	1	1	0	3
Zoochoric	55	77	107	91	121	33	76
(Mammal)	(31)	(36)	(44)	(32)	(27)	(23)	(13)
Anemochoric	34	62	52	60	51	127	24
Combination	27	14	18	22	50	37	3
Unknown	2	2	2	3	0	5	0
Total	118	169	183	177	223	202	106

ranging between 17 to 24 species. The abundance of different dispersal categories based on number of individuals per site changed significantly between tropical dry forest sites. La Flor was clearly dominated by wind-dispersed individuals with very few zoochoric-dispersed individuals. The opposite was true for Ometepe, which had a very high number of zoochoric-dispersed individuals. The other five sites all had relatively similar proportions of anemochoric and zoochoric dispersal types based on abundance.

The percentage of zoochoric-dispersed and anemochoric-dispersed lianas and trees are relatively similar to other data from tropical dry forests. In twelve Neotropical dry forest sites, Gentry (1996) found that nearly 80% of all lianas and a third of all trees were wind-dispersed (Gentry 1996). When species encountered in this study are compared with the complete flora at Santa Rosa, the ratio of zoochoric- to anemochoric-dispersed is very similar (Table 21). However, when compared to the tropical moist forest on Barro Colorado Island, the percentage of wind-dispersed species decreases for both trees and lianas. This is to be expected because the proportion of wind-dispersed species dramatically declines with increased precipitation (Gentry 1988).

4.4 Ecological Correlates of Breeding Systems and Dispersal Mechanisms

A Spearman's rank correlation identifies ecological and environmental variables correlated with dioecious, zoochoric- dispersed and mammal-dispersed trees and shrubs (Table 22). Dioecious species richness and percentages of total species encountered at each site were significantly correlated with both reserve size and forest cover. There

Table 21. Dispersal mechanisms of trees and lianas in tropical dry and moist forests in Central America.

	This Study	**Santa Rosa**	**Barro Colorado**
Lianas	48 spp.	49 spp.	149 spp.
Zoochoric	21%	22%	40%
Anemochoric	77%	71%	57%
Autochoric	2%	6%	3%
Trees	128 spp.	196 spp.	416 spp.
Zoochoric	64%	68%	82%
Anemochoric	32%	23%	13%
Autochoric	4%	9%	5%

Table 22. Spearman rank correlation for environmental variables and plant breeding systems and dispersal mechanisms. (H. = Hermaphrodite, D. = Dioecious, A. = Anemochoric, Z. = Zoochoric, M. = Mammal).

Variables	**Reserve size**	**Forest cover**	**Precip.**	**Disturb.**
Cover forest	.8571*			
Precipitation	.2143	.2500		
Disturbance	-.1622	-.1081	.1441	
Species richness	.3929	.4286	.2500	-.8829**
Tree richness.	.5000	.5000	.1429	-.8469*
H. richness	.1441	.2883	-.0360	-.6636
H. abundance	-.2500	-.1071	-.2143	-.0901
D. richness	.8524*	.7783*	.0741	-.3740
D. abundance	.4643	.1429	-.4643	-.0541
% Dioecious	.8571*	.7857*	.2857	.1261
A. richness	.2143	.0714	.1429	-.7027
A. abundance	.0000	.0714	-.0357	-.6847
Z. richness	.6728	.7638*	-.2364	-.5872
Z. abundance	.3571	.0714	-.7500	-.1441
% Zoochoric	-.1429	.0714	-.1786	.2162
M. richness	.6307	.8108*	-.3909	.4505
M. abundance	.8214*	.7500	-.5946	-.0714
% M. dispersed	.4286	.7500	-.0901	.5000

*P<.05, **P<.01, ***P<.001

was no correlation between dioecious species richness, abundance, percentage, and precipitation or disturbance. There was no correlation between hermaphroditic plant richness or abundance and area, precipitation or disturbance. Zoochoric species richness was significantly correlated with forest cover. Zoochoric richness and proportion of zoochoric species were not significantly correlated with reserve size, precipitation, or disturbance. Mammal-dispersed richness was correlated with forest cover while mammal-dispersed abundance was strongly correlated with reserve size. There was no correlation between anemochoric richness and abundance and area, precipitation or disturbance.

Plant Sexuality

Dioecious species richness and the proportion of dioecious species at each site were significantly correlated with both reserve size and forest cover. These results support Meave and Kellman's (1994) hypothesis that the dioecious breeding system is disadvantageous in isolated habitats. In theory, a dioecious breeding system promotes cross-pollination and ensures genetic heterozyogosity within a population (Endress 1994). In essence, dioecy prevents plants from looking like the banjo player in the film Deliverance. If there are a low number of dioecious individuals in a forest fragment there is a high probability that cross-pollination will not occur. At this spatial scale, these results suggest that the dioecious breeding systems can be used to identify extinction-prone trees and shrubs in selectively smaller patches of tropical dry forest. These findings may support Janzen's "living dead" hypothesis (Janzen 1986). Janzen noted that many large trees that have long generation times respond slowly to forest fragmentation. This is because many of these trees may persist in a forest fragment for a number of years after fragmentation occurs. These trees will eventually go extinct as co-evolved pollinators and seed dispersers go locally extinct (Laurance and Bierregaard 1997). All the fragments in this study have been isolated for over 50 years; that should be enough time for a number of tree species to go locally extinct. Furthermore, all fragments in this study are spread over a large geographic area and are the best remaining fragments of tropical dry forest in Central America.

These findings should be interpreted with caution for a number of reasons. First, it is not uncommon for seemingly dioecious species to have a low number of flowers from the opposite sex (Policansky 1982; Endress 1994). Since there has been relatively little research into plant breeding systems, some dioecious species may eventually be identified as monoecious. Second, there are a number of physiological phenomena, such as self-incompatibility in perfect or bisexual flowers which may be of equal importance in predicting plant extinction than dioecious species structure. For instance, some hermaphroditic plants such as Casearia and Tabebuia do not self-pollinate and may require pollen from another individual of the same species to reproduce (Bullock 1985; Murcia 1996). In other words, there are a number of hermaphroditic plants that functionally may have breeding systems similar to dioecy. These self-incompatible species may also be extinction prone in small habitat fragments. However, there is currently not enough information on self-incompatibility in hermaphroditic and monoecious plants to determine if they are as vulnerable as dioecious plants.

Caution should also be taken when interpreting the conservation value of using dioecy as an indicator of extinction-prone plants. When examining the list of dioecious species in tropical dry forests, a number of species will never be vulnerable to extinction in Central America because of other natural history characteristics, such as successional status and range. (Table 23). There are a number of dioecious plants, such as Bursera simaruba, Diospyros nicaraguensis, Cecropia peltata, Bernardia nicaraguensis, Myriocarpa bifurca, and Urera baccifera, that are primary and early successional plants (Croat 1979; Janzen 1983). Bawa et al. (1985) found that there was no difference between the number of dioecious species in early successional and mature forests. If this is the case, dioecious species in the families Cecropiaceae, Ebenaceae, Euphorbaceae, and Urticaeae are not the most extinction-prone families in tropical dry forest. Although some species in these families may be rare in late-successional tropical dry forests, they may be common in disturbed forests and landscapes. Second, although it would appear that dioecious species are rare in smaller fragments of tropical dry forest, almost all plants in this study have an extremely wide geographic distribution and occur in other habitats beside the tropical dry forest (Andersen et al. 1997). Only seven dioecious species were restricted to Central America with a majority of all species ranging from Mexico to South America (Croat 1979; Hartshorn 1983; Janzen 1983). Furthermore, many of these species are not restricted to tropical dry forest and can be found in moist forest or in light gaps in wet forest (Croat 1979; McDade et al. 1994). Only Genipa americana, Randia monantha, Agonandra macrocarpa, Coccoloba floribunda, and Alibertia edulis are restricted to tropical dry forest ecosystems.

I hypothesize that dioecious species in the Meliaceae, Nyctaginaceae, Rubiaceae, and Rutaceae families will be exceptionally prone to local extinction in successively smaller habitat fragments. These species are generally restricted to Central America and are rare in small fragments of tropical dry forest and disturbed

Table 23. Dioecious species incidence in seven tropical dry forest sites.

Scientific Name	Cos.	S.R.	P.V.	Chac.	Mas.	L.F.	Ome.
Bursera simaruba	x	x	x	x	x	x	x
Simarouba amara		x	x	x	x	x	x
Cordia panamensis	x	x	x				x
Diospyros nicaraguensis	x			x	x	x	
Astronium graveolens		x	x			x	
Spondias purpurea	x	x	x				
Cecropia peltata	x				x		x
Tetracera volubilis	x	x					x
Bernardia nicaraguensis *		x	x		x		
Margaritaria nobilis			x		x		x
Chlorophora tinctoria	x	x	x				
Trichilia americana		x	x				
Pisonia macranthocarpa	x	x					
Neea fagifolia *	x						x
Triplaris melaenodendron			x			x	
Genipa americana		x				x	
Randia monantha		x	x				
Spondias radlkoferi			x				
Cordia collococca			x				
Bursera graveolens					x		
Ateleia herbert-smithii *		x					
Castilla elastica	x						
Pisonia aculeata							x
Agonandra macrocarpa *		x					
Coccoloba floribunda				x			
Alibertia edulis *		x					
Zanthoxylum monophyllum				x			
Zanthoxylum setulosum *				x			
Alvaradoa amorphoides	x						
Myriocarpa bifurca *					x		
Urera baccifera	x						

* Restricted to Central America

forests. Further research in small habitat fragments in Costa Rica and near the Chamela research station in Mexico could provide considerable insight into this problem. Rather than establishing plots, recording the total number of dioecious species and individuals within a fragment would be the best method to test this hypothesis.

Dioecious species abundance was not correlated with any ecological or environmental variables. Hubbell (1979) also found that there was no relationship between breeding systems and species dispersion or abundance in tropical dry forest of Costa Rica. Dioecious species richness, abundance, and the percentage of dioecious species per site were not significantly correlated with precipitation or disturbance. This is rather surprising considering that total species richness was significantly correlated with disturbance. However, this is in accordance with the findings of Bawa et al. (1985) that there was no difference between the number of dioecious species in early successional forest and mature forest.

Plant Dispersal

The extinction of large mammals in successively smaller tropical forest fragments has been well documented (Eisenberg 1980; Lynam 1997; Terborgh 1997), while the secondary extinction of mammal-dispersed plants, although often proposed, is poorly documented (Janzen 1974; Terborgh 1974; Howe and Smallwood 1982; Howe 1984). A correlation exists between zoochoric-dispersed and mammal-dispersed species richness and forest cover within each reserve. The tropical dry forests on the island of Ometepe had only three of the 34 mammal-dispersed species recorded in all seven plots. The Santa Rosa had 17 mammal-dispersed species in a 0.1 ha plot and the flora of Santa Rosa includes all but one of the mammal-dispersed species recorded from all seven plots (Janzen and Liesner 1980). This would lead one to believe that mammal-dispersed species may be rarer in smaller fragments. However, Meave and Kellman (1994) found that the proportion of mammal-dispersed species, not mammal-dispersed species richness, was lower in naturally fragmented riparian forests than in contiguous forest. There was no correlation between the proportion of zoochoric- or mammal-dispersed species and area.

Although results from this study found a correlation between the number of mammal-dispersed plants and area of forest cover within each fragment, one can not automatically assume that it is due to a loss of dispersal vectors. First, I believe that there are no obligate mammal-dispersed plants in tropical dry forests of Central America. The list of mammal-dispersed trees and shrubs was created following Janzen and Martin (1981) and Gentry (1988), and by assigning all fleshy diaspores larger than 2 cm to the mammal-dispersed category following Gentry (1988). The resulting Table 24 is probably the most accurate list of plants dispersed by mammals that can be compiled, but there are currently no empirical data on obligate dispersal by mammals in tropical dry forest. Most data on seed dispersal in tropical forests are casual anecdotes of birds and mammals often based on one or two tree species or individuals (Janzen 1983; Howe 1986). Most fruits are eaten and dispersed by many animals, not one or a few species (Howe 1986). Second, there is little evidence that the low numbers of mammal-dispersed plants are due to the extinction of native tropical dry forest mammals. The tapir (Tapirus bairdii) and, to a lesser extent, the peccary (Tayasu tajacu) are sensitive to local extinction in smaller fragments of

Table 24. Mammal-dispersed species incidence in seven tropical dry forest sites.

Scientific Name	Cos.	S.R.	P.V.	Chac.	Mas.	L.F.	Ome.
Spondias mombin	x	x	x		x	x	x
Guazuma ulmifolia	x	x	x	x		x	
Diospyros nicaraguensis	x			x	x	x	
Annona purpurea	x	x	x	x			
Astronium graveolens		x	x			x	
Annona reticulata	x				x		x
Spondias purpurea	x	x	x				
Chlorophora tinctoria	x	x	x				
Randia monantha		x	x				
Guettarda macrosperma		x				x	
Jacquinia nervosa		x		x			
Zizyphus guatemalensis			x	x			
Genipa americana		x				x	
Licania arborea		x			x		
Enterolobium cyclocarpum	x	x					
Ficus ovalis	x						x
Manilkara zapota		x				x	
Sideroxylon capiri				x	x		
Capparis pachaca				x			
Apeiba tibourbou	x						
Caesalpinia coriaria (G1173)				x			
Bunchosia cornifolia		x					
Bactris guineensis			x				
Byrsonima crassifolia					x		
Acacia farnesiana	x						
Alibertia edulis		x					
Spondias radlkoferi			x				
Sapranthus palanga						x	
Pithecellobium saman	x						
Brosimum alicastrum		x					
Ficus sp.						x	
Ximenia americana				x			
Agonandra macrocarpa		x					
Randia sp.						x	

tropical dry forest. Other seed dispersing mammals such as agouti (Dasyprocta punctata), pacas (Agouti paca), deer (Odocoileus virginianus), and monkeys (Cebus capucinus, Alouatta palliata) still maintain populations in intermediate and small forest fragments. Furthermore, domestic horses and cattle disperse the same plants as native mammals (Janzen and Martin 1981). Cattle historically may have been the dominant large mammal in the tropical dry forest region over the last one hundred years (Janzen and Martin 1981; Parsons 1983). Past land use history by exotic grazers probably had a more profound effect on contemporary forest composition than the recent extinction of native fauna. Finally, from my qualitative judgment of vulnerable tropical dry forest trees, a majority of the mammal-dispersed trees and shrubs are rare because of factors other than loss of dispersal vectors. A number of studies have found a correlation between seed size and successional status of forest trees (Whitmore 1990; Hammond and Brown 1995; Gibson and Rundel 1996). The large-seeded plants may be rare because most are late successional species that may occur in low densities in smaller or more disturbed fragments. Although there was no correlation between anthropogenic disturbance and mammal-dispersed species richness, the classification of tree species' successional status may be a better predictor of rarity than dispersal vector. Unfortunately, little empirical data exists on the successional status of tropical dry forest trees. Therefore, all trees and shrubs encountered during this study can not be classified as early or late successional species. Establishing more plots in other small fragments less than 500 hectares would significantly improve the resolution of this study.

CHAPTER 5. AVIAN DIVERSITY AND ABUNDANCE

5.1 Introduction

There has been little biogeographical or ecological research on resident bird communities in the tropical dry forest of Central America apart from simple checklists (Howell 1983; Stiles 1983; Ceballos 1995). This is especially true for avian communities in the tropical dry forests of Nicaragua. The majority of studies on tropical bird communities has been undertaken in lowland rainforest and there are no studies on the effects of forest fragmentation on species richness in tropical dry forest. Since tropical dry forest has been reduced to less than 0.1% of its original range in Central America, analysis of species richness and abundance in remaining fragments of forest may provide insight as to how to best preserve avian diversity in Costa Rica and Nicaragua.

This analysis of terrestrial breeding birds of the tropical dry forest regions of Central America has three primary objectives: 1) to discuss biogeographic and life history characteristics of resident birds recorded in the tropical dry forest regions of Central America, 2) to summarize species richness, biogeography, and life history characteristics of tropical dry forest birds encountered during point counts in eight forest fragments, and 3) to identify ecological and environmental variables correlated with bird species richness and abundance.

Biogeographic and life history characteristics for all terrestrial breeding birds are compared. Species richness and abundance of resident birds recorded in eight fragments of tropical dry forest during point counts are compared. A Spearman's rank correlation is used to identify correlates of bird species richness and abundance at seven tropical dry forest sites. In particular, I examine how bird species richness and abundance are associated with area, precipitation, disturbance, plant diversity, and vegetation structure.

5.2 Biogeography and Life History Traits of Resident Birds

A total of 166 terrestrial breeding birds have been recorded in the tropical dry forest region on the Pacific side of Nicaragua and Costa Rica (Howell 1983; Stiles 1983; Gillespie and Nicholson 1996). All species had a variety of geographic range sizes that can be quantified by latitudinal and longitudinal extents (Brown 1995; Gaston 1996). Resident birds recorded in the tropical dry forest region of Nicaragua and Costa Rica had latitudinal extents ranging from three degrees for Hoffmann's woodpecker (Melanerpes hoffmannii), green parakeet (Aratinga holochlora), and blue-tailed hummingbird (Amazilia cyanura) to 116 degrees for house sparrow (Passer domesticus). There were 18 birds (11%) with small latitudinal extents that covered 10 degrees or less and 63 birds (38%) with ranges of 20 degrees or less (Figure 5). Twenty-four birds (14%) had large latitudinal extents greater than 60 degrees.

The northern limits of breeding ranges for birds in the tropical dry forest region vary, but most species have breeding ranges between 25 and 30 degrees north. This latitude roughly corresponds with the boundary between woodland and desert ecosystems in Mexico (Rzedowski 1981). It is interesting to note that as species range increases, most birds have their northernmost breeding ranges at 20 degrees north. This is tightly correlated with the tropical dry forests of Jalisco and the Yucatan in Mexico. The southern latitudinal extents of avian breeding ranges

Figure 6. Latitudinal extent of breeding birds recorded in the tropical dry forest region.

exhibit a relatively different pattern. Thirty-two bird species (19%) recorded in tropical dry forest regions of Central America have their southernmost breeding ranges at 10 degrees north. This corresponds with the extent of tropical dry forest in Costa Rica. Tropical dry forest birds with large ranges have slightly greater latitudinal extents in the southern hemisphere. Of these 166 total bird species, there were 93 species (56%) with breeding ranges extending south of the equator. These southern ranges below the equator vary, but generally can be correlated with the extent of tropical dry forest and woodlands in Paraguay, Argentina, Uruguay, and Brazil.

Longitudinal extent, based on a species' incidence in the Pacific, Central, or Atlantic region of Nicaragua, demonstrates that few resident birds were restricted to the Pacific region (Table 25). Four birds, the pearl kite (Gampsonyx swainsonii), white-belllied chachalaca (Ortalis leucogastra), white-browed wren (Thryothorus ludovicianus), and ruddy-breasted seedeater (Sporophila minuta), were only recorded in the Pacific region. This is a dramatic contrast to the number of breeding birds restricted to the Central and Atlantic regions of Nicaragua. There are 58 resident birds restricted to the Central region and 132 resident birds restricted to the Atlantic region (Gillespie and Nicholson 1996; Gillespie 1998). A majority of birds recorded in the tropical dry forest region have wide longitudinal extents, with 93 birds recorded in all three biographic regions: the Pacific, Central, and Atlantic region. Longitudinal extent identifies species intolerant to different climatic and vegetation regimes, as the three biogeographic regions in Nicaragua (Pacific, Central, and Atlantic) are closely correlated with forest type (tropical dry forest, cloud forest,

Table 25. Longitudinal extent of birds in the tropical dry forest region of Nicaragua and Costa Rica.

Biogeographic regions	**All birds**	**Forest birds**	**% forest birds**
Pacific	4	1	25%
Pacific, Atlantic	19	13	68%
Pacific, Central	50	36	72%
Pacific, Central, Atlantic	93	51	55%

and lowland rainforest, respectively). It would appear that most birds found in the Pacific region are habitat generalists and are not restricted to the tropical dry forest.

According to Stiles' classification system of bird dependence on forest, only eight species or 5% of birds require solid forest, 55% of birds require patchy forest, while 39% of birds do not require forest (Table 26). When all species were classified into six guild categories, a number of interesting patterns emerged (Table 26). Omnivores accounted for 37% of all tropical dry forest birds, followed by insectivores (31%). Carnivores and frugivores each accounted for approximately 11% of all birds while nectarivores and granivores each accounted for approximately 5% of all birds. When species that do not require forest were excluded, the proportions of guild categories for most of the 101 forest birds were similar to non-forest birds except for granivores and frugivores. Most granivores do not require forest while 89% of all frugivores require at least patchy forest.

Avian body mass varied by forest preference and guild categories for all species recorded in the tropical dry forest region of Costa Rica and Nicaragua. Most birds that required solid forest generally had a body mass greater than 100 grams (Figure 6). Birds that required patchy forest have a higher body mass than non-forest birds. This difference in body mass may be due to greater resource abundance and higher productivity in forest ecosystems compared to non-forest ecosystems. A similar pattern occurred for species guilds. Carnivores in the tropical dry forest region of Central America clearly have the highest body mass with no species weighing less than 100 grams (Figure 7). Frugivores were the next largest body class with only six species weighting less than 100 grams. Omnivores as a group

Table 26. Forest preference and guild of birds in the tropical dry forest region of Nicaragua and Costa Rica.

Natural history characteristics	All birds	Forest birds	% forest birds
Forest preference			
Solid forest	8		
Patchy forest	93		
Non-forest	65		
Guild			
Carnivores	18	12	67%
Frugivores	18	16	89%
Granivores	9	2	22%
Insectivores	52	34	65%
Nectarivores	8	5	63%
Omnivores	61	32	52%

Figure 6. Forest preference and mass for resident tropical dry forest birds

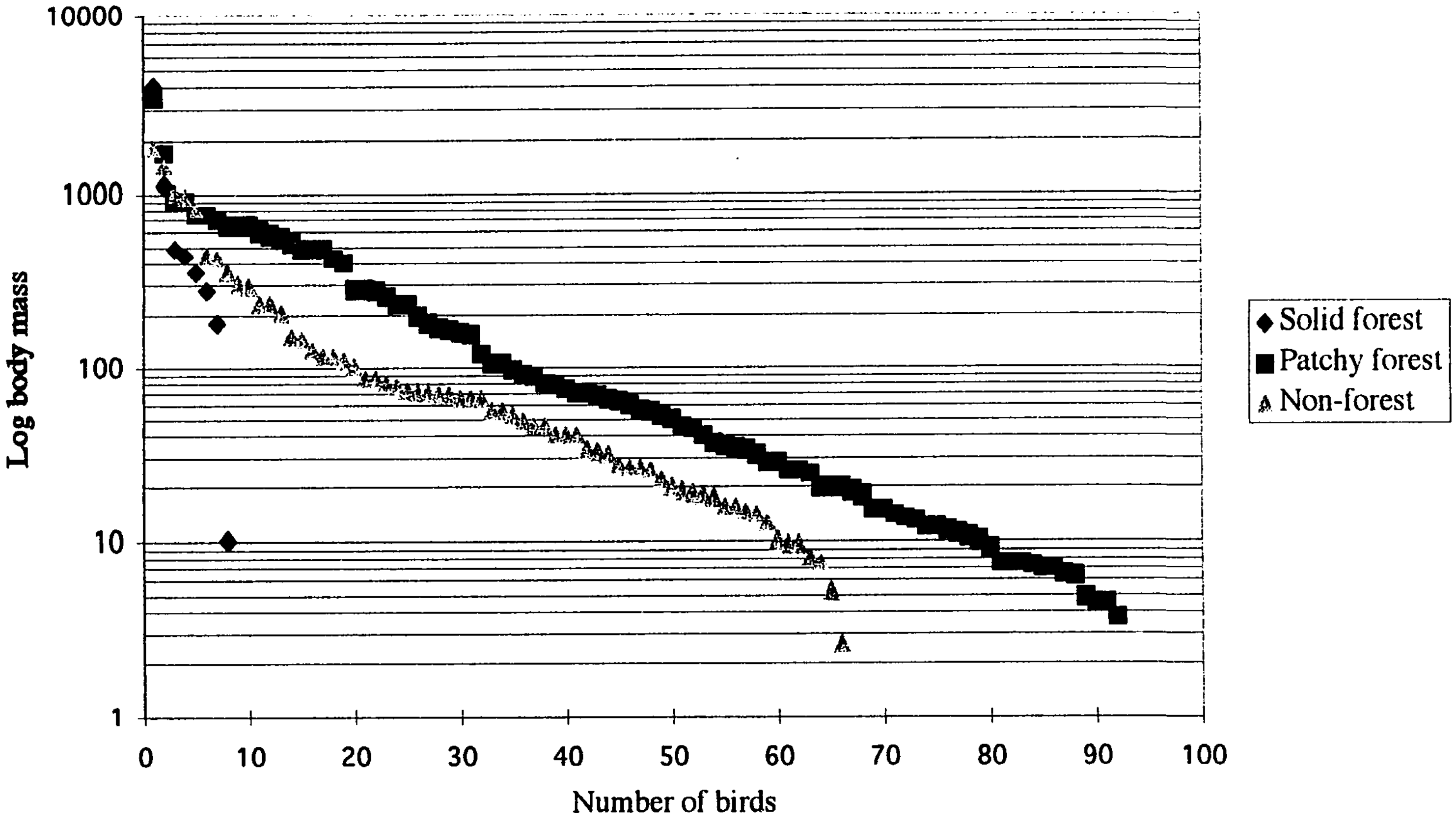
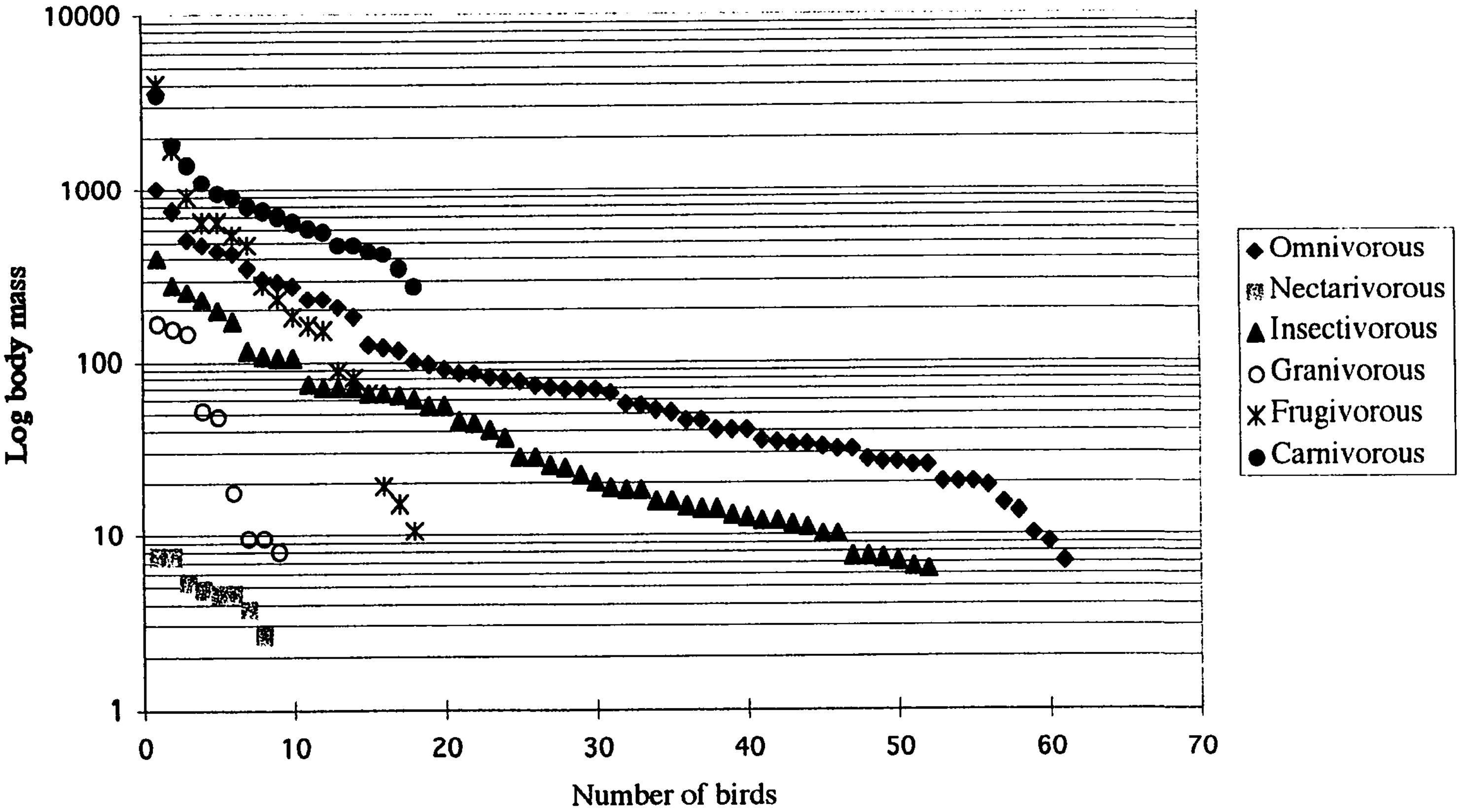


Figure 7. Guild catergories and log body mass for resident tropical dry forest birds.



had notably higher body mass than insectivores. Nectarivores were the smallest, as would be expected.

A number of conclusions can be made about the breeding birds in the tropical dry forest region of Costa Rica and Nicaragua. First, most resident breeding birds do not have specialized forest preference. This summary indicates that the tropical dry forest region of Central America is clearly dominated by habitat generalists. This generalist nature of most tropical dry forest birds can be attributed to the seasonality of dry forest and extensive deforestation that has occurred in the region. The tropical dry forest of Central America is deciduous; its trees lose a majority of their leaves for four to six months per year. This is a marked contrast to tropical dry forest in Australia and Southeast Asia that are evergreen during the dry season. This pronounced dry season prevents many species from requiring solid forest. Few tropical dry forest birds appear to have evolved unique ecological or behavioral adaptations that can be found with forest-interior birds in cloud and lowland rainforests (Willis 1974; Stiles 1983). However, since only 0.1% of tropical dry forest remains in Central America, most species that require solid forest may have gone locally extinct a number of years ago. The seasonal nature and extent of deforestation in the region may provide dry forest birds with an important selective advantage over birds in other biogeographic regions. Stiles (1983) noted that some tropical dry forest birds have expanded their range into the Meseta Central of Costa Rica as humid areas have been deforested. I have observed the same pattern in the deforested lowland areas on the Atlantic side of Nicaragua. In essence, evergreen forests are being converted into fragmented forests with similar vegetation structures as savannas and tropical dry forest. For this reason, a number of tropical dry forest birds will most likely expand their ranges as deforestation continues in the Central and Atlantic regions of Central America.

Seasonality may also explain the generalist nature of species guild. The high proportion of omnivores and relatively low proportion of specialized insectivores and frugivores is again probably best explained by the seasonal nature of the region. The intermittent nature of insect and fruit abundance prevent some species from residing in the region year round. A number of ecological guilds, such as frugivores and certain insectivores, may be unable to persist year round in tropical dry forests due to the pronounced dry season and associated lack of resources. Tropical dry forests have a higher percentage of wind-dispersed plants than wetter forest types and fruit production is markedly seasonal (Opler et al. 1980). Insect abundance and diversity also significantly decrease during the dry season in tropical dry forests (Janzen 1968). Low insect diversity and abundance may also be correlated with lower avian diversity. Most species in tropical dry forest regions have to rely on a diversity of resources to persist in the region year round. This shift in diet in response to seasonality has been noted for a number of vertebrates in seasonal dry forests (Ceballos 1996).

5.3 Resident Birds in Tropical Dry Forest Fragments

A total of 240 point counts totaling 40 hours were undertaken in eight tropical dry forests in Central America from April 23 to July 15, 1997. Seventy-two resident bird species were recorded. Eight migratory bird species were encountered but excluded from the final analysis, which focuses on resident breeding birds. Santa Rosa had the highest species richness of all tropical dry forest sites and the highest mean number of species per point (Table 27). Palo Verde, Chacocente, and Cosiguina were the second richest sites with a similar species richness. The smallest forest fragments of La Pacifica, Ometepe, and La Flor had the lowest species richness.

A total of 1,776 individuals were recorded in the eight sites of tropical dry forest. Santa Rosa had the highest species abundance, followed by Ometepe. La Flor had the lowest species abundance of all sites. The orange-fronted parakeet (Aratinga canicularis), banded wren (Thryothorus pleurostictus), white-lored gnatcatcher (Polioptila albiloris), rufous-naped wren (Campylorhynchus rufinucha), and white-throated magpie-jay (Calocitta formosa) were the most abundant birds in the tropical dry forest, accounting for 38% of all individuals encountered. There were 29 species with 5 or fewer individuals recorded between all tropical dry forests. These rare species accounted for less than 4% of all individuals.

There was no significant difference between the latitudinal extents of birds recorded in large and small forest fragments (Table 28). The mean latitudinal extent of resident birds in Santa Rosa and Palo Verde was similar to the mean latitudinal extent of species in La Pacifica and Ometepe. Resident birds appeared to decrease proportionally for all latitudinal extent categories from larger to smaller fragments. However, the number of birds in the smallest (3°-10°) and largest (61°+) range categories remained relatively constant from larger to smaller fragments. There appears to be little difference in longitudinal extents of species distributed in each of the eight forest fragments (Table 28). There were a similar number of birds recorded in three biogeographic regions as in two biogeographic regions from larger

Table 27. Summary of species richness and abundance in eight fragments of tropical dry forest in Central America.

Sites	**Number of points**	**Resident species**	**Mean number of resident species per point**	**Number of individuals**
Cosiguina	30	35	5.6 ±1.4	245
La Pacifica	30	27	3.9 ±1.3	185
Palo Verde	30	37	4.3 ±0.9	177
Santa Rosa	30	46	6.5 ±1.6	360
Masaya	30	24	3.7 ±1.4	181
Ometepe	30	21	5.7 ±1.0	251
La Flor	30	23	4.9 ±0.8	139
Chacocente	30	37	4.7 ±1.6	238
Total	240	72		1776

Table 28. Biogeographic characteristics of resident birds by site.

Biogeographic characteristics	**Cos**	**S.R**	**P.V**	**Chac**	**Mas**	**L.P**	**L.F**	**Ome.**
Latitudinal extent								
3° - 10°	6	7	6	8	6	5	4	5
11° - 20°	15	14	12	14	6	8	8	7
21° - 30°	2	3	2	3	2	0	3	0
31° - 40°	0	2	2	0	0	1	0	0
41° - 50°	0	7	3	0	0	2	0	1
51° - 60°	6	6	6	5	4	5	3	2
61° +	4	7	6	7	6	6	5	6
Mean	28.8	34.7	34	30.9	34.9	36.8	34.3	35.1
Longitudinal extent								
Pacific	0	0	0	0	0	0	0	0
Pacific, Atlantic	2	3	2	1	0	1	1	1
Pacific, Central	21	20	17	21	13	15	14	10
Pac., Cen., Atl.	12	23	18	15	11	11	8	10

to smaller sites. Birds recorded in three regions and two regions both proportionally declined with decreasing area.

When the life history characteristics of species at all sites are compared, a number of patterns emerge between tropical dry forest fragments. Forest preference for birds recorded at different sites changed significantly from larger to smaller reserves (Table 29). The proportion of birds that required patchy forest declined from larger to smaller fragments. Approximately 75% of the birds at Santa Rosa and Palo Verde required patchy forest compared to approximately 56% of the birds at La Flor, La Pacifica, and Ometepe. This suggests that small fragments contain a lower proportion of birds that require patchy forest and, conversely, a greater number of birds that do not require forest. Proportion of guild by sites was remarkably constant, with the exception of the most speciose guilds: insectivores and omnivores (Table 29). Omnivores ($r_s = .7904$, $P = .02$) and insectivores ($r_s = .8743$, $P = .005$) both declined with decreasing reserve size. There was no significant decrease in other guild categories. Resident birds with intermediate body sizes, between 10.5 and 150 grams, appeared to decrease from larger to smaller tropical dry forest fragments (Table 29) whereas the number of small resident birds (3.7-10 grams) and large birds (151+ grams) remained constant between fragments of different size.

5.4 Correlates of Avian Diversity and Abundance

A Spearman's rank correlation was used to identify correlates of bird species richness and abundance at seven tropical dry forest sites. La Pacifica was excluded from this analysis since the site was actively being cut for timber, thus precluding the collection of floristic data. Three variables, including canopy cover within each

Table 29. Life history characteristics of resident birds by site.

Life history characteristics	Cos	S.R	P.V	Chac	Mas	L.P	L.F	Ome
Forest preference								
Non forest	11	10	8	12	8	10	13	8
Patchy forest	23	36	29	25	16	17	9	13
Solid forest	1	0	0	0	0	0	1	0
Guild								
Carnivores	1	2	3	2	2	3	3	2
Frugivores	5	6	3	5	2	3	2	3
Granivores	3	2	1	3	1	1	2	1
Insectivores	10	16	14	10	7	8	4	2
Nectarivores	3	2	2	6	3	2	5	3
Omnivores	13	18	14	11	9	10	7	10
Weight in grams								
3.7-10	4	5	5	8	4	4	6	5
10.5-25	5	10	7	6	4	3	3	2
26-75	12	13	12	8	6	10	4	4
76-150	5	7	5	4	3	3	2	2
151-250	5	3	2	3	3	2	2	4
251-500	3	5	3	4	2	2	2	2
500-1000	0	1	1	1	0	1	1	0
1000+	1	2	2	3	2	2	3	2

reserve, tree diversity, and number of trees higher than 20 meters, were significantly correlated with species richness (Table 30).

Species Richness

A simple measure of vegetation structure based on tree height was significantly correlated with bird species richness. The number of trees greater than 20 meters in a 0.1 hectare plot at each site was the most significant variable correlated with the number of resident bird species. It should be noted that the number of trees greater than 10 meters in a 0.1 hectare plot was also significantly correlated with species richness ($r_s = .8829$, $P<.008$). Over the last 20 years there has been a number of studies that examine the relationship of tropical rainforest structure and avian diversity. Initially, vegetation structure, which is generally measured using foliage height diversity, was used to explain patterns of avian diversity in both temperate and tropical locales (MacArthur and MacArthur 1961; Recher 1969). Recently, a number of studies have concluded that vegetation structure is not the best predictor of avian diversity in wet forests (Orians 1969; Karr and Roth 1971; Howell 1971; Stiles 1983; Terborgh 1985). However, vegetation structure may be of central importance in the tropical dry forest for a number of reasons. The relationship between vegetation structure and bird diversity is well documented in the northeastern forests of the United States, and it may be the case that a similar relationship occurs in tropical dry forests (MacArthur and MacArthur 1961; MacArthur et al. 1966). First, tropical dry forest structure is very similar to northeastern forests. Although tropical dry forests and eastern deciduous forests differ in species diversity, temperature, and precipitation regimes, both forests have approximately the same height, density, and tree architecture (Whittaker 1975).

Table 30. Spearman's rank correlations (*r*2) between environmental variables and species richness of resident tropical dry forest birds.

Variables	***r*2**
Reserve area	.6847
Canopy cover in reserve	.7748*
Precipitation	-.1982
Elevation	.3964
Disturbance	-.6091
Plant species richness	.6847
Tree diversity	.7568*
Number of trees > 10 cm dbh	.5818
Tree abundance	.0180
Number of tree > 20 m height	.8727**
Zoochoric tree abundance	.3784

* P < .05, ** P< .01, *** P <.001

Secondly, there may be a greater similarity in species guilds between tropical dry forest and eastern deciduous forest than between tropical dry forest and lowland rainforest. For instance, there are a number of wet forest guilds (ant-followers, small obligate frugivores, and dead leaf-gleaners) that are rare or absent from tropical dry forests. With the exception of the frugivore guild, the percentages of tropical dry forest birds in each guild on the east coast of the United States and Pacific side of Central America are relatively similar (Stiles 1983; Wiens 1989). Finally, many species in the eastern deciduous forest of the United States and tropical dry forests of Central America require only patchy forest to persist, not solid forest. As indicated in Table 26, there are only eight resident birds recorded in the tropical dry forest of Nicaragua that require solid forest, while there are 50 resident birds recorded in the Central and Atlantic region in Nicaragua that require solid forest (Gillespie 1998). Further research that calculates foliage height diversity and compares small stands of tall tropical dry forest trees with large stands of short tropical dry forest may test the importance of vegetation structure in predicting bird species richness.

The species-area relationship for fauna is one of the most extensively studied patterns in ecology (Preston 1962; MacArthur and Wilson 1967; Wiens 1989). The relationship between species richness and habitat area have been identified in a number of studies on the effects of forest fragmentation on avian communities (Diamond 1972; Willis 1979; Newark 1991; Christiansen and Pitter 1997). It is not surprising that this study has yielded similar results. It should be noted that reserve area is not the best predictor of species richness, because a number of reserves in Nicaragua and Costa Rica contain other ecosystems such as wetlands and successional shrub vegetation. The extent of canopy area is more strongly correlated with diversity of tropical dry forest birds than is reserve area (Table 30).

A significant correlation exists between tree species richness and bird species richness in tropical dry forest of Central America. There have been few studies of plant species diversity as it relates to avian species richness in the temperate or tropical regions. Holmes and Robinson found an important relationship between insectivorous birds and certain tree species in mixed hardwood forests of the east coast of the United States (Holmes and Robinson 1981; Robinson and Holmes 1984). Snow and Snow (1971) found that bird species diversity and floristic diversity was directly correlated in the tropical forests of Trinidad. Floristic diversity is rarely measured to explain avian species richness, especially in the tropics. This is primarily because vegetation structure and area are easier to measure, and probably better explains a majority of variability in predictions of species richness patterns (Wiens 1989). As previously mentioned, the increase in species richness from smaller to larger fragments of tropical dry forests is largely due to an increase in insectivores and omnivores, not frugivores. It may be the case that insect diversity and abundance are correlated with tree diversity (Erwin 1982). This is because a number of insects in the tropical dry forest have specific host plants (Janzen 1983). Thus tree diversity may result in higher insect diversity and abundance in tropical dry forest fragments. It should be noted that the abundance of zoochoric trees in tropical dry forests was not correlated with overall species richness. The abundance of food resources for frugivores and to a lesser extent certain omnivores does not appear to be a good predictor of species richness.

There are a number of variables not correlated with bird species richness that are of equal interest. There was no correlation between species richness and annual precipitation at different sites. Although a number of studies use precipitation as an indicator of ecosystem productivity, within tropical dry forest, there does not appear to be a significant relationship between precipitation and bird species richness (Rosenzweig and Abramsky 1993). This is most likely due to forest fragmentation, which probably overrides the importance of precipitation in predicting species richness.

There was no correlation between bird species richness and anthropogenic disturbance. Cosiguina and Masaya are significantly affected by anthropogenic disturbance, but the extensive canopy cover at the site still permits a diversity of bird species to persist. These findings provide a little food for thought in the over analyzed SLOSS debate (Patterson 1987; Shafer 1990; Simberloff and Martin 1991). It appears that several large reserves, regardless of disturbance, can maintain high levels of faunal diversity, while several small reserves, with low anthropogenic disturbance, can maintain high floristic diversity. In theory, a network of several small reserves should maintain adequate tropical dry forest plant diversity, while one or two large reserves should maintain bird diversity.

Species Abundance

When species abundances between tropical dry forest sites were compared, tree abundance was the only variable significantly correlated with bird species abundance (Table 31). La Flor and Masaya had a high number of tree individuals and a low bird abundance, while Ometepe and Santa Rosa had fewer tree individuals and a higher bird abundance. It is tempting to conclude that a number of bird

Table 31. Spearman's rank correlations (*r*2) between environmental variables and species abundance of resident tropical dry forest birds.

Variables	***r*2**
Reserve Area	-.0901
Canopy cover in reserve	.2342
Precipitation	-.2703
Elevation	.4505
Disturbance	-.0818
Plant species richness	.0180
Tree diversity	-.0901
Number of trees > 10 cm dbh	.6636
Tree abundance	-.7568*
Number of trees > 20 m height	.0364
Zoochoric tree abundance	-.0180

* P < .05, ** P< .01; *** P <.001

individuals may have been missed when undertaking point counts in reserves with a higher density of trees. Although this may be the case, it must be noted that there was no correlation between height or tree size, which generally make avian surveys more difficult (Remsen 1994).

There are two other patterns of species abundance in the tropical dry forest that warrant further discussion. The first is evidence for density compensation between fragments of different size. MacArthur et al. (1972) described evidence for density compensation on islands: 'The summed population density of individuals of all species on islands is equal to the summed mainland density as a result of niche expansions and higher abundances of island species compensating for the absence of many mainland species' (Mac Arthur et al. 1972; Wiens 1992). This phenomenon of density compensation has been noted on a number of islands (Mac Arthur et al. 1972) and habitat fragments (Cody 1983). Although there is little evidence for density compensation between forest fragments of different sizes on the mainland, there is evidence of density compensation on the island of Ometepe. Ometepe contained the smallest fragment with the lowest bird species richness; however, it had the second highest abundance of species after Santa Rosa. Although this study was undertaken over a relatively short time period, there does appear to be evidence that density compensation occurs on islands.

The second pattern that calls for additional discussion is the relationship between species abundance and distribution which has received much attention recently (Brown 1984; Hanski and Gyllenberg 1997). Latitudinal extent of birds and cumulative species abundance from all eight sites revealed that there was no correlation between range size and abundance (Pearson's $r = -.2112$, $P = .07$). The negative correlation actually suggests that species with smaller ranges are the most abundant. The six most abundant birds have latitudinal extents less than 15 degrees while only four of the 29 rare birds (represented by five or fewer individuals) have latitudinal extents less than 15 degrees. The relationship between distribution and abundance is often described as ubiquitous and has been well documented for North American birds (Bock and Ricklefs 1983; Bock 1984; Krebs 1994; Gotelli and Graves 1996). However, it does not seem to be the case for birds in the tropical dry forest of Central America. It may be that the distribution-abundance relationship is more pronounced in the temperate regions and may not occur in the tropics. High species diversity and smaller range size may cause the distribution-abundance relationship to reverse towards the tropics. This anomaly is due to the fact that there are more species with small ranges in the tropics (Stevens 1989). These species, with small ranges, do not necessarily have lower abundance than species with large ranges. Further research using different taxa may reveal a number of surprising results. Although latitudinal extent does not take into account species with disjunct ranges, it appears that for tropical dry forest birds there is no relationship between species abundance and latitudinal extent.

CHAPTER 6. LOCAL AND REGIONAL EXTINCTION OF FOREST BIRDS

6.1 Introduction

Studies on avian extinction in the tropics have been undertaken using two approaches (Kattan et al. 1994). The first compares bird diversity in forest fragments of different size (Willis 1979; Bierregaard and Lovejoy 1989; Newark 1991). This method identifies species that go locally extinct from larger to smaller fragments. The second approach compares historical data of birds recorded in a study area with recent surveys of birds (Willis 1974; Leck 1979; Kattan et al. 1994; Diamond et al. 1987; Stiles and Levey 1994). This method identifies species that have disappeared from the study site or region. This study employs both methods to identify variables correlated with local and regional extinction in the tropical dry forest of Central America.

In order to assess local extinction between tropical dry forests fragments, only birds encountered during point counts that require patchy or solid forest are used. Non-forest birds are excluded. In order to assess regional extinction, forest birds are divided into two major groups: forest birds found and forest birds not found. Forest birds found include all species encountered during 240 point counts in eight fragments of tropical dry forest. Forest birds not found include all forest birds (excluding nocturnal species) historically recorded as permanent residents in the tropical dry forest of Nicaragua and Costa Rica but not encountered during point counts.

This analysis of tropical dry forest birds has two primary objectives: 1) to identify biogeographic and life history characteristics associated with local extinction based on forest bird incidence in eight tropical dry forest fragments, and 2) to identify similarities and differences between biogeographic and life history characteristics of forest birds found and forest birds not found. In particular, I examine if biogeographic characteristics (small range size, distance to edge of range) and life history characteristics (body mass, guild) are associated with local and regional extinction.

A Spearman's rank correlation identified biogeographic and life history characteristics associated with forest bird incidence in eight fragments of tropical dry forest. A two-tailed Mann-Whitney *U*-test and chi-square test were used to examine similarities and differences between the latitudinal extent, distance to edge of range, body mass, and guild for forest birds found and forest birds not found.

6.2 Results

Local Extinction

There were 51 resident forest birds recorded during point counts at eight tropical dry forest sites. Twenty-one birds encountered during point counts were excluded from this analysis because they required non-forest habitats and are most likely not threatened with extinction due to tropical dry forest fragmentation. A Spearman's rank correlation identified biogeographic and life history variables associated with forest bird incidence in eight fragments of tropical dry forest (Table 32). Three of the thirteen variables tested were significantly correlated with species incidence. Species cumulative abundance from all sites was strongly correlated with bird incidence. The carnivore guild and longitudinal extent were both negatively

Table 32. Spearman's rank correlations (*rs*) between forest bird incidence in eight fragments of tropical dry forest and biogeographic and life history characteristics.

Variables	*rs*
Latitudinal extent	-.2135
Degrees to edge of Northern range	-.0473
Degrees to edge of Southern range	-.1772
Longitudinal extent	-.2880*
Body mass	-.1297
Abundance	.8193***
Forest preference	.2465
Carnivores	-.3051*
Omnivores	-.0827
Insectivores	-.0687
Frugivores	.0397
Granivores	.1338
Nectarivores	.1424

*P<.05, **P<.01, ***P<.001

correlated with bird incidence. There was no significant correlation between species incidence and latitudinal extent, distance to edge of range, body mass, forest preference, or other guild categories.

Regional Extinction

There were 40 forest birds not found during point counts but recorded as permanent breeding residents in the tropical dry forest in Nicaragua and Costa Rica (Howell 1983; Stiles 1983; Gillespie and Nicholson 1997). These 40 birds occur at low densities and are intuitively vulnerable to extinction in the tropical dry forest region of Central America. This is based on the assumption that these 40 birds once occurred throughout the tropical dry forest region and should have had an equal probability of being recorded during point counts at all tropical dry forest sites.

Biogeographic variables for forest birds found and not found are displayed in Table 33. There was no difference between the latitudinal extent of forest birds found and not found (Mann-Whitney U, $p = 0.13$). There was no difference between the distance to the edge of a species' northern range (Mann-Whitney U, $p = .95$) or the distance to the edge of a species' southern range (Mann-Whitney U, $p = .09$) for forest birds found and not found. There was only one forest bird restricted to the Pacific biogeographic region. Approximately 76% of forest birds recorded in only two biogeographic regions were found while only 43% of the forest birds recorded in all three biogeographic regions were found.

Life history variables on weight, forest preference, and guild for forest birds found and not found are summarized in Table 34. Only 25% of forest birds that require solid forest were found while 60% of the forest birds that require patchy

Table 33. Biogeographic characteristics of forest birds found and not found in tropical dry forest.

Biogeographic variables	Birds found	Birds not found
Latitudinal extent in degrees		
3° - 10°	8	5
11° - 20°	19	8
21° - 30°	4	4
31° - 40°	3	2
41° - 50°	6	9
51° - 60°	8	10
61° +	3	2
Degrees to edge of northern range		
0° - 4°	5	3
5° - 9°	13	13
10° - 14°	17	14
15° - 20°	16	5
20° +	0	5
Degrees to edge of southern range		
0° - 4°	24	14
5° - 9°	5	1
10° - 14°	0	2
15° - 20°	2	1
20° +	20	22
Biogeographic region		
1 Region	0	1
2 Region	31	13
3 Region	20	26

Table 34. Life history characteristics of forest birds found and not found.

Life history variables	Birds found	Birds not found
Forest preference		
Solid forest	2	6
Patchy forest	49	34
Weight in grams		
3.7-10	9	6
10.5-25	10	5
26-75	13	6
76-150	6	2
151-250	4	3
251-500	5	6
500-1000	4	9
1000+	0	3
Guild		
Carnivores	3	9
Frugivores	7	9
Granivores	2	0
Insectivores	18	11
Nectarivores	4	1
Omnivores	17	10

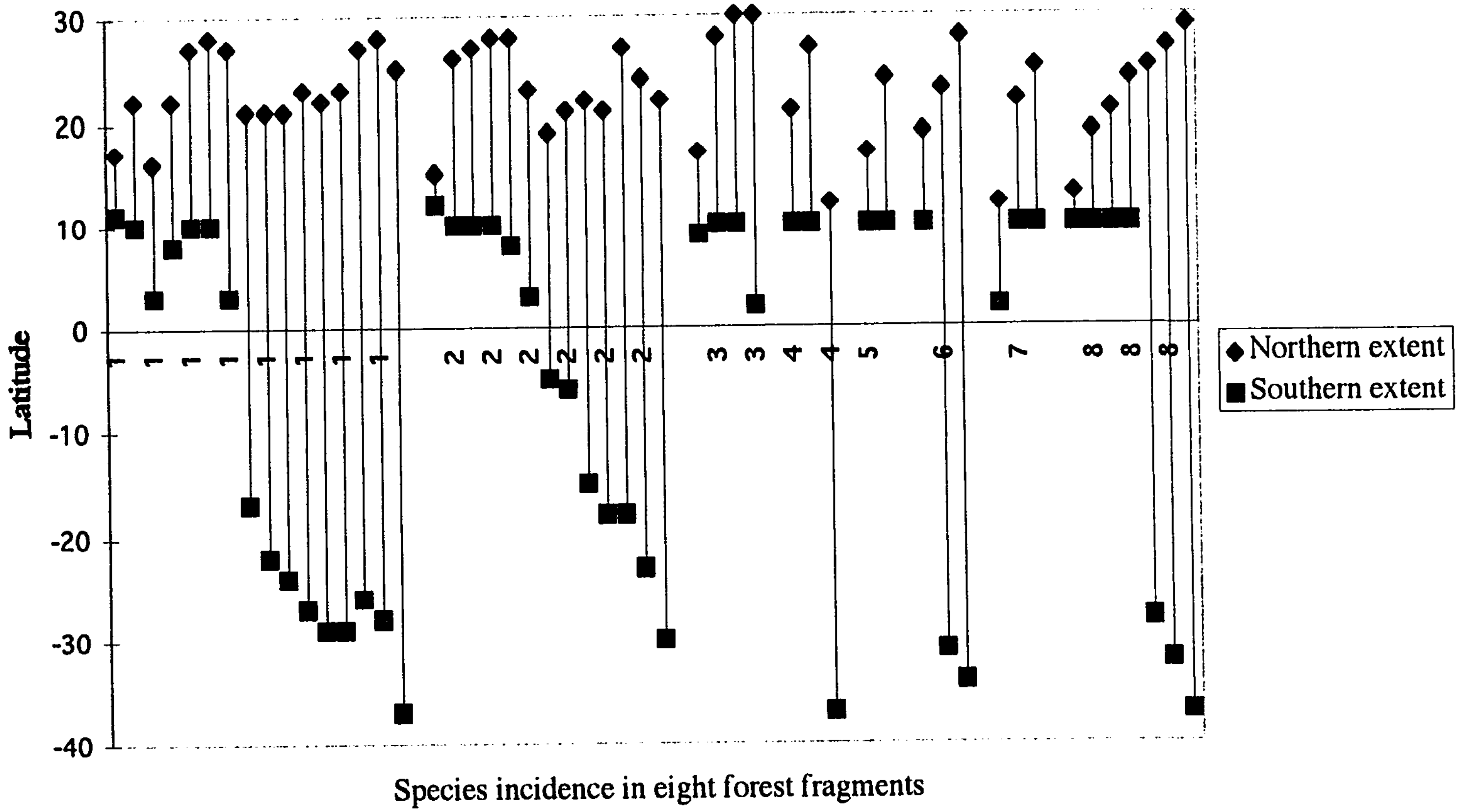
forest were found. Forest birds not found during point counts as a group had greater body masses than forest birds found in tropical dry forest (Mann-Whitney U, p = 0.01). Some guilds were more susceptible to extinction than others. The difference between the observed and expected distribution for guild was significant ($x^2 = 19.81$, df = 4, P <.001) which suggests that some guilds are more susceptible to extinction than others. The carnivores (p = 0.01), frugivores (p = 0.05), and insectivores (p = 0.05) all had significantly lower observed than expected values.

6.3 Discussion

Latitudinal Extent

A number of authors have cited small geographic range as an important variable in predicting extinction prone species (Faaborg 1979; Brown 1995). Birds endemic to islands have restricted geographic ranges, and extinction of island endemics has been well documented (Olson 1989; Olson and James 1991; Paulay 1994). Other studies of endangered birds have found that many birds with small historical ranges on the mainland are vulnerable to extinction (Collar et al. 1992; Stotz et al. 1996). However, small latitudinal extent is not a good predictor of local or regional extinction for tropical dry forest birds. In fact, forest birds with large latitudinal extents appear more vulnerable to both local and regional extinction than species with small latitudinal extents. Latitudinal extent of birds based on species incidence in eight forest fragments revealed that species with large ranges were less common than species with smaller ranges (Figure 8). Sixteen of the 29 forest birds (55%) recorded in two sites or less have large breeding ranges, extending far south of the equator. This can be compared to the fact that only six of the 22 birds (27%)

Figure 8. Latitudinal extent of forest birds encountered during point counts by species incidence in eight fragments.



recorded in three sites or more have breeding ranges south of the equator. A similar pattern also held true for regional extinction. As a group, most forest birds not found had larger latitudinal extents (mean 36.4 degrees ± 21.5) than forest birds encountered during point counts (mean 28.7 ± 19.0). Thus, there is little evidence that latitudinal extent is a good predictor of extinction for tropical dry forest birds.

Latitudinal extent may be a useful tool for identifying Central American endemics which may be important to regional conservation. There were ten forest birds with a latitudinal extent of less than ten degrees (Table 35). Although most are relatively abundant to locally common, five of these species, the green parakeet (*Aratinga holochlora*), blue-tailed hummingbird (*Amazilia cyanura*), white-bellied chachalaca (*Ortalis leucogastra*), Pacific parakeet (*Aratinga strenua*), and spotted-breasted oriole (*Icterus pectoralis*), can be considered uncommon or rare based on observed and published data on species abundance (Stiles 1983; Howell 1983). However, there is only a general consensus on the taxonomy of *Icterus pectoralis* while there is no conclusive evidence that the other birds are actually distinct species (i.e. *Aratinga holochlora* may be *A. rubritoques* or *A. strenua*, *Amazilia cyanura* may be *A. saucerrottei*, and *Ortalis leucogastra* may be *O. vetula* (Stiles and Skutch 1989; Howell and Webb 1995; Stotz et al. 1996). If these species were clumped they would have significantly larger ranges, which would further undermine the use of latitudinal extent for identifying extinction prone birds in Central America. Further taxonomic, ecological, and biogeographic research would illuminate the relevance of range to extinction processes.

Table 35. Forest birds with latitudinal extent less than 10 degrees.

Scientific Name	**Abundance**	**Latitudinal extent**
Melanerpes hoffmannii	Abundant	3
Aratinga holochlora	Rare	3
Amazilia cyanura	Uncommon	3
Ortalis leucogastra	Rare	4
Aratinga strenua	Uncommon	6
Amazona auropalliata	Common	7
Icterus pectoralis	Rare	8
Chiroxiphia linearis	Locally common	8
Campylorhynchus rufinucha	Abundant	9
Thryothorus pleurostictus	Abundant	9

Distance to Edge of Range

Kattan (1994) found that species at the edge of their geographic ranges and altitudinal distributions were particularly vulnerable to extinction in cloud forest in the Andes. This is based on the fact that species at the edge of their range may be at their physiological or ecological limits (Wiens 1989; Kattan 1994). Many species exhibit this type of range pattern, in which a species' abundance gradually declines from the center to the boundaries of its range (Brown 1984). The distance to the edge of a species' breeding range was not a good predictor of either local or regional extinction. There was no correlation between species incidence and distance to the edge of their ranges. This was also the case for forest birds found and not found. Most forest birds found and not found had a similar distance to the northern edge of their breeding range. However, a majority of the forest birds not found had greater distance to the southern end of their ranges. There is little evidence that distance to the edge of range is an important macroecological variable for predicting extinction prone birds in tropical dry forests of Central America. This may be due to the fact that the largest, best preserved forest fragments are in the south of the study area. The Santa Rosa and Palo Verde sites are located at the southern end of Central America's continuous tropical dry forest habitat. This may be the reason species with their southernmost range limits at 10 degrees did not go locally or regionally extinct. This study does not take into account extinction of species at their altitudinal limits, because tropical dry forests are restricted to areas below 400 meters. It may be the case that edge of a species' altitudinal range is a better predictor of extinction than the edge of its geographic range.

Longitudinal extent

Restricted longitudinal extent was not a good predictor of local or regional extinction in the tropical dry forest region. This is mainly due to the fact that there was only one forest bird, the white-bellied chachalaca (Ortalis leucogastra), restricted to the Pacific region. This is not a large enough sample size to test the important of longitudinal extent. Nevertheless, it appears that forest birds with greater longitudinal extents are more vulnerable to both local and regional extinction. Forest birds recorded in two biogeographic regions had a higher incidence in fragments of tropical dry forest than species recorded in all three biogeographic regions. This is because many forest birds that occur in all three biogeographic regions do not have a preference for tropical dry forest. Most of the forest birds recorded in all three biogeographic regions generally occur at higher densities in moist or wet forests and have only small populations in fragments of tropical dry forest (Stiles 1983; Stiles and Skutch 1989). For instance, five species recorded at only one site, the rose-throated becard (Pachyramphus aglaiae), Montezuma oropendola (Psarocolius montezuma), violoaceous trogon (Trogon violaceus), barred antshrike (Thamnophilus doliatus), and tropical parula (Parula pitiayumi), occur in all three biogeographic regions and generally prefer wet forest or evergreen gallery forest (Howell 1983; Stiles and Skutch 1989).

A similar pattern was observed when comparing forest birds found and forest birds not found. Species recorded in three biogeographic regions appear rarer than species recorded in only two biogeographic regions. There are two possible explanations for why forest birds with greater longitudinal extent appear more extinction prone. First, as previously mentioned, the longitudinal extent classification system does not account for forest bird abundance in different forest types. For instance, the bright-rumped attila (Attila spadiceus), lesser greenlet (Hylophilus decurtatus), common tody-flycatcher (Todirostrum cinereum), long-billed gnatwren (Ramphocaenus melanurus), collared aracari (Pteroglossus torquatus), keel-billed toucan (Ramphastos sulfuratus), and plain xenops (Xenops minutus) are common to abundant in moist and wet forests; however, they only maintain small populations in tropical dry forest. In essence, a number of moist forest birds "spill over" into tropical dry forests (Cody 1993). Second, forest birds not found, such as the 11 Accipitridae species, have large territories or home ranges (Appendix 7). These species are rare wherever they occur and have been recorded in tropical dry forests at low densities (Stiles 1983, Thiollay 1989). In conclusion, since there are few birds restricted to the tropical dry forest region, longitudinal extent is not a useful macroecological variable for identifying extinction prone birds. However, it does identify which forest birds will be rare in tropical dry forest fragments of Central America because they prefer moister forest.

Abundance

Species abundance is often cited as the single most important variable in predicting extinction prone birds (Diamond 1984; Pimm et al. 1991; Warburton 1997). The results from this study also found that natural abundance is the best predictor of species incidence in tropical dry forest. Most forest birds recorded in one or two fragments had less than ten individuals. The inverse was true for species recorded in five or more sites. No forest birds recorded in five or more sites had a cumulative abundance less than 15 individuals (mean 69 ± 50). This pattern may also hold true for regional extinction, given that forest birds not found occur at low densities in tropical dry forest. This underscores the importance of field surveys on the distribution of avian abundance for identifying extinction prone birds. It also emphasizes the limitations of undertaking point counts for studies of extinction. Ten minute counts were undertaken at different points or stations in all forest fragments. To ensure that individuals were not counted twice, no censuses were undertaken at the same point and all points were 100 meters apart. Only 30 points could be undertaken in small forest fragments, because any more point counts would have been made in an area already censused. In the large reserves, over 100 point counts could have been undertaken without censusing the same area twice. However, comparison of data from small to large fragments would be biased if more intensive surveys were conducted in larger fragments. I believe that simply recording species presence/absence and relative abundance in fragments for a designated time period (i.e. 30 hours for each site) is a more appropriate method than point counts when studying avian extinction (Beehler et al. 1995). Although recording species incidence as such does not provide abundance data as accurate as that from point counts, it would likely provide a more accurate overall account of avian communities in different forest fragments.

Body mass

Weight is often cited as one of the most important variables in predicting extinction prone birds (Leck 1979; Karr 1990; Gaston and Blackburn 1995; Brown 1995). However, body mass was not a significant variable in identifying local extinction based on species incidence. It may be the case that larger birds in tropical dry forest are more mobile than smaller birds, thus they have a higher probability of being found in isolated forest fragments. Body mass was a significant variable in identifying forest birds vulnerable to regional extinction based on forest birds not found. Forest birds not recorded during point counts had a larger body mass (mean 475 ± 843) than forest birds found in tropical dry forest (mean 127± 188). This is primarily because weight can be correlated with r and K selection. In general, large-bodied birds in Nicaragua and Costa Rica have low population densities, low reproductive rates, and require large territories. Weight is also an important surrogate variable for identifying vulnerable birds based on the impacts of hunting, which may cause local extinction faster than any other biological process (Thiollay 1984; Redford 1992). Large birds, such as guans, tinamous, and quail, are relentlessly hunted in Nicaragua. Furthermore, most birds with high body weights are birds of prey which are shot on site in Nicaragua, because rural Nicaraguans believe they eat domestic animals (Martinez-Sanchez 1986). Thus it would appear that body mass is one of the best predictors of extinction prone species at a regional scale.

Guild

General diet and associated guild are often cited to identify extinction prone species (Willis 1979; Leck 1979; Terborgh and Winter 1980; Estrada et al. 1993; Kattan et al. 1994). However, there is no consensus as to which guild is the most vulnerable to extinction. Raptors and large frugivores have been identified as extinction prone in a number of studies (Leck 1979; Willis 1979; Brash 1987; and Kattan et al. 1994), while other authors have noted a significant loss of understory insectivores (Bierregaard and Lovejoy 1989; Christiansen and Pitter 1997; Canaday 1997). Turner (1996) noted when examining extinction prone guilds from different sites in the Neotropics that no clear trend emerges, because the studies cover forests over a wide range of spatial scales. There was no significant positive correlation between guild and species incidence in tropical dry forest fragments, only a negative correlation for the carnivore guild. The decline of omnivores (r_s = .7904, P = .02), insectivores (r_s = .8743, P = .005), and frugivores (r_s = .6795, P = .06) with decreasing reserve size was noted in chapter five. However, when only forest birds were examined, none of these guilds were significantly correlated with species incidence.

The vulnerability of carnivores, frugivores, and insectivores was noted at a regional scale. The carnivores, frugivores, and insectivores all had significantly lower observed than expected values based on the chi-square test. Approximately 75% of forest carnivores were not encountered during point counts. This can be compared to 56% of frugivores, 38% of insectivores, and 37% of omnivores not found during point counts. Although there can be little question that the carnivores are the most vulnerable guild, there are a number of reasons why guild is a nebulous predictor of extinction prone species. First, due to the generalist nature of tropical dry forest birds, there are few species that have evolved unique dietary requirements or behavioral adaptations as have forest birds in wetter tropical forests. For instance, guilds such as ant-followers, terrestrial insectivores, and dead-leaf gleaners are all but absent in tropical dry forest. Second, with a few exceptions, the classification of guild is relatively subjective. No two studies on avian extinction use the same guild classification system (Willis 1974; Karr 1982; Estrada et al. 1993; Kattan et al. 1994). Most studies that found guild an important predictor of extinction use classifications such as "large frugivores" or "understory insectivores". These terms combine other variables such as body weight and forest preference that are important in predicting extinction prone birds. Third, the census methods used in different studies can significantly affect which guilds appear more susceptible to extinction. Raptors and frugivores appear more extinction prone in studies that compare historical records of birds at a site with recent surveys based on observations of birds over a large area (Leck 1979; Willis 1979; Brash 1987; Kattan et al. 1994). The loss of insectivores is generally cited in studies that use mist nets in small forest fragments smaller than 50 hectares (Bierregaard and Lovejoy 1989; Christiansen and Pitter 1997; Canaday 1997). This aside, there can be no doubt that carnivores are the most vulnerable guild in tropical dry forest, followed by frugivores and insectivores.

Forest preference

A number of authors have noted that forest preference is an important predictor of extinction. Birds that are unable to persist in the landscape surrounding a forest fragment are generally the most vulnerable to extinction (Diamond et al. 1987; Estrada et al. 1997). Approximately 75% of all birds that require solid forest were not encountered during point counts. This can be compared with the fact that only 40% of all birds that require only patchy forest were not encountered. Although there are few birds in tropical dry forest that require solid forest, it does appear that forest preference is important in predicting the most extinction prone species. The eight species that require solid forest, the short-tailed hawk (*Buteo brachyurus*), great black-hawk (*Buteogallus urubitinga*), hook-billed kite (*Chondrohierax uncinatus*), crane hawk (*Geranospiza caerulescens*), double-toothed kite (*Harpagus bidentatus*), gray-headed kite (*Leptodon cayanensis*), great curassow (*Crax rubra*), and stub-tailed spadebill (*Platyrinchus cancrominus*), are extremely rare in tropical dry forest in Central America. More importantly, the forest preference category excludes birds that are not "core" members of forest communities, which should not be included when examining the effects of forest fragmentation on resident birds. These non-forest birds generally thrive in anthropogenic landscapes and are only represented in surveys of forested areas by wandering or dispersing individuals (Remsen 1994). A further subdivision of forest preference based on empirical studies would probably greatly improve the predictive value of using forest preference to identify extinction prone species.

6.4 Conclusions

Results from this study suggest that macroecological variables correlated with extinction prone species differ depending on spatial scale (Table 36). Latitudinal extent and distance to edge of range are poor predictors of both local and regional extinction in tropical dry forest of Central America. However, longitudinal extent identifies forest birds that will be rare in tropical dry forest, but not necessarily the most vulnerable to extinction in Central America. This is because most species recorded in three biogeographic regions maintain healthy populations in wetter forest types. Forest preference is an important category because it identifies forest birds and non-forest birds. More importantly, forest preference identifies birds that require solid forest which are extremely vulnerable to extinction in the tropical dry forest region of Nicaragua and Costa Rica, and possibly Central America. Body mass is an important predictor of regional extinction because most large forest birds occur at low densities where ever they occur. The carnivore guild is the most extinction prone guild in the tropical dry forest region of Central America, followed by frugivores and insectivores. Abundance is intuitively the most important predictor of extinction prone species. Extensive surveys of forest fragments are clearly the best way to

Table 36. Summary of macroecological variables and local and regional extinction. (Ns = not significant, Yes = significant)

Variables	**Local Extinction**	**Regional Extinction**
Small latitudinal extent	Ns	Ns
Degrees to edge of Northern range	Ns	Ns
Degrees to edge of Southern range	Ns	Ns
Longitudinal extent	Yes	Yes
Body mass	Ns	Yes
Abundance	Yes	Yes
Forest preference	Ns	Yes
Carnivores	Ns	Yes
Omnivores	Ns	Ns
Insectivores	Ns	Yes
Frugivores	Ns	Yes
Granivores	Ns	Ns
Nectarivores	Ns	Ns

identify extinction prone species compared to using a single macroecological variable.

CHAPTER 7. SUMMARY

The objectives of this dissertation were to obtain data on plant and avian communities in remaining fragments of tropical dry forests of Central America. In particular, I identified biotic and abiotic variables correlated with plant and avian species richness and selective extinction.

Plants

Although floristic diversity changed significantly between sites, family richness and abundance was predicable in different patches of tropical dry forest. Results from this research support Gentry's hypothesis that Fabaceae is always the most speciose family in Neotropical areas with a strong dry season (Gentry 1986, Gentry 1996). However, it rejects Gentry's hypothesis that Bignoniaceae is always the most speciose liana family in Neotropical areas with a strong dry season. Bignoniaceae was the dominant overall liana family in species richness at five sites. Bursera simaruba was encountered in all plots at each site. However, Bursera simaruba was not always the dominant species by frequency at all sites. These finding support Gentry's hypothesis that species dominance is never predictable in different tropical dry forests and most likely determined by stochastic processes (Gentry 1986, Hubbell 1979).

Anthropogenic disturbance was significantly correlated with total species richness, tree species richness, and liana abundance. There was a significant correlation between reserve size, tropical dry forest cover within each reserve, precipitation and plant species richness. These results suggest that a qualitative assessment of anthropogenic disturbances such as the intensity and frequency of fire, grazing, and wood collection is a better predictor of woody plant richness than reserve size, forest cover, or precipitation.

Structurally, remaining fragments of tropical dry forest in Central America have a significantly lower of number of total individuals, tree individuals, tree and lianas > 10 cm dbh, and basal area than other Neotropical dry forests. Differences in density can most likely be explain by the current disturbance regime and extensive fragmentation of tropical dry forests in Central America. Floristic diversity in Central American dry forests is still relatively high compared to a number of Neotropical forests. Family richness, total plant species richness, liana richness, and tree richness are similar to other Neotropical forests. However, tropical dry forests in Northern South America and Mexico contain a higher species richness.

Dioecious species richness and percentages of total species encountered at each site were significantly correlated with both reserves size and forest cover. There was no correlation between dioecious species richness, abundance, percentage, and precipitation or disturbance. Zoochoric species richness was significantly correlated with forest cover. Zoochoric richness and percentage of zoochoric species were not significantly correlated with reserve size, precipitation, or disturbance. Mammal dispersed richness was correlated with forest cover while mammal dispersed abundance was correlated with reserve size. These results support Meave and Kellman hypothesis that dioecious and mammal dispersed plants are rare in successively smaller habitat fragments.

Birds

A simple measure of vegetation structure based on tree height was significantly correlated with bird species richness. The number of trees greater than 20 meters in a 0.1 hectare plot at each site was the most significant variable correlated with the number of resident bird species. The relationship between species richness and habitat area have been identified in a number of studies on the effects of forest fragmentation on avian communities (Diamond 1972; Willis 1979; Newark 1991; Christiansen and Pitter 1997). It is not surprising that this study has yielded similar results. However, the extent of canopy area is more strongly correlated with diversity of tropical dry forest birds than is reserve area. A significant correlation exists between tree species richness and bird species richness in tropical dry forest of Central America. There was no correlation between species richness and annual precipitation at different sites and anthropogenic disturbance.

Results from this study suggest that macroecological variables correlated with extinction prone species differ depending on spatial scale. Latitudinal extent and distance to edge of range are poor predictors of both local and regional extinction in tropical dry forest of Central America. However, longitudinal extent identifies forest birds that will be rare in tropical dry forest, but not necessarily the most vulnerable to extinction in Central America. This is because most species recorded in three biogeographic regions maintain healthy populations in wetter forest types. Forest preference is an important category because it identifies forest birds and non-forest birds. More importantly, forest preference identifies birds that require solid forest which are extremely vulnerable to extinction in the tropical dry forest region of Nicaragua and Costa Rica, and possibly Central America. Body mass is an important predictor of regional extinction because most large forest birds occur at low densities where ever they occur. The carnivore guild is the most extinction prone guild in the tropical dry forest region of Central America, followed by frugivores and insectivores. Abundance is intuitively the most important predictor of extinction prone species. Extensive surveys of forest fragments are clearly the best way to identify extinction prone species compared to using a single macroecological variable.

Appendix 1. Family and scientific name of plants encountered in tropical dry forest

Family	Scientific Name
Acanthaceae	Acanthaceae sp. (G1264)
	Acanthaceae sp. (G1183)
	Aphelandra deppeana Schl.& Cham.
	Aphelandra scabra (Vahl) Sm.
Agavaceae	Agave angustifolia Haw.
Anacardiaceae	Astronium graveolens Jacq.
	Spondias mombin L.
	Spondias purpurea L.
	Spondias radlkoferi Donn.
Annonaceae	Annona purpurea Moc. & Sesse
	Annona reticulata L.
	Sapranthus palanga R.E.Fr.
Apocynaceae	Forsteronia spicata (Jacq.) G. Mey
	Plumeria rubra L.
	Prestonia mexicana A. DC.
	Stemmadenia obovata (Hook & Arn.) K. Schum.
	Thevetia ovata (Cav.) A. DC.
	Apocynaceae 1
Araliaceae	Sciadodendron excelsum Griseb.
Arecaceae	Bactris guineensis (L.) H.E. Moore
Aristolochiaceae	Aristolochia anguicida Jacq.
Asteraceae	Ageratina crassiramea (B.L. Rob.) R. King & Rob.
	Eupatorium albicaule Sch. Bip. ex Klatt
	Mikania houstoniana (L.) B.L.Robinson
	Helianthinae (G1263)
Bignoniaceae	Adenocalymma inundatum Mart. ex Meisn
	Amphilophium paniculatum (L.) HBK.
	Arrabidaea cf chica (H. & B.) Verl.
	Arrabidaea mollissima (HBK.) Bur. & K. Schum.
	Arrabidaea patellifera (Schlecht.) Sandw.
	Callichlamys latifolia (L. Rich.) K. Schum.
	Ceratophytum tetragonolobum (Jacq.) Spr.& Sandw.
	Cydista diversifolia (HBK.) Miers
	Cydista heterophylla Seib.
	Macfadyena unguis-cati (L.) A. Gentry
	Mansoa hymenaea (DC.) Gentry
	Melloa quadrivalvis (Jacq.) A. Gentry
	Pithecoctenium crucigerum (L.) A. Gentry

	Tabebuia ochracea (Cham.) Standl.
	Tabebuia impetiginosa (Martius ex De Candolle) Standl.
	Tabebuia rosea (Vertol.) DC.
	Tecoma stans (L.) Juss.
	Xylophragma seemannianum (O. Ktze.) Sandw.
	Bignoniaceae 1
	Bignoniaceae 2
	Bignoniaceae 3
	Bignoniaceae 4
Bixaceae	*Bixa orellana L.*
Bombaceae	*Bombacopsis quinata* (Jacq.) Dugand
	Pseudobombax septenatum (Jacq.) Dugand
Boraginaceae	*Cordia alliodora* (Ruiz & Pau) Oken
	Cordia bullata (L.)Roem. & Schult.
	Cordia collococca L.
	Cordia guanacastensis Standl.
	Cordia panamensis Riley
	Tournefortia hirsutissima L.
Burseraceae	*Bursera graveolens* (HBK.) Triana & Planch.
	Bursera simaruba (L.) Sarg.
Cactaceae	*Lemaireocereus aragonii* (Weber) Britt. & Rose
	Acanthocereus pentagonus (L.) Britton & J. Rose
Capparidaceae	*Capparis flexuosa* (L.) L.
	Capparis indica (L.) Druce
	Capparis pachaca ssp. *oxysepala* (C.Wright ex Radlk)?
Cecropiaceae	*Cecropia peltata* L.
Chrysobalanaceae	*Hirtella racemosa* var. *hexandra* (Willd. ex Roem & Schult.) Prance
	Licania arborea Seem.
Cochlospermaceae	*Cochlospermum vitifolium* (Willd.) Spreng
Combretaceae	*Combretum farinosum* HBK.
Connaraceae	*Rourea glabra* HBK.
Dilleniaceae	*Tetracera volubilis* L.
Ebenaceae	*Diospyros nicaraguensis* Standl.
Erythroxylaceae	*Erythroxylon havanense* Jacq.
Euphorbiaceae	*Bernardia nicaraguensis* Standl.& L.O. Williams
	Croton niveus Jacq.
	Euphorbia schlechtendalii Boiss.
	Garcia nutans Vahl in Rohr
	Gymnanthes lucida Sw.
	Hura crepitans L.
	Jatropha curcas L.
	Margaritaria nobilis L.
	Euphorbiaceae sp. (G954)
Fabaceae	*Fabaceae* (G1279)

	Fabaceae sp.
Caesalpinioideae	Bauhinia glabra Jacq.
	Caesalpinia cf coriaria (G1173)
	Caesalpinia eriostachys Benth.
	Senna atomaria (L.) H.S. Irwin & Barney
	Caesalpinioideae sp. (G1198)
Papilionoideae	Acosmium panamense (Benth.) Yakoul.
	Ateleia herbert-smithii Pittier
	Dalbergia glabra (Millsp.) St.
	Diphysa robinioides Benth.
	Erythrina berteroana Urban.
	Gliricidia sepium (Jacq.) Walp.
	Lonchocarpus costaricensis Pittier
	Lonchocarpus minimiflorus Donn. smith
	Lonchocarpus phaseolifolius Benth.
	Lonchocarpus phlebophyllus Standl.& Steyerm.
	Machaerium biovulatum Micheli
	Machaerium kegelii Meisner
	Myrospermum frutescens Jacq.
	Pterocarpus rohrii Vahl.
Mimosoideae	Acacia collinsii Saff.
	Acacia cornigera L.
	Acacia farnesiana (L.) Willd.
	Albizzia/Lysiloma sp.
	Albizzia caribaea (Urban) Britt. and Rose
	Entada polystachya (L.) DC.
	Enterolobium cyclocarpum (Jacq.) Griseb.
	Lysiloma sp.
	Lysiloma divaricatum (Jacq.) J.F. Macbr.
	Pithecellobium dulce (Roxb.) Benth.
	Pithecellobium saman (Jacq.) Benth.
Flacourtiaceae	Casearia corymbosa HBK.
	Casearia praecox Griseb.
	Casearia sylvestris Sw.
	Casearia tremula (Griseb.) Wright
	Prockia crucis P. Br. ex L.
	Flacourtiaceae (G1237)
Hernandiaceae	Gyrocarpus americanus Jacq.
Hippocrateaceae	Hemiangium excelsum (HBK.) A. C. Smith
	Hippocratea cf volubilis L.
Lauraceae	Ocotea veraguensis (Meisn.) Mez
Marcgraviaceae	Souroubea sp. (G1234)
Malpighiaceae	Banisteriopsis muricata (Cav.) Cuatr.
	Bunchosia cf cornifolia H.B.K.

	Byrsonima crassifolia (L.) HBK.
	Hiraea reclinata Jacq.
	Stigmaphyllon lindenianum Juss.
	Stigmaphyllon sp. (G1397)
Malvaceae	*Malvaviscus arboreus* Cav.
Meliaceae	*Cedrela odorata* L.
	Swietenia macrophylla G. King
	Trichilia americana (Sessé & Mociño) Penn.
Moraceae	*Brosimum alicastrum* Sw.
	Castilla elastica Sesse in Cen.
	Chlorophora tinctoria (L.) Gaud.
	Ficus sp.
	Ficus ovalis (Liebm.) Miq.
Nyctaginaceae	*Pisonia macranthocarpa* Donn. Smith
	Pisonia aculeata L.
	Neea fagifolia Heimerl.
Ochnaceae	*Ouratea lucens* (Kunth) Engl.
Olacaceae	*Schoepfia schreberi* J. F. Gmelin
	Ximenia americana L.
Opiliaceae	*Agonandra macrocarpa* L. O. Wms.
Phytolaccaceae	*Stegnosperma cubense* A. Rich.
Polygalaceae	*Securidaca sylvestris* (Schl.)
Polygonaceae	*Coccoloba floribunda* (Benth) Linden.
	Triplaris melaenodendron (Bertol.) Standl. & Steyerm.
Rhamnaceae	*Karwinskia calderoni* Standl.
	Zizyphus guatemalensis Hemsl.
Rubiaceae	*Alibertia edulis* A. Rich.
	Calycophyllum candidissimum (Vahl.) DC.
	Chomelia spinosa Jacq.
	Exostema mexicanum A. Gray
	Genipa americana L.
	Guettarda macrosperma D. Sm.
	Hamelia patens Jacq.
	Psychotria pubescens Sw.
	Randia monantha Benth.
	Randia sp. (G1438)
	Rubiaceae sp.
Rutaceae	*Esenbeckia berlandieri* ssp. *litoralis* (J.D. Sm.) Kaastra
	Zanthoxylum monophyllum (Lam.) P.Wils.
	Zanthoxylum setulosum P. Wilson
Sapindaceae	*Allophyllus occidentalis* (Sw.) Radlk.
	Paullinia cururu L.
	Serjania atrolineata Sauv. & Wr.
	Serjania grosii Schl.

	Serjania lobulata Standl.& Steyerm.
	Serjania schiedeana Schlecht.
	Serjania (G1050)
	Serjania 1
	Serjania 2
	Thouinidium decandrum (Humb. and Bonpl.) Radlk.
	Sapindaceae sp. (G1263)
Sapotaceae	Manilkara zapota (L.) P. Royen
	Sideroxylon capiri (A. DC.) Pittier
Simaroubaceae	Alvaradoa amorphoides Liebm.
	Simarouba amara Aubl.
Solanaceae	Solanaceae sp. (G1264)
Sterculiaceae	Guazuma ulmifolia Lam.
	Sterculia apetala (Jacq.) Karst.
Theophrastaceae	Jacquinia nervosa C. Presl.
Tiliaceae	Apeiba tibourbou Aubl.
	Luehea candida (T.C.) Mart.
Trigoniaceae	Trigonia rugosa Benth.
Ulmaceae	Celtis iquanaea (Jacq.) Sarg.
	Trema micrantha (L.) Blume
Urticaceae	Myriocarpa bifurca Liebm.
	Urera baccifera (L.) Gaud
Verbenaceae	Cornutia grandiflora Steud.
	Lippia cardiostegia Benth.
	Rehdera trinervis (Blake) Mold.
Vitaceae	Cissus sicyoides L.
	Cissus rhombifolia Vahl.
Zygophyllaceae	Guaiacum sanctum L.
Unknown Liana	Liana 1
	Liana 2
	Liana 3
Unknown Tree	Tree (G1238)
	Tree (G1244)
	Tree

Appendix 2. Plant abundance in seven fragments of tropical dry forest.

Family	Scientific Name	S.R.	Cos	Chac.	Mas.	P.V.	L.F	Ome
ACA	Acanthaceae sp. (G1264)						1	
	Acanthaceae sp. (G1183)		5					
	Aphlelandra deppeana						1	
	Aphlelandra scabra			1				
AGA	*Agave angustifolia*				1			
ANA	*Astronium graveolens*	2				25	6	
	Spondias mombin	4	1		2	4	3	8
	Spondias purpurea	1	1			2		
	Spondias radlkoferi					1		
ANN	*Annona purpurea*	1	4	2		2		
	Annona reticulata		2		5			4
	Sapranthus palanga						1	
APO	*Forsteronia spicata*				1			
	Plumeria rubra	9		3				
	Prestonia mexicana				7		1	5
	Stemmadenia obovata					1		
	Thevetia ovata	7	4	22	6	6		
	Apocynaceae 1				3		2	
ARA	*Sciadodendron excelsum*	1			1			2
ARE	*Bactris guineensis*					3		
ARI	*Aristolochia anguicida*				1			1
AST	*Ageratina crassiramea*				2			
	Eupatorium albicaule				3			
	Mikania houstoniana		10					
	Helianthinae (G1263)							1
BIG	*Adenocalymma inundatum*						18	
	Amphilophium paniculatum	2		5		1		
	Arrabidaea cf *chica*	1						
	Arrabidaea mollissima	13		1	4	1	3	
	Arrabidaea patellifera	4		1		1	3	
	Callichlamys latifolia					1		
	Ceratophytum tetragonolobum			2				
	Cydista diversifolia	3						
	Cydista heterophylla						1	
	Macfadyena unguis-cati	3		2		2	6	1
	Mansoa hymenaea	2				2	2	3
	Melloa quadrivalvis	1						
	Pithecoctenium crucigerum	13		8		1	5	5
	Tabebuia ochracea	1						
	Tabebuia impetiginosa			2		1		

	Tabebuia rosea						1	
	Tecoma stans	1						
	Xylophragma seemannianum						1	
	Bignoniaceae 1	6		15		13	16	
	Bignoniaceae 2	1		1		1	1	
	Bignoniaceae 3				2			
	Bignoniaceae 4	7	1			2	4	
BIX	*Bixa orellana L.*							1
BOM	*Bombacopsis quinata*		2		6	3	4	10
	Pseudobombax septenatum					1		1
BOR	*Cordia alliodora*		9			3		1
	Cordia bullata		2					
	Cordia collococca					2		
	Cordia guanacastensis					1		
	Cordia panamensis	4	1			5		1
	Tournefortia hirsutissima		2					1
BUR	*Bursera graveolens*				1			
	Bursera simaruba	10	6	4	57	6	3	14
CAC	*Lemaireocereus aragonii*			2				
	Acanthocereus pentagonus							2
CAP	*Capparis flexuosa*				1			
	Capparis indica			1			2	
	Capparis pachaca ssp. *oxysepala*			10				
CEC	*Cecropia peltata*		1		2			12
CHR	*Hirtella racemosa* var. *hexandra*	2						
	Licania arborea	1			1			
COC	*Cochlospermum vitifolium*	2	2		15	2	17	2
COM	*Combretum farinosum*	2		11	2	3	8	
CON	*Rourea glabra*	1	1					2
DIL	*Tetracera volubilis*	8	2					1
EBE	*Diospyros nicaraguensis*		2	5	15		1	
ERY	*Erythroxylon havanense*	3		10		1		
EUP	*Bernardia nicaraguensis*	6			1	1		
	Croton niveus			1				
	Euphorbia schlechtendalii				13		3	
	Garcia nutans							1
	Gymnanthes lucida					3		
	Hura crepitans	8						
	Jatropha curcas							3
	Margaritaria nobilis	2						10
	Euphorbiaceae sp. (G954)				4	1		2
FAB	Fabaceae (G1279)	3		7		3	25	2
	Fabaceae sp.						2	
	Bauhinia glabra		2					

	Caesalpinia cf coriaria (G1173)	1						
	Caesalpinia eriostachys					1		
	Senna atomaria						2	
	Caesalpinioideae sp. (G1198)	5						
	Acosmium panamense					18		
	Ateleia herbert-smithii			4				
	Dalbergia glabra					10		
	Diphysa robinioides						1	
	Erythrina berteroana	1						
	Gliricidia sepium					1		
	Lonchocarpus costaricensis		2					
	Lonchocarpus minimiflorus	1	1					
	Lonchocarpus phaseolifolius				2			
	Lonchocarpus phlebophyllus			3				
	Machaerium biovulatum	2						
	Machaerium kegelii		6		34		1	
	Myrospermum frutescens	2				2	4	
	Pterocarpus rohrii	3	3	5		2	4	
	Acacia collinsii					12	3	
	Acacia cornigera						3	
	Acacia farnesiana	1			x		4	
	Albizzia/Lysiloma sp.		1	1	10	1		
	Albizzia caribaea	1				1	6	
	Entada polystachya		1					8
	Enterolobium cyclocarpum			7			1	
	Lysiloma sp.			4				
	Lysiloma divaricatum		1					
	Pithecellobium dulce			2				
	Pithecellobium saman	1		1			1	
FLA	Casearia corymbosa		1		1	1		10
	Casearia praecox			2			1	
	Casearia sylvestris	4						
	Casearia tremula			5		1		
	Prockia crucis					1		
	Flacourtiaceae (G1237)		1		3			
HER	Gyrocarpus americanus			11				
HIP	Hemiangium excelsum	14		3	2	2	3	
	Hippocratea cf volubilis				2			
LAU	Ocotea veraguensis	1						
MAR	Souroubea sp. (G1234)	2				2		
MAL	Banisteriopsis muricata	4						
	Bunchosia cf cornifolia				3			
	Byrsonima crassifolia					2		
	Hiraea reclinata						5	

	Stigmaphyllon lindenianum							1
	Stigmaphyllon sp. (G1397)			1				
MAL	*Malvaviscus arboreus*				1			
MEL	*Cedrela odorata*	1						
	Swietenia macrophylla	1						
	Trichilia americana	1				1		
MOR	*Brosimum alicastrum*	1						
	Castilla elastica		4					
	Chlorophora tinctoria	1	2			1		
	Ficus sp.		1					1
	Ficus ovalis						1	
NYC	*Pisonia macranthocarpa*		1					1
	Pisonia aculeata							1
	Neea fagifolia	2	3					
OCH	*Ouratea lucens*							1
OLA	*Schoepfia schreberi*			1				
	Ximenia americana			1				
OPI	*Agonandra macrocarpa*	1						
PHY	*Stegnosperma cubensis*							4
POL	*Securidaca sylvestris*			4				
POL	*Coccoloba floribunda*							1
	Triplaris melaenodendron					1	1	
RHA	*Karwinskia calderoni*	1						
	Zizyphus guatemalensis			2		1		
RUB	*Alibertia edulis*	2						
	Calycophyllum candidissimum	2		2		7	53	5
	Chomelia spinosa	1				1	3	
	Exostema mexicanum	15						
	Genipa americana	2					1	
	Guettarda macrosperma	4					2	
	Hamelia patens							2
	Psychotria pubescens				2			1
	Randia monantha	6				1		
	Randia sp. (G1438)						1	
	Rubiaceae sp.						3	
RUT	*Essenbeckia berlandieri* ssp. *litoralis*			1				
	Zanthoxylum monophyllum			1				
	Zanthoxylum setulosum			1				
SAP	*Allophyllus occidentalis*	1	5	7		38		
	Paullinia cururu	1						
	Serjania atrolineata		2					
	Serjania grosii			1				
	Serjania lobulata				2			
	Serjania schiedeana		3					

	Serjania (G1050)				2			3
	Serjania 1				2			
	Serjania 2							2
	Thouinidium decandrum		3				2	6
	Sapindaceae sp. (G1263)			12		2	2	
SAP	*Manilkara zapota*	1					1	
	Sideroxylon capiri			1	1			
SIM	*Alvaradoa amorphoides*		3					
	Simarouba amara	1		1	1	1	2	3
SOL	Solanaceae sp. (G1264)		3					
STE	*Guazuma ulmifolia*	3	8	2		4	6	
	Sterculia apetala			1		1		2
THE	*Jacquinia nervosa*	1		5				
TIL	*Apeiba tibourbou*		6					
	Luehea candida	7	1	4			1	
TRI	*Trigonia rugosa*	1			2	2		4
ULM	*Celtis iquanaea*				1			
	Trema micrantha		1					
URT	*Myriocarpa bifurca*					1		
	Urera baccifera	1						
VER	*Cornutia grandiflora*						1	
	Lippia cardiostegia						1	
	Rehdera trinervis					1		
VIT	*Cissus sicyoides*					1		
	Cissus rhombifolia				13			
ZYG	*Guaiacum sanctum*		2					
UNK	Liana 1	1						
	Liana 2		8		3			
	Liana 3	9						
	Tree (G1238)		1			1	3	
	Tree (G1244)		1	2				2
	Tree			1				
	Total	75	48	54	44	66	59	45

Appendix 3. Family, scientific name, life forms, dispersal, and sexuality of all plants <2.5 cm dbh encountered in seven fragments of tropical dry forest in Central America. (Life form: T = Tree, S = Shrub, L = Liana; Dispersal mechanism: A = autochoric, Unk = unknown, W = anemochoric, Z = zoochoric, Z(M) = zoochoric/mammal dispersed, / = combination of two dispersal mechanisms; Sexuality: H = hermaphrodite, M = monoecious, M(am) = andromonoecious, M(pm) = polygamomonoecious, D = Dioecious, D(gd) = gynodioecious, D(ad) = androdioecious.

Family	**Scientific Name**	**Life forms**	**Dispersal**	**Sexuality**
ACA	Acanthaceae sp. (G1264)	S	W	H
	Acanthaceae sp. (G1183)	S	W	H
	Aphlelandra deppeana	S	W	H
	Aphlelandra scabra	S	W	H
AGA	*Agave angustifolia*	H	W	H
ANA	*Astronium graveolens*	T	Z(M)	D
	Spondias mombin	T	Z(M)	M
	Spondias purpurea	T	Z(M)	D
	Spondias radlkoferi	T	Z(M)	D
ANN	*Annona purpurea*	T	Z(M)	H
	Annona reticulata	T	Z(M)	H
	Sapranthus palanga	T	Z(M)	H
APO	*Forsteronia spicata*	L	W	H
	Plumeria rubra	T	W	H
	Prestonia mexicana	L	W	H
	Stemmadenia obovata	T	Z	H
	Thevetia ovata	T	Z	H
	Apocynaceae 1	L	Unk	H
ARA	*Sciadodendron excelsum*	T	Z	H
ARE	*Bactris guineensis*	S	Z(M)	M
ARI	*Aristolochia anguicida*	L	W	H
AST	*Ageratina crassiramea*	S	W	H
	Eupatorium albicaule	S	W	H
	Mikania houstoniana	L	W	H
	Helianthinae (G1263)	T	W	H

BIG	*Adenocalymma inundatum*	L	W	H
	Amphilophium paniculatum	L	W	H
	Arrabidaea cf *chica*	L	W	H
	Arrabidaea mollissima	L	W	H
	Arrabidaea patellifera	L	W	H
	Callichlamys latifolia	L	W	H
	Ceratophytum tetragonolobum	L	W	H
	Cydista diversifolia	L	W	H
	Cydista heterophylla	L	W	H
	Macfadyena unguis-cati	L	W	H
	Mansoa hymenaea	L	W	H
	Melloa quadrivalvis	L	W	H
	Pithecoctenium crucigerum	L	W	H
	Tabebuia ochracea	T	W	H
	Tabebuia impetiginosa	T	W	H
	Tabebuia rosea	T	W	H
	Tecoma stans	T	W	H
	Xylophragma seemannianum	L	W	H
	Bignoniaceae 1	L	W	H
	Bignoniaceae 2	L	W	H
	Bignoniaceae 3	L	W	H
	Bignoniaceae 4	L	W	H
BIX	*Bixa orellana L.*	S	Z/A	H
BOM	*Bombacopsis quinata*	T	W	H
	Pseudobombax septenatum	T	W	H
BOR	*Cordia alliodora*	T	W	H
	Cordia bullata	S	Z	H
	Cordia collococca	T	Z	D
	Cordia guanacastensis	T	Z	H
	Cordia panamensis	T	Z	D
	Tournefortia hirsutissima	L	Z	H
BUR	*Bursera graveolens*	T	Z	D
	Bursera simaruba	T	Z	D
CAC	*Lemaireocereus aragonii*	H	Z	H
	Acanthocereus pentagonus	H	Z	H
CAP	*Capparis flexuosa*	T	Z	H
	Capparis indica	T	Z	H
	Capparis pachaca ssp. *oxysepala*	S	Z(M)	H
CEC	*Cecropia peltata*	T	Z	D
CHR	*Hirtella racemosa* var. *hexandra*	T	Z	H
	Licania arborea	T	Z(M)	H
COC	*Cochlospermum vitifolium*	T	W	H
COM	*Combretum farinosum*	L	W	H
CON	*Rourea glabra*	L	Z	H

DIL	Tetracera volubilis	L	Z	D (ad)
EBE	Diospyros nicaraguensis	T	Z(M)	D
ERY	Erythroxylon havanense	S	Z	H
EUP	Bernardia nicaraguensis	S	A	D
	Croton niveus	S	A	M
	Euphorbia schlechtendalii	T	W	M
	Garcia nutans	T	A	M
	Gymnanthes lucida	T	A	M
	Hura crepitans	T	A	M
	Jatropha curcas	S	Z	M
	Margaritaria nobilis	T	Z	D
	Euphorbiaceae sp. (G954)	L	Unk	Unk
FAB	Fabaceae (G1279)	T	Unk	Unk
	Fabaceae sp.	T	Unk	Unk
	Bauhinia glabra	L	A	H
	Caesalpinia cf coriaria (G1173)	T	Z(M)/A	M(am)
	Caesalpinia eriostachys	T	Z/A	M(am)
	Senna atomaria	T	Z	H
	Caesalpinioideae sp. (G1198)	T	Unk	Unk
	Acosmium panamense	T	Z	H
	Ateleia herbert-smithii	T	W	D
	Dalbergia glabra	L	Z/W	H
	Diphysa robinioides	T	W	H
	Erythrina berteroana	T	Z	H
	Gliricidia sepium	T	Z/A	H
	Lonchocarpus costaricensis	T	W	H
	Lonchocarpus minimiflorus	T	W	H
	Lonchocarpus phaseolifolius	T	W	H
	Lonchocarpus phlebophyllus	T	W	H
	Machaerium biovulatum	T	W	H
	Machaerium kegelii	L	W	H
	Myrospermum frutescens	T	W	H
	Pterocarpus rohrii	T	W	H
	Acacia collinsii	T	Z/A	H
	Acacia cornigera	T	Z	H
	Acacia farnesiana	T	Z(M)/A	H
	Albizzia/Lysiloma sp.	T	W	H
	Albizzia caribaea	T	W	H
	Entada polystachya	L	W	H
	Enterolobium cyclocarpum	T	Z(M)	H
	Lysiloma sp.	T	W/A	H
	Lysiloma divaricatum	T	W/A	H
	Pithecellobium dulce	T	Z/A	H
	Pithecellobium saman	T	Z(M)	H

FLA	Casearia corymbosa	T	Z	H
	Casearia praecox	T	Z	H
	Casearia sylvestris	T	Z	H
	Casearia tremula	T	Z	H
	Prockia crucis	S	Z/W	H
	Flacourtiaceae (G1237)	T	Z	H
HER	Gyrocarpus americanus	T	W	M
HIP	Hemiangium excelsum	T	W	H
	Hippocratea cf volubilis	L	W	H
LAU	Ocotea veraguensis	T	Z	H
MAR	Souroubea sp. (G1234)	L	Z	H
MAL	Banisteriopsis muricata	L	W	H
	Bunchosia cf cornifolia	S	Z(M)	H
	Byrsonima crassifolia	T	Z(M)	H
	Hiraea reclinata	L	W	H
	Stigmaphyllon lindenianum	L	W	H
	Stigmaphyllon sp. (G1397)	L	W	H
MAL	Malvaviscus arboreus	S	Z	H
MEL	Cedrela odorata	T	W	M
	Swietenia macrophylla	T	W	M
	Trichilia americana	T	Z	D
MOR	Brosimum alicastrum	T	Z(M)	M
	Castilla elastica	T	Z	D(M)
	Chlorophora tinctoria	T	Z(M)	D
	Ficus sp.	T	Z(M)	M
	Ficus ovalis	T	Z(M)	M
NYC	Pisonia macranthocarpa	T	Z	D
	Pisonia aculeata	L	Z	D
	Neea fagifolia	S	Z	D
OCH	Ouratea lucens	S	Z	H
OLA	Schoepfia schreberi	T	Z	H
	Ximenia americana	T	Z(M)	H
OPI	Agonandra macrocarpa	S	Z(M)	D
PHY	Stegnosperma cubensis	L	Z	H
POL	Securidaca sylvestris	L	W	H
POL	Coccoloba floribunda	T	Z	D(gd)
	Triplaris melaenodendron	T	W	D
RHA	Karwinskia calderoni	T	Z	H
	Zizyphus guatemalensis	T	Z(M)	H
RUB	Alibertia edulis	S	Z(M)	D
	Calycophyllum candidissimum	T	W	H
	Chomelia spinosa	S	Z	H
	Exostema mexicanum	T	W	H
	Genipa americana	T	Z(M)	D

	Guettarda macrosperma	T	Z(M)	H
	Hamelia patens	S	Z	H
	Psychotria pubescens	S	Z	H
	Randia monantha	S	Z(M)	D
	Randia sp. (G1438)	S	Z(M)	Unk
	Rubiaceae sp.	T	Unk	Unk
RUT	Essenbeckia berlandieri ssp. litoralis	T	W	H
	Zanthoxylum monophyllum	T	Z	D
	Zanthoxylum setulosum	T	Z	D
SAP	Allophyllus occidentalis	T	Z	M
	Paullinia cururu	L	Z	M
	Serjania atrolineata	L	W	M
	Serjania grosii	L	W	M
	Serjania lobulata	L	W	M
	Serjania schiedeana	L	W	M
	Serjania (G1050)	L	W	M
	Serjania 1	L	W	M
	Serjania 2	L	W	M
	Thouinidium decandrum	T	W	M
	Sapindaceae sp. (G1263)	L	Unk	M
SAP	Manilkara zapota	T	Z(M)	H
	Sideroxylon capiri	T	Z(M)	H
SIM	Alvaradoa amorphoides	T	W	D
	Simarouba amara	T	Z	D
SOL	Solanaceae sp. (G1264)	S	Z	H
STE	Guazuma ulmifolia	T	Z(M)/A	H
	Sterculia apetala	T	Z	M
THE	Jacquinia nervosa	S	Z(M)	H
TIL	Apeiba tibourbou	T	Z(M)	H
	Luehea candida	T	Z/W	H
TRI	Trigonia rugosa	L	W	H
ULM	Celtis iquanaea	S	Z	M(pm)
	Trema micrantha	T	Z	M
URT	Myriocarpa bifurca	S	Z	D
	Urera baccifera	S	Z	D
VER	Cornutia grandiflora	T	Z	H
	Lippia cardiostegia	S	W/A	H
	Rehdera trinervis	T	W	H
VIT	Cissus sicyoides	L	Z	H
	Cissus rhombifolia	L	Z	H
ZYG	Guaiacum sanctum	T	Z	H
UNK	Liana 1	L	Unk	Unk
	Liana 2	L	Unk	Unk
	Liana 3	L	Unk	Unk

Tree (G1238)	T	Unk	Unk
Tree (G1244)	T	Unk	Unk
Tree	T	Unk	Unk
Total			

Appendix 4. Biogeographic characteristics of resident breeding birds recorded in the tropical dry forest region of Costa Rica and Nicaragua. (BIOG = biogeographic regions: P = Pacific region, C = Central region, A = Atlantic region; N.R. = northern breeding range in degrees latitude; S.R. = southern breeding range in degrees latitude; Lat. E. = latitudinal extent in degrees).

Family	Scientific Name	BIOG	N.R.	S. R.	Lat. E
Accipitridae	Busarellus nigricollis	PA	N24	S32	56
Accipitridae	Buteo albicaudatus	PCA	N28	S43	71
Accipitridae	Buteo albonotatus	PCA	N32	S24	56
Accipitridae	Buteo brachyurus	PCA	N27	S27	54
Accipitridae	Buteo jamaicensis	PCA	N49	N8	41
Accipitridae	Buteo magnirostris	PCA	N25	S37	62
Accipitridae	Buteo nitidus	PCA	N33	S27	60
Accipitridae	Buteogallus anthracinus	PA	N27	N3	24
Accipitridae	Buteogallus urubitinga	PA	N26	S34	60
Accipitridae	Chondrohierax uncinatus	PCA	N27	S28	55
Accipitridae	Elanoides forficatus	PCA	N13	S23	36
Accipitridae	Elanus caeruleus	PCA	N45	S43	88
Accipitridae	Gampsonyx swainsonii	P	N13	S28	41
Accipitridae	Geranospiza caerulescens	PCA	N27	S30	57
Accipitridae	Harpagus bidentatus	PCA	N21	S24	45
Accipitridae	Ictinia plumbea	PCA	N23	S23	46
Accipitridae	Leptodon cayannensis	PA	N23	S29	52
Accipitridae	Parabuteo unicinctus	PCA	N34	S43	77
Apodidae	Chaetura vauxi	PCA	N23	N7	16
Bucconidae	Notharchus macrorhynchos	PA	N21	S25	46
Caprimulgidae	Caprimulgus ridgwayi	PC	N26	N11	15
Caprimulgidae	Chordeiles acutipennis	PC	N28	S27	55
Caprimulgidae	Nyctidromus albicollis	PCA	N27	S34	61
Cardinalinae	Saltator atriceps	PCA	N23	N8	15
Cardinalinae	Saltator coerulescens	PCA	N23	S34	57
Cathartidae	Cathartes aura	PCA	N40	S55	95
Cathartidae	Coragyps atratus	PCA	N40	S43	83
Cathartidae	Sarcorhamphus papa	PCA	N23	S30	53
Columbidae	Claravis pretiosa	PCA	N23	S27	50
Columbidae	Columba flavirostris	PCA	N30	N10	20

Columbidae	Columba livia	PCA	N55	S56	111
Columbidae	Columbina inca	PC	N35	N9	26
Columbidae	Columbina minuta	PCA	N19	S25	44
Columbidae	Columbina passerina	PC	N35	S13	48
Columbidae	Columbina talpacoti	PCA	N27	S28	55
Columbidae	Leptotila plumbeiceps	PC	N23	N3	20
Columbidae	Leptotila verreauxi	PC	N29	S37	66
Columbidae	Zenaida asiatica	PC	N43	S30	73
Corvidae	Calocitta formosa	PC	N20	N10	10
Cracidae	Crax rubra	PCA	N23	S2	25
Cracidae	Ortalis leucogastra	P	N16	N12	4
Cracidae	Ortalis vetula	PC	N27	N10	17
Cracidae	Penelope purpurascens	PCA	N23	S3	26
Cuculidae	Coccyzus minor	PCA	N27	N7	20
Cuculidae	Crotophaga ani	PCA	N26	S30	56
Cuculidae	Crotophaga sulcirostris	PCA	N30	S23	53
Cuculidae	Dromococcyx phasianellus	PCA	N21	S26	47
Cuculidae	Morococcyx erythropygus	PC	N23	N10	13
Cuculidae	Piaya cayana	PCA	N28	S34	62
Cuculidae	Tapera naevia	PCA	N20	S38	58
Dendrocolaptidae	Dendrocincla homochroa	PC	N21	N7	14
Dendrocolaptidae	Dendrocolaptes certhia	PCA	N21	S18	39
Dendrocolaptidae	Lepidocolaptes souleyetii	PCA	N19	S5	24
Dendrocolaptidae	Sittasomus griseicapillus	PC	N22	S30	52
Dendrocolaptidae	Xiphorhynchus flavigaster	PC	N28	N10	18
Emberizinae	Aimophila botteri	PA	N28	N10	18
Emberizinae	Aimophila ruficauda	PC	N22	N10	12
Emberizinae	Ammodramus savannarum	PA	N35	0	35
Emberizinae	Arremonops rufivirgatus	PC	N27	N10	17
Emberizinae	Guiraca caerulea	PCA	N33	N10	23
Emberizinae	Sporophila minuta	P	N22	S5	27
Emberizinae	Sporophila torqueola	PCA	N26	N8	18
Emberizinae	Volatinia jacarina	PCA	N26	S34	60
Falconidae	Falco sparverius	PCA	N52	S56	108
Falconidae	Herpetotheres cachinnas	PCA	N27	S26	53
Falconidae	Micrastur semitorquatus	PCA	N22	S29	51
Falconidae	Polyborus plancus	PCA	N32	S57	89
Formicariidae	Thamnophilus doliatus	PCA	N23	S27	50
Fringillidae	Carduelis psaltria	PC	N45	S8	53
Furnariidae	Xenops minutus	PCA	N21	S28	49
Hirundinidae	Progne chalybea	PCA	N23	S37	60
Hirundinidae	Stelgidopteryx serripennis	PCA	N27	N10	17
Hirundinidae	Tachycineta albilinea	PA	N27	S8	35
Icteridae	Cacicus holosericeus	PCA	N23	S17	40

Icteridae	Dives dives	PC	N23	N8	15
Icteridae	Icterus mesomelas	PA	N22	S9	31
Icteridae	Icterus pectoralis	PC	N18	N10	8
Icteridae	Icterus pustulatus	PC	N28	N10	18
Icteridae	Molothrus aeneus	PCA	N32	N10	22
Icteridae	Psarocolius montezuma	PCA	N22	N8	14
Icteridae	Quiscalus mexicanus	PCA	N37	S4	41
Icteridae	Sturnella magna	PCA	N42	S3	45
Momotidae	Eumomota superciliosa	PC	N21	N10	11
Momotidae	Momotus momota	PC	N24	S23	47
Nyctibidae	Nyctibius griseus	PA	N23	S32	55
Parulidae	Basileuterus rufifrons	PCA	N30	N2	28
Parulidae	Euthlypis lachrymosa	PC	N26	N12	14
Parulidae	Geothlypis poliocephala	PCA	N24	N8	16
Parulidae	Parula pitiayumi	PCA	N25	S37	62
Passeridae	Passer domesticus	PCA	N60	S56	116
Phasianidae	Colinus cristatus	PC	N16	N10	6
Picidae	Campephilus guatemalensis	PCA	N28	N8	20
Picidae	Dryocopus lineatus	PCA	N28	S28	56
Picidae	Melanerpes aurifrons	PC	N35	N13	22
Picidae	Melanerpes hoffmannii	PC	N13	N10	3
Pipridae	Chiroxiphia linearis	PC	N17	N9	8
Polioptilidae	Polioptila albiloris	PC	N22	N10	12
Polioptilidae	Polioptila plumbea	PA	N22	S15	37
Polioptilidae	Ramphocaenus melanurus	PA	N22	S25	47
Psittacideae	Amazona albifrons	PC	N27	N10	17
Psittacideae	Amazona auropalliata	PA	N17	N10	7
Psittacideae	Ara macao	PCA	N21	S14	35
Psittacideae	Aratinga canicularis	PC	N24	N10	14
Psittacideae	Aratinga finschi	PCA	N15	N7	8
Psittacideae	Aratinga holochlora?	PC	N16	N13	3
Psittacideae	Aratinga strenua	PC	N17	N11	6
Psittacideae	Brotogeris jugularis	PCA	N17	N3	14
Ramphastidae	Pteroglossus torquatus	PCA	N21	N2	19
Ramphastidae	Ramphastos sulfuratus	PCA	N21	N7	14
Strigidae	Asio clamator	PCA	N19	S34	53
Strigidae	Ciccaba virgata	PCA	N28	S26	54
Strigidae	Glaucidium brasilianum	PCA	N32	S33	65
Strigidae	Lophostrix cristata	PC	N19	S13	32
Strigidae	Otus cooperi	PC	N17	N10	7
Strigidae	Pulsatrix perspicillata	PCA	N19	S27	46
Thrauninae	Cyanerpes cyaneus	PCA	N21	S22	43
Thrauninae	Eucometis penicillata	PA	N21	S24	45
Thrauninae	Euphonia affinis	PC	N28	N10	18

Thrauninae	Euphonia hirundinacea	PCA	N22	N8	14
Thrauninae	Thraupis episcopus	PCA	N20	S13	33
Tinamidae	Crypturellus cinnamomeus	PC	N24	N10	14
Trochilidae	Amazilia cyanura	PC	N15	N12	3
Trochilidae	Amazilia rutila	PCA	N25	N10	15
Trochilidae	Amazilia saucerottei	PC	N12	N2	10
Trochilidae	Amazilia tzacatl	PCA	N20	S2	22
Trochilidae	Anthracothorax prevostii	PA	N21	S6	27
Trochilidae	Chlorostilbon canivetti	PC	N22	N8	14
Trochilidae	Heliomaster constantii	PC	N26	N10	16
Trochilidae	Hylocharis eliciae	PA	N19	N7	12
Troglodytidae	Campylorhynchus rufinucha	PC	N19	N10	9
Troglodytidae	Salpinctes obsoletus	PC	N51	N13	38
Troglodytidae	Thryothorus ludovicianus	P	N42	N13	29
Troglodytidae	Thryothorus modestus	PCA	N17	N7	10
Troglodytidae	Thryothorus pleurostictus	PC	N19	N10	9
Troglodytidae	Thryothorus rufalbus	PC	N16	N3	13
Troglodytidae	Troglodytes aedon	PCA	N38	S56	94
Trogonidae	Trogon elegans	PC	N21	N10	11
Trogonidae	Trogon melanocephalus	PC	N21	N10	11
Trogonidae	Trogon violaceus	PCA	N21	S17	38
Turdidae	Turdus grayi	PCA	N26	N7	19
Tyrannidae	Attila spadiceus	PCA	N26	S23	49
Tyrannidae	Camptostoma imberbe	PC	N28	N10	18
Tyrannidae	Contopus cinereus	PCA	N22	S28	50
Tyrannidae	Elaenia flavogaster	PCA	N22	S30	52
Tyrannidae	Elaenia frantzii	PC	N15	N2	13
Tyrannidae	Legatus leucophaius	PCA	N20	S29	49
Tyrannidae	Megarhynchus pitangua	PCA	N23	S31	54
Tyrannidae	Myiarchus nuttingi	PC	N30	N10	20
Tyrannidae	Myiarchus tuberculifer	PCA	N25	S28	53
Tyrannidae	Myiarchus tyrannulus	PC	N27	S32	59
Tyrannidae	Myiodynastes maculatus	PC	N12	S37	49
Tyrannidae	Myiopagis viridicata	PCA	N23	S28	51
Tyrannidae	Myiozetetes similis	PCA	N23	S27	50
Tyrannidae	Oncostoma cinereigulare	PA	N21	N11	10
Tyrannidae	Pachyramphus aglaiae	PCA	N27	N10	17
Tyrannidae	Pitangus sulphuratus	PCA	N28	S43	71
Tyrannidae	Platyrinchus cancrominus	PCA	N21	N11	10
Tyrannidae	Tityra semifasciata	PCA	N27	S18	45
Tyrannidae	Todirostrum cinereum	PA	N22	S24	46
Tyrannidae	Todirostrum sylvia	PCA	N21	S6	27
Tyrannidae	Tolmomyias sulphurescens	PCA	N21	S30	51
Tyrannidae	Tyrannus melancholicus	PCA	N27	S41	68

Tytonidae	*Tyto alba*	PCA	N50	S56	106
Vireonidae	*Hylophilus decurtatus*	PCA	N21	S5	26
Vireonidae	*Vireo flavoviridis*	PCA	N20	N8	12
Vireonidae	*Vireo pallens*	PA	N28	N9	19

Appendix 5. Life history characteristics of resident breeding birds recorded in the tropical dry forest region of Costa Rica and Nicaragua. (HAB. = forest preference: F = species that require solid forest, P = species that requires patchy forest, O = species that does not require forest; Guild: C = carnivores, O = omnivores, I = insectivores, F = frugivores, N = nectarivores, G = granivores; Grams = body mass in grams).

Family	Scientific Name	HAB.	Guild	Grams
Accipitridae	Busarellus nigricollis	P	C	650
Accipitridae	Buteo albicaudatus	O	C	950
Accipitridae	Buteo albonotatus	P	C	750
Accipitridae	Buteo brachyurus	F	C	480
Accipitridae	Buteo jamaicensis	P	C	900
Accipitridae	Buteo magnirostris	O	O	290
Accipitridae	Buteo nitidus	P	O	425
Accipitridae	Buteogallus anthracinus	O	C	800
Accipitridae	Buteogallus urubitinga	F	C	1100
Accipitridae	Chondrohierax uncinatus	F	C	275
Accipitridae	Elanoides forficatus	P	C	480
Accipitridae	Elanus caeruleus	O	C	350
Accipitridae	Gampsonyx swainsonii	O	O	100
Accipitridae	Geranospiza caerulescens	F	O	350
Accipitridae	Harpagus bidentatus	F	O	180
Accipitridae	Ictinia plumbea	P	I	280
Accipitridae	Leptodon cayannensis	F	O	440
Accipitridae	Parabuteo unicinctus	P	C	700
Apodidae	Chaetura vauxi	P	I	18
Bucconidae	Notharchus macrorhynchos	P	I	105
Caprimulgidae	Caprimulgus ridgwayi	O	I	65
Caprimulgidae	Chordeiles acutipennis	O	I	45
Caprimulgidae	Nyctidromus albicollis	O	I	55
Cardinalinae	Saltator atriceps	O	O	85
Cardinalinae	Saltator coerulescens	P	O	52
Cathartidae	Cathartes aura	O	C	1400
Cathartidae	Coragyps atratus	O	C	1800
Cathartidae	Sarcorhamphus papa	P	C	3500
Columbidae	Claravis pretiosa	O	O	72

Columbidae	Columba flavirostris	O	O	230
Columbidae	Columba livia	O	O	300
Columbidae	Columbina inca	O	G	52
Columbidae	Columbina minuta	O	O	33
Columbidae	Columbina passerina	O	O	40
Columbidae	Columbina talpacoti	O	G	48
Columbidae	Leptotila plumbeiceps	P	G	155
Columbidae	Leptotila verreauxi	P	G	165
Columbidae	Zenaida asiatica	O	G	145
Corvidae	Calocitta formosa	O	O	205
Cracidae	Crax rubra	F	F	4000
Cracidae	Ortalis leucogastra	P	F	650
Cracidae	Ortalis vetula	P	F	650
Cracidae	Penelope purpurascens	P	F	1700
Cuculidae	Coccyzus minor	P	O	65
Cuculidae	Crotophaga ani	O	O	115
Cuculidae	Crotophaga sulcirostris	O	O	80
Cuculidae	Dromococcyx phasianellus	P	O	96
Cuculidae	Morococcyx erythropygus	P	I	63
Cuculidae	Piaya cayana	P	I	105
Cuculidae	Tapera naevia	O	I	55
Dendrocolaptidae	Dendrocincla homochroa	P	I	44
Dendrocolaptidae	Dendrocolaptes certhia	P	I	74
Dendrocolaptidae	Lepidocolaptes souleyetii	P	I	28
Dendrocolaptidae	Sittasomus griseicapillus	P	I	14
Dendrocolaptidae	Xiphorhynchus flavigaster	P	I	60
Emberizinae	Aimophila botteri	O	O	20
Emberizinae	Aimophila ruficauda	P	O	35
Emberizinae	Ammodramus savannarum	O	G	17.5
Emberizinae	Arremonops rufivirgatus	P	O	25
Emberizinae	Guiraca caerulea	O	O	31
Emberizinae	Sporophila minuta	O	G	8
Emberizinae	Sporophila torqueola	O	G	9.5
Emberizinae	Volatinia jacarina	O	G	9.5
Falconidae	Falco sparverius	O	I	115
Falconidae	Herpetotheres cachinnas	P	C	600
Falconidae	Micrastur semitorquatus	P	C	575
Falconidae	Polyborus plancus	O	O	1000
Formicariidae	Thamnophilus doliatus	P	I	28
Fringillidae	Carduelis psaltria	O	O	10
Furnariidae	Xenops minutus	P	I	12
Hirundinidae	Progne chalybea	O	I	40
Hirundinidae	Stelgidopteryx serripennis	O	I	15.5
Hirundinidae	Tachycineta albilinea	O	I	14

Icteridae	Cacicus holosericeus	O	I	70
Icteridae	Dives dives	O	I	108
Icteridae	Icterus mesomelas	O	I	70
Icteridae	Icterus pectoralis	P	O	50
Icteridae	Icterus pustulatus	O	O	45
Icteridae	Molothrus aeneus	O	O	68
Icteridae	Psarocolius montezuma	P	O	520
Icteridae	Quiscalus mexicanus	O	O	230
Icteridae	Sturnella magna	O	O	85
Momotidae	Eumomota superciliosa	O	I	65
Momotidae	Momotus momota	P	O	120
Nyctibidae	Nyctibius griseus	P	I	230
Parulidae	Basileuterus rufifrons	P	I	11.5
Parulidae	Euthlypis lachrymosa	P	O	15
Parulidae	Geothlypis poliocephala	O	I	15.5
Parulidae	Parula pitiayumi	P	O	7
Passeridae	Passer domesticus	O	O	26
Phasianidae	Colinus cristatus	O	O	125
Picidae	Campephilus guatemalensis	P	I	255
Picidae	Dryocopus lineatus	P	I	197
Picidae	Melanerpes aurifrons	P	O	55
Picidae	Melanerpes hoffmannii	P	O	68
Pipridae	Chiroxiphia linearis	P	F	19
Polioptilidae	Polioptila albiloris	P	I	7
Polioptilidae	Polioptila plumbea	P	I	6.5
Polioptilidae	Ramphocaenus melanurus	P	I	10
Psittacideae	Amazona albifrons	P	F	280
Psittacideae	Amazona auropalliata	P	F	480
Psittacideae	Ara macao	P	F	900
Psittacideae	Aratinga canicularis	P	F	80
Psittacideae	Aratinga finschi	O	F	150
Psittacideae	Aratinga holochlora?	P	F	160
Psittacideae	Aratinga strenua	P	F	180
Psittacideae	Brotogeris jugularis	O	F	65
Ramphastidae	Pteroglossus torquatus	P	F	230
Ramphastidae	Ramphastos sulfuratus	P	F	550
Strigidae	Asio clamator	O	C	440
Strigidae	Ciccaba virgata	P	O	275
Strigidae	Glaucidium brasilianum	P	O	70
Strigidae	Lophostrix cristata	P	I	400
Strigidae	Otus cooperi	P	I	170
Strigidae	Pulsatrix perspicillata	P	O	750
Thrauninae	Cyanerpes cyaneus	P	O	13.5
Thrauninae	Eucometis penicillata	P	O	31

Thrauninae	Euphonia affinis	P	F	10.5
Thrauninae	Euphonia hirundinacea	P	F	15
Thrauninae	Thraupis episcopus	O	O	32
Tinamidae	Crypturellus cinnamomeus	P	O	480
Trochilidae	Amazilia cyanura	P	N	4.5
Trochilidae	Amazilia rutila	P	N	4.8
Trochilidae	Amazilia saucerottei	P	N	4.5
Trochilidae	Amazilia tzacatl	O	N	5.2
Trochilidae	Anthracothorax prevostii	O	N	7.5
Trochilidae	Chlorostilbon canivetti	O	N	2.6
Trochilidae	Heliomaster constantii	P	N	7.5
Trochilidae	Hylocharis eliciae	P	N	3.7
Troglodytidae	Campylorhynchus rufinucha	P	I	36
Troglodytidae	Salpinctes obsoletus	O	I	22
Troglodytidae	Thryothorus ludovicianus	O	O	19
Troglodytidae	Thryothorus modestus	O	I	18
Troglodytidae	Thryothorus pleurostictus	P	I	20
Troglodytidae	Thryothorus rufalbus	P	I	25
Troglodytidae	Troglodytes aedon	P	I	12
Trogonidae	Trogon elegans	P	O	78
Trogonidae	Trogon melanocephalus	P	O	90
Trogonidae	Trogon violaceus	P	O	56
Turdidae	Turdus grayi	O	O	76
Tyrannidae	Attila spadiceus	P	O	40
Tyrannidae	Camptostoma imberbe	P	I	7.5
Tyrannidae	Contopus cinereus	O	I	12.5
Tyrannidae	Elaenia flavogaster	O	O	25
Tyrannidae	Elaenia frantzii	P	O	20
Tyrannidae	Legatus leucophaius	O	O	26
Tyrannidae	Megarhynchus pitangua	P	I	70
Tyrannidae	Myiarchus nuttingi	P	I	24
Tyrannidae	Myiarchus tuberculifer	P	O	20
Tyrannidae	Myiarchus tyrannulus	P	O	34
Tyrannidae	Myiodynastes maculatus	P	O	45
Tyrannidae	Myiopagis viridicata	P	I	13
Tyrannidae	Myiozetetes similis	O	O	27
Tyrannidae	Oncostoma cinereigulare	P	I	7.3
Tyrannidae	Pachyramphus aglaiae	P	O	33
Tyrannidae	Pitangus sulphuratus	O	O	68
Tyrannidae	Platyrinchus cancrominus	F	I	10
Tyrannidae	Tityra semifasciata	P	F	88
Tyrannidae	Todirostrum cinereum	P	I	6.3
Tyrannidae	Todirostrum sylvia	P	I	7.5
Tyrannidae	Tolmomyias sulphurescens	O	I	14.5

Tyrannidae	Tyrannus melancholicus	O	O	40
Tytonidae	Tyto alba	O	C	425
Vireonidae	Hylophilus decurtatus	P	O	9
Vireonidae	Vireo flavoviridis	O	I	18.5
Vireonidae	Vireo pallens	P	I	11

Appendix 6. Species abundance in eight fragments of tropical dry forest based on 30 point counts at each site.

Scientific Name	Cos.	S.R.	P.V.	Chac	Mas.	L.P.	L.F	Ome
Aimophila ruficauda	1							
Amazilia cyanura	1			1				
Amazilia rutila		3	1	5	2	1	1	3
Amazilia saucerottei		2	1	11	1	3	2	1
Amazilia tzacatl	6			2	1		2	
Amazona albifrons		21		3		3	3	
Amazona auropalliata	3	2	2	5				5
Aratinga canicularis	29	62	5	8	2	10	1	40
Aratinga strenua					27			
Arremonops rufivirgatus		11	5					
Basileuterus rufifrons		16	10		4			
Brotogeris jugularis	6	3		16		20		28
Buteo magnirostris		3	3	3	1	1	1	3
Buteogallus anthracinus							2	
Calocitta formosa	6	11		12	16	18	19	27
Campephilus guatemalensis		2	2					
Camptostoma imberbe		2	6					6
Campylorhynchus rufinucha	29	20	28	13	15	19		
Cathartes aura		1	1	7	19	1	3	2
Chiroxiphia linearis		7	8	6				
Chlorostilbon canivetti	2			1			1	1
Columba flavirostris	2	1						22
Columbina inca	2			1			8	
Columbina passerina						2		
Coragyps atratus	3	1	1	6	1	3	7	6
Crypturellus cinnamomeus	2	10	8	2	3			
Cyanerpes cyaneus		2						
Dendrocolaptes certhia		2	1					
Dryocopus lineatus	1							
Elaenia flavogaster		2						
Eucometis penicillata		1						
Eumomota superciliosa	10		5			3		
Euphonia affinis	8							
Heliomaster constantii				1			1	
Herpetotheres cachinnas			2					
Icterus pustulatus	5		4		7	2		
Lepidocolaptes souleyetii		1	1					
Leptodon cayannensis	1							
Leptotila plumbeiceps	1			1				

Leptotila verreauxi	9	5	2	9	6	10	10	10
Megarhynchus pitangua	14	10	5	2	9	9		
Melanerpes hoffmannii	16	22	6	9	3	14	4	8
Micrastur semitorquatus						1		
Momotus momota		4	1					
Myiarchus nuttingi		3		4			5	
Myiarchus tuberculifer	2	27	15	9	4	5	11	7
Myiarchus tyrannulus	4	9	3	7	5	7	4	15
Myiodynastes maculatus	7	2	4			2		
Myiozetetes similis		1	1					
Pachyramphus aglaiae			2					
Parula pitiayumi								24
Piaya cayana	6	7	3	3	1	1		
Pitangus sulphuratus	2	0	3	2	1	1		3
Polioptila albiloris	21	29	11	20	30	10	13	
Polioptila plumbea			2			6		
Polyborus plancus				2			1	
Progne chalybea				8			17	
Psarocolius montezuma				8				
Quiscalus mexicanus								1
Sittasomus griseicapillus		5	1					
Thamnophilus doliatus		3						
Thryothorus pleurostictus	21	17	10	27	14	13	22	27
Thryothorus rufalbus				1				
Tityra semifasciata	2	3						
Todirostrum sylvia		2		2				
Tolmomyias sulphurescens	1	7	7	10	2	14		
Trogon elegans	3	7	1	2				
Trogon melanocephalus	7	5	5	9	7	5	1	8
Trogon violaceus		1						
Vireo flavoviridis	6							
Xiphorhynchus flavigaster	2	2						
Zenaida asiatica		3						
UNKOWN	4		1			1		4

REFERENCES

Aizen, M. A., and P. Feinsinger. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. Ecology 75: 330-351.

Andersen, M., A. Thornhill, and H. Koopowitz. 1997. Tropical forest disruption and stochastic biodiversity losses. Pp. 281-291 in W. F. Laurance and R. O. Bierregaard, Jr., eds., Tropical Forest Remnants. The University of Chicago Press, Chicago.

Ashton, P. S. 1969. Speciation among tropical forest trees: Some deductions in light of recent evidence. Biological Journal of the Linnean Society 1: 155-196.

Bawa, K. S. 1974. Breeding systems of tree species of a lowland tropical community. Evolution 28: 85-92.

Bawa, K. S., and P. A. Opler. 1977. Spatial relationships between staminate and pistillate plants of dioecious tropical forest trees. Evolution 31: 64-68.

Bawa, K. S., D. R. Perry, and J. H. Beach. 1985. Reproductive biology of tropical lowland rain forest trees, Part 1: Sexual systems and incompatibility mechanisms. American Journal of Botany 72: 331-345.

Bawa, K. S., S. H. Bullock, D. R. Perry, R. E. Coville, and M. H. Grayum. 1985. Reproductive biology of tropical lowland rain forest trees, Part 2: Pollination systems. American Journal of Botany 72 (3): 346-356.

Beehler, B. M., J. B. Sengo, C. Filardi, and K. Merg. 1995. Documentation of the lowland rainforest avifauna in Papua New Guinea: effects of patchy distribution, survey efforts, and methodology. EMU 95: 149-161.

Bierregaard, R. O., Jr. 1990. Avian communities in the understory of Amazonian forest fragments. Pp. 333-343 in A. Keast, ed., Biogeography and Ecology of Forest Bird Communities. Academic Publishing, The Hague, Netherlands.

Bierregaard, R. O., Jr., and T. E. Lovejoy. 1989. Effects of forest fragmentation on Amazonian understory bird communities. ActaAmazonica 19: 215-241.

Bierregaard, R. O., Jr., T. E. Lovejoy, V. Kapos, A. A. dos Santos, and R. W. Hutchings. 1992. The biological dynamics of tropical rain forest fragments. Bioscience 42: 859-866.

Bock, C. E. 1984. Geographical correlates of abundance vs. rarity in some North American winter landbirds. The Auk 101: 266-273.

Bock, C. E., and R. E. Ricklefs. 1983. Range size and local abundance of some North American songbirds: a positive correlation. The American Naturalist 122: 295-299.

Brash, A. R. 1987. The history of avian extinction and forest conversion on Puerto Rico. Biological Conservation 39: 97-111.

Brown, A. D., S. C. Chalukian, and L. M. Malmierca. 1985. Estudio floristico-estructural de un sector de selva semidecidua del Noreste Argentina 1. Composicion floristica, densidad, y diversidad. Darwiniana 26: 27-41.

Brown, J. H. 1971. Mammals on mountain-tops: Non-equilibrium insular biogeography. American Naturalist 105: 467-478.

-----. 1984. On the relationship between abundance and distribution of species. American Naturalist 124: 253-279.

-----. 1995. Macroecology. The University of Chicago Press, Chicago.

Brown, J. H., and A. C. Gibson. 1983. Biogeography. The C. V. Mosby Company, St. Louis, Missouri.

Brown, K. S., Jr., and G. G. Brown. 1992. Habitat alteration and species loss in Brazilian forests. Pp. 119-142 in T. C. Whitmore and J. A. Sayer, eds., Tropical Deforestation and Species Extinction. Chapman and Hall, London.

Brown, S., and A. E. Lugo. 1980. Preliminary estimates of the storage of organic carbon in tropical ecosystems. Pp. 65-117 in S. Brown, A. E. Lugo, and B. Liegel, eds., Carbon Dioxide Effects Research and Assessment Program: The role of tropical forests on the world carbon cycles. Center for Wetlands, University of Florida, Gainesville.

Budowski, G. 1966. Fire in tropical lowland areas. Proceedings of the Annual Tall Timbers Fire Ecology Conference 5: 5-22.

-----. 1970. The distinction between old secondary and climax species in tropical Central American lowland forests. Tropical Ecology 2 (1): 44-48.

Bullock, S. H. 1985. Breeding systems in the flora of a tropical deciduous forest in Mexico. Biotropica 17: 287-301.

-----. 1995. Plant reproduction in neotropical dry forests. Pp. 277-303 in S. H. Bullock, H. A. Mooney, and E. Medina, eds., Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge.

Bullock, S. H., H. A. Mooney, and E. Medina, eds. 1995. Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge.

Canaday, C. 1997. Loss of insectivorous birds along a gradient of human impact in Amazonia. Biological Conservation 77: 63-77.

Carlquist, S. 1974. Island Biology. Columbia University Press, New York.

Ceballos, G. 1995. Vertebrate diversity, ecology and conservation in neotropical dry forests. Pp. 195-220 in S. H. Bullock, H. A. Mooney, and E. Medina, eds., Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge.

Christiansen, M. B., and E. Pitter. 1997. Species loss in a forest bird community near Lagoa Santa in southeastern Brazil. Biological Conservation 80: 23-32.

Clark, D. A., and D. B. Clark. 1984. Spacing dynamics of a tropical rainforest tree: Evaluation of the Janzen-Connell model. American Naturalist 124: 769-788.

Clinebell, R. R., O. L. Phillips, A. H. Gentry, N. Starks, and H. Zuuring. 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. Biodiversity and Conservation 4: 56-90.

Cody, M. L. 1983. Bird diversity and density in South African forests. Oecologia 59: 201-215.

-----. 1993. Bird diversity components within and between habitats in Australia. Pp. 147-158 in R. E. Ricklefs and D. Schluter, eds., Species Diversity in Ecological Communities: Historical and Geographical Perspectives. The University of Chicago Press, Chicago.

Coen, E. 1983. Climate. Pp. 35-46 in D. H. Janzen, ed., Costa Rican Natural History. The University of Chicago Press, Chicago.

Collar, N. J., L. P. Gonzaga, N. Krabbe, A. Madrono Nieto, L. G. Naranjo, T. A. Parker III, and D. C. Wege. 1992. The ICBP/IUCN Red Data Book. 3rd ed., part 2, Threatened Birds of the Americas. International Council for Bird Preservation (ICBP), Cambridge.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

Corlett, R. T. 1995. Tropical secondary forests. Progress in Physical Geography 19: 159-172.

Corlett, R. T., and I. M. Turner. 1997. Long-term survival in tropical forest remnants in Singapore and Hong Kong. Pp. 333-345 in W. F. Laurance and R. O. Bierregaard, Jr., eds., Tropical Forest Remnants. The University of Chicago Press, Chicago.

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. American Naturalist 137 (1): 27-49.

Dallmeier, F., ed. 1992. Long-Term Monitoring of Biological Diversity in Tropical Forest Areas. UNESCO, Paris.

Daubenmire, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in northeastern Costa Rica. Journal of Ecology 60: 147-170.

Denslow, J. S. 1985. Disturbance mediated coexistence of species. Pp. 307-323 in S. T. A. Pickett and P. S. White, eds., The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Diamond, J. M. 1980. Patchy distributions of tropical birds. Pp. 57-74 in M. E. Soule and B. A. Wilcox, eds., Conservation Biology: An Evolutionary-Ecological Perspective. Sinauer Associates, Sunderland, Massachusetts.

-----. 1989. The present, past and future of human-caused extinction. Philosophical Transactions of the Royal Society of London B 325: 469-477.

Diamond, J. M., K. D. Bishop, and S. Van Balen. 1987. Bird survival in an isolated Javan woodland: Island or mirror? Conservation Biology 1 (2): 132-142.

Dirzo, R., and A. Miranda. 1990. Contemporary neotropical defaunation and forest structure, function, and diversity--A sequel to John Terborgh. Conservation Biology 4 (4): 444-447.

Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. Ecology 75 (3): 615-626.

Dodson, C. H., and A. H. Gentry. 1992. Florula de Capeira. Banco Nacional de Ecuador, Quito.

Dunning, J. B., Jr. 1993. Handbook of avian body masses. CRC Press, Boca Raton, Florida.

Ehrendorfer, F. 1979. Reproductive biology in island plants. Pp. 293-306 in D. Bramwell, ed., Plants and Islands. Academic Press, London.

Eisenberg, J. F. 1980. The density and biomass of tropical mammals. Pp. 35-55 in M. E. Soule and B. A. Wilcox, eds., Conservation Biology: An Evolutionary-Ecological Perspective. Sinauer Associates, Sunderland, Massachusetts.

Endress, P. K. 1994. Diversity and Evolutionary Biology of Tropical Flowers. Cambridge University Press, Cambridge.

Erwin, T. 1982. Tropical forests: Their richness in Coleoptera and other arthropod species. Coleopterists' Bulletin 36 (1): 74-75.

Estrada, A., R. Coates-Estrada, and D. A. Meritt, Jr. 1997. Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. Biodiversity and Conservation 6 (1): 19-44

Estrada, A., R. Coates-Estrada, D. Meritt, Jr., S. Montiel, and D. Curiel. 1993. Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. Vegetatio 107/108: 245-257.

Faaborg, J. 1979. Qualitative patterns of avian extinction on neotropical land-bridge islands: Lessons for conservation. Journal of Applied Ecology 16: 99-107.

Fensham, R. J. 1995. Floristics and environmental relations of inland dry rainforest in north Queensland, Australia. Journal of Biogeography 22: 1047-1063.

Foster, R. B. 1990. Heterogeneity and disturbance in tropical vegetation. Pp. 75-92 in M. E. Soule and B. A. Wilcox, eds., Conservation Biology: An Evolutionary-Ecological Perspective. Sinauer Associates, Sunderland, Massachusetts.

Galli, A., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. The Auk 93: 356-364.

Gaston, K. J. 1996. Species-range-size distributions: Patterns, mechanisms and implications. Trends in Ecology and Evolution 11: 197-201.

Gaston, K. J., and T. M. Blackburn. 1995. Birds, body size and the threat of extinction. Philosophical Transactions of the Royal Society of London B 347: 205-212.

Gentry, A. H. 1982. Patterns of Neotropical plant species diversity. Evolutionary Biology 15: 1-84.

-----. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75: 1-34.

-----, ed. 1990. Four Neotropical Rainforests. Yale University Press, New Haven, Connecticut.

-----. 1991. The distribution and evolution of climbing plants. Pp. 3-42 in F. E. Putz and H. A. Mooney, eds., The Biology of Vines. Cambridge University Press, Cambridge.

-----. 1993. A Field Guide to the Families and Genera of Woody Plants of Northwest South America. Conservation International, Washington, D. C.

-----. 1995. Diversity and floristic composition of neotropical dry forests. Pp. 146-194 in S. H. Bullock, H. A. Mooney, and E. Medina, eds., Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge.

Gerhardt, K., and H. Hytteborn. 1992. Natural dynamics and regeneration methods in tropical dry forests: An introduction. Journal of Vegetation Science 3: 361-364.

Gessner, F. 1956. Wasserhaushalt der Epiphyten und Lianen. Pp. 915-950 in H. Ruhland, ed., Handbuch der Pflanzenphysiologie, Vol. III. Springer-Verlag, Berlin.

Gibson, A. C., ed. 1996. Neotropical Biodiversity and Conservation. Mildred E. Mathias Botanical Garden 1, UCLA, Los Angeles.

Gillespie, T. W. 1994. A Biogeographical and Cultural Ecological Assessment of Nature Reserves on the Island of Ometepe, Nicaragua. Master's Thesis, California State University, Chico.

-----. 1995. Fauna Silvestre de Ometepe, Technical Report 11. Ministry of Natural Resources and the Environment, Managua, Nicaragua.

-----. 1998. An application of extinction and conservation theories for forest birds in Nicaragua. In review, Ecological Applications.

Gillespie, T. W., H. Walter, and J. C. Martinez-Sanchez. 1996. Flora y Vegetacion del Isla de Ometepe, Technical Report 13. Ministry of Natural Resources and the Environment, Managua, Nicaragua.

Gillespie, T. W., and K. Nicholson. 1997. Checklist, biogeography, and natural history characteristics of herpetofauna, avifauna, and mammals in Nicaragua, Technical Report 18. Ministry of Natural Resources and the Environment, Managua, Nicaragua.

Gillespie, T.W. and B. Prigge. 1998. Flora and vegetation of a primary successional community along an altitudinal gradient. In press, Brenesia

Glander, K. E. 1996. The Howling Monkeys of La Pacifica. Duke University Primate Center, Durham, North Carolina.

Gotelli, N. J., and G. R. Graves. 1990. Body size and the occurrence of avian species on land-bridge islands. Journal of Biogeography 17: 315-325.

-----. 1996. Null Models in Ecology. Smithsonian Institution Press, Washington, D. C.

Greenberg, R. 1992. Forest migrants in non-forest habitats on the Yucatan peninsula. Pp. 273-286 in J. M. Hagan III and D. W. Johnston, eds., Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington, D. C.

-----. 1996. Managed forest patches and the diversity of birds in southern Mexico. Pp. 59-90 in J. Schelhas and R. Greenberg, eds., Forest Patches in Tropical Landscapes. Island Press, Washington, D. C.

Greenberg, R., P. Bichier, and J. Sterling. 1997. Bird populations in rustic and planted shade coffee plantations of eastern Chiapas, Mexico. Biotropica 29 (4): 501-514.

Hammond, D. S., and V. K. Brown. 1995. Seed size of woody plants in relation to disturbance, dispersal, soil type in wet Neotropical forests. Ecology 76 (8): 2544-2561.

Hanski, I., and M. Gyllenberg. Uniting two general patterns in the distribution of species. Science 275: 397-400.

Harrington, G. N., A. K. Irvine, F. H. J. Crome, and L. E. Moore. 1997. Regeneration of large-seeded trees in Australian rainforest fragments: A study of higher-order interactions. Pp. 292-303 in W. F. Laurance and R. O. Bierregaard, Jr., eds., Tropical Forest Remnants. The University of Chicago Press, Chicago.

Hartshorn, G. S. 1983. Plants: Introduction. Pp. 118-157 in D. H. Janzen, ed., Costa Rican Natural History. The University of Chicago Press, Chicago.

Hartshorn, G. S., and B. E. Hammel. 1994. Vegetation types and floristic patterns. Pp. 73-89 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds., La Selva: Ecology and Natural History of a Neotropical Rainforest. University of Chicago Press, Chicago.

Heybrock, G. 1984. Der Tayrona-Trockenwald Nord-Kolumbiens. Eine Okosystemstudie unter besonderer Berucksichtigung von Biomasse und Blattflachenindex (LAI). Giessener Geographische Schriften 55: 1-104.

Heywood, V. H., ed. 1993. Flowering Plants of the World. Oxford University Press, New York.

Heywood, V. H., G. M. Mace, R. M. May, and S. N. Stuart. 1994. Uncertainties in extinction rates. Nature 368: 105.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr. 1971. Forest environments in tropical life zones. Pergamon Press, New York.

Holmes, R. T., and S. K. Robinson. 1981. Tree species preference of foraging insectivorous birds in a northern hardwood forest. Oecologia 48: 31-35.

Hopkins, B. 1983. Successional processes. Pp. 605-616 in F. Bourliere, ed., Tropical Savannas. Elsevier, New York.

Howe, H. E. 1984. Implications of seed dispersal by animals for tropical reserve management. Biological Conservation 30: 261-281.

Howe, H. E., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13: 201-228.

Howell, S. N. G., and S. Webb. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford University Press, Oxford.

Howell, T. R. 1969. Avian distribution in Central America. The Auk 86: 293-326.

-----. 1971. An ecological study of the birds of the lowland pine savanna and the adjacent rain forest in northeastern Nicaragua. The Living Bird 10: 185-242.

-----. 1983. Birds of Nicaragua. Unpublished manuscript, Los Angeles, California.

Hubbell, S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. Science 203: 1299-1309.

Hubbell, S. P., and R. B. Foster. 1986. Commonness and rarity in a Neotropical forest: Implications for tropical tree conservation. Pp. 205-231 in M. E. Soule, ed., Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts.

Huston, M. 1980. Soil nutrients and community structure in Costa Rican forests. Journal of Biogeography 7: 147-157.

Incer, J. B. 1975. Geographia ilustrada de Nicaragua. Editora y distribuidora, Nicaraguauense S. A., Managua, Nicaragua.

IRENA (Instituto de Recursos Naturales y del Ambiente). 1990. El sistema de areas silverstres protegidas de Nicaragua. IRENA, Managua, Nicaragua.

-----. 1994. Plan de Accion Ambiental. IRENA/ECOT-PAF, Managua, Nicaragua.

IUCN (International Union for the Conservation of Nature and Natural Resources). 1992. Protected Areas of the World: A Review of National Systems. Vol. 4, Nearctic and Neotropical. IUCN, Gland, Switzerland.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. American Naturalist 101: 233-249.

-----. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54 (3) 687-708.

-----. ed. 1983a. Costa Rican Natural History. The University of Chicago Press, Chicago.

-----. 1983b. No park is an island: Increase in interference from outside as park size decreases. Oikos 41: 402-410.

-----. 1986a. The future of tropical biology. Annual Review of Ecology and Systematics 17: 305-324.

-----. 1986b. Guanacaste National Park: Tropical Ecological and Biocultural Restoration. Editorial Universidad Estatal a Distancia, San Jose.

-----. 1988a. Tropical dry forests: The most endangered major tropical ecosystem. Pp. 130-137 in E. O. Wilson, ed., Biodiversity. Natural Academy Press, Washington, D. C.

-----. 1988b. Management of habitat fragments in a tropical dry forest: Growth. Annals of the Missouri Botanical Garden 75: 105-116.

-----. 1988c. Guanacaste National Park: Tropical ecological and biocultural restoration. Pp. 143-192 in J. Cairns, Jr., ed., Rehabilitating Damaged Ecosystems. CRC Press, Boca Raton, Florida.

Janzen, D. H., and R. Liesner. 1980. Annotated checklist of lowland Guanacaste Province, Costa Rica, exclusive of grasses and nonvascular cryptograms. Brenesia 18: 15-90.

Janzen, D. H., and P. S. Martin. 1982. Neotropical anachronisms: The fruits the Gomphotheres ate. Science 215: 19-27.

Jordano, P. 1995. Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interactions. American Naturalist 145: 163-191.

Jiménez, Q. 1993. Arboles Maderables en Peligro de Extinction en Costa Rica. INBio 121. San Jose, Costa Rica.

Karr, J. R. 1977. Ecological correlates of rarity in a tropical forest bird community. The Auk 94: 240-247.

-----. 1982. Avian extinction on Barro Colorado Island, Panama: A reassessment. American Naturalist 119 (2): 220-239.

-----. 1990. Avian survival rates and the extinction process on Barro Colorado Island, Panama. Conservation Biology 4: 391-396.

Karr, J. R., S. K. Robinson, J. G. Blake, and R. O. Bierregaard, Jr. 1990. Birds of four Neotropical forests. Pp. 237-269 in A. H. Gentry, ed., Four Neotropical Rainforests. Yale University Press, New Haven, Connecticut.

Karr, J. R., and R. R. Roth. 1971. Vegetation structure and avian diversity in several New World areas. American Naturalist 105: 423-435.

Kattan, G. 1992. Rarity and vulnerability: The birds of the Cordillera Central of Colombia. Conservation Biology 6: 64-70.

Kattan, G. H., H. Alvarez-Lopez, and M. Giraldo. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. Conservation Biology 8 (1): 138-146.

Keel, S., A. H. Gentry, and L. Spinzi 1993. Using vegetation analysis to facilitate the selection of conservation sites in eastern Paraguay. Conservation Biology 7 (1): 66-75.

Kramer, E. A. 1997. Measuring landscape changes in remnant tropical dry forests. Pp. 386-399 in W. F. Laurance and R. O. Bierregaard, Jr., eds., Tropical Forest Remnants. The University of Chicago Press, Chicago.

Krebs, C. J. 1994. Ecology: The Experimental Analysis of Distribution and Abundance, 4th ed. Harper Collins, New York.

Lanly, J. P. 1984. Quantifying changes in forest cover in the humid tropics: Overcoming current limitations. Journal of World Forest Resources 1: 3-63.

Laurance, W. F. 1997. Hyper-disturbed parks: Edge effects and the ecology of isolated rainforest reserves in tropical Australia. Pp. 71-90 in W. F. Laurance and R. O. Bierregaard, Jr., eds., Tropical Forest Remnants. The University of Chicago Press, Chicago.

Laurance, W. F., and R. O. Bierregaard, Jr. 1997. Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. The University of Chicago Press, Chicago.

Leck, C. F. 1979. Avian extinctions in an isolated tropical wet-forest preserve, Ecuador. The Auk 96: 343-352.

Lerdau, M., J. Whitbeck, and N. M. Holbrook. 1991. Tropical deciduous forest: Death of a biome. Trends in Ecology and Evolution 6 (7): 201-202.

Lott, E. J., S. H. Bullock, and J. A. Solis Magallanes. 1987. Floristic diversity and structure of a tropical deciduous forest of coastal Jalisco. Biotropica 19: 228-235.

Maass, J. M. 1995. Conversion of tropical dry forest to pasture and agriculture. Pp. 399-422 in S. H. Bullock, H. A. Mooney, and E. Medina, eds., Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge.

MacArthur, R. H. 1964. Environmental factors affecting species diversity. American Naturalist 98: 387-97.

MacArthur, R. H., J. M. Diamond and J. R. Karr. 1972. Density compensation in island faunas. Ecology 53: 330-342.

MacArthur, R. H., H. Recher, and M. L. Cody. 1966. On the relation between habitat selection and species diversity. The American Naturalist 100: 319-332.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey.

Maldonado, T., J. Bravo, G. Castro, Q. Jimenez, and O. Saborio. 1995. Evaluacion Ecologica Rapida Region del Tempisque, Guanacaste, Costa Rica. Fundacion Neotropica, Costa Rica.

MARENA (Ministerio del Ambiente y Recursos Naturales). 1997. Plan de manejo: Refugio de vida silvestre "La Flor". MARENA, Managua, Nicaragua.

Martinez-Sanchez, J. C. 1986. Causes affecting the survival of birds of prey in Nicaragua. Birds of Prey Bulletin 3: 43-47.

McBirney, A. R., and H. Williams. 1965. Volcanic History Of Nicaragua. University of California Press, Berkeley, California.

McDade, L. A., K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds. 1994. La Selva: Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago.

Meave, J., and M. Kellman. 1994. Maintenance of rain forest diversity in riparian forests of tropical savannas: Implications for species conservation during Pleistocene drought. Journal of Biogeography 21: 121-135.

Medina, E. 1995. Diversity of life forms of higher plants in neotropical dry forests. Pp. 221-242 in S. H. Bullock, H. A. Mooney, and E. Medina, eds., Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge.

Meffe, G. K., and C. R. Carroll. 1994. Principles of Conservation Biology. Sinauer Associates, Sunderland, Massachusetts.

Murcia, C. 1996. Forest fragmentation and the pollination of neotropical plants. Pp. 19-36 in J. Schelhas and R. Greenberg, eds., Forest Patches in Tropical Landscapes. Island Press, Washington, D. C.

Murphy, P. G., and A. E. Lugo. 1986a. Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17: 67-88.

-----. 1986b. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18: 89-96.

-----. 1995. Dry forests of Central America and the Caribbean. Pp. 9-34 in S. H. Bullock, H. A. Mooney, and E. Medina, eds., Seasonally Dry Tropical Forests. Cambridge University Press, Cambridge.

Myers, N. 1980. Conversion of Tropical Moist Forests. National Academy of Sciences, Washington, D. C.

Nason, J. D., P. R. Aldrich, and J. L. Hamrick. 1997. Dispersal and the dynamics of genetic structure in fragmented tropical tree populations. Pp. 304-320 in W. F. Laurance and R. O. Bierregaard, Jr., eds., Tropical Forest Remnants. The University of Chicago Press, Chicago.

Newmark, W. D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara Mountains, Tanzania. Conservation Biology 5 (1): 67-78.

Nietschmann, B. 1990. Conservation by conflict in Nicaragua. Natural History (November): 42-49.

Olson, S. L. 1989. Extinction on islands: Man as a catastrophe. Pp. 50-53 in D. Western and M. C. Pearl, eds., Conservation for the Twenty-first Century. Oxford University Press, New York.

Olson, S. L., and H. F. James. 1991. Descriptions of thirty-two new species of birds from the Hawaiian islands, Part 1: Non-passeriformes. Ornithological Monographs 45: 1-88.

Opler, P. A., G. W. Frankie, and H. G. Baker. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 68: 167-188.

Orians, G. H. 1969. The number of bird species in some tropical forests. Ecology 50: 783-801.

Parsons, J. J. 1983. Beef cattle. Pp. 77-79 in D. H. Janzen, ed., Costa Rican Natural History. The University of Chicago Press, Chicago.

Parthasarathy, N., and R. Karthikeyan. 1997. Plant biodiversity inventory and conservation of two tropical dry evergreen forests on the Coromandel coast, south India. Biodiversity and Conservation 6: 1063-1083.

Patterson, B. D. 1987. The principle of nested subsets and its implications for biological conservation. Conservation Biology 1 (4): 323-334.

Phillips, O. L., and P. H. Raven. 1996. A strategy for sampling Neotropical forests. Pp. 141-165 in A. C. Gibson, ed., Neotropical Biodiversity and Conservation. Mildred E. Mathias Botanical Garden 1, UCLA, Los Angeles.

Pickett, S. T. A., and P. S. White, eds. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Pimm, S .L., H. L. Jones, and J. M. Diamond. 1988. On the risk of extinction. American Naturalist 132: 757-785.

Policansky, D. 1982. Sex change in plants and animals. Annual Review of Ecology and Systematics 13: 471-495.

Preston, F. W. 1962. The canonical distributors of commonness and rarity, Parts 1 and 2. Ecology 43: 185-215, 410-432.

Primack, R. B. 1993. Essentials of Conservation Biology. Sinauer Associates, Sunderland, Massachusetts.

Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65: 1713-1724.

Rabinowitz, D., S. Cairns, and T. Dillion. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. Pp. 182-204 in M. Soule, ed., Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts.

Raven, P. H. 1987. The scope of the plant conservation problem world-wide. Pp. 19-29 in D. Bramwell, O. Hamann, V. H. Heywood, and H. Synge, eds., Botanic Gardens and the World Conservation Strategy. Academic Press, New York.

Redford, K. 1992. The empty forest. BioScience 42: 412-422.

Remsen, J. V., Jr. 1994. Use and misuse of bird lists in community ecology and conservation. The Auk 111: 225-227.

Ricklefs, R. E., and D. Schluter, eds. 1993. Species Diversity in Ecological Communities: Historical and Geographical Perspectives. The University of Chicago Press, Chicago.

Robinson, J. G. 1996. Hunting wildlife in forest patches: an ephemeral resource. Pp. 111-130 in J. Schelhas and R. Greenberg, eds., Forest Patches in Tropical Landscapes. Island Press, Washington, D. C.

Robinson, J. G., and K. H. Redford. 1986. Body size, diet, and population density of Neotropical forest mammals. The American Naturalist 128: 665-680.

Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. The Auk 101: 672-684.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.

Rosenzweig, M. L., and Z. Abramsky. 1993. How are diversity and productivity related? Pp. 52-65 in R. E. Ricklefs and D. Schluter, eds., Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago.

Rundel, P. W., and A. C. Gibson. 1996. Adaptive strategies of growth form and physiological ecology in neotropical lowland rain forest plants. Pp. 33-71 in A. C. Gibson, ed., Neotropical Biodiversity and Conservation. Mildred E. Mathias Botanical Garden 1, UCLA, Los Angeles.

Rzedowski, J. 1988. Vegetacion de Mexico. Editorial Limusa, D. F., Mexico.

Sabogal, C. 1992. Regeneration of tropical dry forests in Central America, with examples from Nicaragua. Journal of Vegetation Science 3: 407-416.

Sakai, A. K., W. L. Wagner, D. M. Ferguson, and D. R. Herbst. 1995. Biogeographical and ecological correlates of dioecy in the Hawaiian flora. Ecology 76 (8): 2530-2543.

Sauer, J. D. 1969. Oceanic islands and biogeographic theory: a review. Geographical Review 59: 582-593.

Sauer, J. D. 1979. Living fences in Costa Rican agriculture. Turrialba 29 (4): 255-261.

Savage, M. 1992. Germination of forest species under an anthropogenic vine mosaic in Western Samoa. Biotropica 24 (3): 460-462.

Schelhas, J., and R. Greenberg, eds. 1996. Forest Patches in Tropical Landscapes. Island Press, Washington, D. C.

Shafer, C. L. 1990. Nature Reserves: Island Theory and Conservation Practice. Smithsonian Institution Press, Washington, D. C.

Simberloff, D. S. 1986. Are we on the verge of a mass extinction in tropical rainforests? Pp. 165-180 in D. K. Elliot, ed., Dynamics of Extinction. Wiley-Interscience, New York.

Simberloff, D. S., and J. Martin. 1991. Nestedness of insular avifaunas: Simple summary statistics masking complex species patterns. Ornis Fennica 68: 178-192.

Snow, B. K., and D. W. Snow. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. The Auk 88: 291-322.

Soule, M. E., and B. A. Wilcox, eds. 1980. Conservation Biology: An Evolutionary-Ecological Perspective. Sinauer Associates, Sunderland, Massachusetts.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: How so many species coexist in the tropics. American Naturalist 133 (2): 240-256.

Stiles, F. G. 1983. Birds: Introduction and checklist. Pp. 502-544 in D. H. Janzen, ed., Costa Rican Natural History. The University of Chicago Press, Chicago.

-----. 1985. Conservation of forest birds in Costa Rica: Problems and perspectives. Pp. 141-168 in A. W. Diamond and T. E. Lovejoy, eds., Conservation of Tropical Forest Birds. ICBP Technical Publication no. 4, Cambridge.

Stiles, F. G., and D. J. Levey. 1994. Birds of La Selva and vicinity. Pp. 384-393 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds., La Selva: Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago.

Stiles, F. G., and A. Skutch. 1989. A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, New York.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. Neotropical Birds: Ecology and Conservation. The University of Chicago Press, Chicago.

Swaine, M. D. 1992. Characteristics of dry forest in West Africa and the influence of fire. Journal of Vegetation Science 3: 365-374.

Swaine, M. D., D. Lieberman, and J. B. Hall. 1990. Structure and dynamics of a tropical dry forest in Ghana. Vegetatio 88: 31-51.

Taylor, B. W. 1963. An outline of the vegetation of Nicaragua. Journal of Ecology 51: 27-54.

Talyor, C. M., and N. J. Gotelli. 1994. The macroecology of Cyprinella: correlates of phylogeny, body size and geographic range. American Naturalist 144: 549-569.

Terborgh, J. W. 1974. Preservation of natural diversity: The problem of extinction prone species. Bioscience 24: 715-722.

-----. 1985. Habitat selection in Amazonian birds. Pp. 311-338 in M. L. Cody, ed., Habitat Selection in Birds. Academic Press, Orlando, Florida.

-----. 1988. The big things that run the world--A sequel to E. O. Wilson. Conservation Biology 2: 402-403.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pp. 119-133 in M. Soule, ed., Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA.

Thiollay, J.-M. 1984. Raptor community structure of a primary rain forest in French Guiana and effect of human hunting pressure. Raptor Research 18 (4): 117-122.

-----. 1989. Area requirements for the conservation of rain forest raptors and game birds in French Guiana. Conservation Biology 3: 128-137.

-----. 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. Conservation Biology 6 (1): 47-63.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: A review of the evidence. Journal of Applied Ecology 33: 200-209.

Turner, I. M., K. S. Chua, J. S. Y. Ong, B. C. Soong, and H. T. W. Tan. 1996. A century of plant species loss from an isolated fragment of lowland tropical rain forest. Conservation Biology 10: 1229-1244.

Turner, I. M., and R. T. Corlett. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends in Ecology and Evolution 11: 330-333.

Turner, I. M., H. T. W. Tan, Y. C. Wee, A. bin Ibrahim, P. T. Chew, and R. T. Corlett. 1994. A study of plant species extinction in Singapore: Lessons for the conservation of tropical biodiversity. Conservation Biology 8: 705-712.

Van der Pijl, L. 1982. Principles of dispersal in higher plants. Springer-Verlag, Berlin.

Veblen, T. T. 1982. The effects of introduced wild animals on New Zealand forests. Annals of the Association of American Geographers 72: 372-397.

Veblen, T. T., T. Kitzberger, and A. Lara. 1992. Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. Journal of Vegetation Science 3: 507-520.

Veblen, T. T., and D. C. Lorenz. 1986. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. Physical Geography 7: 1-24.

Veblen, T. T., M. Mermoz, C. Martin, and E. Ramilo. 1989. Effects of exotic deer on forest structure and composition in northern Patagonia. Journal of Applied Ecology 26: 711-724.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver & Boyd, Edinburgh.

Warburton, N. H. 1997. Structure and conservation of forest avifauna in isolated rainforest remnants in tropical Australia. Pp. 190-206 in W. F. Laurance and R. O. Bierregaard, Jr., eds., Tropical Forest Remnants. The University of Chicago Press, Chicago.

Watts, I. E. M. 1954. Line squalls of Malaya. Journal of Tropical Geography 3: 1-14.

Weyl, R. 1980. Geology of Central America. Gebruder Borntraeger, Berlin.

White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: An introduction. Pp. 17-33 in S. T. A. Pickett and P. S. White, eds., The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Whitmore, T. C. 1997. Tropical forest disturbance, disappearance, and species loss. Pp. 3-12 in W. F. Laurance and R. O. Bierregaard, Jr., eds., Tropical Forest Remnants. The University of Chicago Press, Chicago.

Whittaker, R. H. 1975. Communities and Ecosystems, 2nd ed. Macmillan, New York.

Wiens, J. A. 1989. The Ecology of Bird Communities, Vol. 1: Foundations and Patterns. Cambridge University Press, Cambridge.

Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs 44: 153-169.

-----. 1979. The composition of avian communities in remanescent woodlots in southern Brazil. Papeis Avulsos Zoologia 33: 1-25.

IMAGE EVALUATION
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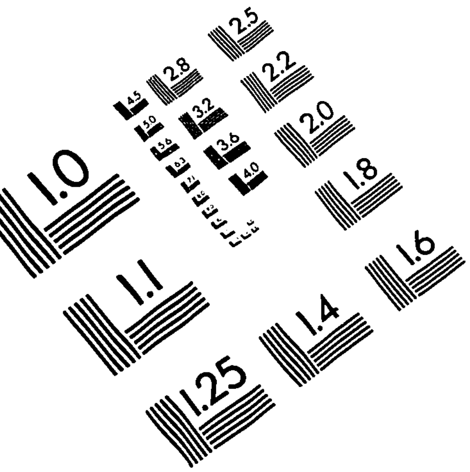

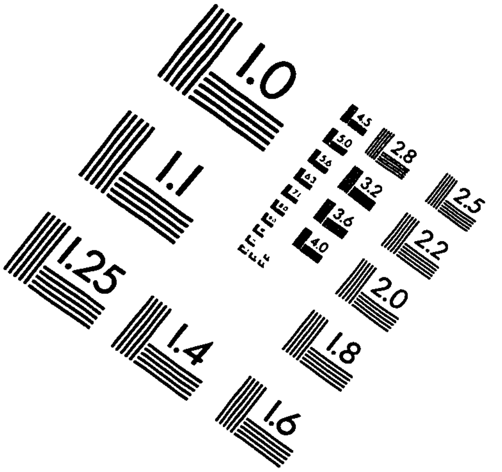

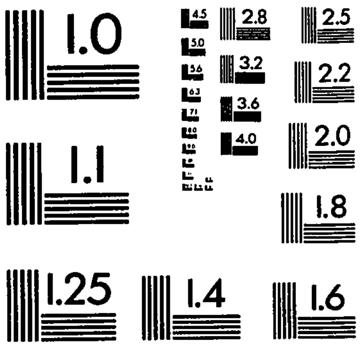

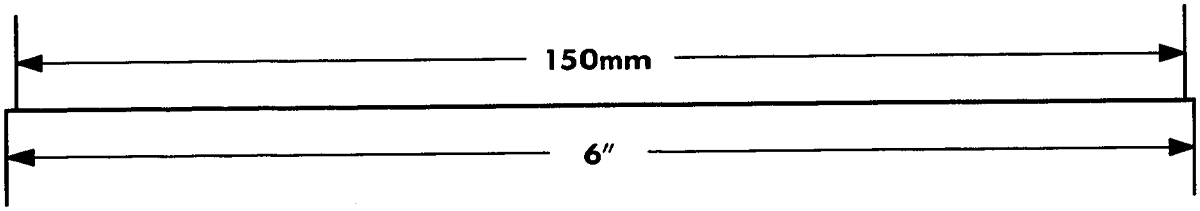

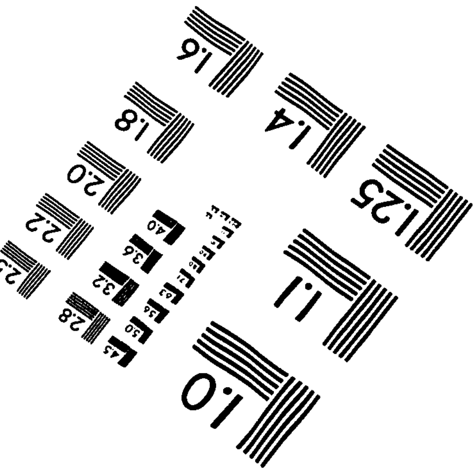

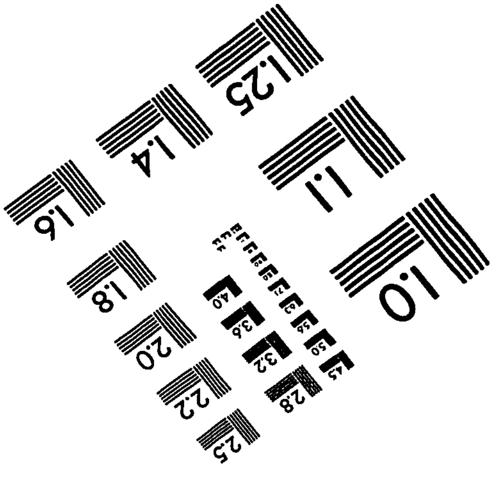

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