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Phytosociology of Vascular Plants on an International Biosphere Reserve: Virgin Islands National Park, St. John, US Virgin Islands

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ABSTRACT.—We investigated the relationships of vegetation communities to environmental variables and compared the relative contribution of native and introduced species in extant forest communities on St. John, US Virgin Islands, using an island-wide forest vegetation inventory and monitoring network of permanent plots. We detected 2,415 individuals of 203 species, 5 percent of which were introduced. Cluster analysis, Indicator Species Analysis, and Nonmetric Multidimensional Scaling (NMS) ordination detected four broad species communities divided primarily by moisture and disturbance gradients. Group 1 was characterized by rocky, low-to-mid elevation dry scrub forest on soils with fairly low soil nutrient content; Group 2 was distinguished by low soil nutrient content, high-elevation moist basin forests on steep slopes; Group 3 was indicative of disturbed communities on a wide range of elevations with gentle or no slope across a range of soil types; and Group 4 represented mid-elevation moist forests across a range of steep slopes on nutrient-rich soils. Though introduced species are present and widespread on the island, they do not appear to be dominating most plant communities. Exceptions may be those communities with long-standing histories of human disturbance. Achieving an adequate sample of forest types of limited extent or linear spatial patterns such as mangroves and gallery moist forests is difficult with a systematic design. Future sampling should consider some form of stratification targeting these under-sampled forest types.

KEYWORDS.—Caribbean forest vegetation, disturbance, introduced species, inventory and monitoring, phytosociology, Virgin Islands National Park

INTRODUCTION

Extant Caribbean forests have been shaped by natural disturbances, specifically hurricanes, and a more recent history of human exploitation (Lugo et al. 2000). Land use history on St. John is similar to that of other islands in the Lesser Antilles. Forests on St. John were first utilized by pre-Columbian native Taino Indians for food, shelter, and raw materials for boat construction. Danish settlers arrived in the early 1700's and cleared large areas of forest for agriculture, farming, and building construction (Ray and Brown 1995; Woodbury and Weaver 1997). A favorable climate contributing to long growing seasons lent itself to sugarcane, cotton, tobacco, and coffee cultivation (Woodbury and Weaver 1997). As a result, the vegetation has been dramatically altered through time, and many of the current island landscapes are dominated by secondary forest (Weaver and Chinea-Rivera 1987; Ray and Brown 1995; Rogers and Reilly 1998). Some Antillean forest types, such as the once-common subtropical dry forest, have been impacted to the point that they are now considered endangered ecosystems (Murphy and Lugo 1986; Ray et al. 1998; Linares-Palomino and Ponce Alvarez 2005). On many of the islands, forest cover consists of fragments scattered across the landscape and much of what remains are secondary forests containing various introduced species whose long-term impacts on species composition and ecosystem function are

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yet to be understood (Chinea and Helmer 2003; Grau et al. 2003; Lugo and Helmer 2004).

Though St. John shares a history of disturbance-dominated landscapes common in the Lesser Antilles, it has avoided the subsequent urban development that has occurred across the Caribbean basin. In 1956 approximately 65 percent of St. John was donated to the U.S. National Park Service for the creation of the Virgin Islands National Park (VINP) (National Park Service 2005). In recognition of its uniqueness, in 1976 the park was designated an international biosphere reserve by the United Nations Educational, Scientific and Cultural (UNESCO) Man and Biosphere (MAB) program. With the addition of offshore areas in 1962 and the establishment of the Virgin Islands Coral Reef National Monument in 2001, the VINP mission "to protect, manage, interpret and preserve the park's unique natural and scenic resources and values unimpaired for the education, enjoyment and inspiration of present and future generations" extends from the island's highest point, Bordeaux Mountain at 389 m, into the surrounding Caribbean tropical marine ecosystems (National Park Service 2005). The result has been the protection from development of one of the larger contiguous forest areas in the Lesser Antilles, and a unique opportunity for the study of island flora and fauna.

The species composition and vegetation structure in St. John's forests, considered a global biodiversity "hotspot" (Myers et al. 2000, Helmer et al. 2002), are of substantial importance to understand current biodiversity in the Caribbean basin, and to evaluate availability of habitat for multitudes of wildlife species. In addition to contributing to global wildlife and vegetation biodiversity, the Greater and Lesser Antilles are an important archipelago for wintering neotropical migratory songbirds (Askins et al. 1992; Wunderle and Waide 1993; Rappole 1995). Studies have suggested that deforestation has led to losses of wintering habitat for many warbler species in the Caribbean, and to population declines in these species (Rappole 1995).

Despite the need to understand the present Caribbean forest landscape, surprisingly few studies have documented patterns and composition of island vegetation, particularly in the U.S. Virgin Islands. Studies that have explored species-environment relationships and forest productivity in the Caribbean have focused primarily on woody species (Weaver and Chinea-Rivera 1987; Ray et al. 1995; Ray et al. 1998; Rivera et al. 1998; Lugo et al. 2004; Linares-Palomino et al. 2005). Aside from a limited number of field guides, taxonomic floral descriptions, and broad scale community maps, the result has been a general paucity of information regarding non-woody vascular plant species, their relationships to woody species, and plant community-environment relationships in this region. Current VINP management objectives that could benefit from a comprehensive phytosociological study and vegetation monitoring include: reduction of soil erosion, landslides, and freshwater runoff that damage near-shore coral reefs and reduce their value as an ecotourism resource (National Park Service 2005); elimination or reduction of feral white-tail deer (*Odocoileus virginianus*), donkey (*Equus asinus*), domestic goat (*Capra hircus*), wild hog (*Sus scrofa*), and domestic sheep (*Ovis aries*) populations that threaten forest regeneration and soils (National Park Service 2004); an Avian Conservation Implementation Plan, directed toward maintaining and increasing the amount of over wintering habitat for Neotropical migrants (Watson 2003); and monitoring of land use change from construction and over development (U.S. Department of Transportation 2004).

The U.S. Department of Agriculture (USDA) Forest Service, Forest Inventory and Analysis (FIA) program conducts systematic surveys of forestland across the entire United States and its territories. In 2004, FIA initiated a special, intensified study on St. John to investigate the structure and diversity of forest vegetation, and additional forest attributes. This intensified inventory was not limited to within the VINP boundaries, but encompassed the entire island because conditions and management activities in the non-park portions of the island directly and indirectly impact the unique

Caribbean ecosystems the park is meant to preserve. Specifically, our objectives were to: 1) install a permanent forest vegetation inventory and monitoring network across the island of St. John, 2) document the composition, relative abundance, and vertical position of all vascular plants on forested plots, 3) quantify and compare populations of native and introduced vegetation occurring on forestland, and 4) identify environmental variables influencing the distribution of vascular plants across the island.

MATERIALS AND METHODS

Study site

The island of St. John, U.S. Virgin Islands, is located in the Caribbean Sea (13°22′N, 64°40′W) approximately 30 km east of Puerto Rico. St. John is approximately 5180 ha in area and covers rugged terrain ranging in elevation from sea level to 387 m above sea level, and slopes in excess of 30 percent across the bulk of the island (Rankin 2002). The Virgin Islands National Park occupies over half of the volcanically formed island. Primary forest types include mangrove and salt flats; moist upland, gallery, and basin forests; dry evergreen woodlands, thickets, thorn and cactus scrubs, coastal hedges; and pasture (Woodbury et al. 1997). The climate on St. John is primarily subtropical, and the island is subject to tropical trade winds, hurricanes, and variable rainfall. Precipitation on St. John ranges from 890 to 1400 mm y^{-1}, and averaged 1141 mm y^{-1} for the years 1971 to 2000 at the Cruz Bay weather station at the west end of the island (Weaver and Chinea-Rivera 1987; Southeast Regional Climate Center 2005). The majority of rainfall on St. John occurs during late spring, summer, and early fall, with a dry season December through April (Weaver and Chinea-Rivera 1987).

Sample design and data collection

Vegetation and environmental data were collected June through July of 2004 using the USDA Forest Service FIA sample design (USDA Forest Service 2003). In an effort to minimize impacts to forest vegetation, Forest Service FIA protocol does not allow for repeated visits to sample sites within a given year. To minimize any potential effects of seasonality we sampled at the mid-point of the rainy season—the point at which any seasonal growth flushes would have already occurred but drought would not have resulted in senescence. Twenty-six plots were arranged on an unbiased, systematic sample grid across St John. The grid on St. John was composed of hexagons covering approximately 200 ha each, with one sample plot located within each hexagon. Plots were located and mapped using differentially corrected global positioning system (GPS) equipment to ensure a high degree of accuracy. Plots were installed and data collection took place where there was at least 10 percent tree canopy coverage and a minimum forested area of 0.4 ha around each plot center, as designated by USDA Forest Service FIA sample design guidelines. Plots consisted of a cluster of four subplots each with a 7.3 m radius (Fig. 1). There were 167 m^2 per subplot, for a total sampled area of 670 m^2 (0.017 ha) in a fully forested plot.

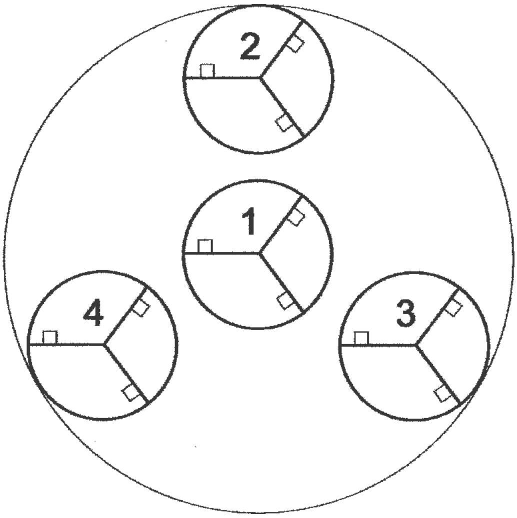

FIG. 1. Forest Inventory and Analysis plot design. Figure recreated with permission of USDA Forest Service, Forest Inventory and Analysis program.

Field crews collected forest inventory, understory structure and composition, and physiographic data on each subplot. Diameter at breast height (DBH) (taken at 1.37 m), total height, crown ratio, crown width, and other parameters were measured on all trees with DBH ≥ 12.5 cm within the subplots; and DBH and total height were measured on saplings with DBH ≥ 2.5 cm within a 2.1 m radius microplot nested in each subplot (Bechtold and Patterson 2005). Details on the plot and subplot-level site characteristic categories used in FIA are found in the USDA Forest Service, FIA-Southern Research Station Field Guide, Supplement C to Southern Research Station Regional Manual 1.62, Field Procedures for Puerto Rico and the Virgin Islands (*http://www.srs.fs.usda.gov/fia/manual/*). Additional environmental information was derived from mapped Soil Survey Geographic Database (SSURGO) soil data (USDA Natural Resources Conservation Service 2004).

All vascular plant species were recorded within each subplot within a 45 minute time limit. The USDA Forest Service FIA program limits the subplot search for vascular plant species to 45 minutes in order to maintain the efficiency of the data collection process, and to standardize the process nationwide (Gray and Azuma 2005). Percent foliar cover was then estimated to the nearest percent for each species on the subplot in each of five categories: total cover, cover in the 0 to 61 cm height layer, cover in the 61 to 183 cm height layer, cover in the 183 to 488 cm height layer, and cover above 488 cm. Voucher specimens for unknown species and species with which the botanist was less familiar were documented in the field, collected, and submitted to a botanist from the University of the Virgin Islands for identification and comparison against herbarium records.

Field methods as designated by FIA allow for multiple conditions on each subplot, resulting in subplots with various percentages of forest acreage. The nonforest portions are not sampled, resulting in "partial" subplots and "partial" plots. Because partially sampled subplots and plots violate statistical assumptions, particularly species-area relationships, we eliminated all subplots that contained less than 100 percent forest area, and analyzed data using subplots as the primary sample unit (Gray and Azuma 2005; Oswalt in press; Rudis et al. in press). Some degree of spatial autocorrelation was expected among subplots comprising a "plot" unit; however, the nonparametric statistical methods used for this analysis helped to avoid this problem, and we were interested in allowing for the potential separation of subplots occurring in different environmental conditions (e.g., aspect or percent slope) (King and Buckney 2002). The remaining sample size consisted of 75 100-percent forested subplots in 20 plots.

Species composition and structure

Species richness values, including jackknife estimates and rarefaction curves, were estimated using PC-Ord and EstimateS 7.5 (McCune and Mefford 1999; Colwell 2005). Nomenclature followed the USDA PLANTS database species list for the U.S. Virgin Islands and Puerto Rico. Species were assigned to life form as given in USDA PLANTS database (http://plants.usda.gov/) and Acevedo-Rodríguez (1996). Rushes and sedges were lumped into the "herb" category, and subshrubs were lumped in the "shrub" category for simplification. Cacti were split into "shrub" or "tree" as given in PLANTS. Species were assigned to three groups: native, introduced, or unknown using the PLANTS database. Definitions of broad forest types (e.g., Secondary Forest) follow Woodbury and Weaver (1997) and Acevedo-Rodríguez (1996).

Community determination

Cluster analysis was used to group subplots by species composition (McCune and Grace 2002). Sample by species matrices were populated using total percent cover values on a subplot basis, arcsine-square root transformed to improve normality (McCune and Grace 2002). Rare species (species occurring in two or fewer plots) were removed from each matrix prior to analysis to reduce noise in the dataset (Weaver and Chinea-Rivera 1987; McCune et al. 2000; McCune and Grace 2002; Picking and Veneman 2004). One subplot was an outlier falling in a dry salt lagoon and containing only one species, *Laguncularia racemosa* (L.) Gaertn. f., and was removed from analysis.

Clustering was performed using Sorenson distance measures with flexible beta set at -0.25, the preferred distance measure for community datasets (McCune et al. 2000; McCune and Grace 2002). We then used nonmetric multiresponse permutation procedures (MRPP) to test within-group homogeneity and to validate the separation between clusters (McCune et al. 2000). Nonmetric MRPP utilizes rank transformed distance matrices rather than raw data (as in MRPP) to calculate test statistics, and has been successfully used for evaluating differences in groups of community data (McCune et al. 2000). The A statistic in MRPP describes "chance-corrected within-group agreement," or the difference in within-group homogeneity compared to random chance (McCune and Grace 2002). The A statistic is significant and $A > 0$ when the within-group homogeneity and between-group heterogeneity is greater than that expected by chance (McCune et al. 2000; McCune and Grace 2002). When $A > 0.3$, differences between groups are considered to be fairly large, though McCune et al. (2000) point out that A values in community data often fall below $A = 0.1$ even if differences between groups exist. Indicator species analysis was used to flag species indicative of each cluster, as determined by importance values and significance levels. We determined where to break the dendrogram by plotting the average P-values from the indicator species analysis by the number of groups to find the level of maximum significance as suggested by (Dufrene and Legendre 1997).

Ordination

Arcsine square root-transformed matrices from the cluster analysis were subjected to nonmetric multidimensional scaling (NMS) to identify environmental characteristics that play a role in determining community composition. One subplot contained no environmental data and was removed from the ordination analysis, resulting in a sample size of 73. The ordination was performed on the "autopilot slow-and-thorough" mode in PC-Ord using Sorenson distance measures, 40 runs with real data and 50 runs of randomized data (McCune and Grace 2002). Average stress and instability were used to determine the best solution, and Pearson and Kendall correlations of environmental variables with axes were used to interpret the ordination (McCune and Grace 2002). Species matrices were initially analyzed at the whole community level. Subsequent analysis separated the species matrix into two life-form categories, trees (overstory) and herb-shrub-epiphyte (understory).

Categorical class variables in the environmental matrix were used like continuous variables by assigning values based on the midpoint of the class in which they fell. Environmental variables used in the community NMS ordination are given in Table 1. Ordination on the understory layer alone also included structural components of the overstory in the environmental matrix, as we suspected that the herb layer was influenced both by the environment and by the structure of the overstory component (Table 1). Ordinations are shown with cluster groups and species as the identifying characteristics.

RESULTS

Species composition and structure

We recorded 2,415 individuals of 203 species (63 families) on St. John forestland. This richness represents 21 percent of all vascular species described on the island (Acevedo-Rodríguez 1996). First-order jackknife estimates indicated the true species richness was 255.3 (± 12.15 standard deviations (SD)). The species area curve for samples recorded on St. John began to plateau at 70 subplots (Fig. 2).

Subplots contained 32.20 (± 8.29 SD) species, on average, and beta diversity (gamma

TABLE 1. Quantitative environmental variables evaluated in the community and understory NMS matrices and correlations to community-level NMS axes.

Variable name	Community matrix	Understory matrix	Community axis correlations 1	Community axis correlations 2	Community axis correlations 3
Slope	Yes	Yes	0.36	0.12	−0.03
Aspect	Yes	Yes	−0.21	0.3	−0.06
Elevation	Yes	Yes	0.41	−0.1	−0.49
Distance to water	Yes	Yes	−0.06	−0.15	−0.11
Distance to improved roads	Yes	Yes	0.07	−0.05	0.55
Distance to urban areas	Yes	Yes	0.07	−0.17	0.17
Distance to agriculture	Yes	Yes	−0.27	0.03	−0.29
Acres of contiguous forest	Yes	Yes	−0.05	0.07	−0.02
Total clay (percent)[a]	Yes	Yes	−0.11	−0.47	−0.44
Bulk density[a]	Yes	Yes	0.13	0.42	0.46
Available water capacity[a]	Yes	Yes	−0.04	−0.48	−0.41
Linear extensibility (percent)[a]	Yes	Yes	−0.13	−0.38	−0.46
Organic matter (percent)[a]	Yes	Yes	−0.14	−0.17	−0.39
Cation exchange capacity[a]	Yes	Yes	−0.1	−0.47	−0.44
pH (water extraction method)[a]	Yes	Yes	0.03	−0.41	−0.33
Calcium carbonate[a]	Yes	Yes	0.14	0.2	0.4
Gypsum[a]	Yes	Yes	−0.13	−0.4	−0.47
Sodium adsorption ratio[a]	Yes	Yes	−0.13	−0.4	−0.47
Overstory trees per hectare	No	Yes		N/A	
Overstory basal area per hectare	No	Yes		N/A	
Aboveground biomass (mg/ha)	No	Yes		N/A	
Belowground biomass (mg/ha)	No	Yes		N/A	
Total biomass (mg/ha)	No	Yes		N/A	
Crown area	No	Yes		N/A	
Crown volume	No	Yes		N/A	
Overstory trees per hectare	No	Yes		N/A	

[a] Denotes variables derived from SSURGO mapped soil data, Natural Resources Conservation Service, 2004.

diversity divided by alpha diversity) was estimated at 7.93. Twenty-six percent of species occurred in only one subplot and 10 percent of recorded species occurred in only two subplots. Twenty-two species were unknown, but distinct, and were assigned generic names as given in the PLANTS database. Eighty-four percent of species detected were native to the Virgin Islands, 5 percent were introduced, and nativity could not be determined for 11 percent of species. Fifty-nine subplots (79%) contained at least one introduced species; 29 subplots (39%) contained two or more. We detected 9 out of 25 known species that are endemic to the combined Virgin Islands and Puerto Rico (Acevedo-Rodríguez 1996).

Guapira fragrans (Dum.-Cours.) Little was the most common vascular plant (and tree) sampled, occurring on 91 percent of subplots, though it never covered more than 25 percent of any single subplot, and averaged 8 percent total foliar cover across subplots. *Randia aculeata* L. was the most common shrub sampled, occurring in 75 percent of subplots sampled; *Acacia retusa* (Jacq.) Howard was the most common liana, oc-

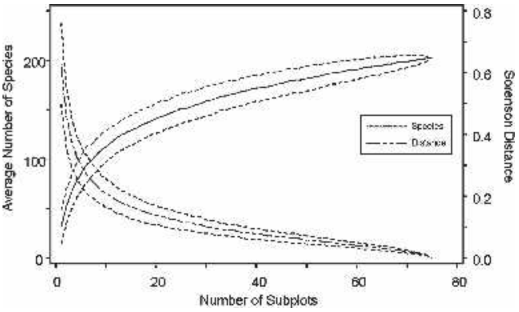

FIG. 2. Species area curve with Sorenson distance measures for samples on St. John, U.S. Virgin Islands, 2004.

curring in 61 percent of subplots; *Anthurium cordatum* (L.) Scott was the most common herb, appearing in 37 percent of subplots; *Lasiacas divaricata* (L.) A.S. Hitchc. was the most common grass, sampled in 55 percent of subplots; and *Tillandsia utriculata* L. was the most common epiphyte, occurring in 52 percent of subplots. The majority of species detected were shrubs, followed by trees and vines.

Species averaged 4.19 (±0.29 SD) percent total foliar cover on subplots, with a range of averages from 1 percent (trace) to 22.14 percent. The maximum cover exhibited by any one species on a given subplot was 90 percent. On subplots containing at least one introduced species, the average cover of introduced species was 1.86 (± 0.22 SD) percent. Average foliar cover on subplots was highest in the 61 to 183 cm vegetation layer, and was lowest in the 0 to 61 cm and >488 cm layers.

Community determination

Clustering and indicator species analysis yielded maximum results at four clusters. The resulting dendrogram was pruned with <25 percent of information remaining (Fig. 3). The four highest scoring indicator

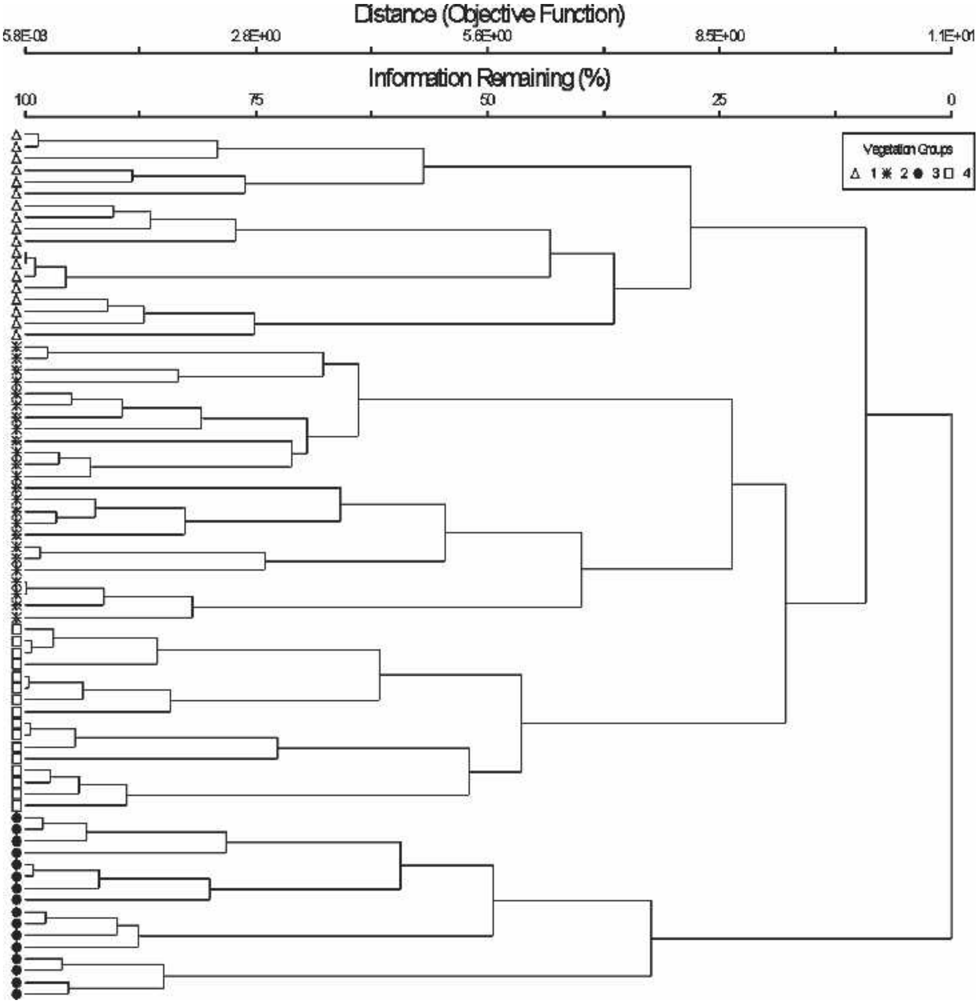

FIG. 3. Results of cluster analysis on community-level data, St. John, U.S. Virgin Islands. The dendrogram was broken into 4 groups with less than 25 percent of information remaining.

species, importance values, and *P*-values for each group are given in Table 2. Major group separations occurred between Group 3 and Groups 1, 2, and 4. Results of the nonmetric MRPP showed a chance-corrected within-group agreement of $A = 0.50$ ($P < 0.0001$), and a T-test statistic of −31.22, thus validating the separation between selected groups.

Group 1 split apart from Groups 2 and 4 along what appeared to be a moisture gradient. Primary indicators of Group 1 were *Acacia muricata* (L.) Willd., *Croton flavens* L. var. *rigidus* Muell.-Arg., *Eugenia cordata* (Sw.) DC., and *Plumeria alba* L.; species indicative of dry scrub forest (Acevedo-Rodríguez 1996). Conversely, indicators of both Groups 2 and 4 were indicative of moist forests, although species of Group 2 were more typical of basin moist forests, while species of Group 4 were more typical of secondary moist forests (Acevedo-Rodríguez 1996). Primary indicators of Group 2 included *Anthurium cordatum* (L.) Schott, *Capparis baducca* L., *Chionanthus compactus* Sw., *Cordia alliodora* (Ruiz &

TABLE 2. Indicator species detected on the island of St. John in June and July, 2005 by cluster analysis group. Life form, indicator value for indicator species analysis, and nativity are denoted.

Group	Scientific name	Plant family	Primary life form	Indicator value[a]	Nativity[b]
1	*Plumeria alba* L.	Apocynaceae	tree	75.7	N
	Acacia muricata (L.) Willd.	Fabaceae	tree	63.9	N
	Eugenia cordata (Sw.) DC.	Myrtaceae	tree	63.8	N
	Croto flavens L. var. *rigidus* Muell.-Arg.	Euphorbiaceae	shrub	52.6	N
	Reynosia guama Urban	Rhamnaceae	shrub	48.3	N*
	Brufelsia americana L.	Solanaceae	shrub	45.1	N
	Oplonia spinosa (Jacq.) Raf.	Acanthaceae	shrub	44.4	N
	Ipomoea eggersii (House) D. Austin	Convolulaceae	vine	43.5	N
	Amyris elemifera L.	Rutaceae	shrub	41.5	N
	Agave missionum Trel.	Agavaceae	herb	41	N*
2	*Morisonia americana* L.	Capparaceae	tree	61.3	N
	Cordia alliodora (Ruiz & Pavón) Oken	Boraginaceae	tree	46.4	N
	Chionanthus compactus Sw.	Oleaceae	shrub	45.9	N
	Anthurium cordatum (L.) Schott	Araceae	herb	40.6	N
	Capparis baducca L.	Capparaceae	shrub	40.5	N
3	*Opuntia repens* Bello	Cactaceae	shrub	69.7	N*
	Leucaena leucocephala (Lam.) de Wit	Fabaceae	tree	65	N
	Schaefferia frutescens Jacq.	Celastraceae	shrub	60.7	N
	Acacia retusa (Jacq.) Howard	Fabaceae	liana	58.1	N
	Erythroxylum brevipes DC.	Erythroxylaceae	tree	51.1	N
	Capparis flexuosa (L.) L.	Capparaceae	shrub	50.1	N
	Serjania polyphylla (L.) Radlk.	Sapindaceae	liana	48.7	N
	Commelina erecta L.	Commelinaceae	herb	46.8	N
	Capparis indica (L.) Druce	Capparaceae	shrub	44.2	N
	Tragia volubilis L.	Euphorbiaceae	vine	43.5	N
4	*Savinea florida* (Vahl) DC.	Fabaceae	shrub	61.2	N
	Ardisia obovata Desv. ex Hamilton	Myrsinaceae	tree	60.7	N
	Guettarda scabra (L.) Vent.	Rubiaceae	shrub	60.6	N
	Eugenia monticola (Sw.) DC.	Myrtaceae	tree	57.5	N
	Psychotria nervosa Sw.	Rubiaceae	shrub	51.9	N
	Nectandra coriacea (Sw.) Griseb.	Lauraceae	shrub	51.4	N
	Cestrum laurifolium L'Hér.	Solanaceae	shrub	48.2	N
	Chiococca alba (L.) A.S. Hitchc.	Rubiaceae	liana	47.8	N
	Lasiacis divaricata (L.) A.S. Hitchc.	Poaceae	grass	47.7	N

[a] Indicator values represent a combination of relative abundance and relative frequency. Values are given where $p \geq 0.001$.

[b] Native species with an asterisk indicate species endemic to the combined U.S. Virgin Islands and Puerto Rico.

Pavón) Oken, and *Morisonia americana* L.. Primary indicators of Group 3 included *Acacia retusa* (Jacq.) Howard, *Capparis flexuosa* (L.) L., *Capparis indica* (L.) Druce, *Commelina erecta* L., *Erythroxylum brevipes* DC., *Leucaena leucocephala* (Lam.) de Wit, *Opuntia repens* Bello, *Schaefferia frutescens* Jacq., *Sejania polyphylla* (L.) Radlk., and *Tragia volubilis* L.. These species are typical of secondary dry forest and disturbed areas (Acevedo-Rodríguez 1996). Significant indicators of Group 4 were *Ardisia obovata* Desv. ex. Hamilton, *Cestrum laurifolium* L'Hér, *Chiococca alba* (L.) A.S. Hitchc., *Eugenia monticola* (Sw.) DC., *Lasiacis divaricata* (L.) A.S. Hitchc., *Nectandra coriaceae* (Sw.) Griseb., and *Sabinea florida* (Vahl) DC.

Ordination

Ordination was performed on two separate species matrices. Community is used here to describe the plant composition of combined understory and overstory species, including all woody and nonwoody species. Understory is used here to describe all non-tree woody and nonwoody species. Nonmetric multidimensional scaling of subplots in community species space resulted in a three-dimensional solution. The final stress for the three-dimensional solution after 108 iterations was 13.52, and the final instability was 0.00001. Overall, the three-dimensional solution explained 78 percent of the variation in the dataset. Axis one explained 27 percent of the variation, and was positively correlated with slope and elevation (Table 1). Axis two explained 18 percent of the variation, and was negatively correlated with percent total clay, available water capacity (AWC), linear extensibility or shrink-swell (LEP), cation exchange capacity (CEC), pH, gypsum, and sodium adsorption ratio (SAR), and positively correlated with bulk density, and weakly positively correlated with aspect (Table 1). Axis three explained 32 percent of the variation, and was positively correlated with distance to improved roads, bulk density, and calcium carbonate, and negatively correlated with percent total clay, organic matter content, elevation, AWC, LEP, CEC, pH, gypsum, and SAR (Table 1). Group 1 subplots were relegated across low-to-mid elevations over a range of slopes, and were distinguished by higher bulk densities, lower clay content, low AWC, low CEC, and slightly acidic soils. Group 2 subplots were generally arrayed towards higher elevations with steep slopes, and were characterized by high bulk densities, lower clay content, low AWC and CEC, and higher pH values. The subplots in Group 2 were scattered across southeast to northwest aspects. Group 3 subplots occurred primarily at the gradient between lower elevation dry forests and higher elevation moist forests on areas with gentle to no slopes, higher organic content, and spanning a range of nutrient contents. The subplots in Group 3 fell on sites with moist, northwesterly aspects. Group 4 subplots occurred primarily at higher elevations with less-steep slopes, fell on south—or east-facing sites, and were on soils distinguished by low bulk densities, high clay content, high organic matter content, high AWC, LEP, and CEC, and neutral pH values (Fig. 4).

Nonmetric multidimensional scaling of subplots in understory species space with tree species removed and environmental variables related to forest structure added to the environmental matrix resulted in a three-dimensional solution, as well (Fig. 5). Final stress for the three-dimensional model was 14.50, and final instability was 0.00001. Combined axes explained 76 percent of the variation in the dataset. Axis one explained 33 percent, and was negatively correlated with overstory basal area, overstory biomass, overstory crown area and volume, and elevation. Axis two explained 22 percent, and was positively correlated with overstory basal area, overstory biomass, total percent clay, AWC, LEP, CEC, pH, gypsum, and SAR, and was negatively correlated with bulk density. Axis three explained 20 percent, and was negatively correlated with distance to agricultural land, total clay, AWC, LEP, organic matter, CEC, gypsum, and SAR, and was positively correlated with bulk density and calcium carbonate. Slope and aspect, which were important in the model when overstory species were included, were no longer strongly correlated to ordination axes.

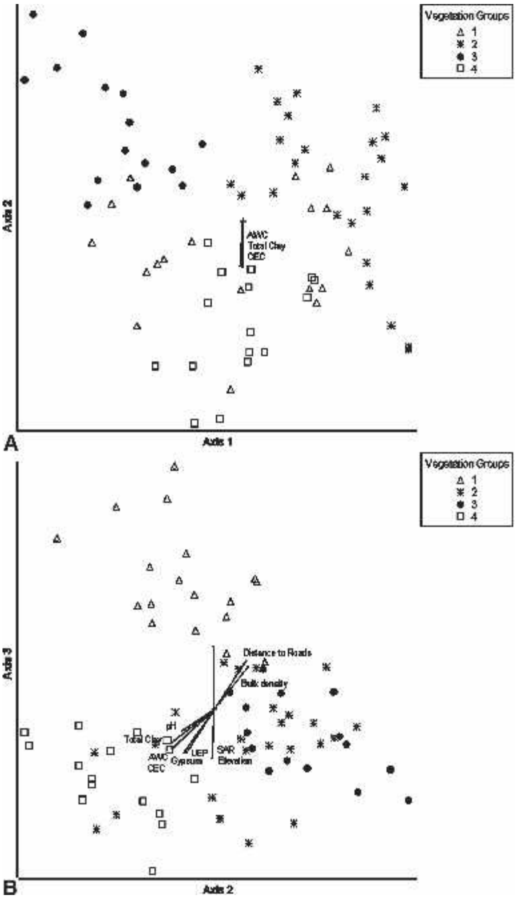

FIG. 4. Vegetation community (combined overstory and understory) joint biplot ordination along NMS axes, coded by cluster analysis groups. Vector length and direction indicates the strength and direction of relationships with environmental axes. Plot (a) shows ordinations for axes 1 and 2, and plot (b) shows ordinations for axes 2 and 3.

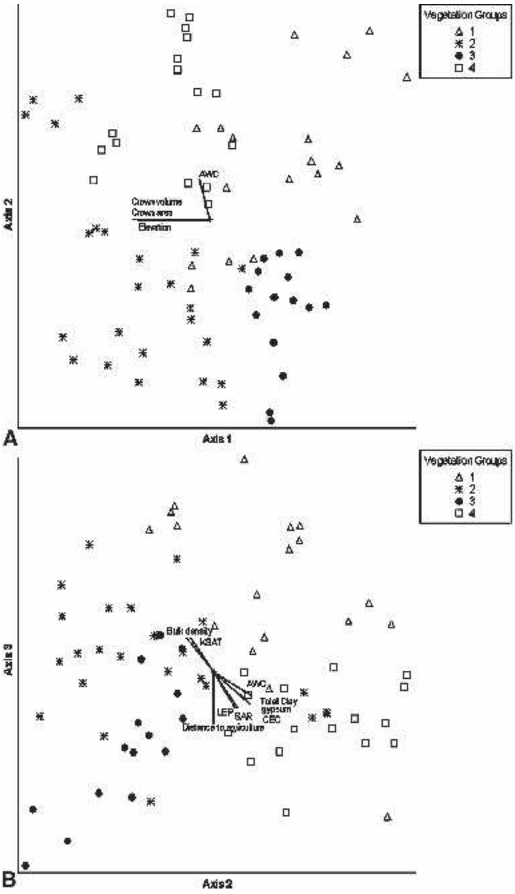

FIG. 5. Understory vegetation joint biplot ordination along NMS axes, coded by cluster analysis groups. Vector length and direction indicates the strength and direction of relationships with environmental axes. Plot (a) shows ordinations for axes 1 and 2, and plot (b) shows ordinations for axes 2 and 3.

Subplots grouped by community from the cluster analysis, and understory species were plotted simultaneously on the ordination axes (Fig. 5). Subplots in Group 1 appeared to have lower basal areas, crown volumes, and crown areas, and—as in the whole community ordination—fell along lower elevations. Subplots in Group 2 covered a range of basal areas, but tended to have large crown volumes and crown areas. Subplots in Group 3 exhibited fairly low basal areas and crown volumes and areas in the middle of the range of values. Finally, Group 4 exhibited higher basal areas overall, and a wide range of crown volumes and crown areas. Group relationships to other environmental variables did not change between the community ordination and the understory ordination.

DISCUSSION

The island of St. John contains diverse vascular plant assemblages covering a range of forest structures, all of which are important to the maintenance of species biodiversity in the Caribbean. The flora on St. John is important because of the loss of tropical and subtropical dry forests and the level of preservation afforded those forests on St. John as a result of federal protection through the VINP.

Cluster analysis, indicator species analysis, and NMS ordination detected four broad species communities on St. John. Group 1 was characterized by rocky, low-to-mid elevation dry-scrub forest on soils with fairly low nutrient content; Group 2 was distinguished by nutrient poor, high-elevation moist basin forests on steep slopes; Group 3 was indicative of disturbed communities on a wide range of elevations with gentle or no slope across a range of soil types; and Group 4 represented mid-elevation moist forests across a range of steep slopes on nutrient-rich soils. Due to the systematic nature of the FIA sample design, we probably undersampled rare communities or communities that form linear features on the landscape. For instance, we probably undersampled mangrove forests, which tend to form linear bands along the coast, as well as gallery moist forests, which form linear bands in riparian areas (Woodbury and Weaver 1997). We may also have under-represented partially forested areas due to FIA rules for installing plots. However, the systematic design was useful in that we sampled disturbed communities and transitions that other studies may have overlooked by sampling discrete stands based on aerial photography, landowner constraints, or study objectives. For example, though Ray et al. (1998) conducted thorough woody-species botanical surveys of dry forest communities on St. John, the sample design was necessarily constrained by the study objectives to minimize effects of human alterations, thereby missing portions of the vegetation community. Similarly, Woodbury and Weaver (1997) produced a thorough report with maps describing vegetation communities on St. John. Their study focused on verifying, describing, and delineating communities derived from aerial photographs, however, and again, their approach minimized the potential for detecting transitions and disturbed vegetation, and did not focus on the environmental factors that structure the communities, their structure, development, and occurrence. Our study differs in scope from many studies conducted on St. John. Rather than focusing on a single landform or landholding, our study crossed physiographic and political boundaries. Moreover, our study included all vascular plant species.

The major division in our dendrogram, rather than occurring along a moisture gradient, occurred between "disturbed" forests (Group 3) and "undisturbed" forests in both dry and moist forests (Fig. 3). From there, the larger group of "undisturbed" forests was divided along a moisture gradient, as others have found in studies of subtropical and tropical vegetation (Woodbury and Weaver 1997; Sánchez-Sánchez and Islebe 2002). Group 3 is of interest to us because disturbed forest community types appear to have been overlooked in most previous studies. Species composition in Group 3 consisted primarily of weedy species typical of roadsides and other open, disturbed areas. While introduced species were so widespread they were not strong indicators of any group (>50 percent Indicator Value), Group 3 was the only group that contained any introduced species indicators at significant levels ($P < 0.5$) (Table 2). Our species associations in cluster groups were fairly closely aligned descriptively with the Woodbury and Weaver species lists for species associations (1997). However, preliminary mapping indicates that the spatial distribution of our vegetation communities does not necessarily agree with vegetation maps produced in 1997 by Woodbury and Weaver. Future research will attempt to further compare and contrast forest community typing based on extensive, systematically-collected forest inventory data and with previous mapping efforts that used more intensive, selective sampling.

All subplots classified in Group 3 (disturbed subplots) fell on the north side of the island, though they were scattered from the far west end of the island, near Cruz Bay, to the northeast side of the island near Brown Bay, and not all disturbed subplots were facing the same aspect. This surprised us, given that hurricanes are an important, naturally-occurring periodic disturbance in Caribbean forests, and major hurricanes, like Hurricane Hugo in the late 1980s, tend to approach the island from the south (Reilly 1991). Reilly (1991) found that elevation, slope, and aspect played a more important role in the relative damage caused by Hurricane Hugo, though, than did latitude or longitude on the island. In the Reilly (1991) study, lower elevation windward slopes received more damage than did higher elevation leeward slopes. However, the north side of St. John is flatter and more suitable for agricultural and residential development, and has more attractive white sand beaches. By contrast, the south side is composed primarily of rocky beaches and cliffs. As a result, more development has occurred along the north side of the island, and human impacts are probably more heavily concentrated there, even within National Park boundaries. Four of the 16 Group 3 subplots fell on Mary Point, a site with a history of over 250 years of grazing and cultivation (Ray and Brown 1995). Vegetation profiles in 1995 indicated a young forest characterized by a sparse canopy and dominated by nonnative species and thorny vines (Ray and Brown 1995). Authors noted that grazing by feral donkeys still occurred frequently at Mary Point (Ray and Brown 1995). At least one Group 3 subplot occurred near Cruz Bay in an area affected by a blowdown, presumably associated with a tropical storm or hurricane. Four subplots were located near historic ruins, and signs of feral donkeys (scat, tracks) suggested grazing may have affected the vegetation.

Beyond major divisions that appear to be based on moisture and land-use or land-history patterns, species groups were structured primarily on the basis of elevation, slope, soils, and aspect, which strongly influence vegetation development in the subtropics (Lugo et al. 2000). Influential soil parameters were primarily indicative of the texture and productivity of sites on which each community fell, which is related, in part, to moisture and topography. Although distance to agriculture and distance to improved roads were important in the community ordination and appeared as vectors on ordination graphs, these features are heavily constrained by topography on St. John and are most likely related to the vegetation only as a byproduct of other topographical features. For instance, the primary road on St. John follows a ridgetop across the length of the island. Subplots falling close to the top of the ridge would be positively autocorrelated with both elevation and close proximity to improved roads, even if the proximity of the road has no ecological impact on the plant community structure. Therefore, topography has a confounding effect on the relationship between plant communities, land-use features, and disturbance on St. John. Group 3 subplots exhibited a strong affinity to axis two, and to axis three, corresponding to mid-elevation areas of low slope with a northern aspect and a wide range of soil parameters. Aspect may be a lesser influence as degree of slope declines. It is logical that mid-elevation areas with lower percent slope on a rugged island would be subject to higher rates of disturbance, as those areas would be most attractive for cultivation, development, and recreational activities, particularly if soil productivity is relatively high compared to other island soils. The same sites might also be more attractive to grazing mammals like feral donkeys, goats, and cows, particularly if the sites are already characterized by sparse canopies and lush understory growth (Rudman 1998). Highly disturbed community types like Group 3 could be priority areas for VINP rehabilitation activities. Long term re-measurement and monitoring directed at understanding the disturbed communities detected in Group 3 will be valuable, particularly with regards to the impacts of feral grazing mammals on island flora.

When canopy tree species were removed and overstory characteristics were added to the environmental matrix, understory communities were primarily influenced by elevation, soil characteristics, tree species basal area, and canopy characteristics. Therefore, it is reasonable to expect that understory species that occur at similar elevations at similar moisture gradients vary in relation to the characteristics of the forest overstory, which are partially dictated by aspect, slope, stand age, disturbance, and overall tree morphology. Fine-scale soil parameters like macronutrient availability, which we were unable to include in analysis, might also, play an important role in structuring the understory community. Chemical extraction of macronutrients on the subplots measured in this study is currently underway for future analyses. Factors which we were not able to measure, like precipitation at various locations across the island, also play a role, but are closely correlated with the characteristics we did measure.

This study provides a more comprehensive look at St. John's forests, as well as a baseline for future vegetation monitoring. The island-wide network of permanent plots captures not only the relatively undisturbed forests but also the more heavily disturbed, secondary forests that do not necessarily fit into traditional Caribbean vegetation classes, but reflect each island's unique land use history. We hope that the knowledge gained by this inventory and monitoring network will contribute to the planning efforts underway for other public lands in the Virgin Islands, and potentially for the wider Caribbean basin.

The FIA sample design is valuable for sampling vegetation without bias. However, even using intensified sampling protocols; it may be too coarse to allow for the detection of subtle differences in vegetation communities and environmental gradients. Further planned data collection might help to classify community differences and relationships to environmental variation, as well as begin the sampling of non-forest (<10% canopy coverage with tree species) vegetation. Analysis of soil macro- and micro-nutrient characteristics and spatial comparisons of our results with previous vegetation mapping efforts will allow for further understanding of the spatial extent of various species and forest types.

Achieving an adequate sample of forest types of limited extent or linear spatial patterns such as mangroves and gallery moist forests is difficult with a systematic design. Future sampling should consider some form of stratification targeting these undersampled forest types, and extending the inventory and monitoring network to include samples of all vegetation types found on the island.

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