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Climate shapes the novel plant communities that form after deforestation in Puerto Rico and the U.S. Virgin Islands

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ABSTRACT

Environmental and past land use controls on tree species assemblages on the Commonwealth of Puerto Rico and the U.S. Virgin Islands were characterized to determine whether biophysical factors or land-use history has been more important in determining the species composition of secondary tropical forests after large-scale forest clearing for agriculture, widespread species introduction, and landscape-scale forest fragmentation. Post-deforestation, secondary forest assemblages are comprehensively described, both as broad general assemblages and island-specific variations by calculating species importance values from forest inventory data. Hierarchical clustering and indicator species analysis defined species assemblages, and then correlations between species assemblages and environmental variables were explored with non-metric multidimensional scaling, analysis of variance and χ^2 testing. These assemblages are arrayed along environmental gradients of decreasing spring moisture stress, decreasing maximum temperatures, and increasing minimum temperatures. Land-use history is not as important to determining variation in species composition across climatic zones, although several species assemblages are associated with certain geology types or land-use histories. Naturalized tree species are prominent in these secondary forests and contribute to the formation of some novel assemblages, but native late and early successional species also colonize former agricultural land, all influenced by the degree of disturbance. We conclude that environmental factors have an overarching effect on forest species composition across the broader range of climatic, geologic and topographic conditions and larger geographic scales, while land-use history influences subtropical secondary forest species assemblages within a specific climatic zone or set of relatively narrow environmental conditions.

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1. Introduction

In many tropical regions, clearing of old-growth tropical forests for agriculture has accelerated over the last decade. Deforestation for industrial-scale agriculture clears larger areas faster than the forest clearing for small-scale or subsistence agriculture that dominated in earlier decades. In some countries, however, secondary tropical forests are recovering on much of the land previously cleared for agriculture (Kauppi et al., 2006), including several countries in the Caribbean, which is the location of this study (Helmer et al., 2008). These secondary forests provide our best opportunities to answer questions about the relative influences of land-use history *vs.* climate and other biophysical influences on secondary forest species composition. Yet understanding the relative importance of these factors sheds light on secondary forest successional processes, biodiversity maintenance, and introduced species dynamics across the tropics where secondary forests are expected to cover increasingly large areas.

The forests of Puerto Rico and the U.S. Virgin Islands, the subject of this research, have undergone near complete clearing since European colonization began in the early 1500s. Since the 1950s, there has been large-scale agricultural abandonment and forest recovery. In some instances, the secondary forests that have emerged are novel species assemblages, distinct from the pre-colonization forests due to the widespread introduction and naturalization of many tree species (Aide et al., 1996; Zimmerman et al., 2000; Chinea and Helmer, 2003; Lugo and Helmer, 2004). We need to better understand how these emerging secondary forests have formed if we are to manage them for the sustainable delivery of ecosystem services (Hobbs et al., 2006).

Most previous studies of the influence of land-use history on secondary forests communities in Puerto Rico are limited to samples selected along land-use gradients within small landscapes that encompass only one climatic zone and substrate type (García-Montiel and Scatena, 1994; Rivera and Aide, 1998;

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Pascarella et al., 2000; Thompson et al., 2002, 2007; Molina and Lugo, 2006). These studies find that past land use has an overriding impact on secondary forest species composition. Though we know from this previous work that land-use history can strongly influence the species composition of secondary tropical forests, we do not know whether previous land use contributes significantly to variation in species composition across large landscapes. No studies characterize the relative influences of land-use history *vs.* biophysical variables on secondary forest communities over environmental gradients that, for example, include both dry and wet climatic zones. A systematic sample of secondary forest communities across two humid climatic zones and two main geologic classes of Puerto Rico, however, concludes that previous land-use interacts with climate and substrate to determine tree species composition (Chinea and Helmer, 2003).

In this study, we test a suite of environmental and land-use history variables to learn which factors contribute most to explaining variation in the species composition of secondary tropical forests across a more diverse environmental gradient than previous work. In addition, instead of selecting sites along gradients designed to test whether previous land use is important, we use a systematic sample based on forest inventory data. With a systematic sample design, the forest stand data quantitatively represent the actual variation in species composition that exists across a landscape. Consequently, this sample design should help reveal what will most influence tropical forest communities when secondary forests recover after large-scale clearing, agricultural use and abandonment. We expect that climate will explain much of the variation in forest community structure in the systematic sample of forest stands across a steep environmental gradient, but that land-use history will still be important. To test this hypothesis, the objectives of this study are to (1) describe forest communities of Puerto Rico and the U.S. Virgin Islands that have developed after land-use histories characterized by deforestation for agriculture, abandonment, and subsequent forest regeneration; (2) determine which environmental and land-use history factors best correlate with the gradients that define these forest assemblages; and (3) test whether forest assemblage is related to land use as mapped in 1951, 1977, 1991 and 2000.

2. Methods

We used hierarchical clustering and indicator species analysis to define species assemblages in data from systematically placed forest inventory plots across Puerto Rico and the U.S. Virgin Islands. Differences between assemblage trees per hectare (TPH), basal area per hectare (BAH), live aboveground biomass per hectare (AGBH), and average canopy height (HT) were tested with analysis of variance (ANOVA). We explored the correlations between species assemblages and environmental variables with non-metric multidimensional scaling (NMS), and further explored assemblage distribution across land cover types over 4 time periods; 1951, 1977, 1991 and 2000 on mainland Puerto Rico with χ^2 testing.

2.1. Study area

The Commonwealth of Puerto Rico consists of the islands of Puerto Rico, Vieques, Culebra (the latter two sometimes referred to as the Spanish Virgin Islands), and a number of smaller islands centered on 18°15′N by 66°30′W (Fig. 1). The U.S. Virgin Islands, an unincorporated territory of the United States, are made up of St. Croix, St. John, St. Thomas and many smaller islands centered on the geographic coordinates of 18°20′N by 64°50′W (Fig. 1).

Extensive deforestation for agriculture began on Puerto Rico with European colonization and continued until the early 1950s when it was estimated that the island was 96% deforested (Wadsworth, 1950; Birdsey and Weaver, 1982). Widespread abandonment of agricultural land due to socioeconomic changes has allowed forest recovery (Thomlinson et al., 1996; López et al., 2001; Helmer, 2004; Kennaway and Helmer, 2007; Helmer et al., 2008) to such an extent that forest cover had reached 32% by 1980 (Birdsey and Weaver, 1982) and 57% by 2003 (Brandeis et al., 2007). The forests of the U.S. Virgin Islands also experienced a

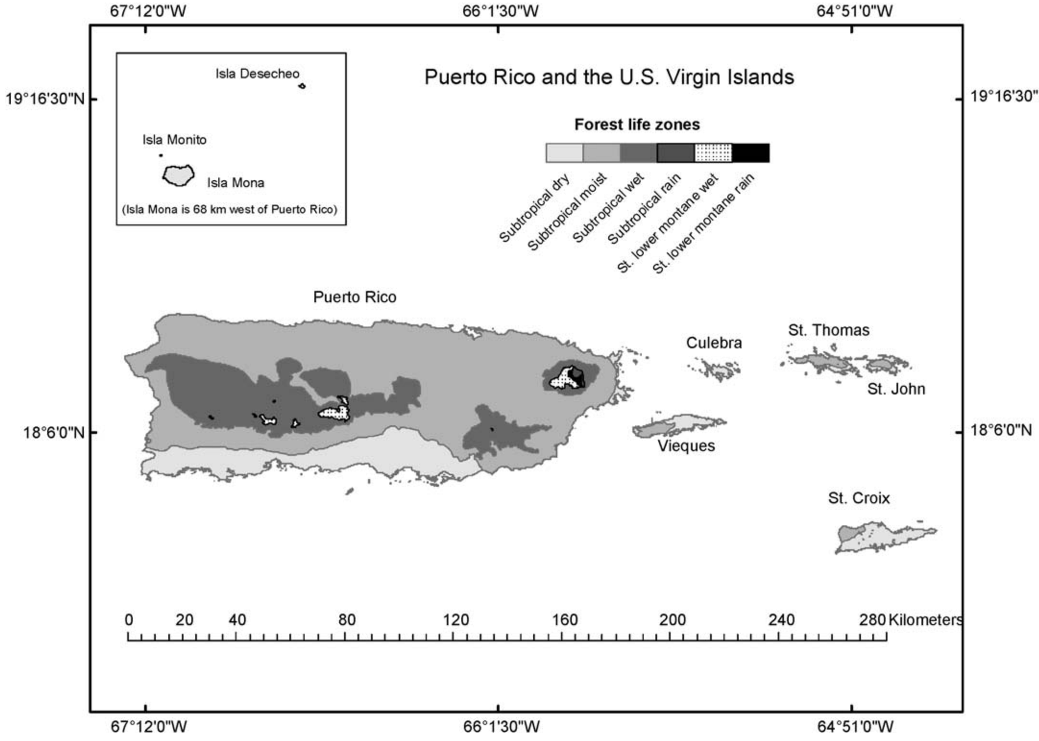

Fig. 1. Map of Puerto Rico and the U.S. Virgin Islands with forest life zones derived from Ewel and Whitmore (1973).

colonial period of deforestation for export agriculture followed by forest recovery (Weaver, 2006a,b). Forest cover had increased to 68% in 1994, but decreased to 61% by 2004 from other development pressures (Brandeis and Oswalt, 2007).

High species endemism, high physiographic complexity over relatively small areas, and a natural disturbance regime of hurricanes, and less frequently drought, created diverse forest communities (Lugo et al., 2000; Myers et al., 2000). The addition of anthropogenic disturbance and naturalized species further increased the complexity of Caribbean forest successional processes and the resulting tree species assemblages (Lugo and Helmer, 2004; Lugo and Brandeis, 2005; Brandeis, 2006).

Many researchers recognize the relationships between the rugged topography, climatic gradients, and forest vegetation of Puerto Rico. Forest vegetation reflects the marked environmental and climatic gradients resulting from the interaction between Trade Winds and abrupt elevation changes. Birdsey and Weaver (1982), Ewel and Whitmore (1973), and Little and Wadsworth (1989) give excellent descriptions of the forest associations found on Puerto Rico, though they focus on mature forest communities (Ewel and Whitmore, 1973). Holdridge life zones are commonly used to describe vegetation zones in these islands, and they have been the basis for reporting forest categories in the previous forest inventories. These categories will also be used here to group forest assemblages.

Subtropical dry forest conditions predominate at lower elevations along coasts and in southwest Puerto Rico, over most of Vieques, all of Culebra, and most of the U.S. Virgin Islands (Ewel and Whitmore, 1973; Birdsey and Weaver, 1982; Brandeis et al., 2007). Subtropical moist forest occurs at higher elevations on Vieques, St. Croix, St. John and St. Thomas where higher elevations cause the orographic cooling of moisture carried on the Trade Winds, increasing precipitation. Subtropical wet forests and subtropical rain forests occur at the higher elevations found only on mainland Puerto Rico. Additionally, subtropical lower montane wet forests and subtropical lower montane rain forests are found in the Luquillo Mountains of Puerto Rico.

2.2. Forest inventory

Field crews installed 369 permanent forest inventory plots spread across mainland Puerto Rico, Vieques, Culebra, St. Croix, St. John and St. Thomas. Field crews visited all sampling points and installed plots on mainland Puerto Rico in the months of January through July in 2001–2003. Sampling points on Vieques, Culebra, St. Croix, St. John and St. Thomas were visited from February to October in 2004.

Generally, plots were equally spaced on a systematic sampling grid (see McCollum, 2001; Brandeis, 2003 for details). While most inventory plots were systematically placed in an un-biased sample, 24 plots were added as a stratified sample in subtropical lower montane forests, forests on ultramafic (serpentine) substrate, and more mature subtropical dry forests on mainland Puerto Rico. In addition, sampling intensity on St. John was double that of the other Virgin Islands to benefit management of the Virgin Islands National Park (Oswalt et al., 2006). Plots could not be installed on substantial portions of eastern Vieques because of past U.S. Navy activity.

The permanent plots consisted of a four-subplot cluster. Each subplot in the cluster has a 7.3 m radius, so total sampled area is 0.067 ha per permanent plot for trees with diameter at breast height (d.b.h., measured at 1.37 m) $\geq$12.5 cm. Trees with d.b.h. $\geq$ 2.5 cm were measured in a 2.1 m radius microplot nested within each subplot. Detailed information on plot location, installation, and monumentation, and site descriptions, tree measurement, tree damage description, and other data collected at each forested plot can be found in the USDA Forest Service's Forest Inventory and Analysis, Southern Research Station Field Guide, Field Procedures for Puerto Rico and the Virgin Islands (USDA Forest Service, 2002) or in Bechtold and Scott (2005).

Species nomenclature was based on the USDA-NRCS PLANTS database (USDA Natural Resource Conservation Service, 2009), with supplemental reference to Little and Wadsworth (1989) and Little et al. (1974). Molina and Alemañy (1997) was used as an additional reference to determine which tree species were native or introduced to the U.S. Virgin Islands. The species relative importance value (IV) was calculated for each inventory plot by taking the average of relative dominance (each species' basal area (BA) divided by the total BA) and relative density (each species' trees per hectare divided by total trees per hectare), multiplied by 100 (Curtis and McIntosh, 1951; Whittaker, 1975).

2.3. Clustering, indicator species analyses and assemblage structural characteristics

The full primary species matrix consisted of species' IV by inventory plot for 369 inventory plots and 328 species. Hierarchical agglomerative cluster analysis was performed using a Flexible Beta linkage method (beta = -0.25) and Sørensen distance measure (PC-Ord Version 5.0, McCune and Mefford, 1999). Preliminary analyses of the full primary species matrix revealed outlying points that exceeded 2 standard deviations in Euclidean distance which were then deleted from the matrices. Plots that fell in mangrove forest were removed from the analysis because the inventory had few plots in mangrove and the composition of mangrove forest is already well defined. Preliminary ordinations showed stronger correlations between species assemblages and environmental variables after removal of rare species. Relatively rare species that were found in less than 5 plots were removed from the primary matrix to reduce "noise" in the data and strengthen the extraction of pattern from the data (McCune and Grace, 2002). After all of these reductions, final cluster and indicator species analyses were run on a data set consisting of all islands combined, and then on the data split into two data sets; the 270 plots and 92 species on mainland Puerto Rico and the 89 plots and 45 species on Vieques, Culebra and the U.S. Virgin Islands, which henceforth will be referred to simply as the Virgin Islands. Splitting the data allowed us to show both the broadly defined, general species assemblages that span multiple islands and the unique variations created by local environmental factors and differing land-use histories on the Virgin Islands that might otherwise be lost within the larger, mainland Puerto Rico dominated dataset.

DuFrêne and Legendre (1997) indicator species analysis was used both to ascertain which species defined the clusters and to help guide the selection of an optimum number of clusters as per the description given in McCune and Grace (2002). The final decision on the optimal number of ecologically meaningful clusters was based the methods outlined in McCune and Grace (2002), the indicator species analysis results, field experience, literature review and mapping in a GIS to better visualize their spatial distribution.

Mean structural characteristics (quadratic mean diameter (QMD), TPH, BAH, AGBH, HT) were calculated for each assemblage identified by the cluster analyses. Assemblage QMD (d.b.h. in centimeters), TPH (number of stems per hectare), BAH (m^2/ha) and AGBH (oven-dry Mg per hectare, including foliage) are for all stems with d.b.h. $\geq$ 12.5 cm. Methods and allometric equations used for estimating AGBH are described in Brandeis et al. (2007). Canopy height is the average height (m) for all trees that were considered dominant or co-dominants in the stand. Assemblage mean values were estimated and compared with SAS using the General Linear Model procedure (PROC GLM) for uneven sample sizes and Least Squares Means pairwise comparisons (Freund and Littel, 1981; SAS Institute, 2004).

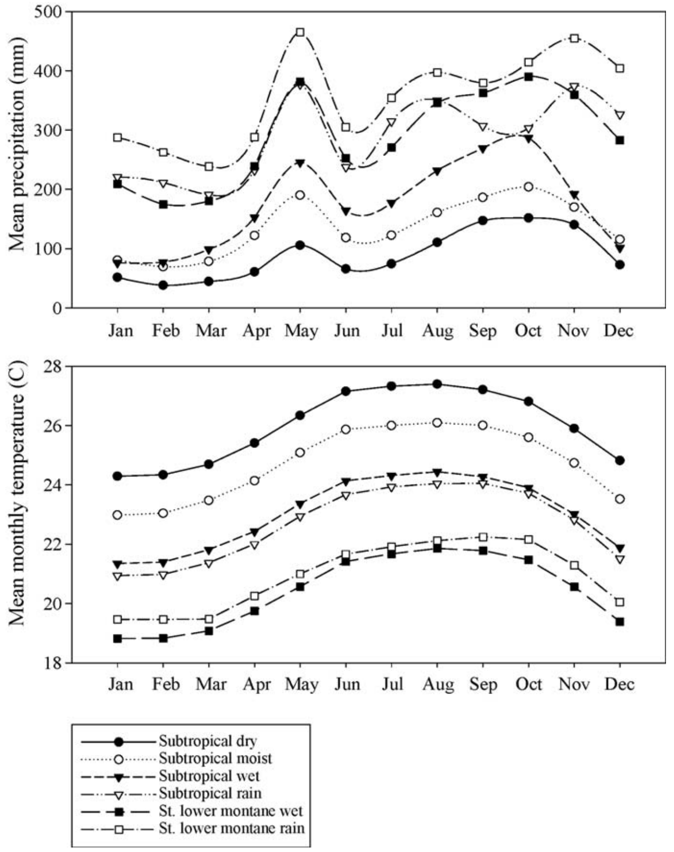

Fig. 2. Thirty-year average monthly precipitation (mm) and average monthly temperature (°C) on Puerto Rico and the U.S. Virgin Islands by Holdridge life zone.

2.4. Non-metric multidimensional scaling and assemblage frequency distributions

A secondary environmental matrix was filled with continuous and categorical variables collected at the plot by field crews or extracted from GIS coverages. We used plot center coordinates to extract the environmental attributes of each plot from digital maps of climate, topography, geology, historical land-cover and nearest distance to a coastline. Climate data included 30-year average monthly and annual precipitation as well as minimum, maximum and mean temperatures (Fig. 2) for both Puerto Rico (Daly et al., 2003) and the Virgin Islands (Fig. 3).

Topographic variables included elevation, percent slope, aspect, cosine aspect, degrees from North, and slope position (Hatfield, 1999), and they were extracted from 30-m digital elevation models (Gesch et al., 2002). Land-cover data included generalized land cover in 1951, 1977, 1991 and 2000, as well as forest age class derived from the four land-cover maps (Kennaway and Helmer, 2007). Generalized geology came from the map of Krushensky (1995) for Puerto Rico, and from a hard copy map (Garrison et al., 1972) digitized by Colorado State University and later edited.

To better represent growing conditions at each plot, annual and seasonal moisture stress indices were calculated as in Ohmann and Spies (1998). The annual moisture stress was represented by dividing the average annual temperature by the average annual precipitation. Seasonal moisture stress indices for spring (March, April, May), summer (June, July, August), fall (September, October, November), and winter (December, January, February) were also calculated by dividing the average monthly temperature for the three-month period by the average monthly precipitation for that period.

Non-metric multidimensional scaling was run with the Sørensen distance measures (PC-Ord Version 5.0, McCune and Mefford, 1999). Preliminary NMS runs (using the autopilot, thorough mode) established the best dimensionality and starting coordinates (McCune and Mefford, 1999) for the final NMS runs.

Frequency distribution tables of assemblage occurrence in different life zones, age classes, and land cover classes were generated with frequency procedure (PROC FREQ) in the Statistical Analysis System (SAS, Version 9.1) package (SAS Institute, 2004). Chi-Squared (χ^2) and Cochrane–Mantel–Haenszel tests were employed to look for significant (α-level = 0.05) differences in the distribution of each assemblage across life zones, geologic substrates, and 3 past land uses (specifically, that last land use

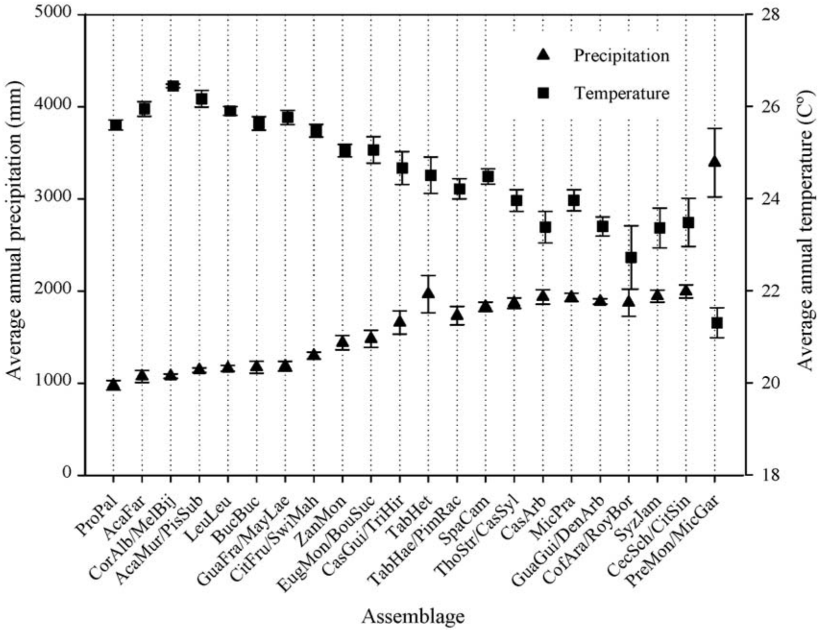

Fig. 3. Average annual precipitation (mm) and average annual temperature (°C) with standard errors of the mean at forest inventory plots where each tree species assemblage was encountered. Assemblages are the result of hierarchical clustering on the combined data from Puerto Rico and the U.S. Virgin Islands.

before reversion to forest). Plots were grouped into 5 life zone/geologic substrate categories to aid in interpretation, as was done in Helmer et al. (2002). These groups are subtropical dry on alluvial, volcanic and sedimentary substrates (Dry/AVS), subtropical dry on limestone (Dry/Lime), subtropical dry–moist on ultramafic (Dry, Moist/Ultra), subtropical moist on alluvial, volcanic and sedimentary (Moist/AVS), subtropical moist–wet on limestone (Moist, Wet/Lime), subtropical wet on alluvial, volcanic and sedimentary (Wet/AVS), subtropical lower montane on alluvial, volcanic and sedimentary (LM/AVS), and subtropical wet–subtropical lower montane on ultramafic (Wet, LM/Ultra).

3. Results

3.1. Tree species assemblages and their characteristics

Clustering resulted in 22 tree species assemblages in the combined, all-islands dataset (Table 1); 14 assemblages from mainland Puerto Rico data (Table 2); and 8 assemblages from the Virgin Islands data (Table 3). (Assemblage names were taken from the first 3 letters of the 2 most significant indicator species ($P < 0.05$), or single significant indicatory species if only one was present.) The assemblages found in clustering the combined data from all islands are distributed along gradients of increasing average annual precipitation and decreasing average annual temperature (Fig. 2) that correspond to increases in elevation. Assemblages are ordered in the tables by decreasing mean annual moisture stress at the inventory plots where they were found, and origin (native to the islands or introduced post-European colonization) is included for each species. The mean structural characteristics (QMD, TPH, BA, AGB, and HT) for assemblages found across all the islands, on mainland Puerto Rico and in the Virgin Islands (Table 4) show the wide range in forest structure.

3.2. Environmental correlations with ordination axes

Scree plots and stress statistics indicated that a three-dimensional solution best fit the combined and separate data sets for the NMS ordination. After ranking by R^2 of the first ten most significant environmental variables and tree species correlated with each of the 3 ordination axes, we found that only environmental variables were significant, specifically the climate variables (Tables 5–7).

Ordination of data from all the islands combined resulted in a cumulative R^2 value of 0.434 for 3 axes. All-islands ordination axis 1 was negatively correlated with spring and annual moisture stress (Table 5), and positively correlated with mean monthly precipitation in April, distance from the coast, and May precipitation. Tree species that were negatively correlated with this axis included *Leucaena leucocephala* (Lam.) de Wit, *Acacia farnesiana* (L.) Willd., and *P. pallida*, species found in lower elevation, degraded areas in subtropical dry and moist forest zones. Species that were positively correlated with these axes included *Guarea guidonia* (L.) Sleumer and *Casearia guianensis* Aubl., which occur in subtropical moist and subtropical wet forest zones. All-islands axis 2 showed positive correlations with minimum monthly temperature in March, January and November. Positively correlated species included *Bursera simaruba* (L.) Sarg. and *Tabebuia heterophylla* (DC.) Britt., species found in both subtropical moist and subtropical dry forest. At the other end of the axis were higher elevation, subtropical wet species such as *G. guidonia* and *Cecropia schreberiana* Miq. All-islands axis 3 was negatively correlated with mean maximum temperatures in September and June, and it positively correlated with elevation. The species *L. leucocephala* and *Spathodea campanulata* Beauv. were negatively correlated with axis 3 while

Table 1

Tree species assemblages for all islands combined, with importance value (IV), indicator species *P* (values of $P < 0.05$ are highlighted), and species origin (N = native to the islands before European colonization, I = introduced).

Assemblage	Species	IV	P	Origin
ProPal	**Prosopis pallida**	88.5	0.001	I
	Acacia macracantha	11.6	0.108	I
	Cordia laevigata	6.2	0.326	N
AcaMur/PisSub	**Acacia muricata**	81.8	0.001	N
	Pisonia subcordata	62.2	0.001	N
	Eugenia cordata	53.8	0.001	N
	Capparis cynophallophora	47.9	0.001	N
	Myrciaria floribunda	45.6	0.001	N
	Amyris elemifera	19.1	0.013	N
	Cassine xylocarpa	10.8	0.087	N
	Capparis hastata	8.3	0.209	N
	Pilosocereus royenii	5.1	0.465	N
AcaFar	**Acacia farnesiana**	87.0	0.001	I
	Albizia lebbeck	3.8	0.665	I
LeuLeu	**Leucaena leucocephala**	58.9	0.001	N
	Samanea saman	3.7	0.642	I
CorAlb/MelBij	**Cordia alba**	91.1	0.001	N
	Melicoccus bijugatus	24.8	0.010	I
	Croton astroites	15.2	0.029	N
	Adelia ricinella	13.8	0.071	N
	Eugenia rhombea	12.8	0.070	N
	Tecoma stans	9.3	0.188	N
	Krugiodendron ferreum	8.9	0.152	N
EugMon/BouSucc	**Eugenia monticola**	67.7	0.001	N
	Bourreria succulenta	23.2	0.005	N
	Sabinea florida	21.3	0.005	N
	Guettarda scabra	16.4	0.018	N
	Randia aculeata	13.2	0.040	N
	Coccothrinax alta	4.3	0.556	N
	Ocotea floribunda	4.1	0.601	N
	Casearia decandra	3.8	0.620	N
	Tabebuia heterophylla	65.4	0.001	N
	Coccoloba diversifolia	9.7	0.116	N
	Cordia sulcata	5.1	0.482	N
	Casearia guianensis	56.4	0.001	N
	Trichilia hirta	20.2	0.021	N
	Guazuma ulmifolia	19.3	0.009	N
	Andira inermis	12.5	0.044	N
	Myrcia splendens	8.1	0.159	N
	Cupania americana	4.8	0.496	N
	Thouinia striata	41.1	0.002	N
	Casearia sylvestris	30.5	0.003	N
	Ficus citrifolia	13.4	0.055	N
	Myrsine coriacea	9.8	0.145	N
	Eugenia biflora	9.5	0.115	N
	Tetrazygia elaeagnoides	8.6	0.181	N
	Trichilia pallida	3.5	0.684	N
	Delonix regia	3.4	0.686	I
	Casearia arborea	21.9	0.010	N
	Psidium guajava	13.0	0.081	N
	Ocotea leucoxylon	8.8	0.119	N
	Ormosia krugii	8.8	0.218	N
	Trema micranthum	6.7	0.328	N
	Hymenaea courbaril	6.0	0.376	N
	Buchenavia tetraphylla	4.4	0.503	N
	Quararibea turbinata	2.4	0.840	N
	Coffea arabica	91.6	0.001	I
	Roystonea borinquena	14.5	0.025	N
	Homalium racemosum	13.7	0.044	N
	Petitia domingensis	8.9	0.169	N
	Miconia prasina	11	0.12	N
	Piper amalago	3.3	0.733	N
GuaFra/MayLae	**Guapira fragrans**	58.8	0.001	N
	Maytenus laevigata	48.2	0.001	N
	Cordia alliodora	29.5	0.005	N
	Bursera simaruba	22.4	0.004	N

Table 1 (*Continued*)

Assemblage	Species	IV	P	Origin
	Capparis indica	20.2	0.040	N
	Ocotea coriacea	13.0	0.069	N
	Chionanthus compactus	12.4	0.077	N
	Faramea occidentalis	9.5	0.118	N
	Capparis baducca	6.4	0.316	N
	Chrysophyllum pauciflorum	2.5	0.865	N
ZanMon	**Zanthoxylum monophyllum**	22.0	0.014	N
	Exostema caribaeum	6.6	0.264	N
	Ardisia obovata	6.3	0.299	N
	Senna siamea	6.3	0.345	I
	Pictetia aculeata	5.0	0.470	N
	Cinnamomum elongatum	4.2	0.599	N
CitFru/SwiMah	**Citharexylum fruticosum**	71.2	0.001	N
	Swietenia mahagoni	19.0	0.006	I
	Ziziphus mauritiana	9.8	0.157	I
	Tamarindus indica	5.1	0.468	I
BucBuc	**Bucida buceras**	13.8	0.033	N
	Pithecellobium dulce	12.1	0.099	I
	Albizia procera	7.7	0.201	I
SpaCam	**Spathodea campanulata**	60.9	0.001	I
	Thespesia grandiflora	5.8	0.389	N
	Terminalia catappa	2.4	0.844	I
	Erythroxylum rotundifolium	1.6	0.972	N
TabHae/PimRac	**Tabebuia haemantha**	52.3	0.001	N
	Pimenta racemosa	45.9	0.002	N
	Neolaugeria resinosa	42.8	0.001	N
	Clusia rosea	23.9	0.007	N
	Licaria parvifolia	10.7	0.078	N
	Annona muricata	9.3	0.177	N
	Ocotea sintenisii	4.5	0.458	N
	Coccoloba microstachya	3.4	0.667	N
GuaGui/DenArb	**Guarea guidonia**	46.3	0.001	N
	Dendropanax arboreus	18.7	0.017	N
	Inga vera	16.2	0.021	N
	Mangifera indica	12.4	0.056	I
	Urera baccifera	12.2	0.073	N
	Artocarpus altilis	7.6	0.248	I
	Erythrina poeppigiana	3.2	0.773	I
CecSch/CitSin	**Cecropia schreberiana**	45.7	0.001	N
	Citrus sinensis	28	0.004	I
	Inga laurina	11.9	0.057	N
	Cyathea arborea	9.9	0.121	N
	Persea americana	6.6	0.325	I
SyzJam	**Syzygium jambos**	71.4	0.001	I
	Zanthoxylum martinicense	7.9	0.172	N
	Schefflera morototonii	7.6	0.266	N
	Croton rigidus	5.7	0.375	N
	Calophyllum antillanum	4.5	0.556	I
PreMon/MicGar	**Prestoea montana**	71.5	0.002	N
	Micropholis garciniifolia	62.5	0.001	N
	Sloanea berteriana	61	0.001	N
	Micropholis chrysophylloides	46.4	0.001	N
	Henriettea squamulosum	43.6	0.001	N
	Byrsonima spicata	32.6	0.002	N
	Dacryodes excelsa	25.1	0.003	N
	Psychotria berteriana	22.5	0.01	N
	Alchornea latifolia	14.9	0.051	N
	Cordia borinquensis	12	0.076	N
	Clusia clusioides	8.4	0.216	N
	Myrcia citrifolia	4.3	0.536	N

Table 2

Tree species assemblages for mainland Puerto Rico, with importance value (IV), indicator species P (values of $P < 0.05$ are highlighted), and species origin (N = native to the islands before European colonization, I = introduced).

Species	IV	P	Origin
Acacia farnesiana	87.5	0.001	I
Prosopis pallida	47.9	0.001	I
Albizia lebbeck	4.8	0.428	I
Leucaena leucocephala	76.7	0.001	N
Albizia procera	6.2	0.268	I
Citharexylum fruticosum	46.0	0.001	N
Exostema caribaeum	29.8	0.001	N
Ardisia obovata	16.9	0.007	N
Zanthoxylum martinicense	11.8	0.028	N
Pithecellobium dulce	7.4	0.178	I
Swietenia mahagoni	4.6	0.492	I
Bursera simaruba	37.6	0.001	N
Bucida buceras	25.9	0.001	N
Amyris elemifera	16.0	0.018	N
Coccoloba diversifolia	15.0	0.019	N
Ocotea sintenisii	9.4	0.054	N
Myrsine coriacea	8.3	0.122	N
Licaria parvifolia	8.2	0.098	N
Senna siamea	7.4	0.202	I
Pictetia aculeata	7.2	0.141	N
Ocotea coriacea	4.6	0.396	N
Thouinia striata	85.2	0.001	N
Ficus citrifolia	9.7	0.092	N
Petitia domingensis	7.0	0.185	N
Trichilia pallida	5.1	0.346	N
Eugenia rhombea	4.0	0.501	N
Coccoloba microstachya	3.4	0.605	N
Casearia guianensis	62.3	0.001	N
Andira inermis	16.9	0.018	N
Guazuma ulmifolia	15.9	0.018	N
Guapira fragrans	11.4	0.059	N
Myrcia splendens	9.4	0.096	N
Cupania americana	6.5	0.318	N

Assemblage	Species	IV	P	Origin
NeoRes/GueSca	**Neolaugeria resinosa**	52.5	0.001	N
	Guettarda scabra	42.3	0.001	N
	Eugenia monticola	37.8	0.001	N
	Tabebuia haemantha	25.5	0.001	N
	Pimenta racemosa	15.6	0.013	N
	Randia aculeata	13.8	0.022	N
	Clusia rosea	13.6	0.022	N
	Casearia decandra	7.8	0.120	N
	Bourreria succulenta	7.4	0.159	N
	Ocotea floribunda	6.6	0.237	N
	Annona muricata	3.7	0.607	N
	Homalium racemosum	3.7	0.567	N
SpaCam	**Spathodea campanulata**	76.6	0.001	I
	Terminalia catappa	4.6	0.381	I
TabHet/CasArb	**Tabebuia heterophylla**	62.9	0.001	N
	Casearia arborea	19.5	0.005	N
	Roystonea borinquena	6.0	0.301	N
	Myrcia citrifolia	5.2	0.333	N
CasSyl/PsiGua	**Casearia sylvestris**	20.5	0.004	N
	Psidium guajava	11.9	0.046	N
	Coffea arabica	11.6	0.039	I
	Ormosia krugii	8.5	0.161	N
	Eugenia biflora	7.2	0.212	N
	Thespesia grandiflora	4.6	0.448	n
	Buchenavia tetraphylla	3.6	0.583	N
	Hymenaea courbaril	3.6	0.672	N
	Tetrazygia elaeagnoides	2.3	0.907	N
	Piper amalago	1.9	0.953	N
GuaGui/DenArb	**Guarea guidonia**	49.0	0.001	N
	Dendropanax arboreus	21.0	0.003	N
	Mangifera indica	13.2	0.023	I
	Artocarpus altilis	10.1	0.082	I
	Cordia sulcata	6.4	0.368	N
	Quararibea turbinata	4.2	0.470	N
	Erythrina poeppigiana	3.0	0.786	I
	Cordia alliodora	2.1	0.913	N

Table 3
Tree species assemblages for the Virgin Islands, with importance value (IV), indicator species P (values of $P < 0.05$ are highlighted), and species origin (N = native to the islands before European colonization, I = introduced).

Assemblage	Species	IV	P	Origin
ProPal	**Prosopis pallida**	86.6	0.001	I
AcaFar	**Acacia farnesiana**	81.2	0.001	I
	Albizia lebbeck	8.0	0.676	I
	Inga laurina	6.3	0.794	N
LeuLeu	**Leucaena leucocephala**	71.4	0.001	N
	Samanea saman	7.3	0.752	I
AcaMur/PisSub	**Acacia muricata**	84.5	0.001	N
	Pisonia subcordata	62.1	0.001	N
	Eugenia cordata	55.4	0.001	N
	Capparis cynophallophora	49.6	0.001	N
	Myrciaria floribunda	47.8	0.001	N
	Amyris elemifera	41.5	0.010	N
	Guettarda scabra	26.5	0.032	N
	Bucida buceras	15.3	0.322	N
CorAlb	**Cordia alba**	84.6	0.001	N
	Melicoccus bijugatus	25.2	0.089	I
	Croton astroites	16.4	0.154	N
	Eugenia rhombea	15.4	0.218	N
	Adelia ricinella	14.0	0.164	N
	Tecoma stans	8.8	0.597	N
EugMon/CapBad	**Eugenia monticola**	41.8	0.011	N
	Capparis baducca	35.3	0.014	N
	Bursera simaruba	32.1	0.018	N
	Maytenus laevigata	32.1	0.027	N
	Sabinea florida	29.4	0.019	N
	Ocotea coriacea	27.7	0.037	N
	Bourreria succulenta	26.0	0.069	N
	Chionanthus compactus	17.3	0.119	N
	Cordia alliodora	15.7	0.269	N
	Krugiodendron ferreum	14.5	0.213	N
GuaFra/CapInd	**Guapira fragrans**	64.7	0.001	N
	Capparis indica	34.7	0.039	N
	Cassine xylocarpa	19.0	0.128	N
	Tabebuia heterophylla	9.6	0.514	N
	Capparis hastata	9.3	0.466	N
CasGui/ZanMon	**Casearia guianensis**	48.0	0.001	N
	Zanthoxylum monophyllum	42.3	0.009	N
	Citharexylum fruticosum	40.0	0.009	N
	Ziziphus mauritiana	39.0	0.023	I
	Trichilia hirta	35.7	0.017	N
	Zanthoxylum martinicense	26.4	0.030	N
	Acacia macracantha	24.9	0.063	I
	Andira inermis	23.7	0.081	N
	Randia aculeata	12.4	0.336	N
	Swietenia mahagoni	10.6	0.385	I

Micropholis guyanensis (A. DC.) Pierre and *C. schreberiana* were positively correlated.

Ordination results of the plots on mainland Puerto Rico and all-islands data were similar (cumulative $R^2 = 0.435$). Axis 1 for this ordination was negatively correlated with spring minimum temperatures, similar but opposite in sign to the correlations found in all-islands axis 2 (Table 6). *G. guidonia* (positive correlation) and *L. leucocephala* (negative correlation) were associated with this axis. Puerto Rico axis 2 was positively correlated with distance from the coast, and negatively correlated with spring and annual moisture stress, and axis 3 was negatively correlated with winter and spring moisture stress, and it was positively correlated with latitude.

Ordination of the Virgin Islands plots showed environmental variable correlations with different axes from those of the all-islands axes or mainland Puerto Rico (Table 7). In addition, the correlations were stronger (cumulative $R^2 = 0.632$). Axis 1 was notably correlated with latitude, average monthly temperature in November, and slope. *L. leucocephala* was positively correlated with this axis, while a suite of dry forest species that included *B. simaruba*, *Guapira fragrans* (Dum.-Cours.) Little and *A. farnesiana* were negatively correlated with the axis. Axis 2 was correlated with precipitation in October and July, and latitude. *A. farnesiana* and *Acacia muricata* (L.) Willd. were positively correlated with this axis, and *L. leucocephala* was negatively correlated. Virgin Islands ordination axis 3 is significantly correlated with maximum spring and fall temperatures, and winter precipitation to a lesser extent.

3.3. Life zone, geology, forest age and land cover distribution

The frequency with which each species assemblages was found within the 8 life zone/geologic substrate combinations on Puerto Rico and the 4 life zone/geologic substrate combinations on the Virgin Islands is presented in Tables 8 and 9, respectively. The distribution of forested plots by the land cover type found before to reversion to forest shows the prevalence of abandoned pasture across mainland Puerto Rico (Table 10). All assemblages except the subtropical lower montane PreMon/MicGar were found on sites that had formerly been pasture or herbaceous agriculture. Some assemblages, notably GuaGui/DenArb, were frequently found in areas of abandoned coffee shade. Three assemblages (AcaFar/ProPal, LeuLeu and CecSch/CitSin) were not found in undisturbed (since 1951) forest.

There was strong indication that the AcaFar/ProPal assemblage of mainland Puerto Rico was found more frequently in the subtropical dry forest life zone ($P = 0.0588$), and that it had little preference as to geologic substrate ($P = 0.8669$). In all cases, the AcaFar/ProPal assemblage was found on land that had reverted from agriculture or pasture. Similarly, there was a strong indication that the AcaFar assemblage found on the Virgin Islands was preferentially distributed in subtropical dry forest ($P = 0.0588$), and showed no differences in distribution by substrate. The ProPal assemblage of the Virgin Islands was found entirely within the subtropical dry forest life zone on all substrates.

The Puerto Rico LeuLeu assemblage was distributed in both the subtropical dry and moist forest life zones on a variety of substrates, entirely on land that was formerly herbaceous agricultural/pasture. The LeuLeu assemblage was distributed similarly in the Virgin Islands, however, with a markedly higher frequency on extrusive volcanic substrates than on limestone, intrusive volcanic or alluvial substrates ($P = 0.0003$).

Some of the Virgin Islands assemblages were found with equal frequency in the subtropical dry and moist forest life zone (AcaMur/PisSub, EugMon/CapBad, and CasGui/ZanMon), and two other assemblages (CorAlb and GuaFra/CapInd) might also straddle these life zones but there were too few occurrences for statistical testing. There were significant differences in the distribution by substrate of these Virgin Island assemblages. The AcaMur/PisSub assemblage occurred exclusively on extrusive volcanic substrates. The EugMon/CapBad assemblage was more common on extrusive volcanic substrates ($P = 0.0076$), while the CasGui/ZanMon assemblage showed greater frequency of occurrence on intrusive volcanic substrates ($P = 0.0464$).

Puerto Rico mainland assemblages that straddled the subtropical dry and moist forest life zones were CitFru/ExoCar, BurSim/BucBuc, and ThoStr. Additionally, there was some indication that the CitFru/ExoCar assemblage was more frequently found on former herbaceous agricultural/pasture land ($P = 0.0578$), but it was also found in areas that had been forest since 1951. This assemblage showed little preference for substrate type within the subtropical dry and moist forest life zones. The BurSim/BucBuc assemblage was found on both limestone and extrusive volcanic substrates, but had a markedly higher occurrence on limestone in the subtropical moist forest life zone ($P = 0.0186$). This assemblage

Table 4
Number of plots sampled, quadratic mean diameter (QMD, cm), and mean values for trees per hectare (TPH), basal area per hectare (BA, m^2/ha), aboveground live biomass per hectare (AGBH, Mg/ha), canopy height (HT, m), and annual moisture stress index (MS), with standard errors of the mean for groups on all islands, mainland Puerto Rico and the Virgin Islands.

Island group	N	QMD	TPH	BAH	AGBH	HT	MS
All islands							
ProPal	7	5.3	2231 (705)	5.0 (2.0)	25.2 (10.8)	4.4 (0.5)	0.0267 (0.0016)
AcaFar	15	5.4	2471 (554)	5.6 (1.1)	22.9 (4.9)	5.0 (0.5)	0.0253 (0.0013)
CorAlb/MelBij	4	4.9	4862 (1379)	9.3 (3.7)	33.1 (13.0)	4.4 (0.3)	0.0246 (0.0005)
AcaMur/PisSub	7	6.5	6191 (344)	20.4 (2.1)	75.9 (9.6)	6.3 (0.5)	0.0230 (0.0007)
LeuLeu	41	4.8	4235 (478)	7.6 (0.8)	31.3 (3.4)	5.3 (0.2)	0.0228 (0.0005)
BucBuc	15	5.9	4102 (740)	11.1 (2.2)	47.7 (10.2)	6.4 (0.7)	0.0226 (0.0010)
GuaFra/MayLae	12	8.4	3741 (547)	21.0 (3.0)	80.9 (10.7)	8.2 (0.8)	0.0221 (0.0008)
CitFru/SwiMah	7	10.3	1608 (620)	13.5 (4.0)	44.0 (12.8)	8.8 (0.8)	0.0197 (0.0007)
ZanMon	31	7.1	4190 (433)	16.7 (1.7)	71.4 (8.8)	8.7 (0.6)	0.0187 (0.0009)
EugMon/BouSuc	15	6.0	4891 (729)	14.0 (2.1)	53.1 (7.8)	7.5 (0.5)	0.0179 (0.0011)
CasGui/TriHir	15	7.4	4228 (627)	18.1 (3.3)	74.3 (15.2)	10.2 (0.6)	0.0163 (0.0015)
TabHet	8	7.8	2510 (1031)	11.9 (2.7)	48.6 (12.5)	9.7 (1.4)	0.0145 (0.0030)
TabHae/PimRac	9	6.9	4677 (674)	17.4 (3.1)	77.6 (15.4)	9.0 (1.3)	0.0144 (0.0009)
SpaCam	27	10.8	3740 (533)	34.3 (3.4)	151.7 (17.4)	13.4 (1.0)	0.0137 (0.0004)
ThoStr/CasSyl	23	9.6	3461 (351)	25.0 (7.7)	86.1 (17.7)	10.7 (0.6)	0.0132 (0.0005)
CasArb	25	10.4	2755 (417)	23.3 (3.2)	94.9 (12.7)	11.1 (0.8)	0.0128 (0.0009)
MicPra	24	8.8	2961 (354)	18.1 (2.0)	77.7 (8.8)	11.9 (0.8)	0.0126 (0.0003)
GuaGui/DenArb	41	10.9	3078 (335)	28.8 (2.9)	114.1 (11.0)	13.0 (0.5)	0.0125 (0.0002)
CofAra/RoyBor	4	10.1	1299 (437)	10.3 (4.4)	33.6 (12.2)	11.3 (1.5)	0.0124 (0.0011)
SyzJam	10	12.2	2541 (463)	29.7 (6.8)	123.3 (27.8)	13.6 (1.4)	0.0122 (0.0005)
CecSch/CitSin	11	11.3	1579 (452)	15.9 (3.5)	70.3 (18.0)	11.6 (1.4)	0.0120 (0.0006)
PreMon/MicGar	8	11.6	2519 (389)	26.6 (3.7)	111.7 (17.2)	10.8 (0.8)	0.0070 (0.0009)
Puerto Rico							
AcaFar/ProPal	8	6.4	1977 (436)	6.4 (1.8)	27.6 (8.2)	5.7 (0.9)	0.0252 (0.0028)
LeuLeu	19	5.4	3359 (755)	7.7 (1.9)	34.3 (8.9)	6.2 (0.6)	0.0205 (0.0012)
CitFru/ExoCar	14	7.0	3587 (649)	13.9 (2.3)	57.1 (10.1)	8.9 (0.9)	0.0190 (0.0013)
BurSim/BucBuc	20	7.1	4389 (558)	17.3 (1.9)	77.4 (9.0)	9.3 (0.7)	0.0184 (0.0010)
ThoStr	7	7.3	3808 (900)	15.9 (1.9)	64.7 (9.1)	8.7 (0.8)	0.0158 (0.0022)
CasGui/AndIne	13	7.5	4331 (720)	19.2 (3.8)	79.3 (17.2)	10.7 (0.6)	0.0155 (0.0016)
NeoRes/GueSca	17	6.6	4025 (626)	13.7 (2.2)	58.5 (10.2)	8.6 (0.8)	0.0138 (0.0006)
SpaCam	43	10.2	3635 (372)	29.6 (2.5)	130.0 (12.3)	12.8 (0.7)	0.0133 (0.0003)
TabHet/CasArb	12	8.7	3060 (747)	18.0 (3.7)	69.8 (15.2)	10.0 (0.9)	0.0130 (0.0020)
CasSyl/PsiGua	29	10.1	3002 (407)	24.1 (6.2)	84.0 (15.4)	10.8 (0.7)	0.0129 (0.0006)
GuaGui/DenArb	46	11.1	3066 (316)	29.6 (2.7)	117.8 (10.3)	13.4 (0.5)	0.0126 (0.0002)
SyzJam	19	11.0	2425 (315)	23.2 (4.4)	97.9 (19.3)	12.6 (0.9)	0.0120 (0.0004)
CecSch/CitSin	14	11.0	1476 (365)	14.0 (2.9)	62.7 (14.7)	11.8 (1.1)	0.0119 (0.0005)
PreMon/MicGar	9	11.1	2570 (347)	25.0 (3.7)	103.6 (17.2)	10.4 (0.8)	0.0073 (0.0009)
Virgin Islands							
GuaFra/CapInd	5	7.7	2349 (225)	10.9 (4.2)	38.2 (13.3)	5.4 (0.7)	0.0262 (0.0013)
ProPal	6	5.4	2479 (780)	5.7 (2.2)	29.0 (11.9)	4.6 (0.5)	0.0254 (0.0012)
CorAlb	4	4.9	4862 (1379)	9.3 (3.7)	33.1 (13)	4.4 (0.3)	0.0246 (0.0005)
AcaFar	7	4.0	2768 (1137)	3.5 (1.2)	11.9 (4.3)	3.7 (0.5)	0.0243 (0.0007)
LeuLeu	29	4.9	4670 (521)	8.7 (0.9)	35.2 (3.9)	5.3 (0.2)	0.0236 (0.0003)
AcaMur/PisSub	7	6.5	6191 (343)	20.4 (2.1)	75.9 (9.6)	6.3 (0.5)	0.0230 (0.0007)
CasGui/ZanMon	14	7.6	2465 (250)	11.1 (1.8)	40.0 (5.6)	6.4 (0.4)	0.0229 (0.0007)
EugMon/CapBad	17	7.0	5397 (535)	20.7 (2.1)	79.9 (7.2)	7.5 (0.3)	0.0222 (0.0004)

most frequently originated on land that had formerly been in herbaceous agriculture or pasture, followed by land that had remained forested since 1951 ($P = 0.0078$). The ThoStr assemblage had broad distributions across the subtropical dry, moist and wet/rain forest life zones, and was found on both volcanic and limestone substrates, and all past land uses, with no significant differences.

Other mainland Puerto Rico assemblages showed more general distributions across the broad subtropical moist forest life zone. The CasiGui/AndIne assemblage occupied abandoned herbaceous agricultural/pasture land ($P = 0.0012$) in the subtropical moist forest life zone ($P = 0.0388$) with equal frequency on volcanic, alluvial and limestone substrates ($P = 0.7212$). The NeoRes/GueSca assemblage was found primarily in the subtropical moist forest life zone ($P = 0.0221$) on former herbaceous agricultural/pasture land, land that has been forested since 1951, and to a lesser extent, abandoned coffee shade ($P = 0.0468$). While there is some indication that this assemblage primarily forms on limestone and ultramafic substrates ($P = 0.0897$), it was found on alluvial and volcanic substrates as well. The TabHet/CasArb assemblage had broad distributions across the subtropical dry, moist and wet/rain forest life zones, was found on both volcanic and limestone substrates, and all past land uses, with no significant differences. Although the CasSyl/PsiGua assemblage was frequently found on abandoned pasture, it was not exclusive to the former land use, being found on abandoned coffee shade and relatively undisturbed forest ($P = 0.1690$). It did, however, show greater frequency of occurrence in the moist forest life zone on extrusive volcanic, followed by limestone, substrates ($P < 0.0001$).

The plots with high relative importance of the introduced species *S. campanulata*, the SpaCam assemblage, occurred most frequently in the subtropical moist forest life zone on both limestone and extrusive volcanic substrates, with a very strong affinity for former herbaceous agricultural/pasture land ($P = 0.0006$). This assemblage was also found, although much less frequently, in subtropical wet forest on extrusive volcanic substrates in abandoned coffee shade.

A number of assemblages were encountered on lands formerly managed for shade coffee production, particularly the GuaGui/DenArb assemblage. This assemblage was found in the subtropical

Table 5
Non-metric multidimensional scaling ordination axes correlations with environmental variables and tree species, for all islands.

Axis 1			Axis 2			Axis 3		
Variable	r	r^2	Variable	r	r^2	Variable	r	r^2
Moisture stress—Spring	−0.550	0.303	Temperature, min.—March	0.440	0.193	Temperature, max.—September	−0.277	0.077
Moisture stress—Annual	−0.539	0.291	Temperature, min.—January	0.436	0.190	Temperature, max.—June	−0.277	0.077
Moisture stress—Summer	−0.463	0.215	Temperature, min.—November	0.435	0.189	Elevation	0.272	0.074
Moisture stress—Winter	−0.464	0.215	Temperature, min.—Annual	0.432	0.187	Temperature, max.—May	−0.271	0.074
Moisture stress—Fall	−0.444	0.197	Temperature, min.—December	0.432	0.187	Temperature, max.—October	−0.273	0.074
Precipitation—April	0.411	0.169	Temperature, min.—February	0.432	0.186	Temperature, max.—April	−0.270	0.073
Coast distance	0.398	0.158	Temperature, min.—September	0.431	0.186	Temperature, max.—August	−0.268	0.072
Precipitation—May	0.393	0.154	Temperature, min.—April	0.430	0.185	Temperature, avg.—June	−0.265	0.070
Temperature, min.—June	−0.384	0.147	Temperature, min.—October	0.426	0.181	Temperature, avg.—May	−0.264	0.070
Temperature, min.—October	−0.371	0.138	Temperature, min.—August	0.420	0.176	Temperature, max.—July	−0.264	0.070
Axis 1			Axis 2			Axis 3		
Species	r	r^2	Species	r	r^2	Species	r	r^2
Leucaena leucocephala	−0.501	0.251	*Guarea guidonia*	−0.366	0.134	*Spathodea campanulata*	−0.594	0.353
Guarea guidonia	0.449	0.202	*Bursera simaruba*	0.325	0.106	*Leucaena leucocephala*	−0.250	0.062
Casearia guianensis	0.325	0.106	*Cecropia schreberiana*	−0.322	0.103	*Inga laurina*	−0.234	0.055
Acacia farnesiana	−0.287	0.082	*Ing a vera*	−0.319	0.101	*Micropholis guyanensis*	0.224	0.050
Andira inermis	0.281	0.079	*Tabebuia heterophylla*	0.308	0.095	*Cecropia schreberiana*	0.223	0.050
Dendro panax arboreus	0.251	0.063	*Guettarda scabra*	0.307	0.094	*Ocotea leucoxylon*	0.218	0.047
Mangifera indica	0.225	0.051	*Spathodea campanulata*	−0.279	0.078	*Prestoea montana*	0.211	0.045
Prosopis pallida	−0.219	0.048	*Coccolo ba diversifolia*	0.269	0.072	*Inga laurina*	0.211	0.044
Bursera simaruba	−0.216	0.047	*Ardisia obovata*	0.265	0.070	*Tabebuia heterophylla*	−0.209	0.044
Bucida buceras	−0.216	0.047	*Citrus sinen sis*	−0.246	0.060	*Albizia procera*	−0.205	0.042
	Axis r^2 = 0.198			Axis r^2 = 0.146			Axis r^2 = 0.09	

moist and wet/rain forest life zones on all substrates except for ultramafic. This assemblage showed markedly high frequency of occurrence in the subtropical moist forest life zone on extrusive volcanic soils on former herbaceous agricultural/pasture land, followed closely by a strong presence in the subtropical wet/rain forest life zone, on extrusive volcanic substrates in abandoned coffee shade ($P = 0.0011$). Another assemblage found in the former coffee producing lands was the CecSch/CitSin. This assemblage was found most frequently in abandoned coffee shade on volcanic substrates in the subtropical wet/rain life zone, and less frequently on former herbaceous agricultural/pasture land on limestone substrates ($P = 0.0159$) in the subtropical moist life zone.

The assemblage SyzJam, with its high relative importance of the introduced *S. jambos*, was also found most frequently on former agricultural/pasture land, with fewer occurrences in abandoned coffee shade, and two instances in land that had been forest since

Table 6
Non-metric multidimensional scaling ordination axes correlations with environmental variables and tree species, for mainland Puerto Rico.

Axis 1			Axis 2			Axis 3		
Variable	r	r^2	Variable	r	r^2	Variable	r	r^2
Temperature, min.—April	−0.547	0.300	Coast distance	0.389	0.152	Moisture stress—Winter	−0.259	0.067
Temperature, min.—May	−0.547	0.300	Moisture stress—Spring	−0.363	0.132	Moisture stress—Spring	−0.233	0.055
Temperature, min.—March	−0.544	0.296	Moisture stress—Annual	−0.347	0.120	Latitude	0.229	0.052
Temperature, min.—Annual	−0.543	0.295	Moisture stress—Winter	−0.316	0.100	Moisture stress—Annual	−0.199	0.040
Temperature, min.—October	−0.543	0.295	Moisture stress—Summer	−0.282	0.080	Slope	0.197	0.039
Temperature, min.—February	−0.536	0.288	Precipitation—April	0.277	0.077	Slope position	0.182	0.033
Temperature, min.—June	−0.537	0.288	Moisture stress—Fall	−0.278	0.077	Moisture stress—Summer	−0.164	0.027
Temperature, min.—September	−0.536	0.287	Latitude	0.246	0.061	Slope percent	0.162	0.026
Temperature, min.—November	−0.531	0.282	Precipitation—May	0.235	0.055	Precipitation—April	0.133	0.018
Temperature, min.—August	−0.530	0.281	Temperature, min.—October	−0.220	0.049	Precipitation—December	0.130	0.017
Axis 1			Axis 2			Axis 3		
Species	r	r^2	Species	r	r^2	Species	r	r^2
Guarea guidonia	0.445	0.198	*Spathodea campanulata*	0.601	0.361	*Casearia guianensis*	0.393	0.154
Leucaena leucocephala	−0.425	0.181	*Guarea guidonia*	0.373	0.139	*Leucaena leucocephala*	−0.360	0.130
Cecropia schreberiana	0.341	0.116	*Bucida buceras*	−0.289	0.084	*Andirainermis*	0.333	0.111
Eugenia jambos	0.307	0.094	*Bursera simaruba*	−0.277	0.076	*Acacia farnesiana*	−0.293	0.086
Ingavera	0.305	0.093	*Exostema caribaeum*	−0.240	0.057	*Tabebuia heterophylla*	0.264	0.070
Ingalaurina	0.302	0.091	*Clusiarosea*	−0.235	0.055	*Myrcia splendens*	0.255	0.065
Ocotea leucoxylon	0.293	0.086	*Eugenia monticola*	−0.233	0.054	*Citharexylum fruticosum*	0.232	0.054
Tabebuia heterophylla	−0.270	0.073	*Casearia sylvestris*	0.211	0.044	*Spathodea campanulata*	−0.220	0.049
Bursera simaruba	−0.264	0.070	*Guettarda scabra*	−0.210	0.044	*Citrussinensis*	−0.205	0.042
Dendropanax arboreus	0.240	0.057	*Pictetia aculeata*	−0.202	0.041	*Ardisiaobovata*	0.200	0.040
	Axis r^2 = 0.163			Axis r^2 = 0.144			Axis r^2 = 0.128	

Table 7
Non-metric multidimensional scaling ordination axes correlations with environmental variables and tree species, for the Virgin Islands.

Axis 1			Axis 2			Axis 3		
Variable	r	r^2	Variable	r	r^2	Variable	r	r^2
Latitude	−0.558	0.311	Precipitation—October	−0.318	0.101	Temperature, max.—May	−0.623	0.389
Temperature, avg.—November	0.504	0.254	Latitude	0.272	0.074	Temperature, max.—November	−0.621	0.385
Slope	−0.503	0.253	Precipitation—July	−0.243	0.059	Precipitation—February	0.619	0.383
Elevation	−0.478	0.228	Moisture stress—summer	0.216	0.047	Temperature, max.—March	−0.600	0.360
Moisture stress—Spring	0.474	0.225	Moisture stress—Fall	0.210	0.044	Temperature, max.—April	−0.591	0.350
Slope percent	−0.472	0.222	Precipitation—June	−0.207	0.043	Longitude	0.589	0.347
Temperature, avg.—May	0.431	0.186	Slope position	−0.207	0.043	Temperature, max.—October	−0.573	0.328
Temperature, avg.—December	0.414	0.172	Precipitation—September	−0.197	0.039	Temperature, max.—June	−0.563	0.317
Precipitation—April	−0.394	0.155	Temperature, max.—August	0.184	0.034	Precipitation—November	0.562	0.316
Temperature, avg.—March	0.392	0.154	Distance from coast	−0.181	0.033	Temperature, max.—Annual	−0.564	0.310
Axis 1			Axis 2			Axis 3		
Species	r	r^2	Species	r	r^2	Species	r	r^2
Leucaena leucocephala	0.597	0.357	*Leucaena leucocephala*	−0.630	0.397	*Prosopis pallida*	−0.675	0.455
Bursera simaruba	−0.496	0.246	*Acacia farnesiana*	0.542	0.293	*Bourreria succulenta*	0.417	0.174
Guapira fragrans	−0.487	0.237	*Acacia muricata*	0.320	0.103	*Ziziphus mauritiana*	−0.350	0.122
Acacia farnesiana	0.363	0.132	*Cassine xylocarpa*	0.288	0.083	*Trichilia hirta*	−0.273	0.074
Myrciaria floribunda	−0.327	0.107	*Prosopis pallida*	0.249	0.062	*Guettarda scabra*	0.267	0.071
Maytenus laevigata	−0.319	0.102	*Melicoccus bijugatus*	−0.233	0.054	*Eugenia monticola*	0.260	0.068
Capparis baducca	−0.319	0.101	*Amyris elemifera*	0.232	0.054	*Pisonia subcordata*	0.253	0.064
Capparis cynophallophora	−0.289	0.083	*Guapira fragrans*	0.222	0.049	*Krugiodendron ferreum*	0.245	0.060
Cordia alliodora	−0.279	0.078	*Guettarda scabra*	0.212	0.045	*Acacia farnesiana*	−0.235	0.055
Acacia muricata	−0.276	0.076	*Eugenia cordata*	0.213	0.045	*Casearia guianensis*	−0.235	0.055
	Axis r^2 = 0.269			Axis r^2 = 0.189			Axis r^2 = 0.174	

Table 8
Frequency distribution of species assemblages by Holdridge life zone and geology on mainland Puerto Rico.

Assemblage	Life zone/geologic substrate								
	Dry/AVS	Dry/Lime	Dry, Moist/Ultra	Moist/AVS	Moist, Wet/Lime	Wet/AVS	LM/AVS	Wet, LM/Ultra	Totals
AcaFar/ProPal	4	2	0	2	0	0	0	0	8
LeuLeu	5	4	3	7	0	0	0	0	19
CitFru/ExoCar	0	2	2	4	6	0	0	0	14
BurSim/BucBuc	4	3	0	2	11	0	0	0	20
ThoStr	0	1	0	3	3	0	0	0	7
CasGui/AndIne	1	0	0	4	5	3	0	0	13
NeoRes/GueSca	1	0	3	2	7	0	0	4	17
SpaCam	0	0	0	17	14	12	0	0	43
TabHet/CasArb	0	1	0	5	1	5	0	0	12
CasSyl/PsiGua	0	1	0	12	8	7	0	1	29
GuaGui/DenArb	0	0	0	20	7	19	0	0	46
SyzJam	0	0	0	3	7	9	0	0	19
CecSch/CitSin	0	0	0	0	3	9	2	0	14
PreMon/MicGar	0	0	0	0	0	4	4	1	9
Totals	15	14	8	81	72	68	6	6	270

These groups are subtropical dry on alluvial, volcanic and sedimentary substrates (Dry/AVS), subtropical dry on limestone (Dry/Lime), subtropical dry–moist on ultramafic (Dry, Moist/Ultra), subtropical moist on alluvial, volcanic and sedimentary (Moist/AVS), subtropical moistwet on limestone (Moist, Wet/Lime), subtropical wet on alluvial, volcanic and sedimentary (Wet/AVS), lower montane on alluvial, volcanic and sedimentary (LM/AVS), and subtropical wet—lower montane on ultramafic (Wet, LM/Ultra).

1951. It occurred with equal frequency in the subtropical moist and wet/rain life zones ($P = 0.6374$), but most frequently on extrusive volcanic substrates ($P = 0.0155$). Finally, the assemblage distributed at the highest elevation and highest precipitation, the PreMon/MicGar, was found in the subtropical wet/rain and subtropical lower montane life zones with equal frequency, entirely on volcanic substrates. All of the sites with this assemblage had been forested since 1951.

4. Discussion

The new forest tree species assemblages that formed on Puerto Rico and the U.S. Virgin Islands show broadly defined, general species assemblages that span multiple islands, with unique variations created by local environmental factors and differing land-use histories.

4.1. Highly disturbed subtropical dry forest assemblages

Assemblages characterized by the importance of *A. farnesiana*, *P. pallida* and *L. leucocephala* were found on all islands on relatively flat, lowland sites with greater spring moisture stress, grazing and herbaceous agriculture land-use histories and, in some cases, succession arrested by chronic disturbance. These are resilient, successional species capable of persisting and competing successfully with other taxa in pastures and disturbed sites along the islands' coastlines and dry limestone areas (Dansereau, 1966; Skolmen, 1990; Parrotta, 2000a,b). Dense stands of *L. leucocephala* forming on drier, highly disturbed lands have been described on Puerto Rico (Molina and Lugo, 2006) and the U.S. Virgin Islands (Ray and Brown, 1995; Adam and Ryan, 2003; Thomas and Devine, 2005; Weaver, 2006a). The *A. farnesiana* and *P. pallida* stands had relatively low TPH and BAH (2231–2471 stems/ha and

Table 9
Frequency distribution of species assemblages by Holdridge life zone and geology in the Virgin Islands.

Assemblage	Life zone/geologic substrate				
	Dry/ AVS	Dry/ Lime	Moist/ AVS	Moist, Wet/Lime	Totals
GuaFra/CapInd	4	0	1	0	5
ProPal	6	0	0	0	6
CorAlb	3	1	0	0	4
AcaFar	4	2	1	0	7
LeuLeu	12	8	8	1	29
AcaMur/PisSub	4	0	3	0	7
CasGui/ZanMon	8	0	6	0	14
EugMon/CapBad	7	0	10	0	17
Totals	48	11	29	1	89

Life zone/geologic substrate groups are subtropical dry on alluvial, volcanic and sedimentary substrates (Dry/AVS), subtropical dry on limestone (Dry/Lime), subtropical moist on alluvial, volcanic and sedimentary (Moist/AVS), subtropical moist–wet on limestone (Moist, Wet/Lime).

Table 10
Frequency distribution of forested inventory plots by last land cover class before reverting to forest, by assemblage, on mainland Puerto Rico.

Assemblage	HerbAg/ pasture	Coffee shade	Not disturbed	Other	Total
AcaFar/ProPal	7	0	0	1	8
LeuLeu	15	0	0	4	19
CitFru/ExoCar	8	0	3	3	14
BurSim/BucBuc	13	2	5	0	20
ThoStr	4	1	1	1	7
CasGui/AndIne	10	1	1	1	13
NeoRes/GueSca	9	1	6	1	17
SpaCam	27	8	1	7	43
TabHet/CasArb	5	5	1	1	12
CasSyl/PsiGua	13	5	9	2	29
GuaGui/DenArb	22	16	6	2	46
SyzJam	11	5	2	1	19
CecSch/CitSin	4	9	0	1	14
PreMon/MicGar	0	0	8	1	9
Totals	148	53	43	26	270

5.0–5.6 m^2/ha, across all islands). *L. leucocephala*, while forming denser stands (4235.1 stems/ha), had the lowest QMD (4.8 cm) and low BAH (7.6 m^2/ha).

There are surprisingly few assemblages found entirely within the subtropical dry forest life zone on mainland Puerto Rico beyond the highly impacted forests dominated by introduced species previously mentioned. Instead, Puerto Rico's subtropical dry forest life zone held assemblages that were also found in the subtropical moist forest life zone, or more correctly stated, across the broad transition zone between subtropical dry and subtropical moist forest.

4.2. Subtropical dry and dry–moist transition forest assemblages

Within the broad transition zone between the subtropical dry and subtropical moist forest life zones in Puerto Rico, and to a lesser extent the Virgin Islands, there has been the formation of more diverse assemblages of Caribbean dry forest species on lower slopes less impacted by human land use and disturbance and less dominance by introduced pioneer species. There is indication of some species composition continuity across the subtropical dry and moist forests on all the islands. Broad assemblages defined by the relatively higher importance of *C. guianensis*, *Eugenia monticola* (Sw.) DC. and *G. fragrans* were found on all islands. The *Bucida buceras*–*G. fragrans* community described by Gould et al. (2006) has species from both the Puerto Rico mainland and Virgin islands subtropical dry to moist forest assemblages found in this study.

Natives *B. buceras* L. and *B. simaruba* are often dominant trees in Caribbean subtropical dry to moist forests (Francis, 2000a,b; Gould et al., 2006), and these species figure prominently in some of the assemblages found in this study. On mainland Puerto Rico, the distribution of the BurSim/BucBuc assemblage reflects interplay between climate and substrate. The assemblage was found in both life zones, but in the subtropical moist forest it was more frequently found on droughty limestone substrates. This assemblage was more common on limestone substrates and on sites in the oldest forest class.

The Virgin Islands showed some unique subtropical dry–moist transitional forest assemblages that had a markedly different species composition than those on mainland Puerto Rico, for example, AcaMur/PisSub, EugMon/CapBad, CorAlb and GuaFra/CapInd. This may be due to differing patterns of land use, rates of forest recovery, and geographic isolation of each island. The Virgin Islands subtropical dry to moist assemblages found here were similar to those found by Weaver (2006b) in the Cinnamon Bay watershed, St. John. But, we did not observe the same patterns of species distribution by topography seen by Weaver and Chinea (1987) and Weaver (2006b), assemblage differentiation into the toposequences described by Ray and Brown (1995), or the correlations between assemblages and substrates found by Woodbury and Weaver (1987).

Although we did not have the detailed land-use history for these islands that we had for mainland Puerto Rico, we do know from historical sources that agriculture abandonment began sooner and proceeded quicker on St. John than on the other Virgin Islands, meaning the secondary forests have been recovering there for a longer time (Weaver, 2006b). This decreased level of recent disturbance, particularly within the protected Virgin Islands National Park, presents a skewed, but species-rich, example of Virgin Islands subtropical dry and subtropical moist forest under reduced human impacts and after greater recovery times.

4.3. Subtropical moist forest assemblages

The assemblages in the extensive subtropical moist forest life zone on Puerto Rico often occupied a variety of substrates and were found across multiple life zones. The ThoStr, CasGui/AndIne, TabHet/CasArb and CasSyl/PsiGua assemblages, while predominately found in the subtropical moist forest life zone, are also found to a lesser degree in the adjacent subtropical dry and subtropical wet life zones. The NeoRes/GueSca assemblage represents the vegetation on a combination of karst and ultramafic substrates in the subtropical moist to wet life zone of mainland Puerto Rico. This assemblage has species typically found on the droughty substrates of karst "mogote" hilltops and sides (Chinea, 1980; Álvarez Ruiz et al., 1997; Brandeis, 2006; Aukema et al., 2007).

Many subtropical moist and some wet forest sites on mainland Puerto Rico shared a relatively high importance of *S. campanulata*, particularly in the subtropical moist forest life zone on both limestone and extrusive volcanic substrates in former agricultural and pasture land, and in the subtropical wet forest on extrusive volcanic soil in abandoned coffee shade. The increase in importance of *S. campanulata* throughout the subtropical moist and wet forest life zones on mainland Puerto Rico has been observed since forest inventories began in 1980, and the species has held the position of most prevalent forest tree since the 1990 forest inventory (Birdsey and Weaver, 1982; Franco et al., 1997; Brandeis et al., 2007). *S. campanulata* grows best on deep, fertile, well-drained substrates, can colonize highly eroded sites, and commonly colonizes abandoned pastures (Dansereau, 1966; Francis, 2000c; Abelleira Martínez and Lugo, 2008). The *S.*

campanulata stands inventoried by this study were particularly productive, having the highest average AGBH (130 Mg/ha) and one of the highest BAH (29.6 m^2/ha). This is impressive considering that 81.4% of these stands were agricultural land in 1951, and 25.6% were still under agriculture as late as 1977. Abelleira Martínez and Lugo (2008) observed even higher productivity in *S. campanulata* stands growing on land formerly cultivated for sugar cane that averaged 91.9 m^2/ha of basal area.

Growth and regeneration of *S. campanulata* is limited, however, by shade intolerance that restricts its ability to replace itself in a mature stand (Francis, 2000c), even those periodically disturbed by hurricanes (Thompson et al., 2007). Brandeis (2006) observed that in the northwestern karst region *S. campanulata* was the most important tree species on the valley areas between mogote hills, but not on moderate, moister slopes where GuaGui/DenArb assemblage predominates, or on the drier, strongly sloped hilltops occupied by assemblages indicated by the relative importance of *T. heterophylla*. Despite their ability to persist in the understory for many years, *S. campanulata* seedlings and saplings are kept from regenerating by residual coffee shade canopies and replaced over time by more shade tolerant species, particularly *G. guidonia* (Rivera and Aide, 1998; Aide et al., 2000; Francis, 2000c; Marcano Vega et al., 2002), and *T. heterophylla* tolerates poorer soils (Weaver, 2000b) than *S. campanulata*.

4.4. Subtropical wet forest assemblages

This life zone holds young secondary forests where some overstory canopy has been maintained but that is now reverting to a more closed canopy condition with native species, and similar forests that have had their canopies more severely disturbed and opened to early successional native species. It also has forests that are typified by a naturalized shade tolerant species that is replacing itself well and becoming dominant in stands.

The GuaGui/DenArb assemblage is found on moderate, wetter mountain slopes and often indicates sites that were managed for coffee shade but that have now been largely abandoned. The maintenance of a tree overstory for coffee shade and high site productivity explain why this assemblage has the greatest HT (13.6 m), as well as high QMD (11.1 cm), BAH (29.6 m^2/ha), and AGBH (118 Mg/ha). These forests frequently grow on fertile volcanic substrates, experience low levels of moisture stress, and have been managed to maintain a tree overstory. Half of plots measured were still coffee shade or forest in 1951, and 84.8% were still coffee shade in 1977. By 1991, however, none of the plot locations were still being managed for coffee shade and all sites had reverted to unmanaged forest.

The importance of *G. guidonia* is a possible indication of how much the forests of Puerto Rico have been modified by former land uses, in this case coffee cultivation. Normally, *G. guidonia* is an uncommon component in undisturbed humid lowland and subtropical lower montane forests throughout its extensive natural range (Weaver, 2000a). In Puerto Rico, the species is found in association with *Dacryodes excelsa* Vahl and the other species typical of the "tabonuco" forest type and regeneration appears to be related to disturbance (Weaver, 2000a). *G. guidonia*, a native species that was maintained for coffee shade along with native *Inga laurina* (Sw.) Willd., and the introduced *Inga vera* Willd. and *Erythrina poeppigiana* (Walp.) O.F. Cook, has increased in importance to become the second most important species island-wide, indicating an ability to successfully regenerate in abandoned coffee shade and out-compete those other species (Birdsey and Weaver, 1982; Franco et al., 1997; Pascarella et al., 2000; Brandeis et al., 2007). This native species has responded to the regeneration opportunities provided by human forest management and disturbance that might have otherwise been taken by introduced species.

The CecSch/CitSin assemblage is an even more disturbed forest community within the former coffee shade areas. *C. schreberiana* is an early invader of disturbed areas and is often associated with other secondary forest species like *Schefflera morototonii* (Aubl.) Maguire, Steyermark & Frodin and *Ochroma pyramidale* (Cav. ex Lam.) Urban (Crowe, 1980; Liegel, 2000; Silander and Lugo, 2000). The presence of species that require light in the understory for germination and early growth like *C. schreberiana* indicate frequent canopy openings due to human activities or hurricanes (Crowe, 1980; Dallmeier et al., 1998; Weaver, 1998). This assemblage has a low TPH (1476 stems/ha) and low BAH (14.0 m^2/ha) relative to other assemblages in this life zone, but still a relatively high QMD (11.0 cm) and HT (11.8 m). These structural characteristics also point to a forest with more open canopy comprised of fewer, large trees that have been purposely retained or that have survived disturbances. Popper et al. (1999) found large, old, *C. schreberiana*, *S. morototonii* and *I. laurina* trees in association with coffee shade, and postulated that these trees were remnants of the prior, undisturbed forest, or that they had become established soon after abandonment.

An assemblage indicative of human impact and introduced species naturalization is characterized by the importance of the introduced species *Syzygium jambos* (L.) Alston. This shade tolerant species is capable of reproducing under closed canopies and of self-replacement to form dense, monospecific stands (Wadsworth, 1943; Aide et al., 2000; Pascarella et al., 2000; Brown et al., 2006; Thompson et al., 2007). We can see how the *S. jambos*-dominated assemblage is present not only on lands that were in agriculture in 1951 and 1977, but also on lands that had been coffee shade. This species has formed well-developed stands on fertile volcanic substrates. *S. jambos* has grown in importance since being described as a potentially important timber species by Wadsworth (1943) and currently ranks as the 8th most important species island-wide in the subtropical moist forest life zone and the 4th most important species in the subtropical wet forest life zone (Brandeis et al., 2007).

4.5. Subtropical lower montane forest assemblages

At higher elevations above the region of coffee cultivation, anthropogenic disturbances were limited to pasturing and wood cutting, so modifications to the forest were less notable. The sites with the PreMon/MicGar assemblage were all forested in 1951 and have remained so until today. The extensive, objective sampling of the entire landscape used in this study was not intensive enough within the upper elevation forests (even after some sampling intensification), to separate the traditionally described forest types of "tabonuco", "palo colorado", palm brake and elfin forests (Ewel and Whitmore, 1973; Weaver and Murphy, 1990; Weaver, 1991), or into the groups defined by the finer scale recent study by Gould et al. (2006). Instead, species indicative of all of these forest types such as *Prestoea montana* (Graham) Nichols., *Micropholis garciniifolia* Pierre, *Sloanea berteriana* Choisy ex DC., *D. excelsa* and many others were clustered together in one large, assemblage.

4.6. Environmental correlations to the species assemblages

Forest ecosystems on Puerto Rico and the U.S. Virgin Islands consist of broad tree species assemblages that can be found across all islands, and variations that have been created by differing land uses and individual island environmental conditions. Spring moisture stress was a prominent factor in the formation of assemblages, but so were maximum and minimum temperatures, and the topographic variables such as elevation and distance from the coast that are confounded with them. Highly disturbed, dry, relatively flat, lowland sites with greater spring moisture stress with assemblages indicated by *A. farnesiana*, *P. pallida* and *L. leucocephala* occupy one end of a climatic gradient. At moister sites along this gradient are disturbed upland sites in the subtropical dry to moist forest transition zone indicated by *C. guianensis*, followed by disturbed moist forest of SpaCam and TabHet/CasArb assemblages. This gradient ends in the wet forest assemblage GuaGui/DenArb that was formerly managed for coffee-shade. Another important gradient represents a variation on the preceding one where monthly minimum temperatures, particularly in the spring, differentiate in assemblage distribution.

While similar trends can be seen in the Virgin Islands, there is also an additional separation of *L. leucocephala*-dominated stands and the CorAlb assemblage on St. Croix, which is at a lesser latitude than the other Virgin Islands. Decreasing spring moisture stress, decreasing average monthly temperatures in fall, winter and spring, and increasing in slope and elevation also influence assemblages along this gradient. This gradient ends with the more species-rich dry forest found on St. Thomas. Another Virgin Islands gradient begins with *P. pallida* and *A. farnesiana* assemblages found on flat, highly disturbed areas with less annual precipitation (particularly in the summer and fall months) and moves up into dry–moist transition forests located at higher slope positions. Spring and fall maximum monthly temperatures also played a minor role in assemblage formation and distribution in the Virgin Islands.

Broad ecotones exist on these islands, particularly between the subtropical dry and subtropical moist life zones, and many tree species have equally broad environmental niches along these ecotones. The assemblages are not tightly correlated with specific Holdridge life zones or soil types; rather they tend to occur in multiple life zones and geological parent materials. None of the assemblages were limited to only one life zone, and six assemblages were found in three different life zones. Some assemblages did occur more frequently on certain substrates, but none were restricted to a single substrate, not even those found on ultramafic substrates. Assemblages in the Virgin Islands fit more closely into specific life zones and soil types, but this is probably due to the limited life zones and soil types found on these smaller islands.

4.7. Land-use history correlations to the species assemblages

Land-use history can strongly influence tropical forest succession within a climatic zone (Álvarez Ruiz et al., 1997; Rivera and Aide, 1998; Aide et al., 2000; Chinea, 2002; Marcano Vega et al., 2002; Thompson et al., 2007; Abelleira Martínez and Lugo, 2008). When considering differences in species composition across climatic zones, land use and climate are confounded because climate influences land use. In Puerto Rico and the U.S. Virgin Islands, for example, coffee cultivation was limited to moist and wet climatic zones. Sugar cane cultivation occurred in dry and moist zones. Pasture occurs in dry, moist and wet climates. Because these major land uses extend over two or more climatic zones, we conclude that climate is more important to determining variation in species composition across climatic zones than is land-use history. Nevertheless, it still must be recognized that land use and climate are not completely separable.

Several species assemblages were significantly associated with certain geology types or land-use histories in the χ^2 tests but not in the ordinations. The most likely explanation for why land-cover history was not significant here, but was significant in ordinations from other studies, is a combination of the sample design and of the prevalence of certain land covers and trends across mainland Puerto Rico. Most of the forest inventory plots in Puerto Rico were under cultivation for coffee or pasture/herbaceous agriculture before reverting to forest. It follows that the source of most of the variability in our systematic sample is not differences in land use but differences in climate, because the data set in this study span a climate gradient that ranges from very dry forest to cloud forest. In contrast, most other studies, for example, Chinea and Helmer (2003) and Thompson et al. (2002) spanned narrower environmental gradients, such as only humid or only dry climatic zones and two or three geological substrates, and accordingly, land use or geology explains more of the variability in species composition in their plots than in this study. Moreover, in most tree community studies in Puerto Rico, collections of plots were specifically designed to test for differences in land-use or geomorphology by including more equal numbers of plots with different land-use histories. Finally, none of the other studies mentioned use monthly climate data as environmental explanatory variables, which would leave room for more non-climate variables to explain more variation in species composition.

Pasture has been a prominent land cover in Puerto Rico and remains so to this day, because while pasture has reverted to forest at higher elevations, sugar cane has transitioned to pasture in the lowlands (Kennaway and Helmer, 2007). The proportional representation of land-use histories in the mostly systematic sample of inventory plots reflects these land-cover data. In 1951, 41.1% of the points sampled were in pasture, and it has remained a common land cover class until the present day (Table 8). Herbaceous agriculture had largely disappeared from our sample by 1977, and coffee shade by 1991 (Table 10), which is consistent with the findings of Kennaway and Helmer (2007). Of those forest plots where we have mapping data, 35.6% of the forest fell in the 23–49 year old age class. So, while we have data from multiple years for multiple land cover classes, the trends at the majority of the sampled points were all very similar. Additionally, the past land use categories used here might mask a land use that preceded pasture. For example, abandoned herbaceous agriculture might be used as unmanaged pasture before complete abandonment and reversion to forest.

5. Conclusions

The long history of forest disturbance on Puerto Rico and the U.S. Virgin Islands makes it impossible to know precisely how much the currently observed tree species assemblages reflect pre-European colonization forest types and their local variations. However, we know that after large-scale deforestation and forest recovery, at least some novel forests have formed. Naturalized tree species play prominent roles in the recovery and secondary succession of these forests but in differing ways depending on their abilities to regenerate under increasingly closed canopies.

Environmental factors have an overarching effect on forest species composition across the broader range of climatic, geologic and topographic conditions and larger geographic scales, while land-use history also influences subtropical secondary forest species assemblages within a specific climatic zone or set of relatively narrow environmental conditions. More intensive sampling within each land-use history category might be needed to more fully characterize its influence on species composition.

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