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ON THE NATURE OF THE DRY EVERGREEN FOREST (COPPICE) COMMUNITIES OF NORTH ANDROS ISLAND, BAHAMAS[1]

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ABSTRACT

As a part of our continuing research on the vegetation of the Bahamas and in an effort to better characterize the various components of the vegetation of the Bahamas, a detailed investigation of the Coppice Communities of North Andros, Island, Bahamas was initiated. The vegetation of fifteen stands of dry evergreen forest was sampled by quadrats and the data analyzed by dominance-type classification and Detrended Correspondence Analysis. We found that coastal stands are generally at lower elevations, have fewer sinkholes, are less dense and rich in species, have lower species diversity, and have more multi-stemmed trees than interior stands. Coastal stands were divided into two communities: METOPIUM - COCCOLOBA (COASTAL) and COCCOLOBA and interior stands into three: METOPIUM - COCCOLOBA (INTERIOR), METOPIUM - EXOTHEA and EXOTHEA - BURSERA - METOPIUM. Within the Bahamas, the dry evergreen forest of North Andros is more similar to vegetation which occurs on the northern and central Bahamas Islands than to scrubbier vegetation on the southern islands. Outside the Bahamas, it is similar to the tropical hardwood hammocks of southern Florida and some communities on limestone soils in the Greater Antilles.

INTRODUCTION

Although the flora of the Bahamas has been studied since 1725 (Coker 1905), the plant communities on Andros Island, Bahamas have been described only in broad qualitative terms. Correll and Correll (1982) mentioned nine communities for all of the Bahamas, and Northrop (1902) noted five for New Providence and Andros Island. Only Nickrent et al. (1988) and Eshbaugh and Wilson (1990) have described communities for Andros specifically: pineland, saltwater marsh, savanna, scrub, freshwater swamp, beach/strand, coastal rock, mangrove, coastal coppice, and interior coppice.

The two most prevalent natural terrestrial plant communities are the pineland and what historically has been termed the "coppice." The pineland, or pine barrens of Northrop (1902), is the most widespread community on Andros and is dominated by Pinus caribaea (Nomenclature after Correll and Correll 1982). Some woody plants characteristic of the pinelands include Metopium toxiferum, Duranta repens, and Tetrazygia bicolor. Stands of pine occur on loose limestone rock substrate and cover a large portion of central and eastern Andros (Sauleda and Adams 1979).

The coppice communities are examples of dry evergreen forests (DEF) and are also termed thickets or woodlands. They consist primarily of broad-leaved shrubs and trees. Coastal DEF occurs behind the beach/strand or coastal rock communities on limestone rock or a mixture of rock and sand (Nickrent et al. 1988). The vegetation is dominated by large shrubs and trees which often support many bromeliad and orchid epiphytes (Eshbaugh and Wilson 1990). Stands of interior DEF, the blackland community of Correll and Correll (1982), generally occur as "islands" within pinelands away from the coastline. Based on canopy height, stands have been divided into low (2-4 m) and high (5-12 m) DEF (Coker 1905; Sauleda and Adams 1979). Low DEF is similar in appearance to scrub communities (Eshbaugh and Wilson 1990), but is more dense, less thorny, and generally occurs on jagged rock substrates (Nickrent et al. 1988). High DEF is often found on more elevated limestone land forms ("sea ridges") containing many sinkholes up to 7 m in diameter and depth. These sinkholes support a

[1] This paper is an expanded and slightly modified version of an earlier paper by Smith, I.K. and J. Vankat. In Press. Dry evergreen forest (coppice) communities of North Andros Island, Bahamas. Bull. Torrey Bot. Club.

major portion of the fern flora of Andros (Eshbaugh and Wilson 1990).

The term "coppice" has been applied to DEF vegetation from at least the early part of this century (cf. Northrop 1902, Cocker 1905), presumably as a result of British influence in the Bahamas. The existing DEF on Andros, along with most of the vegetation in the Bahamas, is thought to be secondary growth. Formerly, based upon Columbus' descriptions, trees in the Bahamas were known to be larger than those now present. DEF vegetation with today's structural characteristics has been present on North Andros at least throughout the life span of the island's oldest inhabitants. Today, the DEF continues to be disturbed by human activities. Cutting for firewood seldom occurs on Andros, but economically valuable trees such as Swietenia mahagoni (mahogany) and Lysiloma sabicu (horseflesh) are extracted to make wood carvings and Coccothrinax argentata (silver-top palm) is used to make baskets, hats, mats, and picture frames. Moreover, large sinkholes with decaying vegetation are used for agriculture, such as banana and papaya plants. Stands are commonly cleared for home sites. Fires rarely but occasionally invade DEF sites.

Recently, the Bahamian government has been considering initiating sustained-yield logging and agriculture in the pinelands and possibly clearing around Swietenia mahagoni and Lysiloma sabicu in DEF in order to favor growth for eventual harvesting. Conservation concerns on Andros include protection of some land from development and consideration of the introduction of the endangered Bahamas parrot (Amazona leucocephala bahamensis) into DEF. Informed decisions on these economic and conservation issues require better descriptions of the vegetation than are currently available.

The objective of this investigation was to quantitatively describe the dry evergreen forest (coppice) communities on North Andros Island, Bahamas. Specifically, we characterize DEF composition and structure and determine whether different community types or vegetation gradients are present.

STUDY AREA

Andros Island is 210 km southeast of Miami, Florida and is the largest of the 35 inhabited Bahamas Islands. It is 45 X 165 km and covers approximately 6000 km^2. It is divided by a series of shallow channels called "bights" into three main sections: North Andros (the largest), Middle Cay, and South Andros (Sealey 1985; Eshbaugh and Wilson 1990).

Mean annual temperature in the Bahamas is about 25° C (Correll and Correll 1982) and the humidity is relatively high (Patterson and Stevenson 1977). North Andros has infrequent frosts, but the climate is considered subtropical by Nickrent et al. (1988) and others. Annual precipitation is 1300 mm (Sealey 1985), most of which occurs between May and October (Campbell 1978).

The substrate of Andros is of oolitic limestone and the soil is usually sandy or stony and poorly developed (Sealey 1985). The soil is also low in organic matter (Patterson and Stevenson 1977), with a pH of 7-8 (Henry 1974). Although the topography of Andros has relatively little variation, Sealey (1985) has recognized four major landscape types: ridgeland, rockland, wetland, and coastland. The ridgeland contains a series of rocky ridges up to 18 m in height extending along the east coast (Northrop 1902; Eshbaugh and Wilson 1990). Rockland landscapes are flat and rocky and often have a soft limestone substrate suitable for farming. In both ridgelands and rocklands, karstic weathering (the dissolving of limestone by rainwater) produces platted, pitted, or honeycombed rock surfaces (Correll 1979), as well as solution holes or sinkholes that often extend down to the (fresh) water table. Wetland landscapes occur in both inland and coastal areas covered by shallow water for at least part of the year, and coastland landscapes consist of various types of beaches. Only the wetland landscape type lacks DEF vegetation.

METHODS

Data Collection. During 1989 and 1990 summers we sampled 15 coastal and interior stands of DEF on North Andros Island (Figure 1), five each from the coastland, ridgeland, and rockland landscape types (Smith 1991). Stands with a canopy generally <4 m were not sampled because they were nearly impenetrable. For each stand, elevation and distance from the coast were determined using topographic maps and aerial photographs.

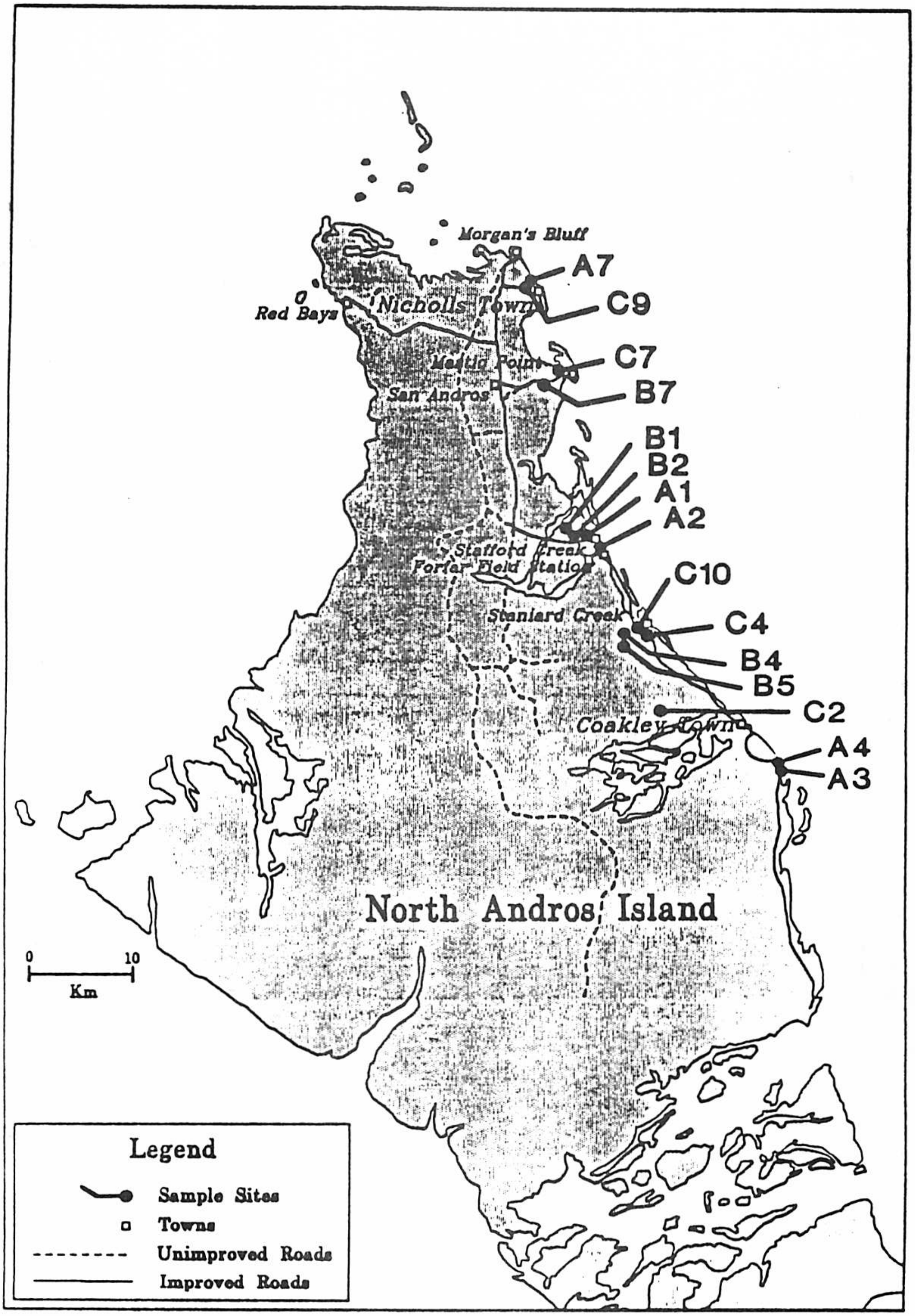

Figure 1. Map of North Andros Island, Bahamas and locations of the 15 stands sampled. A = coastland, B = ridgeland, and C = rockland. Original base map compiled by D.R. McRitchie, 1988; this version by Miami University Geographic Information Systems Laboratory, 1991.

We identified and measured the diameter at breast height (dbh) of all trees and palms ≥ 5 cm dbh in either a 20x25 or 20x50 m plot, depending on plot size. In each plot, the cover and number of sinkholes ≥ 2 m deep and the abundance of bromeliads, ferns, orchids, and rocks were estimated visually. In a 5x5 m subplot in each corner of a plot, all trees and shrubs ≥ 1 m tall were identified and counted with the canopy height being measured with a clinometer. Herbarium specimens and all data, including plot locations, are deposited in the Willard Sherman Turrell Herbarium (MU), Miami University, Oxford, Ohio.

Data Analysis. Three data sets were examined: 1) overstory species (plot data; species with individuals > 5 cm dbh), 2) understory species (subplot data minus species with individuals ≥ 5 cm dbh in any plot), and 3) overstory and understory species combined (subplot data; species with individuals ≥ 1 m tall). Density and basal area values were calculated for the overstory species; however, because sinkholes were often inaccessible for sampling, we subtracted the areas of sinkholes ≥ 2 m deep from the area of the sample plots and adjusted absolute values of density and basal area accordingly (adjustments ranged from 0 to 4%). The mean of the relative density and basal area values was used as an importance percentage for the overstory species; relative density was used as an indication of abundance for understory species and for over- and understory species combined. Species richness was calculated as the total number of species sampled and species diversity as an inverted Simpson's Index (in units of species equivalents).

Community types and vegetation gradients were determined using the dominance-type approach (Whittaker 1973) and Detrended Correspondence Analysis (DCA; Hill 1979). Relative basal area values were used in both analyses, and the minimum value for a dominant was 10%. Regression analysis was used to determine relationships between vegetation gradients and environmental variables and t-tests to determine differences between coastal and interior DEF. All statistical analyses were done with Minitab (Schaefer and Anderson 1989).

RESULTS

1. General Description Of Dry Evergreen Forest Vegetation. Ninety-eight woody plant taxa and two palms representing 80 genera and 42 families were sampled (Table 1). Nearly half (19) of the plant families were represented by only one species. The Rubiaceae had the largest number, 10 species. Most individuals were not in flower or fruit when sampled, and it was especially difficult to differentiate between *Eugenia* and *Calyptranthes* and among individual species of *Calyptranthes*, *Coccoloba*, and *Eugenia*.

Most stands sampled had few bromeliads, but more bromeliads than orchids and more orchids than ferns. The bromeliads (*Tillandsia* spp.) and orchids (e.g., *Encyclia* spp. and *Oncidium* spp.) were primarily epiphytic. The ferns (e.g., *Anemia* spp. and *Adiantum tenerum*) were primarily terrestrial and in sinkholes. None of the stands sampled in the coastland contained ferns. All stands had vines (e.g., *Jacquemontia* spp. and *Smilax* spp.) and/or viney shrubs (e.g., *Chiococca alba* and *Oplonia spinosa*). Although Northrop (1902) and Campbell (1978) stated that cacti were characteristic of stands near the coast, none were observed.

The ground surface of most plots was rocky and had few if any sinkholes. Six stands contained sinkholes ≥ 2 m deep, having a mean relative cover of 2.2% (range 1 to 4%). Only one of the five plots in the coastland had a sinkhole and it was < 2 m deep. a. Overstory species. Of the 100 total species, 65 were present in the overstory. Only 10 of these had an importance percentage ≥ 2%, with the dominants being *Metopium toxiferum* (28%) and *Coccoloba* spp. (25%; Table 2). These two taxa, along with *Bursera simaruba*, occurred in all 15 plots, and *Bumelia salicifolia* occurred in 14. In contrast, 35 species were found in only one or two plots (Figure 2). Ten of the 11 most abundant taxa are broad-leaved and all are evergreen or semi-evergreen.

Species richness of the overstory was 16.0 ± 3.2 species (mean ± standard deviation; range of 13 to 22) in the 20x25 m plots and 23.0 ± 6.5 species (range of 17 to 35) in the 20x50 m plots.

Table 1. Systematic Listing of species collected and the community association of these species.

	(O)	(U)	1	2	3	4	5
ACANTHACEAE							
Oplonia spinosa		+	+		+		
ANACARDIACEAE							
Metopium toxiferum	+		+	+	+	+	+
APOCYNACEAE							
Plumeria obtusa	+			+			
AQUIFOLIACEAE							
Ilex							
I. krugiana	+				+	+	
I. repanda	+		+		+	+	
ASTERACEAE							
Eupatorium bahamense		+					+
Gochnatia ilicifolia		+	+				
BIGNONIACEAE							
Jacaranda coerulea	+				+		
Tabebuia							
T. bahamensis	+		+	+	+	+	
T. lepidota		+			+		
BORAGINACEAE							
Bourreria ovata		+	+	+	+	+	
BURSERACEAE							
Bursera simaruba	+		+	+	+	+	+
CANELLACEAE							
Canella winterana	+			+			
CASUARINACEAE							
Casuarina litorea	+		+				
CELASTRACEAE							
Crossopetalum rhacoma		+			+	+	
Maytenus buxifolia	+		+	+			
Schaefferia frutescens		+				+	+
COMBRETACEAE							
Conocarpus erectus	+		+				
CUPRESSACEAE							
Juniperus barbadensis	+		+			+	
EBENACEAE							
Diospyros crassinervis	+		+	+	+	+	
ERYTHROXYLACEAE							
Erythroxylum							
E. areolatum	+		+		+		+
E. rotundifolium	+		+	+	+	+	
EUPHORBIACEAE							
Ateramnus lucidus	+		+	+			
Bonania cubana	+		+	+	+		
Grimmeodendron eglandulosum		+	+				
Pera bumeliifolia	+		+		+	+	
Phyllanthus epiphyllanthus		+		+	+		
Savia bahamensis	+		+		+		
FLACOURTIACEAE							
Banara minutiflora		+		+		+	+
Casearia nitida		+			+		
Xylosma buxifolium		+			+	+	
GUTTIFERAE							
Clusia rosea	+				+		
LAURACEAE							
Nectandra coriacea	+				+		
LEGUMINOSAE							
Acacia choriophylla	+		+		+	+	
Ateleia gummifera	+					+	
Caesalpinia bahamensis	+				+		

Leucaena leucocephala	+		+	+	+	+	
Lysiloma sabicu	+		+		+	+	
Pithecellobium							
P. bahamense		+			+	+	
P. keyense	+		+	+			
P. unguis-cati		+				+	
MALPIGHIACEAE							
Byrsonima lucida	+		+				
Malpighia polytricha	+		+		+		
MELASTOMATACEAE							
Tetrazygia bicolor		+			+	+	
MELIACEAE							
Swietenia mahagoni	+		+	+	+	+	+
MORACEAE							
Ficus							
F. aurea	+			+	+	+	+
F. citrifolia	+		+	+	+	+	+
F. perforata	+				+	+	+
MYRSINACEAE							
Ardisia escallonioides	+				+		
Myrsine floridana	+		+		+		
MYRTACEAE							
Calyptranthes spp.[1]	+					+	
Eugenia							
E. foetida	+		+				
E. spp.[2]	+		+	+	+	+	+
Myrcianthes fragrans		+	+				
Psidium longipes	+		+				
NYCTAGINACEAE							
Guapira							
G. discolor	+		+	+	+	+	+
G. obtusata		+	+				
OLACACEAE							
Schoepfia chrysophylloides	+		+				
OLEACEAE							
Forestiera segregata	+				+		
PALMAE							
Coccothrinax argentata	+		+				
Thrinax morrisii	+		+				
PINACEAE							
Pinus caribaea var. bahamensis	+				+	+	
POLYGALACEAE							
Polygala oblongata		+				+	+
POLYGONACEAE							
Coccoloba							
C. spp.[3]	+		+	+	+	+	+
C. uvifera	+		+				
RHAMNACEAE							
Colubrina arborescens	+		+				
Krugiodendron ferreum	+		+		+	+	
RUBIACEAE							
Catesbaea spinosa		+			+		
Chiococca alba		+	+		+	+	+
Erithalis fruticosa	+		+				
Guettarda							
G. elliptica		+	+		+	+	
G. scabra		+	+		+	+	+
Neolaugeria densiflora	+				+	+	
Psychotria							
P. ligustrifolia		+	+	+	+	+	+
P. nervosa		+	+		+	+	+
P. pubescens		+			+	+	
Randia aculeata		+	+	+	+	+	+

RUTACEAE							
Amyris elemifera	+		+	+	+	+	
Zanthoxylum							
Z. coriaceum	+		+				
Z. cubense	+				+	+	
Z. flavum	+			+	+		
SAPINDACEAE							
Exothea paniculata	+		+	+	+	+	+
Hypelate trifoliata	+				+	+	
Thouinia discolor	+		+				
SAPOTACEAE							
Bumelia							
B. americana	+				+		
B. salicifolia	+		+	+	+	+	+
Manilkara							
M. bahamensis	+		+				
M. zapota	+			+		+	
Mastichodendron foetidissimum		+			+	+	
SIMAROUBACEAE							
Alvaradoa amorphoides	+				+	+	
Picramnia pentandra		+		+			
Simarouba glauca		+		+			
SOLANACEAE							
Capsicum annuum		+		+	+		
Solanum erianthum	+					+	
THEOPHRASTACEAE							
Jacquinia keyensis	+		+				
UNKNOWNS							
Unknown 1		+		+			
Unknown 2		+				+	
VERBENACEAE							
Duranta repens		+			+	+	+
Lantana involucrata		+			+		+
Petitia domingensis		+			+	+	

(O) = Overstory, (U) = Understory, 1 = Metopium/Coccoloba (coastal), 2 = Coccoloba, 3 = Metopium/Coccoloba (Interior), 4 = Metopium/Exothea, and 5 = Exothea/Bumelia/Metopium.

[1] C. pallens and C. zuzygium

[2] E. axillaris and E. confusa

[3] C. diversifolia with some C. krugii, C. swartzii, and C. tenuifolia

Species diversity was 4.2 ± 1.1 species equivalents (range of 2.4 to 5.7) in the 20x25 m plots and 5.7 ± 2.4 species equivalents (range of 1.9 to 8.2) in the 20x50 m plots.

Overstory stem density was 3089 ± 828 stems/ha (range of 1700 to 3918). Stand basal area averaged 23.0 ± 4.7 m^2/ha (range of 13.6 to 32.8). The largest dbh values were 55.7 cm for a Ficus aurea, 52.7 cm for a Swietenia mahagoni, 46.6 cm for a Metopium toxiferum, and 39.2 cm for a Coccoloba spp.

Thirty-one overstory species had at least one individual with a multiple-stem growth form (≥ 3 stems at breast height). This growth form was especially common in Coccoloba spp., with a total of 83 such individuals occurring in 11 of 15 stands. No other species had > 19 individuals with this growth form or was found in > 7 stands.

b. Understory species. Of the 35 species restricted to the understory, six had a relative density ≥ 5% (Table 3). The most abundant were Psychotria ligustrifolia (15%), Randia aculeata (15%), and Phyllanthus epiphyllanthus (12%). Only P. ligustrifolia was found in all 15 plots, followed by R. aculeata in 13. Twenty-one species were found in only one or two plots Figure 2). In general, the understory species tended to be less widespread than the overstory species.

The richness of over- and understory species combined was 29.2 ± 6.1 species (range of 18 to 38), while the richness of understory species alone was 7.8 ± 2.0 species (range of 4 to 10). Species diversity of the over- and understory combined was 8.3 ± 2.9 species equivalents (range of 4.9 to 13.0), and the diversity of the understory species alone was 4.1 ± 1.5 species equivalents (range of 1.3 to 7.5).

Stem densities were 7478 ± 1298 stems/ha (range of 5150 to 9975) for the under- and overstory combined and 4363 ± 1325 stems/ha (range of 2700 to 6500) for the understory species alone.

2. Dry Evergreen Forest Communities.

Dominance-type classification using relative basal area values produced the following classification of four general community types: 1) METOPIUM - COCCOLOBA; 2) COCCOLOBA; 3) METOPIUM - EXOTHEA and 4) EXOTHEA - BURSERA - METOPIUM

The DCA ordination indicates that the COCCOLOBA and the EXOTHEA - BURSERA - METOPIUM community types are floristically separated from the others (Figure 3). Also, the METOPIUM - COCCOLOBA and the METOPIUM - EXOTHEA community types make up a gradient, as illustrated in the lower left of the ordination figure. Because differences between coastal and interior stands had been recognized previously, we divided the METOPIUM - COCCOLOBA community into COASTAL (< 500 m from coastline) and INTERIOR subdivisions. The final classification, therefore, has two coastal communities, METOPIUM - COCCOLOBA (COASTAL) and COCCOLOBA, and three interior communities, METOPIUM - COCCOLOBA (INTERIOR), METOPIUM - EXOTHEA, and EXOTHEA -BURSERA - METOPIUM.

a.Coastal dry evergreen forest communities. The METOPIUM - COCCOLOBA (COASTAL) community type was represented by three stands which occurred 15-300 m from the coast with elevations of 0-3 m. Canopy heights were 4-10 m, and average stand basal area and density of the overstory were lower than for the other community types (Table 2). Of the 42 overstory taxa, M. toxiferum (33% importance) and Coccoloba spp. (25%) dominated (Table 2). Of a total of 12 understory species, Randia aculeata and Bourreria ovata dominated with 28 and 22% relative density, respectively (Table 3).

The other coastal type, the COCCOLOBA community, was represented by two stands that were 0 and 150 m from the coast at elevations of 0-3 m. Canopy heights were 5-16 m. Of the 24 overstory taxa, Coccoloba spp. (65%) dominated (Table 2). The dominant understory species, of a total of nine, were Phyllanthus epiphyllanthus (44%) and Picramnia pentandra (31%; Table 3).

b.Interior dry evergreen forest communities. The METOPIUM - COCCOLOBA (INTERIOR) community type was represented by six stands located 1700-4200 m from the coast between 0-6 m elevation. Canopy heights were 6-11 m, and average stand basal area and density of the overstory were higher than for the other community types (Table 2). Of the 36 overstory taxa

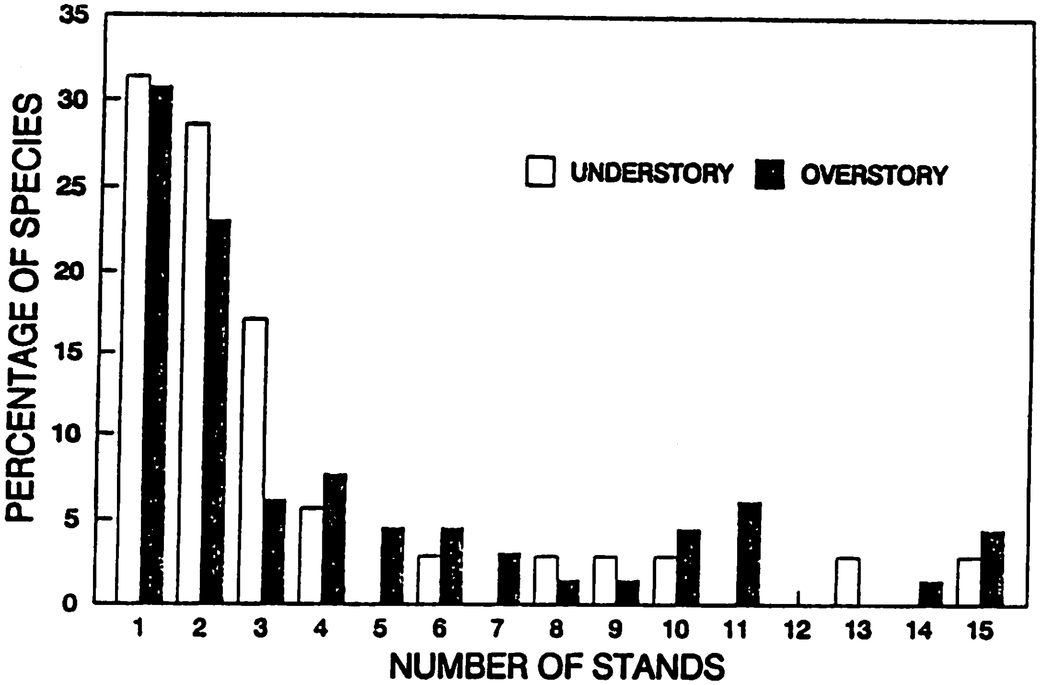

Figure 2. Percentage of the overstory and understory species found in 1 to 15 stands.

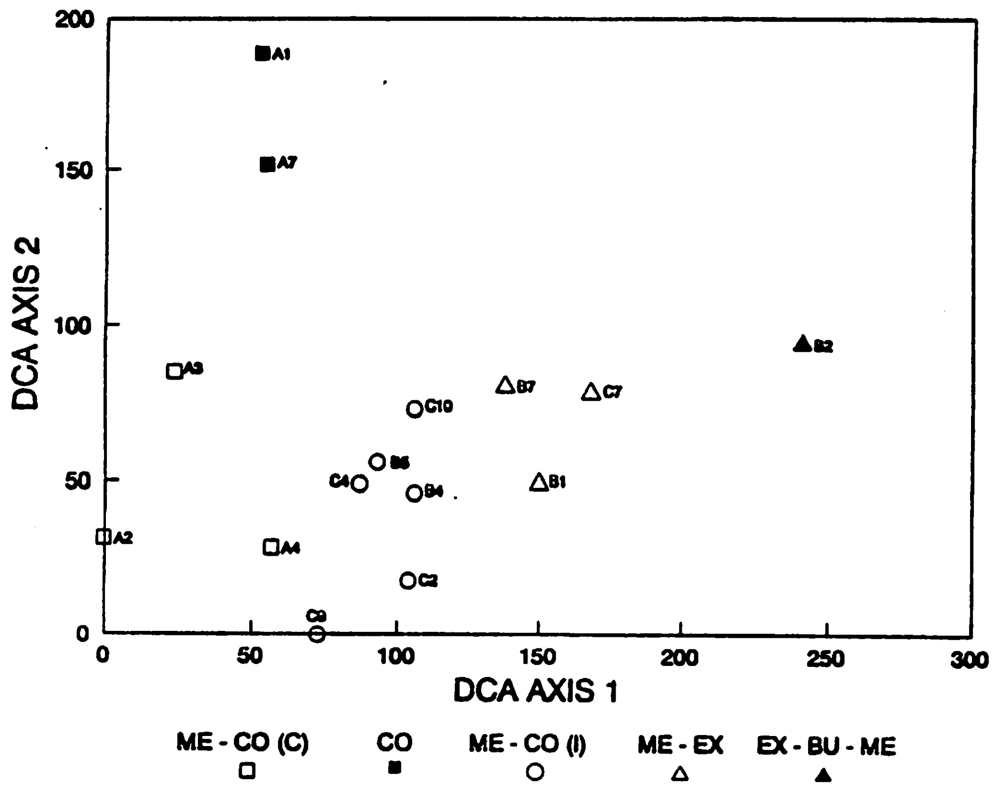

Figure 3. Detrended Correspondence Analysis ordination diagram. Eigenvalues for axes 1 and 2 are .346 and .107, respectively, and represent 89% of the variation accounted for by the first four axes. Names of the community types are the first two letters of the genus of the dominant tree species; BU = *Bursera*, CO = *Coccoloba*, EX = *Exothea*, ME = *Metopium*, C = coastal, and I = interior.

present, M. toxiferum (38%) and Coccoloba spp. (21%) dominated (Table 2). The important understory species (of 20 total) were Guettarda scabra (19%), Psychotria nervosa (18%), and P. ligustrifolia (16%; Table 3).

The METOPIUM - EXOTHEA community type was represented by three stands which occurred at distances of 1300-3700 m from the coast, at elevations of 0-9 m. Canopy heights were 5-13 m. Of the 31 overstory species, M. toxiferum (28%) and E. paniculata (19%) dominated (Table 2). Average stand density of the understory was lower than for other community types (Table 3). The important understory species (of 16 total) were Randia aculeata (19%), Psychotria ligustrifolia (17%), Pithecellobium bahamense (16%), and Phyllanthus epiphyllanthus (14%; Table 3).

The EXOTHEA - BURSERA - METOPIUM community was represented by one stand found 4100 m from the coast over an elevational range of 6-9 m with a canopy height that varied from 4-8 m. This site contrasted with the others in being a ridge, where half the plot was on the ridge top and half on the steep hillside. Of the 13 overstory species, E. paniculata (27%), B. simaruba (18%), and M. toxiferum (16%) dominated, followed by Ficus aurea (14%), (Table 2). Average stand density of the understory was much higher than for the other community types (Table 3). Randia aculeata (24%) dominated the nine understory species (Table 3).

3. Statistical analyses.

Regression analysis revealed significant relationships between stand DCA ordination scores and a few of the 13 biotic and abiotic factors listed in Table 4. The strongest was a positive relationship between first axis scores and distance from the coast ($R^2=0.56$; $p=.001$). This result paralleled the distribution of stands on the ordination figure, where coastal community types are on the left and interior types to the right. The positive relationship between first axis DCA scores and elevation ($R^2=0.48$; $p=.004$) supported this result, in that elevations on North Andros are generally higher inland because of the ridge system. In addition, regression analyses between the first axis DCA scores of interior DEF stands and distance to coast and elevation suggested that elevation may help to account for the gradient of interior community types ($R^2=0.32$; $p=.09$).

First axis DCA scores of all 15 stands were negatively related to the number of individuals with a low-branched or multiple-stemmed growth form ($R^2=0.25$; $p=.056$). Field observations support the generality that multi-stemmed plants are more common in coastal stands, where exposure to environmental stresses such as hurricanes, salt spray, and wind is greater. One coastal stand (A1, Fig. 1) lacked multi-stemmed individuals, but it was located in a protected site next to the mouth of a river.

First axis DCA scores were also positively related to understory species diversity ($R^2=0.37$; $p=.016$), indicating greater diversity in interior than coastal stands. Second axis DCA scores were negatively related to the species richness of the over- and understory combined ($R^2=0.32$; $p=.029$). Therefore, species richness is lower in the COCCOLOBA community than in the other community types.

T-tests used to compare coastal and interior DEF supported the regression findings for the first axis scores (Table 4). T-tests also revealed that interior DEF had greater density of overstory trees and greater richness of understory species; similar findings were obtained for the over- and understory individuals combined. Moreover, interior DEF had a greater total sinkhole area than coastal DEF.

DISCUSSION

Characterization Of Dry Evergreen Forest Vegetation. Two DEF (coppice) community types, coastal and interior, were previously described for North Andros Island by Nickrent et al. (1988) and Eshbaugh and Wilson (1990). Our findings suggest a refined division into several community types.

Coastal DEF, according to Nickrent et al. (1988), has a canopy height of up to 5 m, yet stands sampled in this investigation had canopies ranging from 4 to 16 m. Also contrary to previous descriptions, coastal DEF supported relatively few bromeliads and orchids. Trees with a low-branched or multi-stemmed growth form were common, a trait not previously reported. Of the 11 woody species noted as representative by Nickrent et al. (1988) and Eshbaugh and Wilson

Table 2. Relative basal area (BA), relative density (D), and importance percentage (IP) by community type for overstory taxa having a value ≥ 5% in at least one community type. Dashes (-) denote values <0.5%.

	Overall			Individual Community Types														
Community names				1			2			3			4			5		
	BA	D	IP	BA	D	IP	BA	D	IP	BA	D	IP	BA	D	IP	BA	D	IP
Metopium toxiferum	29	27	28	33	32	33	6	3	4	41	34	38	23	33	28	11	21	16
Coccoloba spp. *	23	27	25	25	24	25	67	62	65	16	26	21	11	12	12	4	11	7
Exothea paniculata	8	8	8	1	1	-	3	3	3	6	6	6	21	17	19	28	27	27
Bursera simaruba	6	6	6	2	3	2	11	11	11	3	4	4	9	6	8	18	19	18
Swietenia mahagoni	6	2	4	4	2	3	-	-	-	8	4	6	10	1	6	3	3	3
Acacia choriophylla	3	3	3	10	9	10				2	2	2	2	4	3			
Bumelia salicifolia	2	4	3	2	3	2	-	-	-	3	4	4	4	6	5	6	11	9
Eugenia spp. **	2	3	3	1	1	1	1	3	2	4	6	5	1	2	1	1	2	1
Pinus caribaea var. *bahamensis*	2	1	2							4	1	3	7	2	4			
Ficus aurea	1	-	1				-	-	-				-	-	-	25	2	24
Alvaradoa amorphoides		1	-										2	5	3			
Absolute basal area (m^2 /ha)	23.0			16.7			24.5			26.0			23.0			20.1		
Absolute density (stems/ha)	3089			2167			2315			3823			3196			2280		
Sample size (N)	15			3			2			6			3			1		

Key to plant community names: 1 = *Metopium/Coccoloba* (coastal), 2 = *Coccoloba*, 3= *Metopium/Coccoloba* (interior), 4 = *Metopium/Exothea*, and 5 = *Exothea/Bumelia/Metopium*.
* Primarily *Coccoloba diversifolia*, with some *C. krugii*, *C. swartzii*, and *C. tenuifolia*.
** *Eugenia axillaris* and *E. confusa*.

Table 3. Relative density by community type for understory species having a value greater than 10% in at least one community type. Dashes (-) denote values < 0.5%.

	Overall	Individual Community Types				
Community names		1	2	3	4	5
Psychotria liqustrifolia	15	16	9	16	17	4
Randia aculeata	15	28	2	11	19	24
Phyllanthus epiphylanthus	12		44	10	14	
Psychotria nervosa	10	9		18	4	10
Guetarda scabra	9	1		19	4	3
Bourreria ovata	7	22	7	3	1	
Guettarda elliptica	4	14		3	-	
Picramnia pentandra	4		31			
Pithecellobium bahamense	3			-	16	
Chiococca alba	2	2		1	2	14
unknown	2				10	
Polygala oblongata	1				3	13
Schaefferia frutescens	1				1	13
Absolute density (stems/ha)	4363	4400	4600	4241	3467	7200

Key to plant community names: 1 = *Metopium/Coccoloba* (coastal), 2 = *Coccoloba*, 3 = *Metopium/Coccoloba* (interior), 4 = *Metopium/Exothea*, and 5 = *Exothea/Bumelia/Metopium*.

Table 4. Values for abiotic and biotic parameters in coastal and interior stands.

Parameter	Coastal	Interior
Abiotic		
Distance from the coast (m)	173***	2535***
Elevation (m)	1.5***	4.2***
Sinkhole area (m^2 /ha)	0**	0.001**
Biotic		
Basal area (m^2 /ha)	19.8	24.5
Canapoy height (m)	7.1	7.9
Low-branched or multiple-stemed growth form (# indiv.)	24.6*	7.4*
Overstory density (stems/ha)	2298***	3484***
Understory density (stems/ha)	4480	4304
Understory richness (# spp.)	4.8**	7.3**
Understory diversity (# spp. equiv.)	2.8**	4.8**
Over- and understory density (stems/ha)	6520*	7957*
Over- and understory richness (# spp.)	24.0**	31.8**
Over- and understory diversity (# spp. equiv.)	8.4	8.2

Statistical significance calculated using t-tests: * p=.10, ** p=.05, *** p=.01.

(1990), only seven were found in the coastal stands sampled in this study. Northrop (1902) and Campbell (1978) stated that cacti were characteristic of stands near the coast, but none were observed in this investigation (Cacti occur in some stands of DEF on North Andros, but are characteristic of DEF only in stands on drier islands further south in the Bahamas e.g Long Island (Personal observation WHE and TKW). Ferns are probably limited in abundance by the lack of sinkholes in coastal DEF, because elsewhere ferns are most often found in sinkholes. Also, coastal influences such as salt spray may be limiting to fern establishment.

The results of this study support the descriptions of interior DEF by Nickrent et al. (1988) and Eshbaugh and Wilson (1990) that stands are dense and dominated by broad-leaved plants with a few scattered pines. We found that stem density in interior stands was higher than in coastal DEF and all taxa were broad-leaved except for Pinus caribaea var. bahamensis and Juniperus barbadensis. Sinkholes or at least shallow depressions were common, as previous reports indicated. The high diversity suggested in earlier studies was also supported, at least in that interior stands were more diverse in understory woody species than coastal stands. Nine of the ten woody species previously reported as common to high interior DEF were found in stands we sampled.

Problems With Comparing Vegetation. The lack of consistent terminology poses a difficulty for comparing DEF vegetation of North Andros with vegetation elsewhere. For example, Seifriz (1943) suggested that the Bahamian DEF was similar to thickets found throughout the American tropics. However, his description of thickets indicates vegetation more similar to the scrub community on Andros and perhaps the scrubby vegetation of the southern Bahamas Islands rather that the DEF of North Andros. We recommend the term "dry evergreen forest", indicating a somewhat arid variant of UNESCO's (1973) tropical and subtropical evergreen seasonal forest (see also Borhidi 1991).

Comparisons are further limited by the scarcity of thorough studies of the composition and structure of the plant communities in the Caribbean.For example, our study is the first quantitative description of any community type in the Bahamas.

The following sections outline comparisons of DEF on North Andros with other vegetation in the Bahamas and elsewhere in the Caribbean. More detailed comparisons are found in Smith (1991).

Comparisons With Bahamian Vegetation. The DEF on North Andros has nearly all the woody plant species listed by Nickrent et al. (1988) and Eshbaugh and Wilson (1990) as common in the scrub and pineland communities on the island. Differences occur in community physiognomy, however, as DEF is taller and less thorny than scrub and more dense than pineland.

Bahamian Islands reported to have vegetation similar to DEF on North Andros include Abaco, Cat, Long, New Providence, and Watlings Islands (Northrop 1902; Cocker 1905). For example, the dominant species and the physiognomy of some woodland communities on Abaco and Cat Islands, as reported by Little et al. (1977) and Byrne (1980), are similar to DEF on North Andros. The similarity of dominant species continues southward in the Bahamas (cf. Little et al. 1977, for Eleuthera); however, canopy height decreases in parallel with decreases in precipitation.

These findings show that DEF vegetation occurs widely in the Bahamas, but there can be significant differences in floristic composition and structure (as well as terminology). In general, the DEF of North Andros Island appears to be more similar to vegetation in the northern and central islands than to the drier, scrubbier vegetation of the southern islands.

Comparisons With Caribbean And North American Vegetation. The DEF of North Andros is also related to vegetation elsewhere in the Caribbean. In general, the Bahamian flora was derived primarily from regions to the south and east, with the strongest influence from Cuba and to a lesser extent from Puerto Rico, Hispaniola, the Yucatan Peninsula, and Florida (Little et al. 1977; Correll and Correll 1982). The influence of North America, although relatively small, was greater in the northwestern islands such as Andros than elsewhere in the Bahamas (Little et al. 1977).

The DEF of North Andros has environmental, physiognomic, and floristic similarities with the tropical hardwood hammocks of southern Florida. Hammocks occur as dense tree islands surrounded by pinelands, swamps, or marshes (Woodall 1980; Tomlinson 1986; Snyder et al. 1990). They are slightly elevated and on limestone soils with numerous cavities and sinkholes (Craighead 1971), as found with the interior DEF of North Andros. Chen and Gerber (1990) considered the climate of Florida to be subtropical, and the precipitation and temperature regimes (including the infrequent occurrence of frost) are similar to North Andros.

Canopy heights of hammocks are up to 18 m on the mainland and decline southward through the Florida Keys (Snyder et al. 1990), paralleling changes in the physiognomy of DEF in the Bahamas. Most tree species are broad-leaved evergreen or semi-evergreen and are common to the Bahamas and Greater Antilles (Snyder et al. 1990). The floristic similarity with North Andros is substantial, as over a third of the woody species reported by Snyder et al. (1990) for the hammocks of southern Florida were sampled in the DEF of North Andros. Also, the two most common trees in the hammocks are Bursera simaruba and Coccoloba diversifolia, and both are very abundant in DEF on North Andros well.

Other Caribbean vegetation is less well studied than in Florida; however, a few comparisons are possible. Robertson (1955), as reported in Snyder et al. (1990), implied that the coastal DEF of the Bahamas is floristically similar to coastal hardwood forests of the Greater Antilles (Puerto Rico, Cuba, Hispaniola, and Jamaica). Individual investigations support this generality; for example, see Murphy and Lugo (1986) for Puerto Rico, Smith (1954) and Borhidi (1991) for Cuba, and Asprey and Robbins (1953) for Jamaica. All these studies describe vegetation very similar to the DEF of North Andros (despite lacking frost) and on soils derived from either limestone or coral. In contrast, there is a low floristic similarity between the DEF of North Andros and the plant communities of the Lesser Antilles, where islands are of volcanic origin and have little limestone soil (Howard 1974).

CONCLUSIONS

The DEF of North Andros Island, Bahamas is dense, closed-canopied, broad-leaved, evergreen, and dominated by Metopium toxiferum and Coccoloba spp. Coastal DEF is generally at lower elevations and has fewer sinkholes than interior DEF. Also, coastal DEF is less dense, less rich in species, lower in species diversity, and has more trees with a low-branched or multi-stemmed growth form. The coastal DEF is divisible into two community types: METOPIUM - COCCOLOBA (COASTAL) and COCCOLOBA. The COCCOLOBA type is unique among all the DEF communities in that M. toxiferum is very low in importance and species richness is low. The interior DEF is divisible into three community types: METOPIUM - COCCOLOBA (INTERIOR), METOPIUM - EXOTHEA, and EXOTHEA - BURSERA - METOPIUM. These differ in a shift in importance from Metopium toxiferum to Exothea paniculata that parallels an increase in elevation.

Within the Bahamas, the DEF of North Andros is more similar to vegetation which occurs on the northern and central islands than to scrubbier vegetation on the drier, southern islands. Outside the Bahamas, the vegetation most similar appears to be the tropical hardwood hammocks of southern Florida.

In the next 10-15 years the human population of Andros Island is expected to expand substantially and increase pressure on native plant communities through agriculture, fire, and development. Correll and Correll (1982) cautioned that agriculture and development has eliminated some native species from DEF and reduced the abundance and distribution of economically valuable tree species such as Swietenia mahagoni, Lysiloma sabicu, and Mastichodendron foetidissimum (see also Campbell 1978).

Jordan (1989) was less alarmed about the effects of development in the Bahamas because he believed that many of the > 600 islands and cays would be left relatively undisturbed, providing representative natural systems, even if others were degraded and lost by human encroachment. However, this argument does not take into account the potential loss of species, species interactions, and plant communities unique to many islands. Little et al. (1977), for example, stated that although the islands are fairly uniform floristically, each has a different set of dominant species. Comparison of our results for North Andros with other islands indicates important differences in vegetation. Moreover, even on North Andros alone, the loss of some stands of DEF could seriously affect biodiversity; not only is DEF reported to have rare and endangered bromeliad, fern, and orchid epiphytes (Nickrent et al. 1988; Eshbaugh and Wilson, 1990), but also most woody plant taxa are restricted to a few stands and thus may be subject to local extinction. Such patterns of extinction are evident on other islands e.g Swietenia mahagoni on San Salvador. Therefore, concern about the effects of future development is more than justified. Our study demonstrates the biological significance of the vegetation of the Bahamas and the importance of minimizing human impact.

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