

Assessing tree species assemblages in highly disturbed Puerto Rican karst landscapes using forest inventory data

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Abstract

Tree species assemblages described by landscape-scale forest inventory data both agreed and differed from those described by intensive, site specific studies in Puerto Rico's highly disturbed northern karst belt. Species assemblages found on hill tops (typified by *Tabebuia heterophylla* or *Bursera simaruba* with *Coccoloba diversifolia*, *Licaria parvifolia*, and *Drypetes alba*), abandoned coffee shade (*Guarea guidonia*, *Dendropanax arboreus*, *Inga vera*, and *Persea americana*), early successional forest (*Tetrazygia elaeagnoides* with *Bucida bursera*), and reverting pasture (*Spathodea campanulata* and *Casearia guianensis*) fit well with previously described forest types. However, systematic sampling captured more marginal forest and showed greater importance of introduced species that comprise/dominate the forest in these areas, particularly *S. campanulata*. Therefore some assemblages were found to be more mixed and less defined than those observed in small scale intensive studies. Because forest inventory sampling includes less defined forest types and areas that are on the margins of environmental gradients, forest inventory data were less able to show the relationships between detailed forest types and environmental gradients observed in other studies. However, at the landscape level, forest inventory data complements and expands on the findings from intensive studies resulting in a clearer, unbiased view of the region's forests.

Introduction

In contrast to many countries in the tropics, forest cover on the island of Puerto Rico has steadily increased over the past 50 years due to economic policies which resulted in the widespread abandonment of agricultural activities and migration from rural to urban areas (Dietz 1986; Thomlinson et al. 1996; Alvarez-Ruiz et al. 1997; Rudel et al. 2000). Land abandonment and reversion to forest occurred throughout the northern karst belt, a region within the subtropical moist and wet forest

life zone with limestone-derived soils and geologic formations which occupies the northwestern portion of Puerto Rico.

Aerial photographs, land use maps, and historical accounts show that the area was almost entirely deforested by the early 1950s (Koenig 1953; Rivera and Aide 1998). There were numerous homesteads throughout the area, with practically every valley under cultivation or used as pasture (Acevedo-Rodríguez and Axelrod 1999). Shaded coffee plantations occupied alluvial terraces and sinkholes, and the surrounding hills were defor-

ested for building materials and fuel wood (Rivera and Aide 1998; Acevedo-Rodríguez and Axelrod 1999).

Since that time the region's small, disturbed forest fragments have grown and coalesced into some of the largest areas of contiguous forest on the island. Although the steep-sided, haystack-shaped mogote hill typifies the karst for many in Puerto Rico, the rugged, diverse landscape also holds cone karst similar to the 'cockpit country' of Jamaica, extensive cave formations, deep sinkholes, and river ramparts (Sweeting 1973; Monroe 1976; Chinaea 1980). Karst terrain and seasonal climate interact to create fine scale environmental patchiness seen as a source of high tree species diversity (Kelly et al. 1988).

The new forests in the karst have higher than average biodiversity for Puerto Rico, with over 1300 plant and animal species (Lugo et al. 2001; Miranda-Castro 2002). These forests provide habitat for 75 species of neotropical migrants, several species endemic to Puerto Rico, and 30 federally listed threatened and endangered species, most notably the endangered endemic Puerto Rican boa (*Epicrates inornatus*) and the soon to be reintroduced Puerto Rican parrot (*Amazona vittata*) (Dugger et al. 1979; Lugo et al. 2001; Miranda-Castro 2002). In addition to the native tree species, many tropical ornamental, forestry and agricultural tree species were introduced to the region and have become naturalized (Francis and Liogier 1991). The impacts these introduced, and often aggressively colonizing, species will have on the future species composition of the karst forests has been explored but is not entirely clear (Lugo and Brandeis 2003; Lugo 2004; Lugo and Helmer 2004).

Most of the information on the forests of the Puerto Rican northern karst belt has come from intensive, relatively small-scale studies which addressed specific hypotheses. There have been several such detailed studies of the vegetation communities in the northern karst belt focusing on specific areas like the Río Abajo public forest, a large protected area near the center of the northern karst belt (Dugger et al. 1979; Alvarez-Ruiz et al. 1997; Acevedo-Rodríguez and Axelrod 1999); studying stands which allowed for the comparison of tree species assemblages on different land uses (Rivera and Aide 1998); or examining differences in karst forest composition

along environmental and topographic gradients (Chinaea 1980).

These studies have provided detailed forest community descriptions for pieces of the northern karst belt. Landscape level studies such as large scale forest inventories can help fill in the blanks between these intensively studied areas. The goal of a forest inventory is to estimate forest parameters, such as basal area, volume or biomass at relatively large scales, such as that of an entire forest, region or nation. Forest inventories rely on extensive rather than intensive sampling, establishing many smaller plots or transects in an unbiased manner across a landscape. This approach to studying forests differs from ecological studies which establish fewer, generally larger, plots in areas of interest in order to address specific hypotheses or describe in detail forest characteristics.

Chinaea and Helmer (2003) took this approach when they analyzed the species composition of systematically-selected forest inventory plots from the island-wide Puerto Rico forest survey of 1990. Chinaea and Helmer (2003) found that the 29 inventory plots on limestone parent materials demonstrated unique species compositions indicative of karst forest.

This study provides a description of the tree species communities that have assembled in Puerto Rico's northern karst belt after the abandonment of agriculture and the introduction of numerous non-native trees species as seen from a landscape scale. Using current forest inventory data I examine the structural characteristics of the naturally regenerated karst forests, the existing tree species assemblages, and what species are indicative of these assemblages. I evaluate tree species assemblages identified using landscape-level forest inventory data and compared to descriptions based on smaller-scale, more intensive, site specific studies of those forests, and karst forests from the Dominican Republic and Jamaica. I assess how well the forest inventory captured the diversity of tree species in those forests, and examine how the assemblages compare in terms of the percentage of native or introduced species and species diversity. Further, I explore correlations of the assemblages with land use and topographic variables collected by the forest inventory.

Methods

Study site

Puerto Rico's northern karst belt is approximately 135 km long from east to west and 23 km at its widest points (page 18 in Monroe 1976), bordered by 66°10' to 67°10' west longitude and 18°30' to 18°18' north latitude (Chinaea 1980) (Figure 1). The study site is almost entirely in the subtropical moist forest life zone, with some sampling in the subtropical wet forest life zone (Ewel and Whitmore 1973). Much of the sampling took place on the steep-sided, sub-conical hills known as mogotes and the flatter areas with between the hills. Capped with hard limestone, mogotes often have only shallow, patchy soil cover while the areas between mogotes often have deeper, more productive soils derived from alluvial deposits (Monroe 1966). The natural forest types found here have been described as a mix of evergreen moist and seasonal forests in lower-lying areas, and dry evergreen forest/scrubland on dryer hill tops (Chinaea 1980; Rivera and Aide 1998; Acevedo-Rodríguez and Axelrod 1999).

The data used in this study were collected in 2001–2003 as part of the USDA Forest Service's Forest Inventory and Analysis (FIA) program's island-wide forest inventory and a supplemental

northern karst belt inventory. The forest inventory uses a computer-generated systematic sample (for details on the inventory design see Brandeis 2003). Additional sampling locations within the northern karst belt were systematically chosen by creating a sampling grid that was three times more intensive than the normal FIA inventory base sampling grid and choosing locations that fell on limestone and carbonate rock according to a Geographic Information System (GIS) map of geological substrates (Brandeis 2003). This sampling intensification produced approximately one sampling point every 800 ha.

Data collection

Field crews located sampling locations with Global Positioning System (GPS) satellite receivers, confirmed that they were on limestone substrate, and installed inventory plots following the protocols of the USDA Forest Service's Forest Inventory and Analysis (FIA) program where there was at least 10% tree canopy coverage and a minimum forested area of 0.4 ha around each plot center. An FIA plot consists of a cluster of four subplots each with a 7.3 m radius (Figure 2). There were 167 m² per subplot, for a total sampled area of 670 m² in a fully forested plot. One subplot was at plot center,

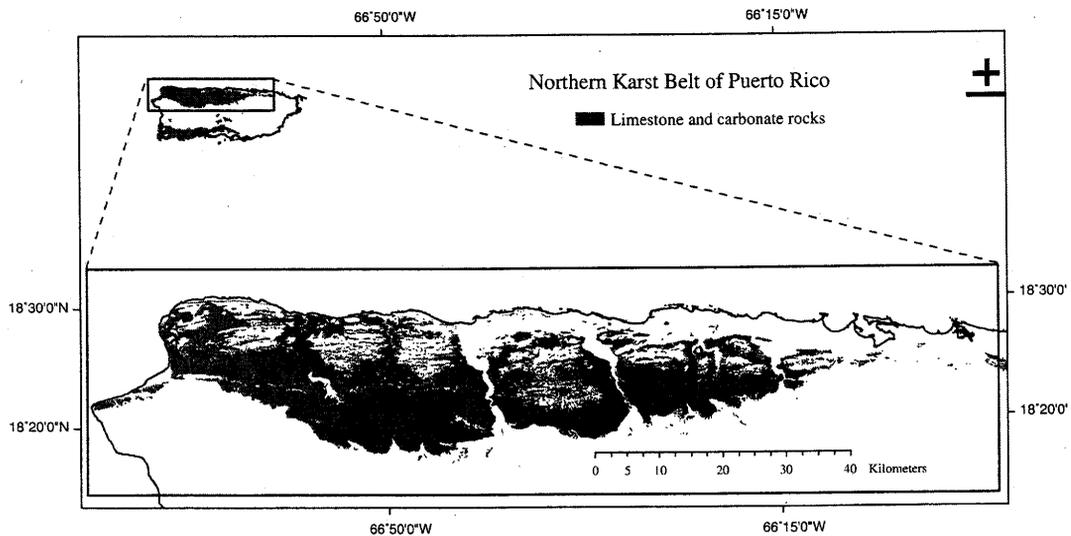


Figure 1. Northern karst belt of Puerto Rico.

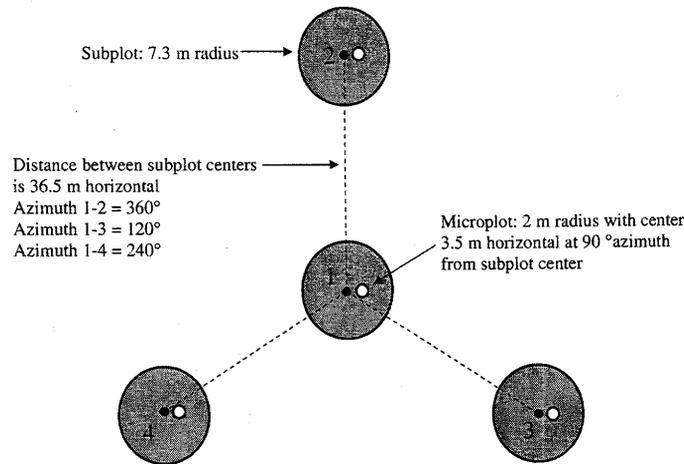


Figure 2. Forest inventory plot, subplot and microplot layout.

and 3 subplots were 36.6 m from the center subplot at 120, 240 and 360 degrees. This configuration was never altered, even if one or more of the subplots fell in a non-forested area. All trees with $D_{BH} \geq 12.5$ cm within the subplots were measured. All saplings with $D_{BH} \geq 2.5$ cm were measured and all seedlings with height ≥ 30 cm were identified and counted within a 2.1 m radius microplot nested in each subplot (Figure 2). For buttressed trees, D_{BH} was taken above the buttress and measurement height noted. Vouchers of unknown species were collected for subsequent identification at the herbarium in the University of Puerto Rico's Botanical Garden and at the International Institute of Tropical Forestry, both in Río Piedras, Puerto Rico. Species nomenclature follows the USDA Natural Resources Conservation Service's PLANTS database (<http://www.plants.usda.gov/>) from 2002. These procedures resulted in the measurement of 2116 trees with $D_{BH} \geq 2.5$ cm and 3541 seedlings at 79 forested plot locations (246 forested subplots). Twelve sampling locations that would have required multiple days to complete due to the distance from the road and rough terrain were not visited.

Field crews noted the following site characteristics for each plot; distance from trails, roads and urban areas, size of surrounding contiguous forest, land use, and ownership type. For each subplot crews noted; slope, aspect, physiographic class (ridge top, upper slope, middle slope, lower slope,

valley cove, valley bottomlands, and valley floodplains), forest type, stand size class, tree density, stand structure, disturbance, and indications of fire or grazing within the past five years. (Guidelines and measurement descriptions appear in the FIA Field Data Collection Manual, Version 1.62 Supplement C for Puerto Rico and the Virgin Islands, which can be downloaded at http://www.srs.fs.usda.gov/fia/manual/2.0_P2Manual.htm.)

Field crews categorized the forest at each inventory plot as either mature secondary forest, young secondary forest, or recent reversions to forest (less than 10% tree canopy coverage) based on size and density of the larger trees, canopy height and closure, and other factors from their experience in the field. Plot center elevation and Holdridge life zone was extracted from digital maps in the GIS.

Analytical methods

Stem density (TPH), basal area per hectare (BAH), and aboveground live tree biomass (AGB) for all trees with $D_{BH} \geq 2.5$ cm were calculated for each subplot, and the values for all 4 subplots were averaged for plot estimates. For partially forested plots, i.e. those that had some subplots in non-forested areas, plot averages represent the average of the forested subplots only. Aboveground live tree biomass (all aboveground parts, including

foliage) was calculated for each individual tree by applying regression equations specific to Holdridge life zone (See Ewel and Whitmore 1973). A species specific AGB equation was available for the palm *Prestoea montana* (Graham) Nichols and used here due to its different growth form.

Subtropical wet forest:

$$\text{AGB} = \exp[0.950 \cdot \ln(D_{\text{BH}}^2 H_{\text{T}}) - 3.282]$$

(Scatena et al. 1993)

Subtropical moist forest:

$$\text{AGB} = \exp[-3.1141 + 0.9719 \cdot \ln(D_{\text{BH}}^2 H_{\text{T}})]$$

(Brown et al. 1989)

Prestoea montana (Graham) Nichols:

$$\text{AGB} = 10.0 + 6.4(H_{\text{T}}) \quad (\text{Frangi and Lugo 1985})$$

To compare species importance throughout the entire sampled area, an importance value (IV) for each species was calculated by taking the average of relative dominance (species BA divided by the total BA), relative density (species TPH divided by total TPH), and relative frequency (number of plots where species occurred divided by total number of plots), multiplied by 100. Species IV was calculated for all stems with $D_{\text{BH}} \geq 2.5$ cm, then separately for trees ($D_{\text{BH}} \geq 12.5$ cm) and saplings ($D_{\text{BH}} < 12.5$ cm). Seedling IV was the average of relative density and relative frequency.

In the rugged karst terrain, a single plot might have subplots that fall in both valleys and on ridges, so to capture the physiographic differences subplots were used as the sampling unit for agglomerative hierarchical clustering and multivariate analyses. For this analysis, each species' tree and sapling (seedlings excluded) subplot IV was calculated by taking the average of only relative density and relative dominance. The primary data matrix consisted of 87 tree and sapling species IVs in 236 subplots after the removal of 65 rare species which each occurred in only one subplot (pp. 75-78 in McCune and Grace 2002). Hierarchical agglomerative cluster analysis, which used the Sorenson and Jaccard distance measure and Flexible Beta linkage where $\beta = -0.25$, was used to group subplots. Indicator species analysis using Dufrene and Legendre's (1997) method and Monte Carlo tests provided statistically significant indicator values for species defining each group. Non-

metric multidimensional scaling (NMS) was then used to explore the relationships between groups and the suite of environmental variables. Preliminary NMS runs (PC-Ord software, thorough autopilot mode) established the best dimensionality and a starting configuration for the final NMS analysis (pp. 115-116 in McCune and Mefford 1999). Scree plots and stress statistics from preliminary NMS runs indicated that a three-dimensional solution best fit the data.

The PC-Ord software was also used to produce species accumulation curves (average number of species found per number of inventory subplots measured), and calculate overall mean Shannon's diversity index, species diversity evenness, and Simpson's diversity index from the data prior to removing rare species from the main matrix for the NMS analysis (McCune and Mefford 1999). Shannon's diversity indices were calculated for each subplot. Once subplots were assigned to species groups by the cluster analysis a mean Shannon diversity index was calculated for each species group, and those means compared using analysis of variance (ANOVA) procedures for models of less than full rank with Least Squares Means pair-wise comparison tests (pp. 85-116 in Freund and Littel 1981).

Results

Seventy-three plots fell within the subtropical moist forest life zone and only 6 fell in subtropical wet forest according to the GIS. Although there was indication that the wet forest stands had higher BAH, the following results do not differentiate between moist and wet karst forest stands. Trees per hectare and AGB were not appreciably different from moist forest stands; multivariate analyses did not find significant correlations between species groupings and life zone; and there was not an adequate sampling of karst wet forest to justify separate analysis.

Karst forest structural characteristics represent a wide range of recovery from varying degrees of anthropogenic disturbance. To better present this range of values, stem density, basal area, and aboveground biomass estimates are presented in three relative stages of forest succession, along with the overall average for all plots, in Table 1. The classification of these stages of forest succes-

Table 1. Stem density (TPH, number of stems/ha), basal area (BAH, m²/ha) and aboveground biomass (AGB, Mg/ha) for trees with $D_{BH} \geq 2.5$ cm in the northern karst belt of Puerto Rico, by successional stage and all plots combined, with standard error for each mean following in parentheses.

	<i>N</i>	TPH	BAH	AGB
Reversions	12	1951.07 (516.97)	11.36 (2.61)	63.44 (22.16)
Young secondary	55	3347.25 (307.56)	19.83 (1.91)	105.50 (13.92)
Mature secondary	12	3997.94 (672.28)	26.97 (3.74)	169.22 (31.43)
All plots combined	79	3234.01 (255.84)	19.63 (1.56)	108.79 (11.67)

sion are admittedly a subjective classification by an experienced forest inventory field crew. But, they do serve to illustrate the spectrum structural characteristics currently found in the karst forest. A total of 210 tree species were found, including overstory trees, saplings and seedlings. The 50 most important species in the $D_{BH} \geq 12.5$ cm class are presented in Table 2, along with their importance in the sapling and seedlings size classes and origins (native or introduced to Puerto Rico). Native species comprised 60.5% of the total importance value of all species in the overstory, 79.5% of saplings, and 86.1% of seedlings. However, the introduced species *Spathodea campanulata* Beauv. (family Bignoniaceae) was the single most important species found in the overstory and midstory of karst forests (29.6% of all overstory stems, 35.1% of the basal area, and occurred in 31.5% of the plots). *S. campanulata* seedlings were also found relatively frequently (Table 2).

Considering just the trees with $D_{BH} \geq 2.5$ cm, there was an average of 3.7 species per inventory subplot. Overall Shannon's diversity index for the karst forest inventoried was 0.952, with an evenness of 0.0707, and Simpson's diversity index of 0.0505. To assess the survey's adequacy in capturing the tree diversity in the northern karst belt, species area (area = number of subplots) curves were plotted for all species found, trees with $D_{BH} \geq 10$ cm, and trees with $D_{BH} < 10$ cm (Figure 3). The upward sloping curves indicate that sampling 4.12 ha of forest in which 152 tree species with $D_{BH} \geq 2.5$ cm were found did not fully describe tree species diversity in the northern karst belt.

Cluster analysis produced 10 clearly defined groups of subplots with 1.95% chaining. Indicator species defining 9 of the 10 groups found in the cluster analysis are presented in Table 3. The tenth group consisted of 80 subplots which did not have any significant indicator species, so it is not

presented in Table 3. Table 4 shows the percentage of each group's IV that is from introduced and native species. The 3 NMS ordination axes produced a cumulative r-squared value of 0.387 (0.086 for axis 1, 0.150 for axis 2, and 0.151 for axis 3) (Figure 4). There were only weak associations with the environmental variables extracted from the inventory data and from GIS coverages (Table 5).

The first and most notable division made in the cluster analysis occurred between subplots heavily dominated by the introduced species *S. campanulata* and all others (Tables 3 and 4). The importance of introduced species in the tree, sapling and seedlings classes of this group was almost entirely due to the presence of *S. campanulata* (Tables 3 and 4). There was a weak correlation in NMS which showed that *S. campanulata* stands occurred predominately at lower and mid-elevations, on less steep lower slopes, floodplains and bottomlands, with few ridge and no upper slope sites (Table 5 and Figure 4).

Spathodea campanulata was important in another subplot grouping, although not directly as an indicator species. The group indicated by *Casearia guianensis* (Aubl.) Urban saplings in the midstory and some larger *Ocotea coriacea* (Sw.) Britt. trees in the overstory also frequently had *S. campanulata* trees in the overstory (Tables 3 and 4). This group had the second highest percentage of introduced species in the overstory due to the presence *S. campanulata* (Table 4).

Subplots where *Tabebuia heterophylla* (DC.) Britt. predominated were separated from the remaining subplots, followed by two groups with species indicative of disturbance and younger stand ages (*Citharexylum fruticosum* L., and *Leucaena leucocephala* (Lam.) de Wit with *Cecropia schreberiana* Miq.). Subplots were grouped by the importance of the indicator species *Bursera simaruba* (L.) Sarg., *Coccoloba diversifolia* Jacq.,

Table 2. Importance values for the 50 most important species in the northern karst belt forest of Puerto Rico, in tree ($D_{BH} \geq 12.5$ cm), sapling ($2.5 \leq D_{BH} < 12.5$), and seedling ($D_{BH} > 2.5$ cm and height ≥ 30 cm) size categories.

Scientific name with authority	Origin	Tree IV	Sapling IV	Seedling IV
<i>Spathodea campanulata</i> Beauv.	I	23.77	9.69	3.20
<i>Bursera simaruba</i> (L.) Sarg.	N	5.05	2.73	0.92
<i>Guarea guidonia</i> (L.) Sleumer	N	4.46	3.37	3.58
<i>Andira inermis</i> (W. Wright) Kunth ex DC.	N	4.25	1.77	3.50
<i>Tabebuia heterophylla</i> (DC.) Britt.	N	3.14	3.62	2.78
<i>Calophyllum antillanum</i> Britt.	I	2.89	1.61	2.66
<i>Ficus citrifolia</i> P. Mill.	N	2.69	0.73	0.46
<i>Neolaugeria resinosa</i> (Vahl) Nicols.	N	2.53	1.46	0.45
<i>Zanthoxylum martinicense</i> (Lam.) DC.	N	2.30	0.48	0.28
<i>Thouinia striata</i> Radlk.	N	2.26	4.12	2.25
<i>Bucida buceras</i> L.	N	2.22	1.29	1.09
<i>Coccoloba diversifolia</i> Jacq.	N	2.21	2.94	2.15
<i>Dendropanax arboreus</i> (L.) Dcne. & Planch. ex Britt.	N	1.91	1.34	1.54
<i>Cecropia schreberiana</i> Miq.	N	1.78	1.73	0.19
<i>Clusia rosea</i> Jacq.	N	1.77	0.45	0.88
<i>Inga laurina</i> (Sw.) Willd.	N	1.62	0.13	0.17
<i>Roystonea borinquena</i> O.F. Cook	N	1.60	0.00	0.60
<i>Citharexylum fruticosum</i> L.	N	1.55	2.85	1.02
<i>Syzygium jambos</i> (L.) Alston	I	1.42	3.03	1.99
<i>Inga vera</i> Willd.	N	1.27	0.58	0.70
<i>Cinnamomum elongatum</i> (Vahl ex Nees) Kosterm.	N	1.23	0.63	1.20
<i>Terminalia catappa</i> L.	I	1.21	0.00	0.13
<i>Senna siamea</i> (Lam.) Irwin & Barneby	I	1.18	0.94	0.08
<i>Persea americana</i> P. Mill.	I	1.08	0.00	0.07
<i>Albizia procera</i> (Roxb.) Benth.	I	1.01	0.00	0.22
<i>Petitia domingensis</i> Jacq.	N	0.99	0.00	0.07
<i>Casearia sylvestris</i> Sw.	N	0.90	3.35	3.72
<i>Adenantha pavonina</i> L.	I	0.88	1.63	0.50
<i>Licaria parvifolia</i> (Lam.) Kosterm.	N	0.81	1.26	0.55
<i>Sideroxylum salicifolium</i> (L.) Lam.	N	0.77	0.00	0.25
<i>Mangifera indica</i> L.	I	0.73	0.00	0.07
<i>Erythrina poeppigiana</i> (Walp.) O.F. Cook	I	0.72	0.00	0.15
<i>Cupania americana</i> L.	N	0.70	0.90	1.48
<i>Mammea americana</i> L.	N	0.69	0.18	0.14
<i>Ocotea coriacea</i> (Sw.) Britt.	N	0.67	0.67	1.08
<i>Delonix regia</i> (Bojer ex Hook.) Raf.	I	0.63	0.16	0.15
<i>Citrus sinensis</i> (L.) Osbeck	I	0.62	0.30	0.07
<i>Myrsine coriacea</i> (Sw.) R. Br. ex Roemer & J.A. Schultes	N	0.61	2.17	1.19
<i>Tetrazygia elaeagnoides</i> (Sw.) DC.	N	0.60	3.05	1.49
<i>Alchornea latifolia</i> Sw.	N	0.59	0.13	0.15
<i>Sapium laurocerasus</i> Desf.	N	0.55	0.72	0.15
<i>Ocotea leucoxyton</i> (Sw.) De Laness.	N	0.44	0.47	0.68
<i>Eugenia biflora</i> (L.) DC.	N	0.41	1.67	2.12
<i>Guapira fragrans</i> (Dum.-Cours.) Little	N	0.40	0.93	0.98
<i>Exothea paniculata</i> (Juss.) Radlk.	N	0.40	0.16	0.42
<i>Chrysophyllum cainito</i> L.	N	0.39	0.14	0.15
<i>Pimenta racemosa</i> var. <i>racemosa</i>	N	0.37	1.00	0.69
<i>Buchenavia tetraphylla</i> (Aubl.) Howard	N	0.32	0.00	0.08
<i>Ocotea sintenisii</i> (Mez) Alain	N	0.31	0.47	0.23

I = introduced species, N = native species.

Licaria parvifolia (Lam.) Kosterm., and *Drypetes alba* Poit., an assemblage that shows few introduced species (Tables 3 and 4).

Subplots grouped by their high importance values of *Guarea guidonia* (L.) Sleumer, *Dendropanax arboreus* (L.) Dcne. & Planch. ex Britt., *Inga*

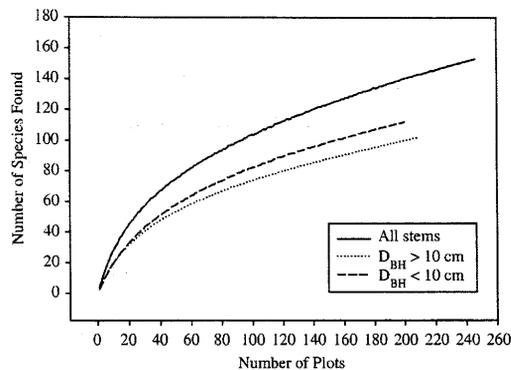


Figure 3. Species accumulation curves (average number of species found per number of inventory subplots measured), for all trees, trees with $D_{BH} \geq 10$ cm, and trees with $D_{BH} < 10$ cm.

vera Willd., and *Persea americana* P. Mill. commonly held *Inga laurina* (Sw.) Willd., *Mammea americana* L., *Citrus sinensis* (L.) Osbeck, and *Coffea arabica* L. (Tables 3 and 4). The low importance of *S. campanulata* in these stands is notable, with a variety of introduced fruit and shade trees making up their exotic component. *G. guidonia* and associates were found at mid-elevations on steeper slopes than where *S. campanulata*-dominated stands were found (Table 5 and Figure 4). *B. simaruba* and associates were found on steeper slopes, as were stands indicated by *T. heterophylla*, but both were at lower elevations than *G. guidonia* and *S. campanulata* stands (Table 5 and Figure 4).

The remaining subplots formed groups based on the indicator species *Myrsine coriacea* (Sw.) R. Br. ex Roemer & J.A. Schultes, *Tetrazygia elaeagnoides* (Sw.) DC. with *Bucida bursera* L., and *Eugenia monticola* (Sw.) DC. with *Bourreria succulenta* Jacq. (Table 2). These groups consisted of species indicative of disturbance, younger stand ages, and the lack of residual trees found in coffee shade (Table 3). These stands showed little correlation with environmental variables.

Comparing the mean Shannon diversity indices of each species group, the group defined by the indicator species *L. leucocephala* and *C. schreberiana* were significantly less diverse than all other groups except those indicated by *C. fruticosum* (Figure 5). Groups defined by *S. campanulata* and *T. heterophylla* also had lower than average Shannon diversity indices (Figure 5).

Discussion

Average stand structural characteristics as found in the forest inventory (average BAH of 11.4–27.0 m^2/ha and TPH of 1951–3998 stems/ha) fall within the broad range of values found by other researchers in the Puerto Rican northern karst belt. China and Helmer (2003) used forest inventory data from 1990 to show that forest on karst sites had an average basal area of 11.7 m^2/ha . Alvarez-Ruiz (1997) found basal areas that ranged from 12.4 to 27.1 m^2/ha for 520–7970 stems with $D_{BH} \geq 2.5$ cm in moist karst forest at varying successional stages and land use histories in the Río Abajo public forest. Basal areas found in this survey were less than those found by Rivera and Aide (1998) in karst forest growing on abandoned shade coffee and pasture sites (average 32.4 m^2/ha) in the Ciales and Morovis municipalities. However, the Rivera and Aide (1998) study included all stems with $D_{BH} \geq 1.0$ cm and had correspondingly higher stem densities (average of 4500 stems/ha). Dugger et al. (1979) also found basal areas that were higher than those found by this survey, ranging from 31.5 m^2/ha in the valleys between mogotes to 0.9 m^2/ha on the mogote tops for stems with $D_{BH} \geq 10$ cm within the Río Abajo public forest.

Several species groupings identified by the cluster analysis correspond to forest types identified in intensive studies of karst forest. Three of the species assemblages found in the survey data are known to occur on mogote tops and upper slopes, and showed some weak positive correlation with higher elevations and steeper slopes. *Tabebuia heterophylla* (group 2) has been found to predominate on pastures and degraded soils, particularly on slopes and exposed karst mogote tops, in the absence of competition from larger, more tolerant species (Weaver 2000; Parker 2003). Alvarez-Ruiz (1997) also describes a seasonal deciduous forest found on mogote tops as consisting of *Neolaugeria resinosa* (Vahl) Nicols., *Calophyllum antillanum* Britt., *Tabebuia haemantha* (Bertol. ex Spreng.) DC., and *T. heterophylla*. Subplots where *B. simaruba* and *C. diversifolia* predominated (group 5) have a species composition that closely fits that of the dry woodland forest type of China (1980), while the subplots with *E. monticola* and *C. rosea* seem to combine the dry woodland and cliff fringe assemblages found on mogote tops and cliff sides.

Table 3. Groups defined by cluster analysis in order of information remaining after each split in the cluster dendrogram, with number of subplots in each cluster and indicator values for species with p -values < 0.05.

GroupID	N	Indicator value	p -value	Origin	Species
Spca	50	82.9	0.001	I	<i>Spathodea campanulata</i> Beauv.
		8.0	0.197	N	<i>Thespesia grandiflora</i> DC.
		9.9	0.200	N	<i>Casearia sylvestris</i> Sw.
		6.8	0.285	I	<i>Terminalia catappa</i> L.
		4.0	0.473	I	<i>Carapa guianensis</i>
		1.6	0.813	N	<i>Cestrum macrophyllum</i> Vent.
		2.0	0.900	I	<i>Erythrina poeppigiana</i> (Walp.) O.F. Cook
		1.8	0.903	I	<i>Delonix regia</i> (Bojer ex Hook.) Raf.
		1.2	0.982	I	<i>Swietenia mahagoni</i> (L.) Jacq.
		0.9	1.000	I	<i>Mangifera indica</i> L.
Tahe	14	79.7	0.001	N	<i>Tabebuia heterophylla</i> (DC.) Britt.
		8.3	0.168	N	<i>Eugenia borinquensis</i> Britt.
		7.3	0.214	N	<i>Psychotria berteriana</i> DC.
		8.2	0.234	N	<i>Neolaugeria resinosa</i> (Vahl) Nicols.
		5.6	0.366	N	<i>Cupania americana</i> L.
		5.1	0.451	N	<i>Roystonea borinquena</i> O.F. Cook
		5.0	0.476	N	<i>Pimenta racemosa</i> var. <i>racemosa</i>
Cifr	8	89.2	0.001	N	<i>Citharexylum fruticosum</i> L.
		6.3	0.257	N	<i>Erythroxylum rotundifolium</i> Lunan
		5.8	0.370	N	<i>Sapium laurocerasus</i> Desf.
Lele	10	5.4	0.394	N	<i>Casearia decandra</i> Jacq.
		53.3	0.001	N	<i>Leucaena leucocephala</i> (Lam.) de Wit
		38.2	0.002	N	<i>Cecropia schreberiana</i> Miq.
Busi	21	4.3	0.559	I	<i>Senna siamea</i> (Lam.) Irwin & Barneby
		69.9	0.001	N	<i>Bursera simaruba</i> (L.) Sarg.
		39.9	0.001	N	<i>Coccoloba diversifolia</i> Jacq.
		22.3	0.011	N	<i>Licaria parvifolia</i> (Lam.) Kosterm.
		19.0	0.008	N	<i>Drypetes alba</i> Poit.
		9.5	0.105	N	<i>Trichilia pallida</i> Sw.
		9.5	0.155	N	<i>Guettarda scabra</i> (L.) Vent.
		6.3	0.294	N	<i>Ocotea sintenisii</i> (Mez) Alain
		3.8	0.537	N	<i>Pseudolmedia spuria</i> (Sw.) Griseb.
		3.5	0.593	N	<i>Picramnia pentandra</i> Sw.
Cagu	11	2.7	0.770	N	<i>Bourreria virgata</i> (Sw.) G. Don
		1.5	0.895	N	<i>Chrysophyllum cainito</i> L.
		85.6	0.001	N	<i>Casearia guianensis</i> (Aubl.) Urban
		11.3	0.090	N	<i>Ocotea coriacea</i> (Sw.) Britt.
		9.5	0.117	N	<i>Randia aculeata</i> L.
		7.4	0.223	N	<i>Myrcia splendens</i> (Sw.) DC.
		6.7	0.226	N	<i>Chrysophyllum oliviforme</i> L.
		6.6	0.272	N	<i>Trichilia hirta</i> L.
		5.8	0.325	N	<i>Ocotea leucoxylon</i> (Sw.) De Laness.
		4.0	0.486	N	<i>Piper amalago</i> L.
Gugu	29	4.7	0.524	N	<i>Ficus citrifolia</i> P. Mill.
		2.1	0.918	N	<i>Petitia domingensis</i> Jacq.
		53.4	0.001	N	<i>Guarea guidonia</i> (L.) Sleumer
		25.4	0.005	N	<i>Dendropanax arboreus</i> (L.) Dcne. & Planch. ex Britt.
		21.1	0.007	N	<i>Inga vera</i> Willd.
		15.1	0.051	I	<i>Persea americana</i> P. Mill.
		13.8	0.060	N	<i>Quararibea turbinata</i> (Sw.) Poir.
		9.7	0.146	N	<i>Inga laurina</i> (Sw.) Willd.
		6.9	0.237	N	<i>Mammea americana</i> L.
		6.6	0.259	N	<i>Cordia sulcata</i> DC.
		4.7	0.495	I	<i>Citrus sinensis</i> (L.) Osbeck
		2.9	0.740	N	<i>Alchornea latifolia</i> Sw.
		2.2	0.849	I	<i>Hyperbaena laurifolia</i> (Poir.) Urban

Table 3. Continued.

GroupID	N	Indicator value	p-value	Origin	Species
Myco	18	2.0	0.870	I	<i>Coffea Arabica</i> L.
		49.3	0.001	N	<i>Myrsine coriacea</i> (Sw.) R. Br. ex Roemer & J.A. Schultes
		46.1	0.001	N	<i>Tetrazygia elaeagnoides</i> (Sw.) DC.
		24.6	0.008	N	<i>Bucida buceras</i> L.
		11.1	0.074	I	<i>Ardisia solanacea</i> Roxb.
		11.1	0.081	N	<i>Coccoloba krugii</i> Lindau
		3.5	0.557	N	<i>Psidium guajava</i> L.
		3.5	0.585	N	<i>Cordia alliodora</i> (Ruiz & Pavón) Oken
		3.0	0.603	N	<i>Pouteria multiflora</i> (A. DC.) Eyma
		95.1	0.001	N	<i>Eugenia monticola</i> (Sw.) DC.
Eumo	5	22.7	0.006	N	<i>Bourreria succulenta</i> Jacq.
		12.4	0.121	N	<i>Andira inermis</i> (W. Wright) Kunth ex DC.
		9.6	0.122	N	<i>Eugenia biflora</i> (L.) DC.
		7.7	0.359	N	<i>Thouinia striata</i> Radlk.
		4.4	0.598	N	<i>Clusia rosea</i> Jacq.

For origin, I = introduced species and N = native species.

Table 4. Percentage of each group's importance value (IV) that is of introduced (I) and native (N) to Puerto Rico in tree ($D_{BH} \geq 12.5$ cm), sapling ($2.5 \leq D_{BH} < 12.5$), and seedlings ($D_{BH} > 2.5$ cm and height ≥ 30 cm) size categories.

GroupID	Origin	Tree IV	Sapling IV	Seedling IV
Spca	I	83.9	57.6	24.8
	N	16.1	42.4	75.6
Tahe	I	0.0	0.0	13.5
	N	100.0	100.0	86.5
Cifr	I	0.0	0.0	9.3
	N	100.0	100.0	90.7
Lele	I	0.0	4.5	11.2
	N	100.0	95.5	88.7
Busi	I	2.7	1.3	2.8
	N	97.3	98.7	97.2
Cagu	I	35.3	4.6	4.0
	N	64.7	95.3	96.0
Gugu	I	12.4	8.0	11.9
	N	87.6	92.0	88.1
Myco	I	16.2	17.3	11.6
	N	83.8	82.7	88.4
Eumo	I	0.0	0.0	0.0
	N	100.0	100.0	100.0
NoInd	I	29.6	22.4	14.2
	N	70.4	77.6	85.8

Group 'NoInd' is for subplots that did not have indicator species.

Subplots with high *G. guidonia* importance values showed species assemblages strongly suggesting stands of inactive coffee shade and agroforestry activities that correspond to Chinaea's (1980) mesic forest type and the abandoned coffee shade of Alvarez-Ruiz et al. (1997) where *G. guidonia*, *Ocotea sintenisii* (Mez) Alain, and *I. vera* made up 80% of the IV. In Alvarez-Ruiz et al. (1997), *Syzygium jambos* (L.) Alston, *O. sintenisii*,

Andira inermis (W. Wright) Kunth ex DC. and others were more common in the midstory of abandoned coffee shade, and many more *I. vera* seedlings were found. There was very little of the otherwise ubiquitous *S. campanulata* in *G. guidonia* dominated sites, probably due to competition with coffee shade and fruit trees, an observation made previously by Rivera and Aide (1998). The native species *G. guidonia* has

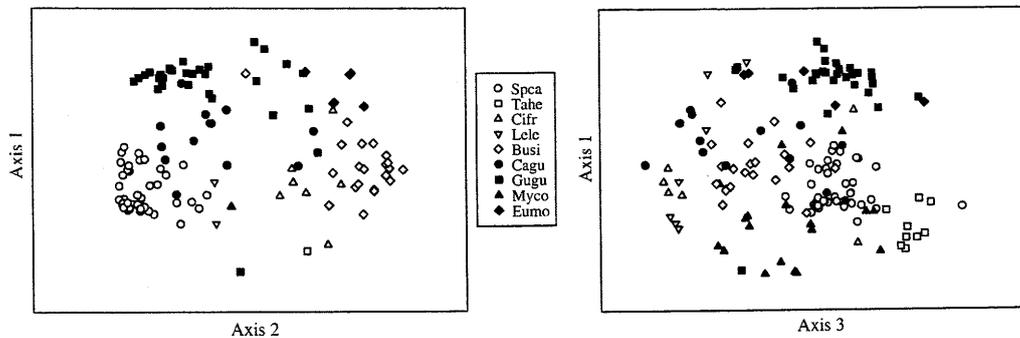


Figure 4. Non-metric multidimensional scaling analysis scatter plot for ordination axes 1 and 2, and for ordination axes 1 and 3. Each point on the figure represents an inventory subplot. Group numbers in the legend correspond to groups described in Table 3.

Table 5. Pearson and Kendall correlations of environmental variables with NMS ordination axes (TPH = trees per hectare, BAH = basal area (m^2) per hectare, distance to water estimated by field crew from aerial photograph, slope % and slope aspect measured in the field, latitude and longitude measured with GPS receiver, and elevation extracted from a digital elevation model in a geographic information system).

Variables	Axis 1		Axis 2		Axis 3	
	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²
TPH	-0.139	0.019	0.148	0.022	0.053	0.003
BAH	-0.025	0.001	-0.234	0.055	0.219	0.048
Dist. water	-0.004	0.000	0.109	0.012	-0.224	0.050
Slope %	0.149	0.022	0.374	0.140	0.110	0.012
Slope aspect	0.107	0.011	-0.103	0.011	-0.035	0.001
Latitude	-0.051	0.003	0.248	0.062	-0.504	0.254
Longitude	-0.106	0.011	-0.070	0.005	-0.139	0.019
Elevation	0.072	0.005	-0.124	0.015	0.385	0.148

regenerated strongly island-wide (Birdsey and Weaver 1987; Franco et al. 1997), and its dominance in inactive coffee shade has possibly prevented further incursions by introduced species into those forests.

Karst sites in early successional stages were dominated by *T. elaeagnoides* (China and Helmer 2003), and the presence of *Psidium guajava* L. (cited as important in former pasture by Rivera et al. (2000)) and *Bucida buceras* L. (a species which competes well on poorer, excessively drained karst soils according to Francis (2000)) would seem to indicate that this group was found on drier sites that were formerly pasture. Additionally, the cluster analysis of forest inventory data produced a wider variety of early successional species assemblages (groups indicated by higher importance of *C. fruticosum*, *L. leucocephala* with

C. schreberiana, and *C. guianensis* with *O. coriacea*) that have formed on sites that were highly disturbed and intensively used in the past.

The overall importance and numerous stands defined by the dominance of *S. campanulata* demonstrate where a landscape-level forest inventory where sampling sites are systematically chosen produces results different from the previous studies of karst forest, and the frequency with which seedlings were found would indicate either continued colonization of recently abandoned agricultural sites or a limited ability to regenerate under some forest canopies. Only Rivera and Aide (1998) showed that *S. campanulata* and *G. guianensis* dominated on sites that were formerly pasture because the abandoned pasture land use was one of the focuses of their study. The studies by China (1980) and Alvarez-Ruiz (1997) focused on

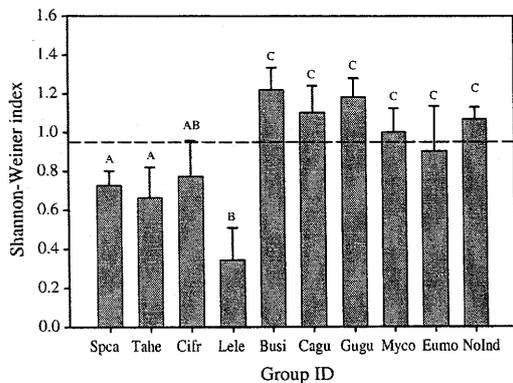


Figure 5. Mean Shannon diversity indices for each group identified by agglomerative hierarchical cluster analysis, with standard errors of each mean. Dashed line represents average Shannon diversity index for all subplots combined. Different letters over each group's histogram represent statistically significant differences at the 0.05 alpha-level found in ANOVA pairwise comparisons. Group number corresponds to groups described in Table 3, and 'NoInd' is for subplots that did not have indicator species.

a more strictly defined karst forest and might not have sampled the former agricultural land on alluvial deposits in the valleys between mogotes where *S. campanulata* dominates. The extent and distribution of *S. campanulata* coverage in low lying areas of the karst region is particularly notable when flying over the area while those trees are flowering because of their large, bright red flowers (E. Helmer, pers. comm.). While native species are prominent in recovery of karst forest, on lower elevation, low slope sites that were probably formerly in pasture, conditions have favored the establishment of introduced species, particularly *S. campanulata*, and the forest inventory results show some indication of that although the correlations with the environmental variables were weak. The importance of disturbance and introduced species in the northern karst belt of Puerto Rican is further highlighted when comparing these forests to other Caribbean karst forests. Puerto Rico karst forest appears to have less BAH than karst forests in the Dominican Republic and Jamaica. Rivera et al. (2000) studied karst forest regenerating on abandoned agricultural land in the Dominican Republic. For all trees with $D_{BH} \geq 1$ cm, Rivera et al. (2000) found basal areas were 44.4 m²/ha on 3510 stems/ha in older forests, 26.7 m²/ha on 3575 stems/ha in cacao

plantations, and 6.6 m²/ha in pastures that had recently reverted back to forest. In Jamaica, Kelly et al. (1988) found basal areas from 28 to 47 m²/ha, with a mean of 35 m²/ha for trees with $D_{BH} \geq 3$ cm.

Species composition of the northern karst belt shared many of the same species as karst in the Dominican Republic, but the lower importance of introduced species in the Dominican Republic karst study site is notable, particularly the lack of *S. campanulata*. *Guarea guidonia* was found on the older forest sites, and in association with *Theobroma cacao* L. plantations similar to its association with Puerto Rican coffee shade (Rivera et al. 2000). *Coccoloba diversifolia* was found in association with *O. coriacea* on mogote tops, which had the highest number of indicator species (Rivera et al. 2000). This species association would seem quite similar to the *C. diversifolia* indicated group in Puerto Rico. However, of the 162 total species observed by Rivera et al. (2000), only 11.7% were introduced. Similarly in Jamaica, Kelly et al. (1988) did not believe that any of the introduced species they found were becoming naturalized.

There are multiple, potentially interacting, reasons for the differences between the karst forests surveyed in Puerto Rico and those of the Dominican Republic and Jamaica. Based on the reported average rainfalls and the overall species compositions, the stands surveyed by Kelly et al. (1988) in Jamaica and by Rivera et al. (2000) in the Dominican Republic might have been wetter, implying the sites have an inherent capacity to support greater basal area. Also, the sites in Jamaica were chosen because they were relatively undisturbed (Kelly et al. 1988). The Dominican Republic karst forest sites were disturbed by agricultural activities, but the lower basal areas in Puerto Rican karst might be indicative of more intensive agricultural activities in the past and more extensive land clearing.

It is also very possible that the differences are again due to the way the forests were sampled. This inventory of Puerto Rican karst forest used an unbiased, systematic sample, while the studies in the Dominican Republic and Jamaica had specific hypotheses to test (e.g. land use history in Rivera et al. 2000) and subjectively chose their study sites according to certain criteria. The Puerto Rican forest sampled might have included more areas of marginal, recently reverted forest that would not

have been considered as study sites on these other Caribbean islands. Valid comparison of the current state of these Caribbean karst forests will not be possible without unbiased samples.

The heavier sampling of highly disturbed forest and areas on the margins of environmental and topographic gradients by the forest inventory might be the reason strong correlations between the forest types and environmental and topographic gradients were not found. For example, some forest inventory subplots fell in stands growing on soils derived from alluvial deposits which are not karst by a strict definition. These subplots do not fall into the topographic categories of mogote top, slope, or valley which have been clearly associated with karst tree assemblages (Chinaea 1980). Weak correlations with percent slope and elevation were found, and species groups fell along those environmental axes as would have been predicted based on the previous studies of karst vegetation. Plot center elevation, which ranged from 10 to 380 m, was extracted from a GIS digital elevation model and was probably not accurate enough or taken at a fine enough scale to capture the effect it might be having on species assemblages. While plot latitude and longitude showed some correlation with the ordination axes, I feel these results might be skewed by the distribution of plots within the asymmetrical karst belt. For example, more plots fell in forest more frequently to the northwest because the karst belt was wider and there was more forest in that area. Additionally, I believe that the environmental variables measured by the inventory did a poor job of capturing the micro-topographic differences potentially captured by a more detailed, in-depth study of each site, and the small sample sizes for some of the variables such as topographic position. Working with a very similar data set, Chinaea and Helmer (2003) concluded that there was not a large influence of forest landscape structure on species diversity and composition at the scale of an island-wide inventory.

Although this forest inventory did not provide sufficient information needed to strongly correlate tree species assemblages to topographic features, it produced a more comprehensive assessment of the extent of introduced species establishment in the northern karst belt by sampling in areas that would be otherwise overlooked by ecological studies that do not use unbiased systematic or

random sampling. The forest inventory sampled more areas of marginal, recently reverted forest that would not have been considered as study sites under different circumstances, and for that reason found a greater variety of early successional species assemblages. Future monitoring of *S. campanulata* and the other introduced species using the forest inventory plots will provide us with valuable insight into their long-term regeneration and interactions with native species.

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