Biodiversity and Conservation (2006) 15:1509–1527
DOI 10.1007/s10531-005-2632-0

Species Composition, diversity and local uses of tropical dry deciduous and gallery forests in Nicaragua

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Received 6 December 2004; accepted in revised form 15 August 2005

Key words: Biodiversity, Central America, Endangered species, Floristic composition

Abstract. The floristic composition and diversity of tropical dry deciduous and gallery forests were studied in Chacocente Wildlife Refuge, located on the Pacific coast in Nicaragua during 1994 and 2000. Density, dominance and frequency as well as species and family important values were computed to characterize the floristic composition. A variety of diversity measures were also calculated to examine heterogeneity in each forest community. A total of 29 families, 49 genera and 59 species were represented in 2 ha dry deciduous forest. In the gallery forest, the number of families, genera and species recorded in 2000 inventory was 33, 48 and 58, respectively and slightly higher than the 1994 inventory. The number of stems ≥10 cm dbh varied from 451 to 489 per hectare in the deciduous forest, and from 283 to 298 per hectare in the gallery forest. The basal area was much larger for species in the gallery than dry deciduous forest. Fabaceae, sub family Papilionoideae, was the most specious family in the deciduous forest while Meliaceae was the dominant family in the gallery forest. Similarity in species composition and abundance between deciduous and gallery forests was low. In terms of species diversity, the gallery forest was found more diverse than the deciduous forest using Fisher's diversity index. Both forest communities were characterized by a typical inverse *J* shape. Therefore, emphasis should be given to the protection of rare species, i.e. as the forests are still under continued human pressure, an immediate action should be taken to conserve the remaining flora.

Introduction

Dry forests once covered more than 40% of the total area of tropical forests (Murphy and Lugo 1986). They are considered to be one of the most threatened of all the major tropical forest habitats and are argued to deserve a high priority for conservation (Janzen 1988; Gillespie et al. 2000). According to the Holdridge system of life zone classification, dry tropical and subtropical forests and woodlands occur in frost-free areas with a mean annual temperature higher than 17 °C, a mean annual rainfall between 250 and 2000 mm, and an annual ratio of potential evapotranspiration to precipitation exceeding unity (Murphy and Lugo 1995).

The area of natural forests in Central America is estimated to be 190,000 km^2, representing ca. 15% of the total land cover. In addition, some 130,000 km^2 deforested land is considered suitable only for forestry, adding to 24% of the total area (Segura et al. 1997). The deforestation rate in Central America is estimated as 0.5 km^2 per year (Roldan 2001). The tendency of human populations to concentrate in drier climates is hastening the rate of dry forest degradation (Murphy and Lugo 1995) and deforestation has increased dramatically with population growth during the last century. Large areas are cleared for grazing and agriculture and only fragments of dry forests remain (Gerhardt 1994).

Nicaragua has 2500 km^2 of tropical dry forests, representing ca. 2% of the total forest cover (Harcourt and Sayer 1996). The dry forests are found mainly on the Pacific coast where ca. 50% of the population also lives. Nicaraguan dry forests have been intensively exploited for commercial timber production. The major commercial timber species are *Swietenia humilis, Cedrela odorata, Bombacopsis quinata, Dalbergia retusa* and *Guaiacum sanctum* (Sabogal 1992). The extraction of valuable commercial trees for export started in early 1900 (Tercero and Urrutia 1994), and continued for decades, resulting in considerable reduction of commercially important species. The Nicaraguan Pacific railway was constructed in the 1950s and most of the railway sleepers used was extracted from the dry forest in Chacocente (Tercero and Urrutia 1994). The dry forests are still major sources of wood for fire, poles and timber, and provide opportunities for hunting and collection of other important non-timber forests products (NTFP). In addition to cutting of trees for wood and related products, the major causes of deforestation have been conversion of dry forests into coffee plantations, crop fields and ranches (Roldan 2001).

Chacocente National Wildlife Refuge was established in 1983 to protect the nesting beach of marine turtles and the last area of the tropical dry forest due to the social, economic, ecological and scientific relevance of this type of ecosystem. During the Sandinista Revolution big ranches were expropriated and became property of the state. In 1990 this land was given to peasant cooperatives. By 1998, the land tenure changed very rapidly since land was being sold and cooperative land was converted into private land (Anonymous 2002). Today, the Chacocente National Wildlife Refuge consists mainly of private farms (84 owners), although some are quite small. The only state land in the refuge is a small property donated to Ministry of Natural Resources and Environment (MARENA) by the International Fauna and Flora Organization. The refuge is not fully protected against human impact and is utilized both legally and illegally by the local people living inside as well as outside the refuge. Anthropogenic disturbances such as burning, grazing, wood collection and illegal cutting are factors affecting plant population density (Gillespie et al. 2000).

The effect of this land use dynamics and forest fragmentation on biological diversity in Chacocente is not well documented (Sabogal and Valerio 1998). An assessment of species composition and diversity provide information for developing guidelines for conservation priorities in the region since few comparative or quantitative studies in remaining forest fragments in Central America have been made (Gillespie et al. 2000). In this study, we described the floristic composition and species diversity of two tropical dry forest types, dry deciduous and gallery forests, at two different times. The vegetation description presented will hopefully contribute to a better understanding of the floristic composition and diversity of the tropical dry forests. Given the threatened status of dry forests throughout the tropics, particularly in Nicaragua, and the fact that dry forests are less studied than moister tropical forest types, this study will provide important baseline data for the region.

Materials and methods

Study area

This study was carried out in Chacocente Wildlife Reserve (11°36′–11°30′ N and 86°08′–86°15′ W) located on the Pacific coast in the department of Carazo, Nicaragua (Figure 1). The refuge consists of closed deciduous forest (1099 ha), gallery forest (471 ha), open low forest (1842 ha), fallows area (554 ha), annual crops (311 ha), grassland (294 ha), and beach area (71 ha) (Anonymous, 2002). Chacocente has a dry period of 7 months with less than 50 mm precipitation per months, and during the rainy season (June–October) rainfall is irregular with many days without rainfall (Anonymous 2002). The mean annual precipitation during the last 13 years has been 1422 mm, with a maximum in 1995

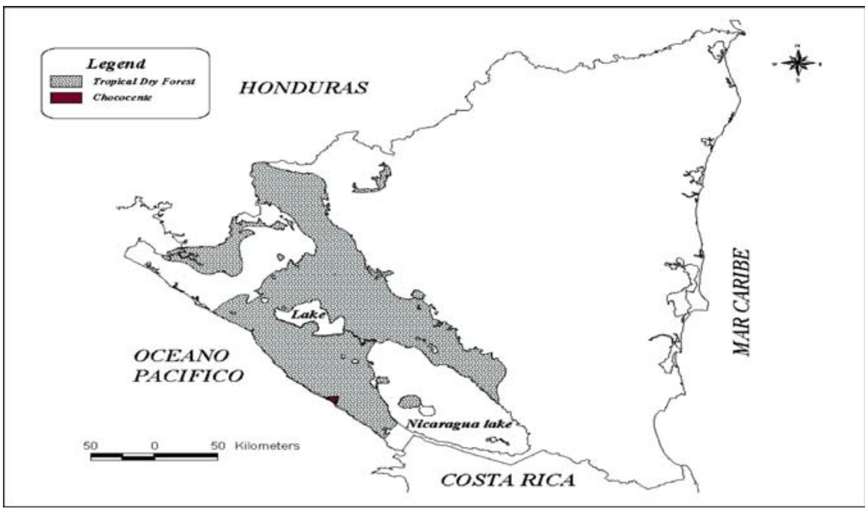

Figure 1. Distribution of tropical dry forests in Nicaragua and location of the study site, Chacocente.

(1962 mm) and the minimum in 1991 (991 mm). During October 1998, hurricane Mitch passed over the area and the precipitation that month was as high as 775 mm. The average annual temperature is 26 °C (Anonymous 2002).

The gallery forest, defined as narrow patches along the fringes of semi-permanent watercourses (Lamprecht 1989), occurs along the main water course, the Río Escalante. It has a different species composition, structure and stand density than the more common deciduous forest. The vegetation is mostly evergreen, the trees are tall and the majority of the trees have a diameter exceeding 35 cm at breast height. The deciduous forest trees totally or partially shed their leaves during the dry season.

Sampling and data analyses

Two permanent plots in each forest type were established by Universidad Nacional Agraria, Managua, Nicaragua in 1989. The area of each permanent plot was 1.0 ha and subdivided into 25 subplots of 20×20 m. Each plot was systematically surveyed by identifying, measuring, and tagging all trees with diameter at breast height (dbh) ≥10 cm. The inventories were made in 1994 and 2000. In addition, local names were recorded and information about uses of the tree species was gathered by consulting a Nicaraguan forest use specialist (Claudio Calero, personal communication) and relevant literature (Salas 1993; Stevens et al. 2001). All scientific names were thoroughly cross-checked in the TROPICOS nomenclatural database (http://mobot.mobot.org/W3T/search/Vast.html) of the Missouri Botanical Garden.

The importance value index (IVI) and family importance value (FIV) were used to describe the species composition of the plots. IVI of a species is defined as the sum of its relative dominance, its relative density and its relative frequency, which in turn are calculated as follows:

Relative dominance= total basal area for a species/total basal area for all species

Relative density= number of individuals of a species/total number of individuals

Relative frequency= frequency of a species/sum frequencies of all species

The frequency of species is defined as the number of subplots (20×20 m) in which the species is present. The theoretical range for relative dominance, relative density and relative frequency is 0–100%, thus IVI of species may vary between 0 and 300%. The FIV was computed in the same way as IVI except that relative frequency was replaced by the relative diversity, computed as the number of species in a family/total number of species. All species encountered during both inventories were clustered into three groups based on the mean number of individuals of a species per hectare as rare (≤4 individuals per hectare), intermediate (4–24 individuals per hectare) and abundant (>24 individuals per hectare). According to Duque and Cavelier (2003), a species with two or fewer individuals in 2.16 ha is considered as locally rare.

A variety of commonly used diversity indices were computed in order to permit a more precise comparison of the alpha diversity between the two forest communities. These indices were Margalef's species richness index, Shannon's measure of evenness, Shannon–Wiener's diversity index, Simpson's diversity index and Fisher's diversity index. These indices are widely employed to measure biological diversity (Magurran 2004). In addition, the species-abundance patterns in each forest community were plotted. Floristic similarity between forest communities was assessed using Jaccard's coefficient of similarity, based on the presence/absence of the species, and Morisita's index of similarity, based on number of individuals per species. Jaccard's coefficient of similarity and Morisita's index vary between 0 and 1 and a value close to 1 indicates greater similarity between forest communities (Krebs 1999). The conservation status of species encountered in our plots was assessed based on the 2004 IUCN Red List of Threatened Species directory (IUCN 2004). In addition, candidate species for future IUCN listing were identified based on their rarity and regional distribution based on Flora of Nicaragua (Stevens et al. 2001) and the Missouri Botanical Garden's TROPICOS database.

Results

Floristic composition

A total of 29 families, 49 genera and 59 species were found in the dry deciduous forest during both inventories (Table 1). While the stem density slightly increased in 2000 inventory, the basal area was relatively less compared to the inventory made in 1994. Fabaceae, sub-family Papilionoideae was the most specious family with higher FIV (Table 2). Other families (sub-families) with ≥4 species were Caesalpinioideae and Boraginaceae. Hernandiaceae, though represented by one species (*Gyrocarpus americanus*), had the second and third higher FIV in 1994 and 2000 inventories, respectively owing to the large stem density per hectare (62 individuals/ha in 1994 and 37 individuals/ha in 2000). *Gyrocarpus americanus* stood out as the most abundant species during both inventories in terms of basal area, relative dominance, relative frequency and IVI (Table 3). While *Tabebuia ochracea* was the second most abundant species during both inventories, *Lonchocarpus minimiflorus* and *Myrospermum frutescens* were more abundant in 1994 and 2000 inventories, respectively. The rarest species during both inventories were *Celtis caudata* and *Zanthoxylum caribaeum* (Table 4). Four species, *Acacia costaricensis*, *Ficus obtusifolia*, *Pithecellobium saman* and *Trichilia hirta*, recorded in 1994 inventory were not encountered in 2000, but four other species, *Adelia barbinervis*, *Casearia*

Table 1. Summary of floristic composition and structure of trees ≥10 cm dbh in dry deciduous and gallery forests inventoried in 1994 and 2000.

Forest types-Inventory time	Families	Genera	Species	Stem density[a]	Basal area[b]
Deciduous-94	29	49	59	451	31.5
Deciduous-00	29	49	59	489	29.0
Gallery-94	33	47	55	298	45.3
Gallery-00	33	48	58	283	49.3

[a]stem density = Number of individuals ha^{-1}.
[b]basal area (m^2 ha^{-1}).

Table 2. The ten most important families (sub-families) in the dry deciduous and gallery forests of Chacocente in 2000 inventory according to decreasing order of family importance value (FIV).

Forest type	Family	Genus	Species	N/ha	IFV
Deciduous	Papilionoideae	8	10	82	58.3
	Caesalpinioideae	3	5	45	29.3
	Hernandiaceae	1	1	37	23.3
	Mimosoideae	2	3	19	20.7
	Bignoniaceae	1	1	40	19.2
	Achatocarpaceae	1	1	23	14.8
	Boraginaceae	1	4	13	14.0
	Apocynaceae	1	1	30	12.7
	Spindaceae	2	2	17	10.4
	Tiliaceae	1	1	12	7.2
Gallery	Miliaceae	3	4	39	40.0
	Capparidaceae	1	1	14	17.6
	Sapindaceae	1	1	13	17.3
	Hernandaceae	1	1	7	15.5
	Sterculiaceae	2	2	8	11.6
	Annonaceae	2	2	15	11.4
	Boraginaceae	1	4	13	14.0
	Simaroubaceae	1	1	16	10.7
	Apocynaceae	1	1	8	10.0
	Rhamnaceae	2	2	8	8.5

corymbosa, *Cordia dentata* and *Trema micrantha*, were found in 2000 inventory (Appendix).

In the gallery forest, the number of families, genera and species encountered in 1994 inventory were 33, 47 and 55, respectively while 48 genera and 58 species were recorded in 2000 inventory (Table 1). The total stem density (298 individuals/ha) was comparatively higher in 1994 inventory than in 2000 inventory while the basal area was relatively larger in 2000 than in 1994 inventory. In both inventories, Meliaceae was the most specious family with higher IFV (Table 2). Most of the important families were represented by 1 or 2 species. The most abundant species, in terms of basal area, relative dominance, and IVI was *Pithecellobium saman*, followed by *Trichilia hirta* (Table 5). In both inventories, *Cordia alliodora* was the rarest species, followed by *Hymenaea courbaril* in the

Table 3. The ten most abundant species in the dry deciduous forest of Chacocente in 1994 and 2000 inventories according to decreasing order of importance value index (IVI) together with structural characteristics.

Species	1994 Inventory				
	Basal area (m^2/ha)	Relative dominance (%)	Relative density (%)	Relative frequency (%)	IVI
Gyrocarpus americanus	6.5326	20.72	13.57	8.12	42.4
Tabebuia ochracea	2.0714	6.57	8.57	7.48	22.6
Lonchocarpus minimiflorus	2.1939	6.96	9.79	5.56	22.3
Stemmadenia obovata	1.2935	4.10	9.23	6.84	20.2
Caesalpinia exostemma	1.8645	5.91	7.45	4.70	18.1
Myrospermum frutescens	1.3467	4.27	6.01	5.34	15.6
Lysiloma divaricatum	2.0737	6.58	3.34	4.70	14.6
Achatocarpus nigricans	1.3346	4.23	5.78	1.92	11.9
Gliricidia sepium	1.8495	5.87	2.78	2.78	11.4
Luehea candida	0.7214	2.29	2.78	4.06	9.1
	2000 Inventory				
Gyrocarpus americanus	3.548	12.23	9.41	8.28	29.9
Tabebuia ochracea	2.1671	7.47	10.04	7.63	25.1
Myrospermum frutescens	1.4233	4.91	6.52	6.10	17.5
Caesalpinia exostemma	1.8082	6.23	7.28	3.92	17.4
Stemmadenia obovata	1.0028	3.46	7.53	5.88	16.9
Achatocarpus nigricans	2.0956	7.23	5.90	3.05	16.2
Lonchocarpus minimiflorus	0.9979	3.44	7.90	4.79	16.1
Gliricidia sepium	1.8574	6.40	2.38	2.83	11.6
Luehea candida	0.6862	2.37	3.14	3.92	9.4
Allophylus psilospermus	0.5432	1.87	2.76	2.40	7.0

1994 inventory, and *Triplaris melaenodendron*in the 2000 inventory (Table 6). Four species, *Casearia tremula*, *Pithecellobium dulce*, *Piper aduncum* and *Randia nicaraguensis* recorded in 1994 inventory were missing in 2000 inventory while seven other species were encountered in 2000 inventory; namely, *Acacia costaricensis, Bursera simaruba, Caesalpinia exostemma, Caesalpinia violacea, Coccoloba* sp., *Licania arborea* and *Tabebuia rosea* (Appendix).

As a whole, the number of species recorded in dry deciduous and gallery forests was nearly the same. However, the stem density in the dry deciduous forest was twice higher than the gallery forest while the basal area was much bigger in the latter. It was found that the similarity in species composition between the two forest communities in both inventories was very low, as shown by low Jaccard's (0.27) and Morisita's (0.35) similarity indices.

Species diversity

The species-abundance patterns of dry deciduous and gallery forests displayed a typical inverse *J*-distribution or the log series distribution (Figure 2). The

Table 4. The ten rarest species in the dry deciduous forest of Chacocente in 1994 and 2000 inventories according to increasing order of IVI together with structural characteristics.

Species	Basal area (m^2/ha)	Relative dominance (%)	Relative density (%)	Relative frequency (%)	IVI
	1994 Inventory				
Zanthoxylum caribaeum	0.0154	0.05	0.11	0.21	0.37
Celtis caudata	0.0305	0.10	0.11	0.21	0.42
Ficus obtusifolia	0.0366	0.12	0.11	0.21	0.44
Coursetia elliptica	0.0266	0.08	0.22	0.43	0.73
Diospyros nicaraguensis	0.0566	0.18	0.22	0.43	0.83
Dalbergia retusa	0.0137	0.04	0.44	0.64	1.12
Calycophyllum candidissimum	0.0113	0.04	0.56	1.07	1.67
Swietenia humilis	0.278	0.88	0.33	0.64	1.85
Chomelia spinosa	0.0715	0.23	0.67	1.07	1.97
Haematoxylon brasiletto	0.6026	1.91	0.56	1.07	3.54
	2000 Inventory				
Celtis caudata	0.0167	0.06	0.13	0.22	0.40
Zanthoxylum caribaeum	0.0191	0.07	0.13	0.22	0.41
Malpighia stevensii	0.0216	0.07	0.13	0.22	0.42
Coursetia elliptica	0.0281	0.10	0.25	0.44	0.78
Dalbergia retusa	0.0097	0.03	0.50	0.65	1.19
Chomelia spinosa	0.0216	0.07	0.63	0.87	1.57
Diospyros nicaraguensis	0.0923	0.32	0.75	0.65	1.72
Calycophyllum candidissimum	0.0113	0.04	0.63	1.09	1.76
Haematoxylon brasiletto	0.1863	0.64	0.50	0.87	2.02
Swietenia humilis	0.3244	1.12	0.50	0.87	2.49

majority of the species in both forest communities were represented by few individuals while few species in both forests were represented by many individuals. In the dry deciduous forest, out of the 59 species recorded during both inventories, 37 species were considered as rare (<4 individuals/ha), 15 species as intermediate (4–24 individuals/ha) and 7 species as abundant (>24 individuals/ha). Of all the species recorded in the gallery forest during both inventories, 43 species was considered as rare (<4 individuals/ha), 8 species as intermediate (4–24 individuals/ha) and 4 species as abundant (>24 individuals/ha). The various diversity measures for each forest community are presented in Table 7. Although the total number of species recorded in both forest communities was very close, the number of individuals in 2 ha plot was much higher in the dry deciduous than gallery forests. In terms of numerical species richness (S/N), the two forest communities differed slightly (cf. 0.1 for gallery and 0.06 for deciduous forest). According to Margalef's index of species richness (D_{Mg}), which combines mathematically number of species (S) and numerical species richness (S/N), the gallery forest (in 2000 inventory) was found to be more diverse than the dry deciduous forest. Shannon's measure of evenness did not differ much between and within forest communities. The Shannon–Wiener diversity index, which combines species richness and

Table 5. The ten most abundant species in the gallery forest of Chacocente in 1994 and 2000 inventories according to decreasing order of importance value index together with structural characteristics.

Species	1994 Inventory				
	Basal area (m^2/ha)	Relative dominance (%)	Relative density (%)	Relative frequency (%)	IVI
Pithecellobium saman	12.462	27.49	0.76	2.34	30.6
Trichilia hirta	4.2525	9.38	7.89	8.31	25.6
Thouinidium decandrum	2.9502	6.51	5.43	6.23	18.2
Simarouba glauca	1.5827	3.49	2.97	9.09	15.6
Capparis pachaca	0.8255	1.82	4.75	6.49	13.1
Gyrocarpus americanus	2.4077	5.31	2.21	4.16	11.7
Astronium graveolens	1.6976	3.74	1.87	5.97	11.6
Stemmadenia obovata	0.7411	1.63	3.99	4.16	9.8
Guarea glabra	0.9649	2.13	2.97	4.16	9.3
Trichilia moschata	0.8863	1.96	2.04	4.68	8.7
	2000 Inventory				
Pithecellobium saman	12.7787	25.89	1.22	2.07	29.2
Trichilia hirta	2.4232	4.91	15.29	8.55	28.8
Capparis pachaca	1.3614	2.76	13.15	7.51	23.4
Thouinidium decandrum	2.9474	5.97	9.63	6.74	22.3
Gyrocarpus americanus	4.6233	9.37	4.43	3.63	17.4
Simarouba glauca	2.01	4.08	4.89	8.29	17.3
Annona reticulata	1.3844	2.80	4.13	6.74	13.7
Astronium graveolens	2.0686	4.19	3.21	5.44	12.8
Stemmadenia obovata	0.8589	1.74	6.57	4.15	12.5
Guarea glabra	1.2341	2.50	5.35	4.40	12.3

evenness into a single value, declined over time within each forest community, and identified the dry deciduous forest as more diverse than the gallery forest. The complement of Simpson's index, which attaches more weight to the abundance of the most common species, also identified the dry deciduous forest as more diverse than the gallery forest. Fisher's diversity index, the most widely recommended measure of diversity, revealed that the galley forest is more diverse than the dry deciduous forest.

Local uses

Although we did not make a systematic ethno-botanical study, the local uses of the tree species in both forest communities were identified based on information gathered from the local people, expert consultation and existing literature. Accordingly, ten major use categories were identified (Figure 3). It was found that the largest number of species in both forest communities (53% of the total species) was used for firewood, followed by timber extraction (35%), rural construction (27%) and charcoal production (23%). Interest-

Table 6. The ten rarest species in the gallery forest of Chacocente in 1994 and 2000 inventories according to increasing order of IVI together with structural characteristics.

Species	1994 Inventory				
	Basal area (m^2/ha)	Relative dominance (%)	Relative density (%)	Relative frequency (%)	IVI
Cordia alliodora	0.0174	0.04	0.1	0.26	0.38
Hymenaea courbaril	0.0287	0.06	0.2	0.52	0.75
Karwinskia calderonii	0.0613	0.14	0.2	0.52	0.83
Triplaris melaenodendron	0.0931	0.21	0.2	0.52	0.90
Guaiacum sanctum	0.0257	0.06	0.3	0.78	1.09
Ceiba pentandra	0.5064	1.12	0.1	0.26	1.46
Cordia gerascanthus	0.09	0.20	0.3	1.04	1.58
Albizia caribaea	0.7178	1.58	0.1	0.26	1.92
Sterculia apetala	0.4611	1.02	0.3	1.04	2.40
Cedrela odorata	1.0955	2.42	0.6	1.82	4.83
	2000 Inventory				
Cordia alliodora	0.0209	0.04	0.15	0.26	0.45
Triplaris melaenodendron	0.0607	0.12	0.15	0.26	0.53
Hymenaea courbaril	0.0264	0.05	0.31	0.52	0.88
Karwinskia calderonii	0.0821	0.17	0.31	0.52	0.99
Cedrela odorata	0.0095	0.02	0.46	0.78	1.26
Guaiacum sanctum	0.2346	0.48	0.31	0.52	1.30
Cordia gerascanthus	0.0804	0.16	0.46	0.78	1.40
Albizia caribaea	0.7854	1.59	0.15	0.26	2.00
Ceiba pentandra	0.8202	1.66	0.31	0.52	2.49
Sterculia apetala	0.4898	0.99	0.61	1.04	2.64

ingly, 24% of the species are not currently under any kind of use. The abundance of species by use group was also examined for each forest community (Figure 3). Given the large number of species used for firewood, the overall abundance was also high. The most interesting part of this result is that the abundance of species used for firewood and timber declined from 1994 to 2000 in both forest communities. Although the abundance of the ''not used'' species in the gallery forest showed an increasing tendency, the reverse held true in the deciduous forest.

Species with high conservation importance

Most of the species in our plots were represented by few individuals (Figure 2). Some of the rarest species were already short-listed in IUCN red list directory as threatened species. Among these threatened species, five species were categorized as vulnerable and six species as endangered (Table 8). *Bombacopsis quinata*, considered as vulnerable, was not encountered in our plots. We also identified seven candidate species that could be included in IUCN red list directory in the future (Table 8).

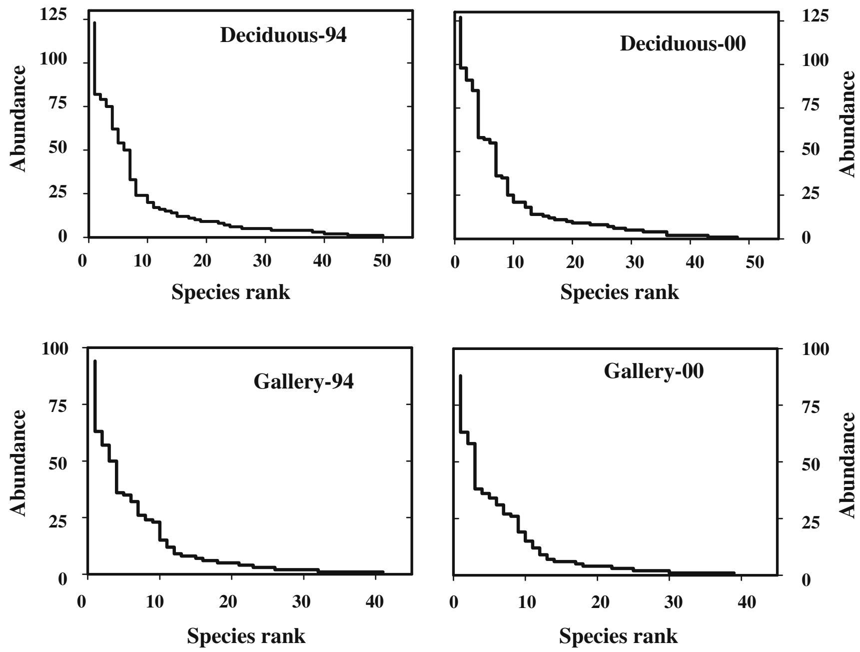

Figure 2. Species abundance plots for dry deciduous and gallery forests inventoried in 1994 and 2000.

Discussion

The number of families, genera and species reported in the present study lies within the range reported earlier in most Neotropical dry forests. For example, Gentry (1988) reported 35 families and 55 species per hectare in a gallery forest in Guanacaste, Costa Rica and Sabogal and Valerio (1998) reported on average 44 species per hectare in Chacocente dry deciduous forest in Nicaragua. The most common family in the deciduous forest was Fabaceae/Papilionoideae with 10 species, a pattern common in most Neotropical dry forests (Gentry 1988). This result also coincides with a study carried out in Central America where Fabaceae was found to be the dominant tree and shrub family in six of seven sites studied (Gillespie et al. 2000). Gillespie et al. (2000) made an inventory in Chacocente and found the same common species as in the present study. However, the present study found *L. minimiflorus* and *C. exostemma* as common species. In tropical dry forest across the north central Yucatan, the following important natural forest species were reported: *Bursera simaruba*, *Caesalpinia gaumeri, Gymnopodium floribundum* and *Piscidia piscipula* (White and Hood 2004), which are also encountered in our study. It was observed that some species recorded in the first inventory (1994) were missing in the subsequent inventory (2000) while new species were encountered in the second inventory. Given the large number of species with 1 or 2 individuals,

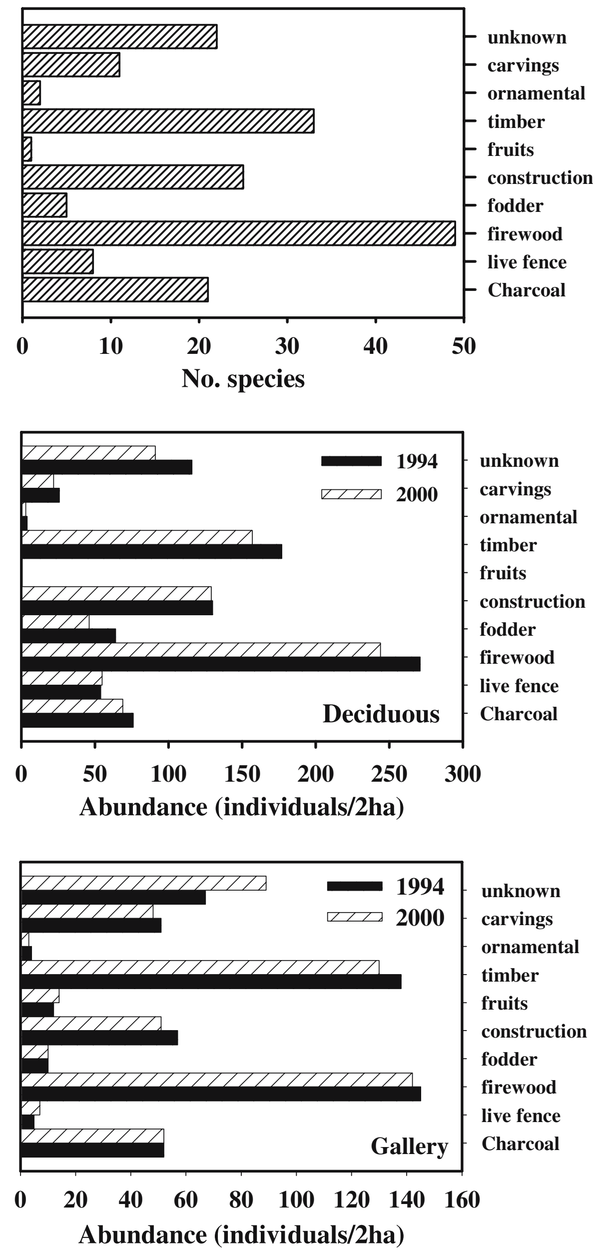

Figure 3. Local uses of tree species and their abundance in dry deciduous and gallery forests in Chacocente, Nicaragua.

Table 7. Diversity measures for trees ≥10 cm dbh in the dry deciduous and gallery forests inventoried in 1994 and 2000 on 2 ha plots.

Diversity Measures	Deciduous		Gallery	
	1994	2000	1994	2000
No. of individuals recorded in 2 ha plots	902	979	597	566
Total number of species recorded	59	59	55	58
Rate of species increase per individual enumerated (S/N)	0.065	0.060	0.092	0.102
Margalef's index of species richness ($D_{Mg} = (S-1)/ln\ N$)	8.52	8.42	8.45	8.99
Shannon's measure of evenness ($J' = H'/ln\ S$)	1.16	1.15	1.17	1.10
Shannon–Wiener's diversity index ($H' = -\sum pi\ log_2 p_i$)	4.71	4.69	4.69	4.48
The reciprocal of Simpson's index ($1/D$)	17.1	16.9	14.6	14.5
Fisher's index of diversity ($\alpha = N(1-x)/x$)	14.1	13.8	14.8	16.2

Table 8. List of threatened species and suggested candidate species for future IUCN listing.

Species	Status
Bombacopsis quinata	Vulnerable
Cedrela odorata	Vulnerable
Dalbergia retusa	Vulnerable
Maclura tinctoria	Vulnerable
Swietenia humilis	Vulnerable
Esenbeckia litoralis	Endangered
Guaiacum sanctum	Endangered
Lonchocarpus minimiflorus	Endangered
Lonchocarpus phlebophyllus	Endangered
Platymiscium pleiostachyum	Endangered
Zanthoxylum belizense	Endangered
Albizia caribaea	Candidate
Celtis caudate	Candidate
Diospyros nicaraguensis	Candidate
Hymenaea courbaril	Candidate
Jacquinia aurantiaca	Candidate
Manilkara achras	Candidate
Phyllostylon brasiliense	Candidate

illegal cutting might have caused the disappearance of this species. However, the plausible explanation for the appearance of species in the second inventory could be ascribed to the transition from seedling class in the 1994 inventory to higher class (trees ≥ 10 cm dbh) in the subsequent inventory.

Tree species richness is difficult to compare for different sample sizes and geographical variation (Murphy and Lugo 1995). Dry forest at Palo Verde on the Pacific side of Costa Rica had approximately 52 tree species per hectare (Murphy and Lugo 1995). Lower values have been found in the drier areas and particularly in insular forests, such as in Southwestern Puerto Rico near Guanica where 30–50 tree species per hectare were found. Gentry (1995) reported an average of 65 tree species per ha in 23 Neotropical dry forests, which is considerably higher than the number of species found in the deciduous forest of Chacocente. However, Gentry's data set included individuals with dbh ≥2.5 cm. In addition, dry forests of Chacocente have a history of severe selective logging which may be the main factor causing the low number of species in this forest. Gillespie and Jaffré (2003) compared species richness in seven different countries using 1000 m^2 area and found that species richness is high in Chamela-Mexico (89), Quiapaca (86) and Chaquimayo-Bolivia (79). The lower species richness was found in Mudumalai (India) with 15 species. The number of species for trees ≥10 cm dbh ranged from 3 to 28 species with a mean value of 16 species per hectare in the Vindhyan dry tropical forest of India (Sagar and Singh 2005). As a whole, the total number of species recorded in the present is comparable with other tropical dry forests.

With regard to stem density and basal area, our result lies with the range of values reported earlier for other tropical dry forests, and in some cases comparably higher. For example, Sabogal and Valerio (1998) reported 389 trees/ha with a basal area of 14.48 m^2/ha in the Chacocente dry deciduous forest, Rundel and Boonpragob (1995) reported 20–88 trees/ha and a basal area ranging from 7 to 42 m^2/ha for tropical dry forest in Thailand. For tropical dry forest at the north central Yucatan, White and Hood (2004) documented the basal area in two sites as 20.7 m^2/ha and 28.4 m^2/ha. Gillespie and Jaffré (2003) inventoried two tropical dry forests of New Caledonia and found the following basal area per hectare for each site: Ouen-Toro 32.7 m^2/ha and Pindai 32.3 m^2/ha. Gillespie and Jaffré (2003) also pointed out that tropical dry forests in the Neotropics have greater structural similarity. In the present study, the similarity in species composition and abundance between dry deciduous and gallery forests was low. The stem density was much higher in the dry deciduous forest while the basal area was much greater for the gallery forest. This could be related to better soil moisture condition in the latter than the former, as moisture is the major environmental factor limiting tree growth in dry areas.

A variety of diversity measures were computed to describe the heterogeneity of the two forest communities, and it was Simpson's index and Fisher's α that consistently differentiated the two communities. According to Simpson's dominance index the dry deciduous forest is more diverse than the gallery forest. This could be related to the relatively large number of abundant species in the deciduous forest than the gallery forest (cf. 7 species in dry deciduous and 4 species in gallery forests with abundance >24 individuals/ha). In 1994 and 2000 inventories of the dry deciduous forest, *Gyrocarpus americanus, Lonchocarpus minimiflorus, Stemmadenia obovata, Tabebuia ochracea* and *Caesalpinia exostemma* represented 49% and 42% of the total individuals per hectare, respectively. While *Trichilia hirta, Capparis pachaca, Thouinidium decandrum* and *Stemmadenia obovata* represented 44% and 45% of the total individuals per hectare found in the gallery forest during 1994 and 2000 inventories, respectively.

Fisher's diversity index showed that the gallery forest is more diverse than the dry deciduous forest. One implication of this finding would be the majority of the species inventoried have irregular and clumped spatial distribution in the deciduous forests, and therefore the gallery forest is characterized by high alpha diversity. The Shannon–Wiener diversity index is usually found to fall between 1.5 and 3.5 and only rarely surpasses 5.0 (Magurran 2004). The values of Shannon–Wiener index for the deciduous and gallery forests falls within the expected range. Gentry (1988) reported values of Shannon–Wiener diversity index for two sites of 0.1 ha in Nicaragua; Cerro Olumo with 5.80 and Cerro El Picacho with 5.22 (Clould forests). These values are higher than the present study; however, the precipitation and altitude of these sites are higher than Chacocente. Hence, the larger diversity of these sites may be due to higher precipitation and low temperature favoring growth and survival of more species.

Almost 50% of Nicaragua's population lives around tropical dry forest and in spite of the partial protection of Chacocente, human pressure on the remaining forests are obvious. The result from the present study provides evidence that the abundance of species used for firewood and timber declined from 1994 to 2000 in both forest communities. For example *Cordia alliodora*, though very common elsewhere in Nicaragua; was one of the rarest species in Chacocente. Even the abundance of the ''not used'' species in the deciduous forest showed a decreasing tendency, indicating an on-going disturbance (anthropogenic and natural) in the forest reserve and loose protection of the forest reserve. It is also important to note that species with high commercial values, such as *Swietenia humilis, Cedrela odorata, Dalbergia retusa* and *Guaiacum sanctum* were among the rarest species in our study. Illegal logging of commercially valuable species is still a common problem in the whole country. Apparently, the continuing loss of biodiversity is attributed to mainly deforestation, as in the case of many tropical dry forests (Thiollay 2002). If this anthropogenic disturbance is not curved as early as possible, the tree species, particularly commercial species that appear almost absent in the forest, will become locally extinct (e.g., *Bombacopsis quinata*). As both forest communities are characterized by many species with few individuals, active management, such as reintroduction of threatened species (Table 8) on private and community lands is highly desirable to maintain viable populations. Simultaneously, an immediate action should be taken to assist the natural regeneration process to restore species diversity of the remaining relics of tropical dry forest in the country. We further recommend a detailed assessment of the suggested candidate species for IUCN listing to determine their conservation status.

Acknowledgements

We thank Claudio Calero for his support during the fieldwork. Also he made a great contribution with his knowledge about species uses. Thanks also to Ali Water and Alvaro Noguera for their help during the fieldwork. The Ministry of Natural Resources and Environment kindly allowed us to carry out this research at Chacocente National Wildlife Refuge. The study was financed by the Swedish International Development Cooperation Agency (UNA-SLU PhD Program). Finally, the anonymous reviewer is highly appreciated for the valuable and constructive comments.

Appendix

Appendix. List of tree species ≥10 cm dbh recorded in 1994 and 2000 inventories in dry deciduous and gallery forests in Chacocente Wildlife Refuge, Nicaragua together with their uses (CH – charcoal; LF – live fence; FW – fire wood; FOD – fodder; RC – rural construction; FRU – fruit; W – timber; P – pole; O – ornamental; HC – handicrafts and carvings).

Species	Family	Deciduous		Gallery		Uses
		1994	2000	1994	2000	
Acacia costaricensis	Mimosoideae	*			*	FW, CH
Achatocarpus nigricans	Achatocarpaceae	*	*			FW, RC
Adelia barbinervis	Euphorbiaceae		*			NO
Albizia caribaea	Mimosoideae			*	*	FW, P, CH
Allophylus psilospermus	Sapindaceae	*	*			FW, CH, RC
Annona reticulata	Annonaceae			*	*	FRU
Ardisia revolute	Myrsinaceae			*	*	NO
Astronium graveolens	Anacardiaceae	*	*	*	*	P, W
Bixa orellana	Bixaceae			*	*	NO
Brosimum alicastrum	Moraceae			*	*	W, FW, CH, HC
Bunchosia cornifolia	Malpighiaceae	*	*			FW, RC, CH
Bursera simaruba	Burseraceae	*	*		*	LF, P
Caesalpinia coriaria	Caesalpinoideae	*	*			FW
Caesalpinia exostemma	Caesalpinoideae	*	*		*	NO
Caesalpinia violacea	Caesalpinoideae	*	*		*	FW, LF, CH
Calycophyllum candidissimum	Rubiaceae	*	*	*	*	FW, CH, O
Capparis odoratissima	Capparidaceae	*	*			FW
Capparis pachaca	Capparidaceae	*	*	*	*	NO
Casearia corymbosa	Flacourtaceae		*			FW
Casearia tremula	Flacourtaceae	*	*	*		FW
Cecropia peltata	Cecropiaceae			*	*	NO
Cedrela odorata	Meliaceae			*	*	W, FW, HC
Ceiba pentandra	Bombacaceae			*	*	W
Celtis caudata	Ulmaceae	*	*	*	*	NO
Chomelia spinosa	Rubiaceae	*	*			NO
Coccoloba caracasana	Polygonaceae			*	*	NO
Coccoloba floribunda	Polygonaceae			*	*	NO
Coccoloba sp.	Polygonaceae				*	FW
Cordia alliodora	Boraginaceae	*	*	*	*	P, HC, W
Cordia collococca	Boraginaceae	*	*	*	*	CH, HC, W
Cordia dentata	Boraginaceae		*	*	*	P, LF
Cordia gerascanthus	Boraginaceae	*	*	*	*	CH, HC, W
Coursetia elliptica	Papilionoideae	*	*			NO
Croton niveus	Euphorbiaceae			*	*	FW
Dalbergia retusa	Papilionoideae	*	*			FW, W, FOD

Appendix. Continued

Species	Family	Deciduous		Gallery		Uses
		1994	2000	1994	2000	
Diospyros nicaraguensis	Ebenaceae	*	*			FW, RC
Erythroxylum havanense	Erythroxylaceae	*	*			FW
Esenbeckia litoralis	Rutaceae	*	*	*	*	FW
Ficus obtusifolia	Moraceae	*				O
Gliricidia sepium	Papilionoideae	*	*			FW, FOD, W
Guaiacum sanctum	Zigophyllaceae			*	*	P, HC, W
Guarea glabra	Meliaceae			*	*	CH, P, HC, W
Guazuma ulmifolia	Sterculiaceae	*	*	*	*	FW, CH, FOD
Gyrocarpus americanus	Hernandiaceae	*	*	*	*	NO
Haematoxylon brasiletto	Caesalpinoideae	*	*			FW
Hippocratea rovirosae	Hippocrataceae	*	*			W, RC
Hymenaea courbaril	Caesalpinoideae			*	*	HC, W
Inga sp.	Mimosoideae			*	*	
Jacquinia aurantiaca	Theophrastaceae	*	*			FW
Karwinskia calderonii	Rhamnaceae	*	*	*	*	W, RC
Licania arborea	Chrysobalanaceae				*	W, HC
Lonchocarpus minimiflorus	Papilionoideae	*	*			FW, FOD, W
Lonchocarpus phlebophyllus	Papilionoideae	*	*			FW, CH, W
Lonchocarpus sp	Papilionoideae	*	*			NO
Luehea candida	Tiliaceae	*	*			RC, W
Luehea seemannii	Tiliaceae			*	*	FW, CH, P, W
Lysiloma divaricatum	Mimosoideae	*			*	FW, CH, RC
Lysiloma sp	Mimosoideae	*	*			FW, CH, RC
Machaerium biovulatum	Papilionoideae	*	*			FW
Maclura tinctoria	Moraceae			*	*	FW, CH, P, W
Manilkara achras	Sapotaceae			*	*	FW, P, W
Malpighia stevensii	Malpighiaceae	*	*			FW, LF
Myrospermum frutescens	Papilionoideae	*	*	*	*	W, RC
Pithecellobium dulce	Mimosoideae	*	*	*		FW, CH
Pithecellobium saman	Mimosoideae	*		*	*	FW, FOD, HC, W
Phyllostylon brasiliense	Ulmaceae	*	*			FW, CH
Piper aduncum	Piperaceae			*		NO
Pisonia macranthocarpa	Nyctaginaceae			*	*	NO
Platymiscium pleiostachyum	Papilionoideae	*	*			FW
Pterocarpus rohrii	Papilionoideae	*	*			FW, LF, W
Randia armata	Rubiaceae			*	*	FW
Randia cookii	Rubiaceae	*	*			FW
Randia nicaraguensis	Rubiaceae			*		FW
Sapranthus nicaraguensis	Annonaceae	*	*	*	*	NO
Senna atomaria	Caesalpinoideae	*	*	*	*	FW, CH
Simarouba glauca	Simaroubaceae			*	*	W, CH
Spondias purpurea	Anacardiaceae	*	*	*	*	NO
Spondias sp.	Anacardiaceae			*	*	NO
Stemmadenia obovata	Apocynaceae	*	*	*	*	FW
Sterculia apetala	Sterculiaceae			*	*	FW
Swietenia humilis	Meliaceae	*	*			W, CH, HC

Appendix. Continued

Species	Family	Deciduous		Gallery		Uses
		1994	2000	1994	2000	
Tabebuia ochracea	Bignonaceae	*	*	*	*	FW, LF, W
Tabebuia rosea	Bignonaceae				*	FW, LF, W
Terminalia oblonga	Combretaceae			*	*	FW, HC, W
Tetrorchidium rotundatum	Euphorbiaceae			*	*	NO
Thouinidium decandrum	Sapindaceae	*	*	*	*	FW, CH, HC
Trema micrantha	Ulmaceae		*			FW, CH, P
Trichilia hirta	Meliaceae	*		*	*	W, FW
Trichilia moschata	Meliaceae	*	*	*	*	P, W
Triplaris melaenodendron	Polygonaceae			*	*	P, LF
Ximenia americana	Olacaceae	*	*	*	*	NO
Zanthoxylum belizense	Rutaceae			*	*	W, RC
Zanthoxylum caribaeum	Rutaceae	*	*	*	*	NO
Ziziphus guatemalensis	Rhamnaceae	*	*			W, FW, P
Zuelania guidonia	Flacourtiaceae	*	*			NO

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