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Vegetation Communities on Little Tobago Island, Republic of Trinidad and Tobago. Composition and Abiotic and Biotic Controls on Distribution

Natalie Boodram[1] and Michael P. Oatham[2]

[1]*Caribbean Environmental Health Institute, P.O. Box. 1111, The Morne, Castries, St. Lucia.*
[2]*Department of Life Sciences, University of the West Indies, St. Augustine, Republic of Trinidad and Tobago.*
Email: mike.oatham@sta.uwi.edu

Abstract- **Trees, ground flora and epiphytes were surveyed across 81 sites on Little Tobago Island, Trinidad and Tobago. Micro-climatic and edaphic parameters were measured at each site. Cluster analysis was used to identify possible vegetation groups. Ordination and logistic regression analysis were used to detect environmental gradients and to describe the influence of the environmental variables on individual plant species. One hundred and sixteen species were found on the island, of which 101 were recorded in this survey. The vegetation community was dominated by native species with individuals of the tree species Coccothrinax barbadensis, Guapira fragrans, Bursera simaruba, and Diospyros inconstans accounting for 66% of all trees surveyed. The sites were classified into five cluster groups based on species composition. One group consisting of 3 sample sites was dominated by the exotic species Bambusa vulgaris and had a significantly different structure due to the multi-stemmed clump habit of the species. No spatial pattern was identified in the distribution of abiotic variables across the island which contributed to the lack of spatial pattern in the distribution of individual plant species. The species found in this survey largely matched those found by Beard in 1944 with a couple of exceptions which may be due to misidentifications in 1944 or decline in species due to disturbance by stochastic events such as hurricanes.**

Keywords- **Dry forest, Trinidad and Tobago, vegetation communities, Caribbean, spatial pattern**

Introduction

The Island of Little Tobago is Trinidad and Tobago's best preserved tropical dry forest ecosystem and forms an valuable wildlife sanctuary and seabird nesting site which is important to the emerging ecotourism industry in the country. The Little Tobago vegetation represents a coastal dry forest community immediately adjacent to littoral communities and is characteristic of many parts of the Lesser Antilles and the northern coast of Venezuela (Oatham and Boodram 2006a). It is important in the context of conservation of tropical dry forests in the eastern Caribbean and northern South America as there are few protected areas for dry forests in this region (Oatham and Boodram 2006b). The World Wild Life Fund for Nature reports the Trinidad and Tobago Dry Forest and the Windward Dry Forest and Leeward Dry Forest ecoregions to be largely cleared, and the remnants heavily impacted, therefore they are classified as critically endangered (Armstrong 2001a,b,c).

The island was last described floristically and ecologically by Beard (1944) following a brief visit to the island. He subsequently used the dry forest vegetation community on the island as a "type" example of dry forest in the SE Caribbean. Apart from Beard (1944) previous vegetation survey work on the island was restricted to opportunistic and non-systematic sampling along the main trails on the island (Boodram 2001). Therefore it was decided to systematically inventory the vegetation communities on the island and investigate the community structure. Given the pressures of global change, both through climate and land-use, this Island offers a unique observatory to determine 'change', largely un-impacted by anthropogenic activity. Our survey contributes to documenting baseline data of this unique island ecosystem.

The specific objectives of this study were to describe the vegetation community or communities of Little Tobago Island and to compare the vegetation communities with those found by Beard in 1944 and to assess the relative impact of environmental variables on community characteristics such as structure and floristics.

Site Description

Little Tobago Island (11° 18’ N, 60° 30’ W) is a 100 ha island 2.4 km off the North East Coast of Tobago which is itself 35 km from the larger island of Trinidad and 115 km from the coast of continental South America. The island experiences a wet-dry tropical climate with an average annual rainfall of 1520 mm with the majority falling between June and December (Bertrand et al. 1991). Diurnal temperatures on the island range from 21°C to 31°C with little seasonal variation (Bertrand et al. 1991). Little Tobago Island has steep coastal slopes rising to an undulating central plateau with a maximum height of 137 m above sea level (Comeau et al. 1992). The rocks on the island are mainly volcanic in origin and consist of pyroclastic tuff breccias and agglomerate volcanics (Maxwell 1948).

Beard (1944) described the vegetation on the island as Deciduous Seasonal Forest of the *Bursera-Lonchocarpus* association (*Coccothrinax* faciation) and specifically noted the trees *Coccothrinax barbadensis*, *Bursera simaruba*, *Lonchocarpus domingensis*, *Diospyros inconstans*, *Pithcellobium ungis-cati* and *Eugenia ligustrina* (and other Myrtaceae) as abundant on Little Tobago Island. Sea-island cotton (*Gossypium barbadense*) was cultivated on Little Tobago Island in the 18th century but cultivation was abandoned after 1781. The island was never again cultivated and was passed into government hands in 1928 on the condition it become a nature reserve. By 1944 the natural vegetation was considered to have fully recovered from cultivation (Woodcock 1867, Beard 1944, Dinsmore 1967). In 1847 a hurricane devastated Tobago with much loss of life and damage to agriculture (Woodcock 1867). No specific mention can be found of damage to Little Tobago as a result of this hurricane, probably because the island was no longer inhabited or cultivated however it can be assumed the vegetation communities suffered some damage. After the island was disturbed in 1963 by Hurricane Flora, Dinsmore (1967) noted that the most damaged areas were characterised by rapidly growing trees like *Cordia collocca* and in the ground flora by the shrub *Aphelandra pulcherrima*. The National Ocean and Atmosphere Agency (NOAA Coastal Services Center 2009) database of historical hurricane tracks also place a tropical storm close to Little Tobago Island in 1878 and a hurricane between Trinidad and Tobago in 1892 however no record of destruction caused by these hurricanes was found in the Tobago historical record apart from landslides and flooding due to excessive rainfall (Beard 1944, Dinsmore 1967, Daniel et al. 2001), so it is assumed Little Tobago suffered few effects from them. Hurricane Ivan in 2004 caused substantial damage on Tobago but occurred after data collection for this study was completed. Currently the island is reserved for conservation and nature-based tourism. Visitors remain on established trails and lookouts so that human disturbances to vegetation on the island are practically non-existent (Boodram 2001).

Materials And Methods

The vegetation communities on Little Tobago Island were sampled using a systematic sampling grid from April 1997 to May 1998. Eighty one sites were studied across a 100m x 100m grid. The grid sampling method was chosen to maximize the chance of covering the full range of vegetation community characteristics such as floristics and structure with the least number of sample points (Mueller-Dombois and Ellenberg 1974; Prince 1986; Causton 1988). The location of the first sample site was selected randomly to introduce randomness into the sample design (Causton 1988). To confirm independence of samples a Mantel type test was performed (Jack Knife with 1000 iterations) using the RELATE module in the PRIMER 5 statistical package (ver. 5.2.8, Plymouth Marine Laboratory, Plymouth, England)to test for spatial autocorrelation among sample sites. A significant correlation between the distance matrix of spatial separation of sample sites and difference matrix of the basal area of individual tree species between sample sites would indicate that sample sites were not independent. A Spearman rank correlation statistic (rho) was calculated and its significance tested using 5000 permutations (Clarke and Warwick 2001; Clarke and Gorley 2002). A non-parametric method was used as the tree data were not normally distributed. In addition, semi-variograms were created to test the independence of the biotic and abiotic data, again checking for auto-correlation and also to check for anisotrophy. Data were analyzed using SgeMS (Boucher 2009), an open source geostatistical software package.

At each site trees, ground flora and epiphyte data were collected. Tree species identity and DBH (at 1.35m above ground level) were collected for trees $\geq$ 5cm DBH at four random points along a 20 m North-South transect using a point centered quarter (PCQ) technique (Bower et al. 1996). A random point was rejected if it included a stem that had been previously measured. The total number of trees recorded at each site was therefore 16 with a total of 1296 trees measured in the survey. From the tree dataset the frequency of occurrence of a species in the 81 sites was calculated along with their density and basal area per site using the methods of Bower et al. (1996). Mean and standard deviation of site density and basal area of each species was derived from the dataset by bootstrapping (1000 samples with replacement) as the method of estimating species density and basal area using the PCQ method gives a highly skewed distribution with many zero values (Bryant et al. 2004). Any epiphyte species visible in the trees sampled were recorded as present at a site in a separate epiphyte dataset. The ground flora at each site was recorded in one 2m x 2m quadrat which was found to be adequate to represent the ground flora at a sample site using a species area curve generated with quadrats of increasing size up to 24 m^2. The ground flora quadrat was located on the right hand side of the centre of the sample site when facing downhill. Within each, all species present with individuals less than 1m in height were recorded along with a percentage cover estimate based on a point-intercept grid of 20cm x 20cm. The frequency of occurrence of ground flora species over the 81 sites and the average percentage cover of each species was calculated.

A cluster analysis was carried out to determine if the sample sites separated into any discrete groups based on the tree vegetation communities (PRIMER 5 statistical package ver. 5.2.8, Plymouth Marine Laboratory, Plymouth, England). Ground flora was excluded from the analysis because over half the ground flora species were transient tree seedlings that may not survive at the sample site and to allow the use of the basal area abundance measure in the analysis. A Bray-Curtis distance metric was used as it satisfies several criteria desirable for ecological studies, in particular; returning a zero similarity between two samples when they have no species in common and being unaffected by the inclusion of species that are absent from both samples which were features of this data set (Faith et al. 1987). Complete linkage (or farthest neighbor) clustering was used as the nearest neighbor and average linkage clustering methods gave chain clusters that were not interpretable ecologically. The clusters generated by the complete linkage method gave clusters that were ecologically meaningful. Tree basal area data were used in the cluster analysis rather than presence/absence or density to allow generation of cluster groups that take into account the influence of dominant species. Cluster groups generated were also generated using presence-absence tree data to compare with the basal area analysis. Non-Metric Multidimensional Scaling (nMDS) Ordination was also carried out in 2 dimensions (Bray-Curtis distance metric, 500 iterations) (PRIMER 5 statistical package ver. 5.2.8) on the same data set to graphically complement the cluster analysis and bring out which groups were more similar. A discriminant analysis was carried out to determine the species contribution to defining the resulting cluster groups (SIMPER module in PRIMER 5 statistical package ver. 5.2.8).

The mean tree DBH, species diversity, stem density, average tree basal area, ground flora species richness and ground flora total percentage cover were determined for each cluster group and tested for significant difference at a 95% confidence level between groups with a Kruskal-Wallis test in the SPSS

12 statistical package (SPSS Inc. 2003) A non-parametric test was used as the parameters could not be transformed to normality. A series of Mann Whitney U tests were used as post-hoc tests to compare the groups for parameters that had tested significantly different in the Kruskal-Wallis test (University of San Francisco 2009). The differences in abiotic variables (see below) between the groups were tested in the same way.

Abiotic data were collected at each site during April to June of 1997. These data included percentage slope, aspect in degrees, altitude in meters, wind speed and salt spray. Wind speed and salt spray at each site were recorded at the same time over a nine day period. Salt spray was measured using a method adapted from Randall (1970) where a piece of towelling material was hung 1.5m above the ground for six hours then transported to the laboratory where the salt accumulated was extracted using water and quantified using a conductivity meter. The sampling was conducted three times so the final value for a site was the average of 3 salt-spray values and 18 wind speed readings generated for each site. Due to logistical constraints the wind speed and salt spray were only measured once for the year in the wet season. It is probable that these parameters would be different in the dry season but it was decided to use the data available. The independence of samples was tested using a Mantel type test (RELATE module in the PRIMER 5 statistical package) by testing for spatial autocorrelation in the abiotic parameters and also by the construction of semi-variograms in the same way as the biotic data (see above).

The contribution of different abiotic parameters and vegetation parameters such as tree density, tree species richness and ground species richness to the distribution of the individual tree species was explored using binary logistic regression. This method was used because the tree basal area data resisted transformation to normality due to the large number of sites that returned zero values for each species. Therefore in each analysis the presence/absence data of a tree species were used as dependent variables and various abiotic variables were entered as independent variables. During model construction independent variables with the least significant partial correlation coefficient were removed from the model in a stepwise fashion until none occurred above a threshold value of $p = 0.10$ (backward stepwise method). Abiotic variables that were found to be spatially auto-correlated were excluded from the analyses. Hosmer and Lemeshow chi-sqare test were performed to test if the model significantly represented the observed value, a non-significant p (>0.05) indicated the model was a good fit to the observed values. A Nagelkerke R^2 estimated the amount of variation explained by the model. The p value for the Wald's statistic was used to indicate if a partial coefficient was significant in the model. The Odds Ratio value was used to explain how the dependent variable varied with the covariate. If it was greater than one it varied positively, less than one it varied negatively. The analyses were carried out using the SPSS 12 statistical package.

At each site the depth of the soil profile was measured. Near surface soil samples were taken from depth layers of 0cm to 15cm. The samples were analyzed for moisture content at field capacity, organic carbon content, total nitrogen, plant available phosphates, calcium, potassium and magnesium cations using techniques after Mitchell and Rue (1979). Electrical conductivity and pH of the samples were determined using a conductivity and pH meter.

Results

Mantel tests for spatial auto-correlation found that *Eugenia monticola* and *Cecropia peltata* were significantly spatially auto-correlated. All other tree species satisfied the independence of samples assumption. Semi-variograms indicated the samples sites were independent for all species however, *E. monticola* and *C. peltata* were still excluded from logistic regression analysis on the basis of results from the previous test. No evidence of anisotropy was revealed by the semi-variograms. Four abiotic parameters were found to be spatially auto-correlated (slope, soil depth, pH and calcium ion concentration) by the Mantel test and were excluded from the logistic regression analyses. Semi-variogram analysis of the abiotic data indicated no spatial structure in the data.

The total flowering plant species richness on Little Tobago was estimated to be 101 species in this survey (Table 1) with an average density of 2642 stems per hectare. The species richness increased to 116 species when species recorded for Little Tobago prior to this survey were included. Of the 116 species 104 were native species and 12 were introduced; 49 were tree species, 24 were shrub species, 40 were herb species and 3 were epiphytes.

The tree species with highest density was *Coccothrinax barbadensis* followed by *Guapira fragrans*, *Diospyros inconstans* and *Bursera simaruba* (Table 2). These four species accounted for 66% of the total tree stems sampled on the island indicating a significant level of dominance. The introduced *Bambusa vulgaris* only occurred at 3 sites but had the largest total basal area of all species which is the result of its multi-stem habit that had a large cumulative DBH and therefore huge basal areas for each individual bamboo "stool". The indigenous multi-stemmed *Coccoloba venosa* also exhibited high basal area for similar reasons. Apart from *B. vulgaris*, no other introduced species was dominant in terms of frequency of occurrence, density or basal area. Only three introduced species occurred in the top thirty tree species by density (Table 2).

In the ground flora data set *Anthurium jenmanii* was the dominant species when ranked by percentage occurrence. It occurred in 72% of the 81 sites surveyed with an average percentage cover of 35% over all sites (Table 3). The seedlings of tree species *Guapira fragrans*, *Diospyros inconstans* and *Coccothrinax barbadensis* were common in the ground flora which mirrored their dominance in the tree species data set. The top ten ground flora species as ranked by percentage occurrence was dominated by tree seedlings with only *A. jenmanii*, *Aphelandra pulcherrima* and *Smilax cumanensis* of the non-tree species occurring at comparable frequency and percentage cover levels to the dominant tree seedlings (Table 3).

The cluster analysis grouped the sites into five groups which were at least 5% different from each other. The groups created should be treated with caution as they were generated using the complete group linkage clustering method which may not be appropriate for this dataset, however the nearest neighbour and average group linkage clustering methods gave chain clusters that were not interpretable ecologically. The cluster analysis using presence-absence tree data generated groups that were not as well defined as the in the basal area cluster analysis, for instance the sample sites that were dominated by *Bambusa vulgaris* were not in separate groups as they were in the basal area cluster analysis. Therefore it was decided that the groups based on the basal area cluster analysis would be used. The groups generated by the complete linkage method did seem ecologically meaningful with groups dominated by species such as *Bambusa vulgaris* separating out into distinct groups. Group F consisted of a single sample site (site 5C), a cultivated garden plot that was dominated by the cultivated species (*Mangifera indica*, *Carica papaya*, *Annona reticulata* and *Psidium guajava*). The nMDS representation of the groups A to E and G (group F removed as an outlier) showed groups A, B, D and G largely discrete but groups C and E overlapped each other and other groups to a large extent (Fig.1). The distortion or stress level of the ordination was relatively high at 0.25 indicting the ordination should be treated with caution (Clarke and Gorley 2001). The discriminant analysis (SIMPER module) showed *Guapira fragrans* and *Clusia palmicida* were common in group A sites, *Bursera simaruba* was characteristic of group B sites, the exotic *Bambusa vulgaris* was characteristic of the three group D sites and *Coccoloba venosa* was characteristic of group G sites (Table 4). Group C and E sites had a broad mix of the dominant species on the island with no one species dominating. When the cluster group classification is superimposed on a map of the sample sites, the group D sites are three sites isolated from one another, the group G sites tend to be clustered on the north-eastern side of the island, the group B sites are concentrated on

TABLE 1. Flowering plant species list for Little Tobago Island. * indicates the species was found on Little Tobago by other collectors but was not found in this survey and (I) indicates the species is introduced to Trinidad and Tobago.

Family	Species	Lifeform
Acanthaceae	*Aphelandra pulcherrima* (Jacq.) Kunth	shrub
Acanthaceae	*Blechum pyramidatum* (Lam.) Urb.	herb
Agavaceae	*Agave* sp.*	shrub
Amaranthaceae	*Alternanthera flavescens* HBK	shrub
Amaranthaceae	*Blutaparon vermiculare* L. Mears	herb
Anacardiaceae	*Mangifera indica* L. (I)	tree
Anacardiaceae	*Spondias mombin* L.	tree
Annonaceae	*Annona muricata* L.	tree
Annonaceae	*Annona reticulata* L.	tree
Araceae	*Anthurium jenmanii* Engl.	herb
Araceae	*Philodendron acutatum* Schott.	epiphyte
Arecaceae	*Coccothrinax barbadensis* (Lodd. ex Mart) Becc.	tree
Arecaceae	*Cocos nucifera* L. (I)	tree
Arecaceae	*Roystonea oleracea* (Jacq.) O.F. Cook	tree
Asteraceae	*Synedrella nodiflora* (L.) Gaertn.	herb
Asteraceae	*Tilesia baccata* (L.) Pruski	herb
Asteraceae	*Cyrtocymura scorpioides* (Lam.) H. Rob.	herb
Azioaceae	*Trianthema portulacastrum* L.	herb
Boraginaceae	*Bourreria succulenta* Jacq.	tree
Boraginaceae	*Cordia collococca* L.	tree
Boraginaceae	*Cordia curassavica* (Jacq.) Roem. & Schult.*	shrub
Bromeliaceae	*Tillandsia flexuosa* Sw.	epiphyte
Burseraceae	*Bursera simaruba* (L.) Sarg.	tree
Cactaceae	*Hylocereus lemairei* (Hook.) Britton & Rose	shrub
Cactaceae	*Melocactus broadwayi* Britton & Rose*	shrub
Cactaceae	*Pilosocereus lanuginosus* (L.) Byles & Rowley	shrub
Caesalpiniaceae	*Senna bacillaris* (L. f.) H.S. Irwin & Barneby	shrub
Capparidaceae	*Capparis flexuosa* (L.) L.	tree
Caricaceae	*Carica papaya* L.	tree
Cecropiaceae	*Cecropia peltata* L.	tree
Celastraceae	*Maytenus tetragonus* Griseb.	tree
Clusiaceae	*Clusia palmicida* Rich. ex Planch. & Triana	tree
Commelinaceae	*Commelina erecta* L.	herb
Convolvulaceae	*Ipomea* sp.	herb
Convolvulaceae	*Iseia luxurians* (Moric.) O' Donnell	herb

Family	Species	Lifeform
Cucurbitaceae	*Psiguria umbrosa* (Kunth) C. Jeffery *	herb
Cyperaceae	*Cyperus ligularis* L.	herb
Ebenaceae	*Diospyros inconstans* Jacq.	tree
Erythroxylaceae	*Erythroxylum cumanense* Kunth in Humb. Bonpl. & Kunth	tree
Erythroxylaceae	*Erythroxylum havanense* Jacq.	tree
Euphorbiaceae	*Codiaeum variegatum* (L.) Rumph. ex A. Juss. (I) *	herb
Euphorbiaceae	*Tragia volubilis* L.	herb
Fabaceae	*Abrus precatorius* L.	tree
Fabaceae	*Andira inermis* (W. Wright) Kunth ex DC.*	tree
Fabaceae	*Desmodium incanum* DC.	shrub
Fabaceae	*Piscidia carthagenensis* Jacq.	tree
Fabaceae	*Rhynchosia phaseoloides* (Sw.) DC.	shrub
Flacourtiaceae	*Casearia decandra* Jacq.	tree
Flacourtiaceae	*Prockia crucis* P. Browne ex L.	tree
Heliconiaceae	*Heliconia bihai* L.	shrub
Malpighiaceae	*Malpighia glabra* L.*	tree
Malvaceae	*Gossypium barbadense* L. (I)*	shrub
Malvaceae	*Hibiscus pernambucensis* Arruda.*	shrub
Malvaceae	*Malvastrum americanum* (L.) Torr	shrub
Marantaceae	*Maranta gibba* Sm. *	herb
Melastomataceae	*Miconia virescens* (M.Vahl) Triana	shrub
Menispermaceae	*Cissampelos pareira* L.	herb
Menispermaceae	*Odontocarya tamoides* (DC.) Miers	herb
Mimosaceae	*Calliandra* sp. *	shrub
Mimosaceae	*Enterolobium cyclocarpum* (Jacq.) Griseb.	tree
Mimosaceae	*Pithecellobium unguis-cati* (L.) Mart.	tree
Moraceae	*Ficus nymphaeifolia* P. Miller	tree
Moraceae	*Maclura tinctoria* (L.) D. Don ex Steudel *	tree
Musaceae	*Musa* sp. (I)	shrub
Myrtaceae	*Eugenia dussii* Krug & Urban	tree
Myrtaceae	*Eugenia ligustrina* (Sw.) Willd.	tree
Myrtaceae	*Eugenia monticola* (Sw.) DC.	tree
Myrtaceae	*Myrcia* sp. *	tree
Myrtaceae	*Pimenta racemosa* (Mill.) J.W. Moore	tree
Myrtaceae	*Psidium guajava* L.	tree
Myrtaceae	*Syzygium malaccense* (L.) Merr. & Perry (I)	tree

Family	Species	Lifeform
Nyctaginaceae	*Guapira fragrans* (Dum. Cours.) Little	tree
Nyctaginaceae	*Guapira eggersiana* (Heimerl) Lundell*	tree
Ochnaceae	*Ouratea guildingii* (Planch.) Urb.	tree
Oleaceae	*Chionanthus compactus* Sw.	tree
Orchidaceae	*Caularthron bicornutum* (Hook.) Raf.	epiphyte
Oxalidaceae	*Oxalis frutescens* L.	herb
Passifloraceae	*Passiflora cyanea* Mast.	herb
Passifloraceae	*Passiflora laurifolia* L.	herb
Passifloraceae	*Passiflora suberosa* L.	herb
Phytolaccaceae	*Rivina humilis* L.	herb
Piperaceae	*Piper guayranum* C. DC.	shrub
Piperaceae	*Piper tuberculatum* Jacq.	shrub
Plumbaginaceae	*Plumbago zeylanica* L. (I)	herb
Poaceae	*Bambusa vulgaris* Schrad. ex J.C. Wendl. (I)	tree
Poaceae	*Cynodon dactylon* (L.) Pers. (I)	herb
Poaceae	*Lasiacis* sp.	herb
Poaceae	*Olyra latifolia* L.	herb
Poaceae	*Oplismenus hirtellus* (L.) P. Beauv.	herb
Poaceae	*Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs (I)	herb
Poaceae	*Paspalum conjugatum* Bergius	herb
Poaceae	*Paspalum vaginatum* Sw.	herb
Poaceae	*Pharus latifolius* L.	herb
Poaceae	*Urochloa fusca* (Sw.) B.F. Hansen & Wunderlin	herb
Polygalaceae	*Securidaca diversifolia* (L.) S.F. Blake	herb
Polygonaceae	*Coccoloba uvifera* (L.) L.	tree
Polygonaceae	*Coccoloba venosa* L.	tree
Pteridiaceae	*Adiantum tetraphyllum* Humb. & Bonpl. ex Willd	herb
Rubiaceae	*Erithalis fruticosa* L.	shrub
Rubiaceae	*Randia aculeata* L.	tree
Rubiaceae	*Borreria remota* (Lam.) Bacigalupo & E.L. Cabral	herb
Sapindaceae	*Melicoccus bijugatus* Jacq.	tree
Sapotaceae	*Chrysophyllum cainito* L. (I)	tree
Sapotaceae	*Manilkara zapota* (L.) P. Royen (I)*	tree
Simaroubaceae	*Picramnia pentandra* Sw.	tree
Smilacaceae	*Smilax cumanensis* Humb. & Bonpl. ex Willd	shrub
Solanaceae	*Cestrum alternifolium* (Jacq.) O.E. Schultz	shrub

Family	Species	Lifeform
Solanaceae	*Solanum adhaerens* Willd. ex Roem. & Schult.	shrub
Solanaceae	*Solanum hirtum* Vahl	shrub
Theophrastaceae	*Jacquinia armillaris* Jacq.	tree
Tiliaceae	*Triumfetta lappula* L.	herb
Urticaceae	*Pilea tobagensis* Urb.*	herb
Verbenaceae	*Citharexylum spinosum* L.	tree
Viscaceae	*Phoradendron trinervium* (Lam.) Griseb.	herb
Vitaceae	*Cissus verticillata* (L.) Nicholson & Jarvis	herb
Vittariaceae	*Vittaria lineata* (L.) Sm.	herb

TABLE 2. Mean density at a sample site, frequency of occurrence and mean basal area of tree species on Little Tobago Island. Mean density and mean basal area derived using bootstapping with replacement (1000 samples). Thirty species of trees with the highest frequency are included in the table. Species marked with a (I) are introduced species.

Species	Frequency (% Sites)	Stem Density (stems per Ha)		Basal Area (m2 per Ha)	
		Mean	StdDev	Mean	StdDev
Coccothrinax barbadensis	95.1	1063.42	118.13	0.0524	0.0039
Guapira fragrans	75.6	283.20	43.44	0.0567	0.0098
Bursera simaruba	69.5	208.93	31.07	0.0903	0.0131
Diospyros inconstans	56.1	274.39	49.45	0.0315	0.0066
Citharexylum spinosum	40.2	84.47	15.89	0.0397	0.0113
Cordia collococca	28.0	93.77	24.53	0.0447	0.0121
Chionanthus compactus	24.4	67.52	17.08	0.0092	0.0025
Coccoloba venosa	23.2	66.03	18.39	0.2702	0.1769
Casearia decandra	20.7	34.71	10.17	0.0065	0.0037
Piscidia carthagenensis	15.9	30.18	10.46	0.0238	0.0106
Clusia palmicida	13.4	59.61	24.07	0.0463	0.0239
Maytenus tetragonus	12.2	40.57	15.01	0.0113	0.0048
Erythroxylum havanense	11.0	41.85	16.99	0.0011	0.0004
Eugenia dussii	8.5	38.35	19.23	0.0022	0.0009
Bourreria succulenta	7.3	29.52	16.79	0.0041	0.0018
Eugenia monticola	7.3	44.34	29.69	0.0032	0.0023
Jacquinia amillaris	7.3	21.47	9.79	0.0014	0.0007
Ouratea guildingii	7.3	25.19	15.06	0.0025	0.0017
Spondias mombin	7.3	13.50	6.25	0.0245	0.0146
Pithecellobium unguis-cati	4.9	19.88	12.47	0.0066	0.0042
Randia aculeata	4.9	4.47	2.45	0.0002	0.0001
Roystonea oleracea	4.9	11.27	6.08	0.0152	0.0076
Bambusa vulgaris (I)	3.7	31.90	18.38	0.7930	0.7126
Eugenia ligustrina	3.7	7.20	4.39	0.0002	0.0001
Mangifera indica (I)	3.7	5.34	2.89	0.0092	0.0058
Picramnia pentandra	2.4	20.97	15.80	0.0006	0.0004
Prockia crusis	2.4	6.29	4.06	0.0001	0.0001
Psidium guajava	2.4	0.96	0.54	0.0010	0.0006
Annona reticulata	1.2	2.04	1.05	0.0140	0.0071
Cocos nucifera (I)	1.2	3.04	1.60	0.0052	0.0027

TABLE 3. Frequency of occurrence and average projected cover of ground flora species occurring on Little Tobago Island. Species marked with a (t) are tree seedlings and species marked with a (I) are introduced species.

Species	Frequency of Occurrence (%)	Projected Cover (%)	
		Mean	Std Dev
Anthurium jenmanii	72	34.451	3.570
Guapira fragrans (t)	35.4	2.204	0.649
Diospyros inconstans (t)	31.7	4.248	1.109
Aphelandra pulcherrima	28	8.283	1.875
Coccothrinax barbadensis (t)	25.6	6.800	1.983
Randia aculeata (t)	25.6	2.218	0.761
Smilax cumanensis	20.7	0.606	0.204
Chionanthus compactus (t)	13.4	0.710	0.255
Casearia decandra (t)	11	1.024	0.629
Capparis flexuosa (t)	9.8	0.867	0.410
Olyra latifolia	9.8	1.834	0.838
Cissus verticillata	8.5	0.201	0.094
Eugenia monticola (t)	8.5	1.458	0.625
Rhynchosia phaseoloides	8.5	0.802	0.551
Cestrum alternifolium var pendulinum	7.3	1.113	0.681
Hylocereus lemairei	7.3	0.799	0.611
Tilesia baccata	7.3	0.784	0.427
Adiantum tetraphyllum	6.1	0.106	0.048
Paspalum conjugatum	6.1	0.800	0.453
Piper guayranum (t)	6.1	0.525	0.361
Bourreria succulenta (t)	4.9	0.108	0.049
Eugenia dussii (t)	4.9	1.092	0.778
Maytenus tetragonus (t)	4.9	0.161	0.077
Ouratea guildingii (t)	4.9	0.414	0.306
Abrus precatorius (t)	3.7	0.623	0.537
Cissampelos pareira	3.7	0.055	0.030
Plumbago zeylanica (I)	3.7	0.474	0.243
Senna bacillaris (t)	3.7	0.148	0.092
Tragia volubilis	3.7	0.119	0.094
Annona muricata (t)	2.4	0.119	0.065

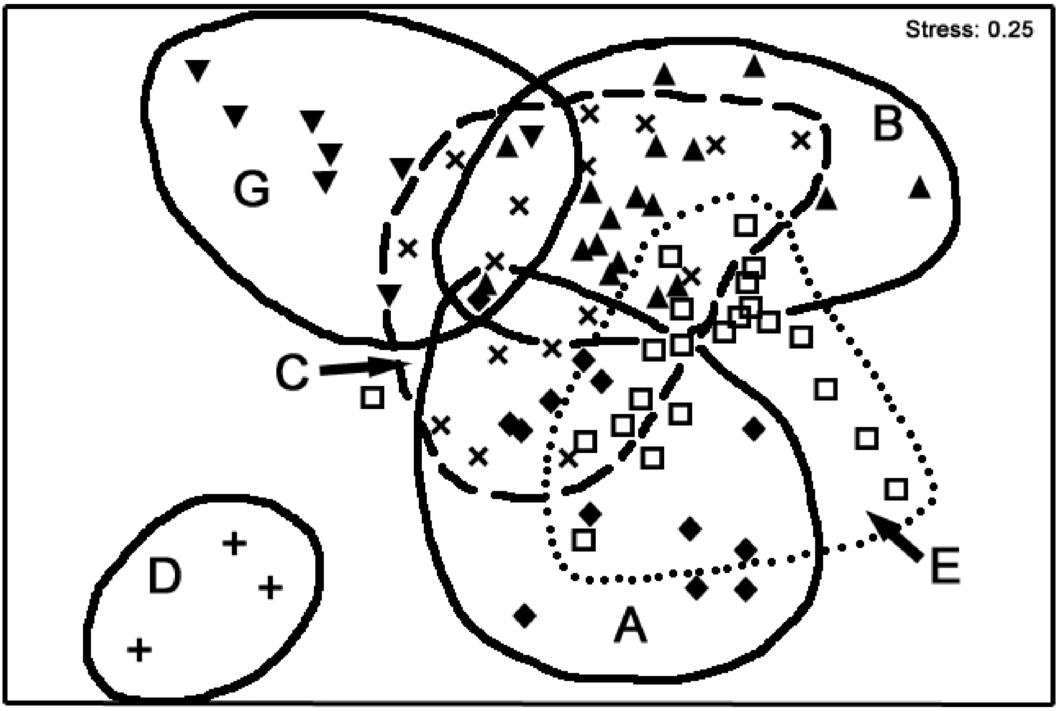

FIG 1. MDS diagram illustrating the separation and overlap between groups of tree vegetation cluster groups on Little Tobago Island.

TABLE 4. Details of species compositions of tree vegetation cluster groups on Little Tobago Island generated by a discriminant analysis.

Group	No. of Sites	Average Similarity	Characteristic Species (Average Basal Area)
Group A	12	40.63	Guapira fragrans (0.17)
			Clusia palmicida (0.28)
			Coccothrinax barbadensis (0.05)
Group B	18	40.19	Bursera simaruba (0.22)
			Coccothrinax barbadensis (0.04)
			Guapira fragrans (0.04)
Group C	17	33.13	Diospyros inconstans (0.09)
			Bursera simaruba (0.08)
			Citharexylum spinosum (0.12)
Group D	3	93.76	Bambusa vulgaris (21.72)
Group E	22	36.89	Coccothrinax barbadensis (0.08)
			Bursera simaruba (0.04)
			Guapira fragrans (0.02)
Group F	1	One site. No similarity calculated	
Group G	8	54.81	Coccoloba venosa (2.56)

the centre and high points of the island and the group F site is found on a sheltered upland site (Fig 2). The group E sites tend to occupy the upland parts of the island to the east of group B sites and group C sites do not appear to follow much pattern.

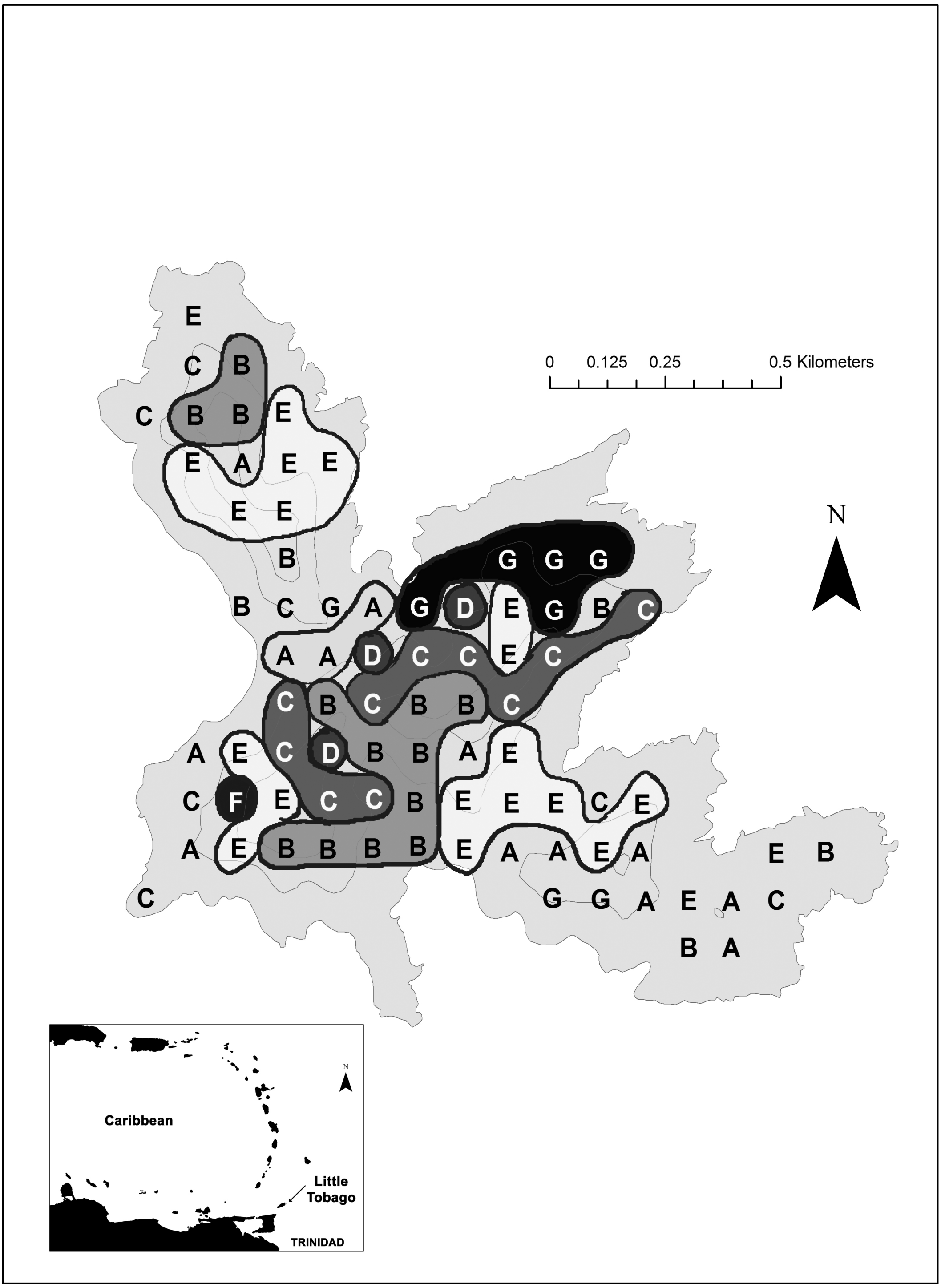

Fig 2. Map of tree vegetation cluster group membership on Little Tobago Island. Where three or more sample sites belong to the same cluster group occur contiguously they are circled except for sites belonging to groups D and F which are circled despite being isolated.

Cluster group D (the *Bambusa vulgaris* group) was very different structurally to all the other groups with a significantly larger average tree DBH, stem density and larger average tree basal area (Table 5). Also cluster group E differed significantly in average DBH compared to all the other groups. It was characterised by a higher density of smaller stems compared with the other non-*Bambusa* groups. There were no significant differences in average species richness of trees or ground flora between the cluster groups (Table 5). There were also no significant differences in abiotic variables between the different groups (Table 6)

Logistic regression analysis was found to be possible only for species with a frequency of occurrence greater than 5% of all sample sites so the rarer species were not analysed. Fourteen species returned models with partial coefficients that significantly affected the species distribution to a greater or lesser extent (Table 7). Tree species richness had a significant effect on the most species distributions (7 species) followed by the soil concentration of soil organic carbon (6 species), aspect and wind speed (4 species each), soil concentrations of N and K (3 species each) and soil conductivity, mean tree DBH and soil concentrations of PO_4 (2 species each). Salt spray and soil nutrient magnesium each had an effect on one species each. According to the odds ratio in the logistic regression tree species richness had a positive effect on the presence of all species for which it had a significant effect. Soil organic carbon had a mixed effect on different species with two species negatively affected (*Citharexylum spinosum* and *Cordia collococca*) and four species positively (*Chionanthus compactus*, *Clusia palmicida*, *Diospyros inconstans* and *Eugenia dussii*). Aspect did not seem to have a very strong influence on the species for which was a significant partial coefficient. Wind speed tended to have a strong affect on the species for which it is a significant partial coefficient. It had a strong negative effect on *Bourreria succulenta* and strong positive effects on *Erythroxylum havanense*, *Ouratea guildingii*, and *Guapira fragrans*. The concentration of K ions in the

TABLE 5. Selected vegetation community parameters for the different tree vegetation cluster groups on Little Tobago Island. Group F excluded because it had only one sample site. A Kruskall-Wallis test H was used to test for significant differences between groups.

Group	N	Tree Height (m)		Tree Average DBH (cm)		Tree Species Richness		Tree Density (stems ha^{-1})		Average BA (m^2)		Ground Species Richness		Ground Species % Cover	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
A	13	7.41	2.4	16.3	3.4	5.5	1.2	2837	1371	0.04	0.03	5.2	1.7	85.1	31.5
B	18	8.19	1.62	17.4	3.8	6.8	1.8	2621	2493	0.04	0.02	5.7	2.6	67.1	35.7
C	17	8.38	1.62	17.7	4.1	6.1	1.5	2249	1476	0.04	0.02	7.4	4.6	87.6	30.3
D	3	8.74	1.73	47.8	38.4	5.3	0.6	4846	873.6	1.38	2.12	4	1	84.1	16.4
E	21	8.37	1.78	12.7	2.1	5.2	1.2	2974	1416	0.02	0.01	5.2	2.9	87.5	46.2
G	8	7.97	0.92	25.8	15.4	5.8	1.5	1848	633.8	0.19	0.31	4.9	1.1	74.5	35
Total	80	8.22	1.66	18.05	10.75	5.86	1.52	2676	1715	0.1	0.43	5.71	3.06	81.12	36.58
H		0.988		35.72		10.43		12.8		43.5		7.927		3.681	
Asymp. Sig.		0.964		< 0.001		0.064		0.025		< 0.001		0.16		0.596	

TABLE 6. Mean of various abiotic variables across all sample sites on Little Tobago Island. No significant differences were detected for the variables between different cluster groups. The Chi-Sqr statistic and Asymtopic significance refer to the Kruskall-Wallis test used to test for differences between groups.

	Mean	SD	Chi-Sqr	Asymp Sig
Altitude (m a.s.l.)	73.67	30.92	4.172	0.525
Dry Season Canopy Closure (%)	89.71	8.49	5.478	0.36
Wet Season Canopy Closure (%)	93.05	8.37	2.831	0.726
Soil Conductivity (Sm^{-1})	0.04	0.06	4.076	0.538
Soil Moisture (%)	42.57	10.11	9.074	0.106
Salt Spray (mg g^{-1})	0.11	0.23	5.477	0.36
Wind Speed (ms-1)	1.01	0.84	4.127	0.531
Soil Nutrient Status				
K (kg ha^{-1})	56.70	29.20	5.055	0.409
Mg (kg ha^{-1})	1335.20	434.60	1.683	0.891
N (kg ha^{-1})	6206.30	3370.20	1.801	0.876
Org C (kg ha^{-1})	106676.30	50474.50	4.148	0.528
C:N Ratio	21.00	16.20	3.011	0.698
PO^{4-} (mg l^{-1})	0.18	0.19	2.367	0.796
Ca kg ha^{-1}	872.60	254.40	2.303	0.806

soil had strong positive effects on the presence of *Diospyros inconstans* and strong negative effects on *Clusia palmicida* and *Chionanthus compactus*. Soil N did not seem to affect the presence of species to such a degree according to the odds ratio.

The model constructed for *Clusia palmicida* explained 60% of the variation in species distribution according to the Nagelkerke pseudo R^2 (Table 7). Soil potassium concentration, aspect, PO_4 soil concentration and organic carbon concentration were the significant partial coefficients in the model and potassium concentration had the largest affect on *C. palmicida* distribution according to the odds ratio for the partial coefficients. Organic carbon had a moderate effect and aspect and PO_4 had little effect. Two other models explained over 50% of the variation observed in the distribution of the species *Erythroxylum havanense* and *Citharexylum spinosum*. *E. havanense* (R^2 = 0.542) was most effected by wind speed (odds ratio = 9.215) with the species showing a preference for windy areas and also by tree species richness (odds ratio = 2.26) and soil N concentration (odds ratio = 2.096). *C. spinosum* (R^2 = 0.501) tended to prefer sites that had a high tree diversity (odds ratio = 3.093) and tended to avoid sites that had a higher organic C concentration in the soil (odds ratio = 0.766) and a north-westerly aspect (odds ratio = 0.989). Five other models explained over 33% of the variation in plant distribution according to the Nagelkerke pseudo R^2 and details of the models can be found in Table 7.

DISCUSSION

The number of species of vascular plants on Little Tobago Island is broadly in line with numbers recorded in similar vegetation surveys in the region. Quigley and Platt (2003) found 103 to 137 species of trees in one hectare sampled in four dry forest sites in the neotropics. They found the density of stems > 1cm DBH was higher in sites at 20° N due to disturbance by hurricanes. Bullock et al. (1995) and Proctor (1989) found between 52 and 94.5 species of trees in 0.1 ha from dry forests around the world and Brandeis and Oswalt (2007) found 105 tree species in dry forest on the U.S. Virgin islands in the Caribbean. Weaver and Chinea (2003) found 103 tree species in 2817 individuals > 2.5 cm DBH in the La Tinaja Dry Forest in Puerto Rico. Fajardo et al. (2006) estimated Venezuelan dry forests contain 110-170 species of plants in a 10 ha area on average. Van Bloem et al. (2004) in a review of tropical dry forest structure in the Caribbean found stems of trees were smaller in diameter (3-15 cm on average) and occurred at higher densities (sometimes exceeding one stem per m^2) than moist tropical forests. They also found that trees were often multi-stemmed and indicated that this type of structure was likely the result of repeated hurricane disturbance. The structure of tree communities on Little Tobago were characterised a lower density (2675 stems per ha) and a higher average DBH (18.1 cm) which probably reflects the lower rates of hurricane disturbance compared to the Greater and Lesser Antilles.

The number of introduced species was low on Little Tobago Island compared to dry forests that tend to suffer more human and natural disturbance (Weaver and Chinea 2003, Breckon 2000). The long period without human disturbance (approximately 200 years) and the separation of the island from sources of introduced species propagules are probably the reasons for the dominance of native species in the vegetation communities. Two hurricanes in 1847 and 1963 disturbed the vegetation on the island but the species that were reported to colonize tree fall gaps (at least after the 1963 hurricane) were native species (Dinsmore 1967). It is not possible to say if the vegetation communities prior to cotton cultivation have completely recovered because of lack of records, but the current vegetation communities are dominated by native species with few scattered exotic species. It is possible that native species such as *Enterolobium cyclocarpum* which is a large long lived tree species may have been more prevalent or even dominant in pre-cotton cultivation vegetation communities and has since declined.

One introduced species that may be a threat to the native vegetation communities on Little Tobago is *Bambusa vulgaris*. Although it is restricted in distribution on the island and is likely only to spread slowly as stools expand vegetatively, it is showing invasive tendencies by persisting on the island and dominating the flora at the sites in which it occurs. *B. vulgaris* has been observed in other parts of Trinidad declining and dying out as it is overtopped and shaded by tree species (Teixeira and Oatham 2001). On Little Tobago Island and perhaps in other dry forests in Tobago it may be able to out compete the shorter stature trees and the take advantage of the opening of the canopy in the dry season. However, *B. vulgaris* is not considered a major invasive species in the invasive species databases (GISD 2009) although it does colonize large areas in Jamaica (GISD 2009).

The survey failed to pick up the only Trinidad and Tobago endemic species that has been collected on the island (*Pilea tobagensis*) (Van Den Eynden et al. 2008). It was last collected in 1989 so a survey should be carried out to determine the status of this species on Little Tobago Island.

In 1944 J.S. Beard spent one day surveying the vegetation of Little Tobago Island (Beard 1944). This was the first and the last comprehensive survey of the vegetation of the Island until this survey. He found *Coccothrinax barbadensis*, *Bursera simaruba*, *Lonchocarpus domingensis*, *Diospyros inconstans*, *Pithcellobium ungis-cati* , *Eugenia ligustrina* (and other Myrtaceae) and *Trichilia trifolia* as the dominants (Table 8). Of these species *L. domingensis* and *T. trifolia* had no clear equivalent in the 1997/8 survey and they seem to have disappeared from the island between 1944 and 1997. The reasons for the difference in the status of the two 1944

TABLE 7. Results of the logistic regression to test for abiotic and vegetation community variable impacts on tree species (presence/absence).

	Overall Model		Partial Coefficients			
Species	H-L Chi-Sq Test (p)	Nagelkerke R^2	Sig Part Coeffs	Wald's Stat	p	Odds Ratio (Exp(B))
Bourreria succulenta	0.945	0.389	Wind Speed	4.336	0.037	0.006
			Tree Avg. DBH	4.061	0.044	1.063
Bursera simaruba	0.68	0.268	Mg	4.398	0.036	0.381
			Tree Species Richness	6.419	0.011	1.691
Casearia decandra	0.865	0.445	Saltspray	4.847	0.028	<0.0001
			Conductivity	5.228	0.022	<0.0001
			Tree Species Richness	6.09	0.014	1.962
Chionanthus compactus	0.124	0.372	Aspect	4.646	0.031	1.008
	0.124	0.372	Organic C	4.615	0.032	1.259
	0.124	0.372	Conductivity	7.427	0.006	<0.0001
	0.124	0.372	K	5.579	0.018	<0.0001
Citharexylum spinosum	0.873	0.501	Aspect	11.187	0.001	0.989
	0.873	0.501	Organic C	6.464	0.011	0.766
	0.873	0.501	Tree Species Richness	18.052	<0.001	3.093
Clusia palmicida	0.562	0.604	K	6.25	0.012	<0.0001
	0.562	0.604	Aspect	5.36	0.021	0.984
	0.562	0.604	Organic C	5.433	0.02	1.548
	0.562	0.604	PO_4	4.122	0.042	0.992
Coccoloba venosa	0.972	0.109		None		
Coccothrinax barbadensis	0.266	0.221	N	5.54	0.019	0.653
Cordia collococca	0.468	0.369	Organic C	4.076	0.043	0.822
	0.468	0.369	Aspect	4.665	0.031	1.007
	0.468	0.369	Tree Species Richness	8.381	0.004	1.944
Diospyros inconstans	0.322	0.35	K	6.707	0.01	30162.581

	0.322	0.35	Organic C	4.325	0.038	1.201
	0.322	0.35	Tree Species Richness	6.832	0.009	1.682
Erythroxylum havanense	0.954	0.542	Wind Speed	7.5	0.006	9.215
	0.954	0.542	N	6.18	0.013	2.096
	0.954	0.542	Tree Species Richness	4.521	0.033	2.26
Eugenia dussii	0.87	0.252	Organic C	4.473	0.034	1.438
	0.87	0.252	Tree Avg. DBH	4.025	0.045	0.781
Maytenus tetragonus	0.83	0.14	None			
Ouratea guildingii	0.302	0.268	Wind Speed	5.545	0.019	4.557
	0.302	0.268	N	5.215	0.022	1.54
Piscidia carthagenesis	0.519	0.219	Tree Species Richness	6.918	0.009	1.925
Guapira fragrans	0.32	0.254	PO_4	5.39	0.02	0.996
	0.32	0.254	Wind Speed	4.506	0.034	2.871
Pithecellobium unguis-cati	0.491	0.298	None			

dominants are not clear. One scenario to explain the discrepancy is that *L. domingensis* and *T. trifolia* have declined and disappeared in the 54 years between the surveys. Reasons for the disappearance are probably not due to human actions as the Island has been protected over the whole of this period so natural stochastic disturbances such as hurricane Flora in 1963 might be responsible. Another scenario is that Beard (1944) did not correctly identify the species in question and *L. domingensis* in 1944 may actually be some other species detected in the 1997 survey. Species that were abundant in 1997 but were not mentioned in 1944 are: *G. fragrans*, *Citharexylum spinosum*, *Coccoloba venosa* and *Piscidia carthagenensis*. These species were either missed or not present in the 1944 survey and have gained dominance since then. *G.fragrans* may have been mistaken as *Pisonia cuspidata, L. domingensis* or both in the 1944 survey. *C.venosa* was patchily abundant on the island in 1997 and may have been missed by Beard if he did not happen to visit a *C. venosa* area.

Beard (1944) considered the vegetation communities to be homogeneous across the island apart from littoral communities that occurred within 30m from the sea on the eastern side of the island. He used this as evidence that the vegetation communities had completely recovered from cotton cultivation because parts of the island that had undergone cultivation were indistinguishable from those that had not although it was not clear how he distinguished between the previously disturbed and undisturbed areas (Beard 1944).

Generally the cluster groups generated on the basis of tree floristics were not very different structurally from one another except group D (the *Bambusa* group) and to a lesser extent group G (the *Coccoloba* group) which had much larger average DBH and average basal area (BA) than the other groups. The reason for the significant difference was the multi-stem habit which meant individuals of these species recorded a very large DBH and BA. Generally multi-stem habit is not a feature of plants on Little Tobago Island as it is elsewhere in the Caribbean. The dry forests of continental South America and Central America have stem densities that are similar to moist forests, i.e., mainly few large single stemmed individuals, while Greater and Lesser Antillean dry forests have a much higher stem density of small DBH stems (Van Bloem and Murphy 2004; Dunphy et al. 2000; Gentry 1995; Murphy and Lugo 1986). The reason for this difference is disturbance by hurricanes in the Antilles that have selected for species that coppice after being snapped off by hurricane force winds resulting in individuals with large numbers of small stems (Van Bloem et al. 2006; Van Bloem and Murphy 2004; Dunphy et al. 2000; Gentry 1995; Murphy and Lugo 1986). The vegetation on Little Tobago Island experiences hurricanes with

TABLE 8. Conspicuous components of the Bursera-Lonchocarpus Association (Coccothrinax faciation) on Little Tobago Island according to Beard (1944). v.a = very abundant, a. = abundant, i.a. = intermittently abundant, o. = occasional, r. = rare.

Species Name According to Beard (1944)	Likely Equivalent Species from 1997-8 Survey	Abundance	Canopy Position	Evergreen or Deciduous
Bursera simaruba	*Bursera simaruba*	v.a.	Upper Story	Deciduous
Coccothrinax barbadensis	*Coccothrinax barbadensis*	v.a.	Upper Story	Evergreen
Lonchocarpus domingensis (Pers.) DC	No clear equivalent	a.	Upper Story	Deciduous
Diospyros inconstans	*Diospyros inconstans*	a.	Lower Story	Evergreen
Eugenia lingustrina	*Eugenia lingustrina*	a.	Lower Story	Evergreen
Pithcellobium unguis-cati	*Pithcellobium unguis-cati*	a.	Lower Story	Evergreen
Trichilia trifolia L.	No clear equivalent	i.a.	Lower Story	Evergreen
Cassia bacillaris L. fil	*Senna bacillaris*	o.	Lower Story	Evergreen
Citharexylum spinosum	*Citharexylum spinosum*	o.	Upper Story	Deciduous
Coccoloba sp.	*Coccoloba uvifera*	o.	Lower Story	Evergreen
Cordia collococca	*Cordia collococca*	o.	Upper Story	Deciduous
Mayepea caribaea (Jacq.) Kuntze	*Chionanthus compactus*	o.	Lower Story	Evergreen
Picramnia pentandra	*Picramnia pentandra*	o.	Lower Story	Evergreen
Pisonia sp. ? cuspidata Heimerl.	*Guapira fragrans*	o.	Upper Story	Evergreen
?		o.	Lower Story	Evergreen
Cassia bicapsularis L.	*Senna bacillaris*	r.	Lower Story	Evergreen
Chlorophora tinctoria Gaud.	*Maclura tinctoria*	r.	Upper Story	Deciduous
Clusia sp.	*Clusia palmicida*	r.	Upper Story	Evergreen
Croton sp.	No clear equivalent	r.	Lower Story	Deciduous
Erythroxylum cumanense	*Erythroxylum cumanense*	r.	Lower Story	Evergreen
Jacquinia barbasco (Loefl.) Mez.	*Jacquinia armillaris*	r.	Lower Story	Evergreen
Ouratea guildingi	*Ouratea guildingi*	r.	Lower Story	Evergreen
Spondias mombin	*Spondias mombin*	r.	Upper Story	Deciduous

less frequency than in the Antilles so either there are fewer species which adopt the coppicing strategy or the coppicing response is less evident over time as dominant coppice shoots suppress other shoots. Instead the vegetation structure is more like continental South America.

The most distinct cluster groups were those dominated by single species most particularly groups D (*B. vulgaris*) and G (*C. venosa*). Group D consists of three sites where *B.vulgaris* has established and still persists. It is likely the natural canopy of the vegetation community on Little Tobago Island is open enough to allow *B. vulgaris* to invade (Teixeira and Oatham 2001) albeit fairly slowly. Group G appears to be found mainly on the NE parts of the island. However according to the logistic regression there are no abiotic variables that significantly explained the distribution of the characteristic species of the group (*C. venosa*). Group A is characterised by a higher than usual occurrence of *Clusia palmicida* but there does not seem to be pattern for the occurrence of this group on the island. The logistic regression indicates *C. palmicida* is more dominant at sites that have low soil potassium ion concentrations. Soil potassium on Little Tobago Island is relatively low compared to similar tropical ecosystems (Baillie 1989; Singh 1989; Baillie 1996). A threshold of 100kg/ha is thought to exist for potassium ion concentration below which it is limiting to plant growth and survival (White 1997). The fact that potassium ions are significant in the distribution of some plant species on Little Tobago Island indicates it may be limiting on Little Tobago Island. *C. palmicida* is a facultative epiphyte so it has the ability to survive with little soil but requires high light environments. It may therefore persist in parts of Little Tobago Island with poor potassium ion concentrations where competition from species that can better utilise higher nutrient status soils is absent. Thus group A may be characteristic of poorer sites with a lower and more broken canopy which is suggested in Table 5A. Group B is characterised by *B. simaruba* and group B sites seem to be found mainly on higher points of the island. The logistic regression analysis found that *B. simaruba* tends to be found where there is a high species richness which may indicate more clement environmental conditions enabling a greater number of species to survive including *B. simaruba*. Tree species richness was positively correlated with about half the dominant species on the island. This is probably an artefact because a more diverse site is more likely to have a species present.

Soil nutrients on the island were found to be generally limiting, particularly potassium, nitrogen and to a lesser extent, phosphorus. Although the amount of N in the soil of Little Tobago Island is relatively large the high C:N ratio (>20:1) indicates that much of it will be bound in complexes with the even greater amount of soil carbon and thus unavailable to the vegetation (Baillie 1996). Nitrogen is therefore probably limiting on the Island. The high levels of soil carbon indicate relatively low rates of organic matter decomposition possibly the result of the seasonal nature of the climate on Little Tobago (Baillie 1996). There are also few legume species that could potentially fix nitrogen in the vegetation communities on the island. Poor levels of K and Ca in the soil indicate the underlying rocks of the island (volcanic breccias and tuffs with few feldspars) are deficient in these nutrients and do not replenish the stock despite the weathering front being relatively close to the soil surface on the island (Burnham 1989). By contrast Mg and to a lesser extent P occur at moderately good concentrations probably indicating a good supply from decomposing rocks or perhaps inputs from bird droppings (guano) from nesting birds. The concentrations of the soil nutrients show no spatial patterning across the island which would help in part to explain the apparent random distribution of the individual species on the island.

Conclusions

The vegetation community on Little Tobago Island is an example of a southern Caribbean basin dry forest that has not been disturbed by humans for over 200 years. It is in good condition with few exotic species and may represent a stable dry forest vegetation community that has been severely reduced in extent and degraded elsewhere in its range in northern South America and the southern Caribbean. The exotic *Bambusa vulgaris* may become a problem in the future and should be removed from the island. There is some evidence that species composition of the vegetation communities may be changing as there are differences in dominant species reported in a 1944 survey compared to the species observed in this study. Possible reasons for the apparent disappearance of two species could be either misidentifications in 1944 or natural disturbances from hurricanes. Despite being disturbed by at least two hurricanes in the last 200 years, the vegetation community does not appear to be adapted to hurricane disturbance as it lacks the coppicing features and numerous small stems of the vegetation communities of more hurricane prone areas.

The composition of the vegetation communities is generally similar across the island but species such as *B. vulgaris* and *Coccoloba venosa* dominate in restricted areas. *Coccothrinax barbadenis*, *Bursera simaruba*, and *Guapira fragrans* dominate the rest of the island with *Clusia palmicida* occurring in scattered patches that may be less favourable to plant growth although this hypothesis needs to be tested. These same species occur across the island but seem to decrease their stature in more exposed situations. The distribution of species appears to be effected by edaphic conditions, particularly soil nutrients. But since the variation in the levels of the edaphic parameters was randomly distributed across the island the distribution of species was also spatially random.

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