Diversity, composition, and structure of tropical dry forests in Central America

Thomas W. Gillespie[1], Alfredo Grijalva[2] & Christine N. Farris[3]
[1]*Department of Geography, 257 Davis Hall, University of South Florida, St. Petersburg, FL 33701-5016, USA;*
[2]*Herbario Nacional, Universidad Centroamericana. Frente a radio Ya, Managua, Nicaragua;* [3]*Department of Geography, University of California, Los Angeles, 1255 Bunche Hall, Los Angeles, CA 90095, USA*

Abstract

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 ecosystem in the lowland tropics. Plots 1000 m^2 were established in seven tropical dry forests in Costa Rica and Nicaragua in order to compare levels of species richness to other Neotropical dry forest sites and to identify environmental variables associated with species richness and abundance. A total of 204 species and 1484 individuals $\geq$ 2.5 cm were encountered. Santa Rosa National Park was the richest site with the highest family (33), genera (69), and species (75) diversity of all sites. Species richness and forest structure were significantly different between sites. Fabaceae was the dominant tree and shrub family at most sites, but no species was repeatably dominant based on number of stems in all fragments of tropical dry forest. Central American dry forests had similar species richness when compared to other Neotropical forests. There was no correlation between forest cover within reserves, or precipitation and plant species richness. There was a significant correlation between anthropogenic disturbance (intensity and frequency of fire, wood collection, grazing) and total species richness, tree and shrub species richness, and liana abundance. These results suggest controlling levels on anthropogenic disturbance within reserves should be a high priority for resource managers in Central America. Further research in forest fragments which examine individual and a combination of disturbance agents would help clarify the importance of anthropogenic disturbance on species richness and abundance.

Introduction

Tropical dry forest in Central America once extended along the Pacific coast from sea level to 400 m from Guatemala to Costa Rica with a disjunct patch in Panama (Murphy & Lugo 1995). Today, tropical dry forests have been reduced to less than 0.1% of their original expanse on the Pacific side of Central America (Janzen 1988a). There is some dispute over the conservation value of Central American tropical dry forest. Some consider Central American tropical dry forest one of the most endangered ecosystems in the lowland tropics, and argue that it deserves a high priority for conservation (Janzen 1986, 1988a). Others believe that tropical dry forest in Central America deserves a relatively low priority for conservation compared to other dry forests in other Neotropical regions (Lott et al. 1987; Gentry 1995). An assessment of species diversity in Central America could provide valuable information on conservation priorities in the region because there have been few comparative or quantitative studies of diversity and structure in remaining forest fragments in Central America (Lerdau et al. 1991; Gerhardt & Hytteborn 1992).

Gentry (1995) noted that the continental subtropical dry forests (along the Tropics of Cancer and Capricorn) of Mexico and Bolivia may be richer in overall number of species 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. 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. For instance, Gentry's data on tropical dry forests of Central America came from only one dry forest sample. This sample was actually a conglomerate of two sites totaling only 700 m^2 and not the standard 0.1 ha plot (Gentry 1982). This may not have been an adequate sample to determine plant species richness for Central American tropical dry forest.

There are few studies on plant alpha diversity in tropical dry forests of Central America. However, research in tropical forests have identified a number of variables associated with plant species richness. Annual precipitation and seasonality are tightly correlated with lowland plant diversity, but this pattern may not occur within neotropical dry forests (Gentry 1988; Fensham 1995; Clinebell et al. 1995). Gentry (1995) noted that once the critical rainfall thresholds needed to maintain a closed-canopy dry forest is achieved, increases in the amount of precipitation have a negligible effect 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 habitat area. A number of studies note that island or habitat area can be correlated with species richness because of stochastic area-dependent extinction that results in lower species richness (MacArthur & Wilson 1967; Shaffer 1981; Pimm et al. 1988). Since tropical dry forests have been reduced to less than 0.1% of their original expanse, the size of remaining fragments may be an important predictor of plant species richness (Janzen 1988a). However, recent studies have noted that small fragments of tropical forest can maintain significant levels of plant diversity even after being fragmented for over 400 years (Turner et al. 1994; Whitmore 1997). Anthropogenic disturbances, such as burning, grazing, and wood collection, may also affect plant species richness (Budowski 1966; Janzen 1986; Sabogal 1992; Swaine 1992; Maass 1995). Yet, most research on disturbance is anecdotal and few researchers quantify or qualitatively rank anthropogenic disturbance as it relates to plant species richness (Murphy & Lugo 1995).

This analysis of tropical dry forest has three primary objectives:
 – to summarize the diversity, floristic composition, and structure of seven remaining tropical dry forest fragments,
 – to compare data on plant species richness in Central American dry forests with other Neotropical dry forests, and
 – to identify ecological and environmental variables associated with plant richness and abundance in Central America.

Methods

Study sites

Study sites were located in seven remaining fragments of tropical dry forests in Costa Rica and Nicaragua (Figure 1). These forests have all been decreed conservation areas and are some of the best and largest remaining patches of tropical dry forest in Central America. Study sites include: (1) Santa Rosa National Park, Costa Rica (10°50' N, 85°40' W), (2) Palo Verde National Park, Costa Rica (10°20' N, 85°20' W), (3) La Flor Nature Reserve, Nicaragua (11°8' N, 85°47' W), (4) Chacocente Wildlife Refuge, Nicaragua (11°32' N, 86°12' W), (5) Reserve on the island of Ometepe, Nicaragua (11°32' N, 85°37' W), (6) Masaya National Park, Nicaragua (11°58' N, 86°06' W) and, (7) Cosiguina Nature Reserve, Nicaragua (12°54' N, 87°32' W).

Field methods

Plots totaling 1000 m^2 were established at each site following Gentry (1982, 1988). Each sample consists of ten 2 × 50 m transects in which all plants ≥ 2.5 cm dbh rooted in the sample plot were censused. Lianas rooted within the transect were measured at their widest point and stems ascending from different rooting points were recorded as separate individuals (Gentry 1982; Lott et al. 1987). The diameter of erect plants (non-climbing) were measured at 1.4 m and the diameter of each stem 2.5 cm or greater was recorded. In each sample, individual transects were laid from a randomly selected starting point. Adjacent transects were separated by 20 m, which resulted in transects covering a diversity of slopes (Gentry 1982, 1988). 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 & Raven 1996). All voucher specimens were deposited in the herbariums of the Universidad Centroamericana (UCA) in Managua and the University of California, Los Angeles (LA). Species names are
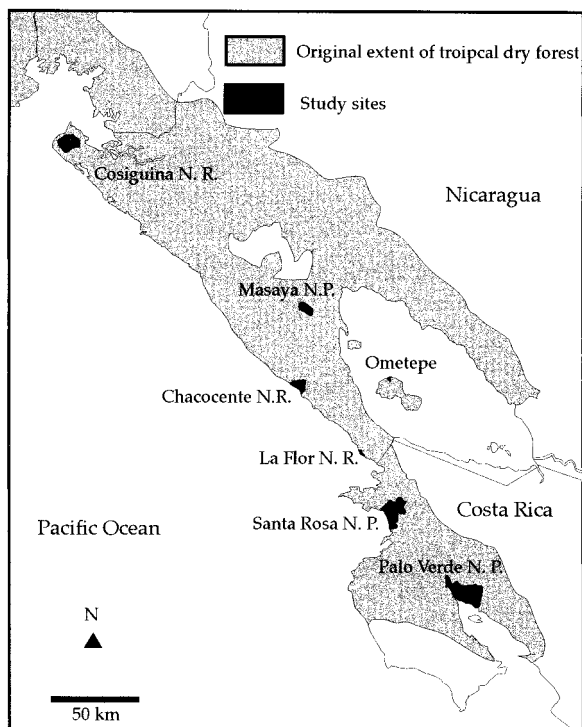
Figure 1. Map of seven conservation areas with tropical dry forest in Central America.

based on those recognized by the Missouri Botanical Garden (Burger 1971; Flora de Nicaragua Project 1998).

Data analysis

Data on plant species richness collected from 0.1 hectare plots from 21 Neotropical dry forest sites were compared with data collected from seven Central American tropical dry forests (Heybrock 1984; Brown et al. 1985; Murphy & Lugo 1986b; Lott et al. 1987; Dodson & Gentry 1992; Keel et al. 1993; Gentry 1995). Although Gentry's 1995 data set contained 28 sites, ten were omitted because they were deemed incomplete. Only sites below 1000 m that totaled 0.1 ha and contained complete floristic data were included. Sites that contain gallery or riparian forest were excluded.

A Spearman's rank correlation was used to identify ecological and environmental variables associated with species richness and abundance at all tropical dry forest sites. All study sites are 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, geologic substrate, and disturbance history (Table 1). Environmental variables of forest area, annual precipitation, and anthropogenic disturbance were collected for all seven study sites. The area of tropical dry forest and semi-deciduous forest cover within each reserve for Costa Rica came from Maldonado et al. (1995) and Kramer (1997) and forest cover in Nicaraguan reserves was calculated from aerial photos following van Wyngaarden (1988). Fire, wood collection, and grazing by livestock are the most important anthropogenic disturbances in tropical dry forest (Murphy & Lugo 1995). All sites were ranked based on the current intensity and frequency of anthropogenic disturbance following Veblen et al. (1992) in which disturbance was qualitatively classified by degree of browsing in three classes, severity of wood collection in three classes, and fire frequency and intensity in three classes. Fire was ranked as (1) for sites with active fire suppression programs and no signs of recent fires, (2) for sites with evidence of only periodic small fires, not annually, and (3) for sites with evidence of large annual fires. Grazing was ranked as (1) for no evidence of any cattle or browsing, (2) for evidence of browsing, cattle seen in the reserve, not daily, and (3) for cattle seen daily in the reserve. Wood collection was ranked as (1) for no current evidence of wood collection, (2) for wood collection heard in reserve and cut trees found in reserve, and (3) wood collection heard daily in the reserve, trees cut in transects after established. The sum of all ranks for each site provided an overall ranking of anthropogenic disturbance within reserves. High ranks signify high levels of anthropogenic disturbance and low ranks signify low levels of anthropogenic disturbance (Table 1).

Results

Diversity

A total of 204 species and morphospecies were encountered in seven fragments of tropical dry forest. Of these, 176 taxa were identified to species or subspecies, eight could only be identified to genus, and 14 could only be identified to family. Six were classified as unknown (an appendix of frequency and density of species sampled is available on the web at www.cas.usf.edu/geography/faculty/tdf.htm). Santa Rosa was the richest site with the highest family, genera, and species richness of all sites (Table 2). The

Table 1. Environmental variables of seven conservation areas with tropical dry forest in Central America

Sites	Forest cover (ha)	Precipitation (mm)	Dry season (months)	Geologic substrate	Fire	Grazing	Wood collection	Anthropogenic disturbance
Palo Verde	1,646	1,717	5	Eocene limestone	2	1	1	4
Cosiguina	5,132	1,827	5	Holocene aeolian ash	3	3	3	9
Santa Rosa	3,556	1,552	6	Pleistocene aeolian ash	1	1	1	3
Masaya	1,300	1,251	6	Holocene *aa* lava	2	2	3	8
Chacocente	1,500	1,362	6	Eocene sandstone	2	1	2	5
La Flor	449	1,805	5	Eocene sandstone	2	1	2	5
Ometepe	420	1,695	5	Holocene *aa* lava	2	1	3	6

Table 2. Summary of floristic diversity for plants $\geq$ 2.5 cm from 0.1 ha samples and mean number of species per transect in seven tropical dry forest sites

Sites	Number of families	Number of genera	Number of species	Mean number of species per 100 m^2 transects($\pm$SD)		
				All forms	Lianas	Trees and shrubs
Cosiguina	27	42	48	10.6 $\pm$ 3.1	2.4 $\pm$ 1.4	9.2 $\pm$ 2.1
Santa Rosa	33	69	75	16.5 $\pm$ 2.9	4.5 $\pm$ 2.1	12.0 $\pm$ 1.3
Palo Verde	29	55	65	14.2 $\pm$ 3.6	3.2 $\pm$ 2.1	11.0 $\pm$ 2.0
Chacocente	28	47	54	13.8 $\pm$ 2.5	2.4 $\pm$ 1.3	11.4 $\pm$ 2.1
Masaya	28	41	44	11.4 $\pm$ 3.1	1.9 $\pm$ 1.0	9.5 $\pm$ 2.8
La Flor	25	52	59	14.1 $\pm$ 2.1	3.7 $\pm$ 1.5	10.4 $\pm$ 1.8
Ometepe	31	42	45	10.8 $\pm$ 3.6	3.7 $\pm$ 1.9	7.1 $\pm$ 2.3

forests in Cosiguina, Masaya, and Ometepe had significantly less species richness than Santa Rosa based on the number of species per transect (Mann–Whitney U, $p = 0.002$, $p = 0.004$, and $p = 0.005$, respectively). There were no significant differences in species richness between Santa Rosa, Palo Verde, La Flor, and Chacocente. However, compared to Santa Rosa, La Flor had significantly less tree and shrub species (Mann–Whitney U, $p = 0.049$) while Chacocente had significantly less liana species (Mann–Whitney U, $p = 0.012$).

Floristic composition

A total of 58 families were identified from all dry forest sites. A majority of these families were not speciose among the sites with approximately 69% of tropical dry forest families represented by two or less species. Fabaceae and Bignoniaceae were the most speciose families followed by Sapindaceae, Rubiaceae, and Euphorbiaceae. When the number of tree and shrub species per family were compared, Fabaceae was the dominant tree and shrub based on number of species per family at all sites except Ome-

tepe (Table 3). Ometepe was dominated by species in the family Rubiaceae and Euphorbiaceae. Bignoniaceae was the most species rich liana family at four sites when liana family richness at all sites were compared. Masaya and Cosiguina both had a higher number of Sapindaceae liana species.

Species composition and number of individuals differed between tropical dry forest sites (Table 4). No species was repeatably abundant based on number of stems per 0.1 ha in all fragments of tropical dry forest. *Bursera simaruba* was the dominant species by frequency at Ometepe and Masaya, among the five most abundant species at Santa Rosa and Cosiguina, and occurred in low densities at Palo Verde, La Flor, and Chacocente. *Bursera simaruba* was also the only species recorded in all tropical dry forest sites. Only three species, *Spondias mombin*, *Cochlospermum vitifolium*, and *Simarouba amara*, were recorded at six sites. A similarity index between tropical dry forest sites (Table 5) revealed that the composition of the Costa Rican sites (Santa Rosa and Palo Verde) were the most similar. Most Nicaraguan tropical dry forest sites had low indices of similarity. The Chacocente and

Table 3. The five most species rich tree and shrub, and liana families by site

Family richness	CS	SR	PV	CH	MA	LF	OM
Number of tree & shrub species							
Fabaceae	6	10	9	9	4	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
Number of liana species							
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

CS = Cosiguina, SR = Santa Rosa, PV = Palo Verde, CH = Chacocente, MA = Masaya, LF = La Flor, OM = Ometepe

La Flor sites on the Pacific coast had the highest similarity within Nicaragua and both sites generally had a higher similarity with Costa Rican sites than with other Nicaragua sites.

Structure

A total of 1484 individuals were encountered from the seven sites (Table 6). Masaya and La Flor had the most tree and shrub individuals while Ometepe and Cosiguina had the lowest number of individuals. Ometepe and Cosiguina had significantly less individuals than all other sites (Mann–Whitney U, $p < 0.05$). Lianas accounted for 20% of all stems in the tropical dry forest. Santa Rosa had the highest number of liana individuals while Cosiguina had the lowest number.

Chacocente and Santa Rosa had the most trees with a dbh $\geq$ 10 cm. La Flor and Palo Verde had the least number of large tree individuals based on total number and proportion of individuals. There were few lianas with a stem diameter $\geq$ 10 cm at all tropical dry forest sites. The average basal area of tropical dry forests in Central America was 22.03 m^2 ha^{-1}. Santa Rosa had the highest basal area of all sites. Chacocente, Cosiguina, La Flor, Masaya, and Palo Verde all had relatively similar basal areas ranging from approximately 21.0 and 23.0 m^2 ha^{-1}. Only Ometepe had significantly lower basal area compared to all other sites (Whitney U, $p < 0.05$).

Table 4. The five most abundant species based on number of stems per 0.1 ha samples at seven tropical dry forest sites

Site	Scientific name	Stems per 0.1 ha
Cosiguina	*Helianthinae* sp.(G895)	10
	Cordia alliodora	9
	Guazuma ulmifolia	8
	Lippia cardiostegia	8
	Bursera simaruba	6
Santa Rosa	*Exostema mexicanum*	15
	Hemiangium excelsum	14
	Arrabidaea mollissima∗	13
	Cydista diversifolia∗	13
	Bursera simaruba	10
Palo Verde	*Allophyllus occidentalis*	38
	Astronium graveolens	25
	Bauhinia glabra∗	18
	Tabebuia ochracea	13
	Lonchocarpus phaseolifolius	12
Chacocente	*Stemmadenia obovata*	22
	Tabebuia ochracea	15
	Thouinidium decandrum	12
	Combretum farinosum∗	11
	Gyrocarpus americanus	11
Masaya	*Bursera simaruba*	57
	Gliricidia sepium	34
	Diospyros nicaraguensis	15
	Cochlospermum vitifolium	15
	Myriocarpa bifurca	13
La Flor	*Calycophyllum candidissimum*	53
	Acacia collinsii	25
	Adenocalymma inundatum∗	18
	Cochlospermum vitifolium	17
	Tabebuia ochracea	16
Ometepe	*Bursera simaruba*	14
	Cecropia peltata	12
	Casearia corymbosa	10
	Bombacopsis quinata	10
	Jatropha curcas	10

∗ = liana

Comparisons to other Neotropical dry forests

Data on plant species richness in tropical dry forest from Central America were compared to other Neotropical dry forests (Table 7). There was no significant difference between the diversity in Central American dry forests compared to a number of Neotropical forests. Family richness, total number of plant species, number of liana species, and number of tree and shrub species were not significantly different than other

Neotropical forests (Mann-Whitney U, $p = 0.61$, $p = 0.16$, $p = 0.65$, $p = 0.11$, respectively). The richest site in Central America, Santa Rosa, was the sixth most diverse site based on family richness and liana richness, and the eighth most diverse site in total species richness and tree and shrub species richness. All other Central American sites, ranked in the bottom half of all sites by categories, with the exception Palo Verde (total species and tree and shrub species) and Ometepe (liana species).

Environmental variables and plant species richness

Environmental variables of area, precipitation, and anthropogenic disturbance were compared to species richness and abundance using a Spearman's rank correlation (Table 8). There was no significant correlation between forest cover within each reserve and plant species richness or abundance. Precipitation was also a poor predictor of species richness at all tropical dry forest sites. Anthropogenic disturbance was significantly correlated with species richness, tree and shrub species richness, and liana abundance.

Discussion

Floristic composition and structure

A number of authors have noted that family richness was predictable in Neotropical dry forests (Murphy & Lugo 1986; Arriaga & León 1989; Gentry 1995). Gentry (1995) found that Fabaceae was consistently the most speciose tree and shrub family, and that Bignoniaceae was the most speciose liana family in Neotropical areas with a strong dry season. Fabaceae was the dominant tree and shrub family at all sites except Ometepe which partially supports Gentry's findings. Bignoniaceae was the dominant liana family in species richness at only four sites. The Masaya and Cosiguina sites each contained only one Bignoniaceae liana species. Disturbance such as cattle grazing and burning may reduce liana diversity most notably Bignoniaceae lianas. Generally, only lianas with high wood density, such as *Combretum farinosum*, and *Serjania* species, are able to persist in areas that are burned. Species abundance based on number of stems per 0.1 ha in dry forest sites was never predictable, and not a single species was repeatably most dominant. *Bursera simaruba* was the only species encountered at all sites but it was only repeatably dominant at two sites. These findings support Gentry's hypothesis that

species dominance is never predictable in different tropical dry forests and is most likely determined by stochastic processes (Hubbell 1979).

Central American tropical dry forest has a lower density of individuals than other Neotropical forests. Gentry (1995) found an average of 370 individuals in 0.1 ha samples of lowland Neotropical dry forest compared to 212 individuals from this study. Differences in tropical dry forest density in Central America may likely be explained by complex interactions of historic disturbances in remaining stands of Central American dry forest. However, direct comparisons are not possible because there are little data on levels of disturbance from other Neotropical sites. Although there was no correlation between tree and shrub abundance and disturbance, there was a correlation for liana abundance. Large lianas are an important physiognomic indicator of mature forests, and the low number of lianas with a dbh $\geq$ 10 cm attests to the fact that there may be no undisturbed or mature tropical dry forests in Central America (Budowski 1970; Gentry 1991). Fire frequency and intensity also affects structure by lowering forest density in different tropical dry forest regions of the world (Sukumar et al. 1992; Swaine 1992; Fensham 1995). In Central American tropical dry forests, fire destroys understory shrubs and lianas that make up a significant portion of the total woody plant structure (Gentry 1982; Bullock 1985; Medina 1995). Most lianas have low wood densities in order to provide higher hydraulic conductivity in their stems and invest resources in growth of length while trees allocate resources to supportive tissue (Gessner 1956; Putz 1984). This low wood density makes 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).

Comparisons to other Neotropical dry forests

Results from this study shared a number of similarities and differences compared to Gentry's (1982) original data on tropical dry forests in Central America. Gentry estimated 22 families, 53 total species, six liana species, and 47 tree and shrub species within 1000 m^2 using a species/area regression to estimate total floristic diversity from a 700 m^2 plot. Gentry's Central American data for total species and tree and shrub species are within the range of our study. However, the number of families and the number of liana species were higher in our study. Although it has been

Table 5. Floristic similarity (Sørensen index) of plants ≥ 2.5 cm dbh tropical dry forests in Central America

Sites	Cosiguina	Santa Rosa	Palo Verde	Chacocente	Masaya	La Flor
Santa Rosa	0.276					
Palo Verde	0.298	0.511				
Chacocente	0.196	0.357	0.417			
Masaya	0.283	0.202	0.255	0.184		
La Flor	0.224	0.418	0.448	0.372	0.252	
Ometepe	0.366	0.250	0.306	0.162	0.337	0.231

Table 6. Summary of forest structure for plants ≥ 2.5 cm from 0.1 ha samples and mean number of individuals and basal area per transect in seven tropical dry forest sites

Sites	Number of individuals per site (1000 m^2)			Individuals per 100 m^2 (±SD)	Total basal area (m^{2}ha^{-1})	Basal area per transects (m^2/100 m^2) (±SD)
	Total	Lianas(≥ 10 cm)	Trees & shrubs(≥ 10 cm)			
Cosiguina	135	17 (0)	118 (52)	13.5 ± 2.9	23.3	0.233 ± 0.095
Santa Rosa	246	77 (1)	169 (61)	24.6 ± 7.0	25.0	0.251 ± 0.042
Palo Verde	227	42 (2)	185 (45)	22.7 ± 6.2	22.8	0.228 ± 0.058
Chacocente	215	38 (1)	177 (62)	21.5 ± 3.1	21.2	0.212 ± 0.032
Masaya	243	20 (1)	223 (52)	24.3 ± 6.1	21.2	0.212 ± 0.065
La Flor	264	62 (1)	202 (42)	26.5 ± 6.4	22.8	0.228 ± 0.057
Ometepe	154	47 (1)	107 (48)	15.4 ± 5.0	17.7	0.162 ± 0.053

noted that subtropical dry forests in the northern hemisphere contain high levels of species richness, the pattern does not necessarily hold true for the subtropical dry forest in the southern hemisphere as proposed by Gentry (1995). When new data from Paraguay were included, the southern subtropical sites had species richness comparable to Central American tropical dry forest (Keel et al. 1993). These results do not support Gentry's finding that Central American tropical dry forests do not have a high priority for conservation based on species richness. For example, Santa Rosa and Palo Verde have a relatively high species richness compared to other Neotropical sites. It should be noted that density per unit area was significantly lower in Central America than other Neotropical sites. If a similar number of stems were counted for all Neotropical dry forest sites, diversity per unit number of stems could result in Central American forest containing an even higher diversity compared to other forests.

Environmental variables and plant species richness

A number of studies have found that annual precipitation is directly correlated with species richness of plants along a gradient from dry to wet tropical forests (Gentry 1988; Clinebell et al. 1995). However, within tropical dry forests of Central America, annual precipitation is a poor predictor of plant diversity. This is in accordance with Gentry's findings that annual precipitation is not a strong predictor of plant richness within Neotropical dry forests (Gentry 1995). Seasonality of rainfall has also been cited as having a significant impact on species richness (Murphy & Lugo 1986a). However, there was little variation in seasonality between Central American sites because all sites have a five or six month dry seasons with less than 50 mm of precipitation (Holdridge et al. 1971; INETER 1997).

There was no correlation between forest cover and species richness in tropical dry forest. 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 (Whitmore 1997). For instance, a 50 ha plot at Pasoh in Malaysia contained 25% of woody flora known from the Malay peninsula and a 6.6 ha plot in Sarawak contained over half of the trees with a dbh of 10 cm known for the whole country (Ashton 1969; Whitmore 1997). The same pattern of species packing may occur in trop-

Table 7. Summary of floristic diversity in 0.1 ha samples from 28 lowland Neotropical dry forest sites

Sites	Families	Total species	Liana species	Tree & shrub species
West Indies				
Guanica, Puerto Rico[1]	19	34	0	34
Mogotes, Puerto Rico[2]	28	49	12	37
Round Hill, Jamaica[2]	32	58	4	54
Mexico				
Chamela, Mexico[3]	37	91	12	79
Chamela, Mexico[3]	34	89	8	80
Central America				
Chacocente, Nicaragua[4]	28	54	11	43
Cosiguina, Nicaragua[4]	27	48	10	38
La Flor, Nicaragua[4]	25	59	14	45
Masaya, Nicaragua[4]	28	44	11	33
Ometepe, Nicaragua[4]	31	45	18	27
Palo Verde, Costa Rica[4]	29	65	17	48
Santa Rosa, Costa Rica[4]	33	75	21	54
Northern South America				
Galerazamba, Colombia[2]	20	55	18	36
Tayrona, Colombia[5]	31	67	18	49
Los Colorados, Colombia[2]	41	121	40	81
Coloso, Colombia[2]	46	113	38	75
Boca de Uchire, Venezuela[2]	20	69	16	53
Blohm Ranch, Venezuela[2]	31	68	17	51
Pacific coast of South America				
Capeira, Ecuador[6]	27	61	19	42
Perro Muerte, Ecuador[2]	33	52	18	54
Cerros de Amotape, Peru[2]	29	57	14	43
Tarapoto, Peru[2]	38	102	27	75
Southern subtropics				
Riachuelo, Argentina[2]	27	47	8	39
Parque El Rey, Argentina[7]	27	40	10	31
Chaquimayo, Bolivia[2]	29	79	29	50
Mbaracayú, Paraguay[8]	30	85	29	56
Tarumá, Paraguay[8]	24	50	13	37
Parabel, Paraguay[8]	28	64	12	52

Sources: 1 = Murphy & Lugo (1986b), 2 = Gentry (1995), 3 = Lott et al. (1987), 4 = this study, 5 = Heybrock (1984), 6 = Dodson & Gentry (1992), 7 = Brown et al. (1985), 8 = Keel et al. (1993).

ical dry forests of Central America. Data from our 0.1 ha plot in the richest site Santa Rosa were within a 20 ha plot in which all plants greater than ≥ 3 cm dbh were inventoried. Our plot included 63% of all species encountered in the 20 ha plot and the 20 ha plot contained approximately 46% of the species able to reach a dbh of 2.5 cm or greater in Santa Rosa

National Park (Janzen & Liesner 1980; Enquist pers. comm.). These results concur with a number of studies which noted that there have been fewer recorded extinctions of plants in tropical rainforests than predicted from a species-area curve (Simberloff 1986; Brown & Brown 1992; Heywood et al. 1994; Turner et al. 1994; Whitmore 1997). 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). Although these data suggest that small fragments can contain relatively high levels of diversity, 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.

The degree of natural disturbance has often been cited as a critical factor in determining tropical forest species diversity (Connell 1978; Pickett & White 1985; Foster 1990). Anthropogenic disturbances, such as burning, grazing, and wood collection, may also significantly lower plant species richness in tropical dry forests (Budowski 1966; Sabogal 1992; Swaine et al. 1990; Jayasingam & Vivekanantharaja 1994; Maass 1995). There was a significant correlation between disturbance and plant species richness, but from this study it is difficult to separate and identify how individual disturbance agents affect forest diversity.

Fire frequency and intensity is often cited as an important predictor of forest diversity (Swaine 1992; Pickett & White 1985) and diversity in different tropical dry forest regions of the world (Janzen 1988b; Sabogal 1992; Swaine 1992; Fensham 1995). Fires in tropical dry forests lower species diversity by selecting for fire resistant species or early successional plants, and destroy understory shrubs and lianas that make up a significant proportion of all woody plants in tropical dry forests (Gentry 1982; Bullock 1985; Swaine et al. 1990; Medina 1995). Fire intensity and frequency was highest at Cosiguina which had significantly lower species diversity than Santa Rosa which has had an active fire suppression program for the last 15 years.

Ungulates, especially cattle, are infamous for compacting soil and destroying understory plant diversity (Veblen 1982; Janzen 1986; Gerhardt & Hytteborn 1992). 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. Intensive grazing by cattle

Table 8. Spearman's rank correlation coefficients between ecological and environmental variables

	FC	PR	DIS	SR	LR	LA	TR
Annual precipitation	0.250						
Anthropogenic disturbance	−0.108	0.144					
Total species richness	0.428	0.250	−0.883 ∗∗				
# of liana species	−0.234	−0.126	−0.736	0.522			
# of liana individuals	−0.285	0.000	−0.775∗	0.643	0.883∗∗		
# of tree and shrub species	0.500	0.142	−0.847∗	0.964∗∗∗	0.396	0.536	
# of tree and shrub individuals	−0.178	−0.321	−0.180	0.000	−0.234	−0.071	0.214

∗P<0.05; ∗∗P<0.01; ∗∗∗P<0.001. FC = forest cover in reserves, PR = annual precipitation, DIS = rank of anthropogenic disturbance, SR = Total species richness, LR = number of liana species, LA = number of liana individuals, TR = number of tree and shrub species, TA = number of tree and shrub individuals.

can also result in an understory dominated by spiny or unpalatable shrubs. Cosiguina and Masaya had the highest intensity of cattle grazing and both sites had significantly less plant diversity than Santa Rosa and Palo Verde. It is still not clear how the presence of cattle in remaining fragments of tropical dry forest in Nicaragua affect the forest composition because Ometepe also had significantly lower plant diversity with no evidence of any cattle or grazing.

A number of studies found that wood collection and logging lowers the species richness of fuelwood and timber species, and favors stress tolerant plants and species that resprout after cutting (Sabogal 1992; Murphy & Lugo 1986a; Ribichich & Protomastro 1998). In many areas where wood collection is intense, weedy lianas and vines tend to smother the tropical forest which further lowers species diversity (Savage 1992; Gentry 1995). In this study wood collection was extremely common in Masaya, Ometepe, and Cosiguina because sites are near towns with high population densities. However, there was no evidence of lianas smothering tropical dry forests because other disturbances, such as fire, may reduce liana densities.

Tropical dry forest that persists in Central America are found in areas where substrates are unsuitable for agriculture (Janzen 1986, 1988b). Remaining forests in Ometepe and Masaya both occur on blocky *aa* lava flows which contains little soil development and this may account for the relatively low tree and shrub species richness at these sites. Tropical dry forest in Palo Verde, La Flor, and Chacocente all occur on Eocene marine sediments which may explain similarities in composition and species richness between the sites. It should be noted that Palo Verde, the richest of these three sites, occurs on rugged limestone outcrops, which has significantly less soil development than La Flor and Chacocente, and physiographically,

the terrain at Palo Verde appears similar to the *aa* lava flows. Santa Rosa and Cosiguina both occur on aeolian ash, but there is greater soil development at Santa Rosa than Cosiguina which may account for higher species richness.

Conclusions and implications for conservation management

Fragments of tropical dry forest in Central America differ significantly in floristic diversity and structure, although Fabaceae is generally dominant based on the number of tree and shrub species per family by site. Santa Rosa National Park and Palo Verde National Park deserve a high priority for conservation within Central America based on plant species richness, while La Flor and Chacocente deserve a high priority for conservation within Nicaragua. It may be the case that if levels of anthropogenic disturbance can be reduced within reserves, many of these dry forests may experience an increase in levels of species richness with time. Fifteen years ago anthropogenic disturbance in the form of grazing and annual burning was extremely common in Santa Rosa National Park (Janzen 1986). Presently, the removal of cattle and an active fire suppression program has resulted in the rapid and dramatic increase of tropical dry forest cover (Kramer 1997). If such intense management had not been undertaken in Santa Rosa, levels of species richness and stand structure would have most certainly been lower than reported in our study. For this reason implementation of similar management programs in Nicaraguan reserves may result in an increase in species richness. Further research in forest fragments that examines individual and combination of disturbance agents would help clarify the importance of

anthropogenic disturbances on species richness and abundance.

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