Caribbean Foresters: A Collaborative Network for Forest Dynamics and Regional Forestry Initiatives
2016 *CARIBBEAN NATURALIST* Special Issue No. 1:116–137

Forest and Community Structure of Tropical Sub-Montane Rain Forests on the Island of Dominica, Lesser Antilles

Saara J. DeWalt[1,*], Kalan Ickes[1], and Arlington James[2]

Abstract - To examine short- and long-term changes in hurricane-prone sub-montane rain forests on Dominica in the Lesser Antilles of the eastern Caribbean, we established 17 permanent, 0.25-ha vegetation plots clustered in 3 regions of the island—northeast, northwest, and southwest. We counted all trees ≥10 cm diameter almost 30 years after Hurricane David caused substantial tree mortality, primarily in the southern half of the island. We identified 1 vegetation association (*Dacryodes–Sloanea*) with 2 variants depending on whether *Amanoa caribaea* was co-dominant. We found that differences in forest structure and species diversity were explained more by region than forest type, with plots in the southwest generally having higher stem density, lower tree height, and greater species diversity than plots in the northeast or northwest. Our results suggest that differences in forest composition in the sub-montane rain forests of Dominica are largely attributable to the presence or absence of the near-endemic canopy-tree species *A. caribaea*, and secondarily to the degree of hurricane-caused disturbance.

Introduction

The Caribbean is considered the third-most important global biodiversity hotspot (Mittermeier et al. 2004, Myers et al. 2000) due to the large number of endemic species, especially plants (Santiago-Valentin and Olmstead 2004), present there. Hurricanes, with their high winds and significant precipitation, are important in determining plant-species composition and forest dynamics throughout the Caribbean (Tanner et al. 1991). The role of storms is likely growing in importance because hurricanes appear to have increased in frequency and intensity in the region (Emanuel 2005, Webster et al. 2005). Little is known about the forest structure, tree-species diversity, composition, or dynamics of tropical forests of the Caribbean Islands, particularly those of the Lesser Antilles. Permanent vegetation plots in the Caribbean, such as those in Puerto Rico (e.g., Thompson et al. 2004) and Jamaica (Tanner and Bellingham 2006), provide opportunities to understand island-specific dynamics. However, more plots on other islands are needed to understand how forests vary across the region and how increased hurricane frequency and intensity may affect Caribbean rain forest dynamics.

Unlike many other islands in the region, over 60% of Dominica's land cover is woodland (Coan et al. 2007), most likely because the rugged terrain and high rainfall make logging nearly impossible (Hodge 1943). Dominica has a diverse

[1]Department of Biological Sciences, Clemson University, Clemson, SC, USA 29634. [2]Forestry, Wildlife, and Parks Division, Roseau, Dominica (retired). [*]Corresponding author - saarad@clemson.edu.

Manuscript Editor: Inés Sastre-de Jesús

flora with various endemic or near-endemic plant species and many regional endemics (Santiago-Valentin and Olmstead 2004); has interesting geo-morphological features, such as an abundance of volcanoes and geothermal activity (Fournier et al. 2009); and is the only Lesser Antillean island with 2 surviving, endemic parrot species—*Amazona arausiaca* Müller (Jac) and *A. imperialis* Richmond (Sisserou) (Wiley et al. 2004).

Like all islands in the Lesser Antilles, Dominica is hurricane-prone. The strongest hurricane to affect Dominica in recent history was Hurricane David, which caused tremendous damage to the island's forests in 1979, particularly its southern portion (Lugo et al. 1983). It was likely the most intense hurricane of the 20th century (Lugo et al. 1983). After Hurricane David, the population of the critically endangered Sisserou was restricted to the forested slopes of Morne Diablotin, the tallest mountain on Dominica (Evans 1986, 1991; Gregoire 1981). Several other hurricanes have impacted Dominica since then, including Hurricane Hugo in 1989, Marilyn in 1995, and Dean in 2007, but none have been as intense as Hurricane David (National Weather Service, NHC Data Archive http://www.nhc.noaa.gov/data/#annual).

In this study, we sought to characterize the sub-montane rain forest of Dominica, which composes nearly 50% of the island's woodlands (Coan et al. 2007). This forest type is found particularly around the 2 tallest mountains on the island, Morne Diablotin and Morne Trois Pitons, and is the primary habitat for nesting and foraging of the 2 endemic parrots (Wiley et al. 2004). Specifically, we investigated whether the sub-montane rain forest should be considered 1 vegetation association across the island, or whether there are finer distinctions that may necessitate different management, conservation, or protection activities for the plants and animals in this habitat. Furthermore, answering this question for Dominica will facilitate inter-island comparisons of species diversity, forest structure, and forest dynamics.

Beard (1949) recognized 2 floristic associations in Domenica's rain forests, 1 of which had 2 faciations. Beard's assessment came from studying trees ≥9.7 cm (≥1 ft) in diameter within 4 ha (10 ac) on Dominica as well as several other Lesser Antillean islands including St. Kitts, St. Lucia, St. Vincent, and Grenada. Although Beard did not enumerate plots or transects on Guadeloupe and Martinique, he visited those islands and incorporated the work of Stehlé (1935, 1945). Based on these data and observations, Beard named 2 floristic associations that occurred at lower elevations (60–900 m) with annual mean precipitation >2200 mm in the Lesser Antilles. He named one *Dacryodes–Sloanea* rain forest, which he noted occurred throughout the Lesser Antilles with the same dominant canopy-tree species at similar relative abundances from island to island. He found this association to be similar to the *Dacryodes–Sloanea* forest found in Puerto Rico. Beard also identified a *Licania–Oxythece* association, which on Dominica could be found with or without the near-endemic canopy tree *Amanoa caribaea.* On other Antillean islands, he found this association (without *A. caribaea*) only on St. Lucia where it was named for the dominant canopy trees *Licania ternatensis* and *Oxythece pallida* (C.F. Gaertn.)

Cronquist, which is now called *Pouteria pallida* (C.F. Gaertn.) Baehni and will be referred to as such henceforth. Beard noted that on Guadeloupe, the only other island where *A. caribaea* is present, the forest was intermediate between the 2 associations with *Dacryodes, Amanoa,* and *Sloanea* as dominant species. However, he did not characterize an association with this mixed assemblage in Dominica.

More recently, the Caribbean Vegetation Ecology Working Group identified only 1 forest alliance in sub-montane rain forests of the Lesser Antilles and called it the *Dacryodes excelsa–Sloanea massoni* Sw. forest alliance (Areces-Mallea et al. 1999). These authors noted that this alliance is related to the *Dacryodes excelsa–Sloanea berteriana* forest alliance found on Puerto Rico—also referred to as tabonuco forest, the Puerto Rican name for *D. excelsa*). The type specimen of *S. massoni* corresponds to *S. dentata* L., and T.D. Pennington (Royal botanical Gardens, Kew, Richmond, UK) recommends using the only other available name, which is *S. truncata* Urb. Therefore, we will call this species *S. truncata* and the forest alliance identified by Areces-Mallea et al. (1999) as the *Dacryodes excelsa-Sloanea truncata* forest alliance.

We used evidence from hierarchical clustering of plots based on tree-species composition, as well as differences in the identity and dominance of the canopy-tree species, in forest structure, and in diversity to determine whether there is 1 rain forest type in Dominica, as suggested by the Caribbean Vegetation Ecology Working Group (Areces-Mallea et al. 1999), or 2 rain forest types as identified by Beard (1949). We also examined the extent of differentiation among the 3 regions. We hypothesized that (1) sites near Morne Trois Pitons in SW Dominica would have more signs of disturbance (shorter canopy height, higher stem density, lower basal area, and higher abundance of pioneer trees) than those in the NE and NW because the southern region was affected more strongly by Hurricane David (Lugo et al. 1983) and (2) windward and lower-elevation sites (NE) and leeward and higher elevation sites (NW) on the sides of Morne Diablotin would differ in composition because of differences in rainfall and elevation. Finally, we made an initial assessment of differences in forest structure and diversity between our Dominica plots and those in the *Dacryodes-Sloanea* forests in the Luquillo long-term ecological research plot in Puerto Rico. We expect that these types of comparisons will be facilitated by additions to the Caribbean Foresters Information Sharing Platform. Like those in Puerto Rico, the permanent plots in Dominica will also provide baseline data to track how forest structure and community structure change over time.

Field-site Description

Dominica is a volcanic island located in the center of the north–south running Lesser Antillean island chain of the eastern Caribbean, between Guadeloupe to the north and Martinique to the south (15°25' N, 61°20' W; Fig. 1). Dominica is a small island: 47 km long, 29 km wide at its widest, and 754 km^2 in area. The terrain of the island is extremely rugged and dominated by Morne Trois Pitons (1424 m asl) in the south and Morne Diablotin (1447 m asl) in the north. These 2 mountains, along with many other smaller mountains and hills, intercept the Atlantic Trade Winds and cause highly variable rainfall. Mean annual rainfall in the interior ranges from 3500 mm to more than 8000 mm, with estimated totals substantially higher towards the summits of the 2 tallest mountains.

We established seventeen 0.25-ha (50 m x 50 m) permanent vegetation plots clustered in 3 geographic regions of Dominica: 6 plots in the northeast (NE) in the Northern Forest Reserve, 4 in the northwest (NW) in the Morne Diablotin National Park and Northern Forest Reserve, and 7 in the southwest (SW) in Morne Trois Pitons National Park. The range in elevation for each region was 224–389 m asl in the NE, 549–747 m in the NW, and 549–732 m in the SW (Table 1). Climatological records are not available for these plots, but mean annual precipitation is likely to be between 3000 and 6000 mm/year, with rainfall amounts in the NE lower than in the SW or NW (Forestry, Wildlife, and Parks Division of Dominica, Roseau, Dominica, unpubl. data). We established plots where there was no sign of current

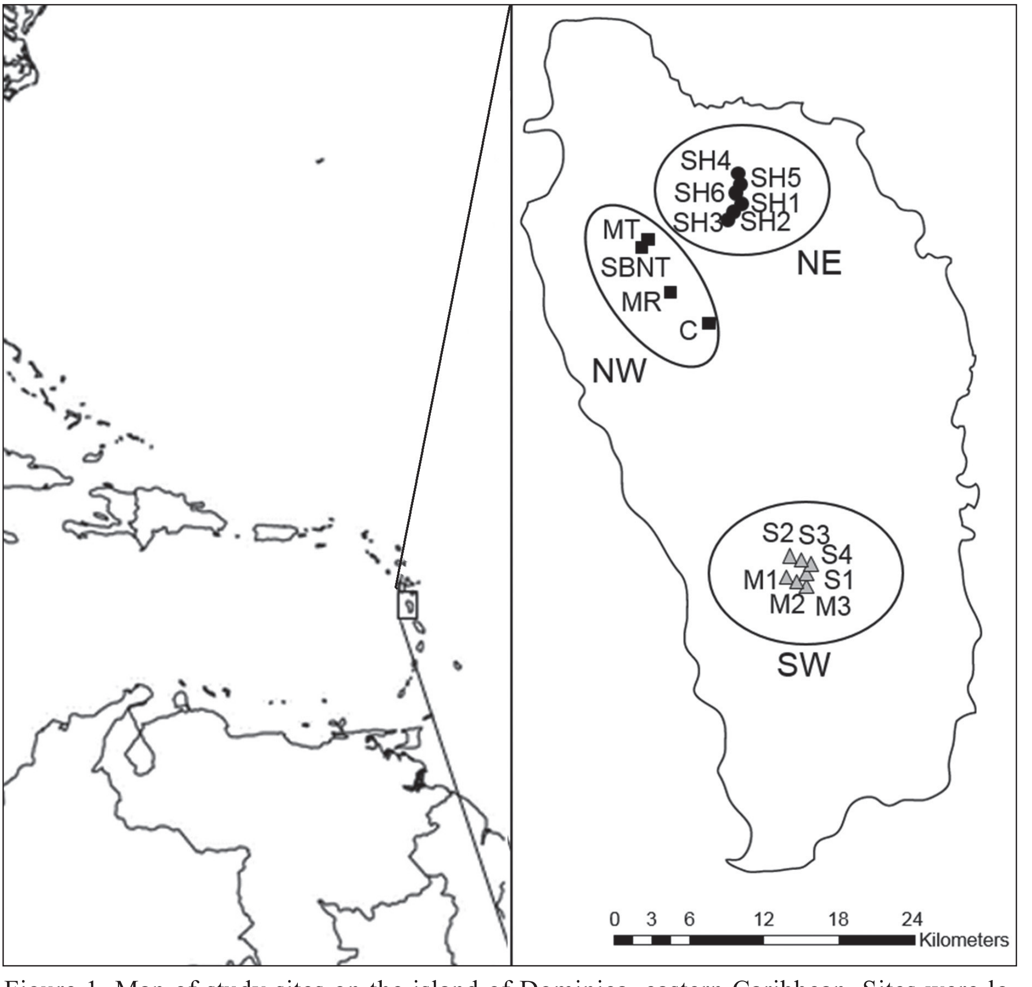

Figure 1. Map of study sites on the island of Dominica, eastern Caribbean. Sites were located in 3 regions: the northeast (NE), northwest (NW), and southwest (SW). Codes for plots correspond with those given in Table 1.

or past human activity (i.e., logging or agriculture), slopes were <45°, large ravines were absent, and soils were not permanently waterlogged. Each plot was at least 400 m from any other plot. We included gaps, but avoided areas that were known or suspected to have nesting Sisserou parrots. Gaps resulted from single treefalls and were too small to substantially influence structure or composition at the plot-level.

We identified plants to species by comparison with voucher specimens deposited in the national herbarium of Dominica (Springfield, Dominica) and the University of Puerto Rico-Río Piedras (UPRRP). We used morphotypes for species that have not been taxonomically well-resolved. We consulted the Taxonomic Name Resolution Service to standardize plant names (Boyle et al. 2013).

Methods

We divided each vegetation plot into 10 m x 10 m subplots for sampling in 2006 or 2007. The average slope of the plots ranged from relatively flat in M3 (average slope = 6.2°) to very steep in S2 (35°) (Table 1).

We tagged and measured all trees ≥1 cm diameter at breast height (dbh), and identified them using standard Center for Tropical Forest Science methods for trees, including measuring tree diameters 50 cm above the last buttresses (Condit 1998), but herein, report only information on trees ≥10 cm dbh. We also measured lianas ≥0.5 cm diameter. We used a laser rangefinder (Impulse, Laser Tech, Inc., Englewood, CO, USA) to measure the height of each tree ≥30 cm dbh that was not leaning and did not have a broken top.

Table 1. Attributes of the seventeen 0.25-ha permanent vegetation plots in sub-montane rain forest of Dominica. Slope was averaged over the twenty-five 10 m x 10 m subplots in each plot.

Code	Plot name	Altitude (m)	Slope (°)
Northeast region			
SH1	Simpa Heights 1	305	18.8
SH2	Simpa Heights 2	366	30.2
SH3	Simpa Heights 3	389	23.2
SH4	Simpa Heights 4	274	11.2
SH5	Simpa Heights 5	233	19.2
SH6	Simpa Heights 6	224	15.8
Northwest region			
C	Carholm	660	23.9
MR	Morne Rachette	747	10.7
MT	Morne Turner	549	27.6
SBNT	Syndicate	602	13.9
Southwest region			
M1	Middleham 1	643	26.6
M2	Middleham 2	655	10.6
M3	Middleham 3	686	6.2
S1	Sylvania 1	709	13.1
S2	Sylvania 2	549	35.2
S3	Sylvania 3	701	25.5
S4	Sylvania 4	732	20.4

We conducted all statistical analyses with the R ver. 3.1.0 software package (R Development Core Team 2014). We first classified the 17 plots into vegetation groups using hierarchical clustering methods. We used the metric $1 - S_{MH}$, in which S_{MH} is the Morisita–Horn (MH) index of community similarity on the species that occurred in at least 2 plots (vegdist function with the horn-distance metric; vegan package ver. 2.0-10) and the Ward method of clustering (hclust function with the ward.D2 method; stats package ver. 3.1.0). We chose the MH index because this metric is very sensitive to the abundance of the most common species in the assemblages (Chao et al. 2005, 2006), and thus, would be particulrly informative for vegetation classification. We used indicator-species analysis to determine which tree species were indicative of the vegetation groups identified by the clustering method (multipatt function with 999 permutations; indicspecies package ver. 1.7.1).

We also visualized community similarity utilizing non-metric multidimensional scaling (NMS) using the MH index and included only species that occurred in at least 2 plots (67 species; metaMDS function; vegan package). We employed permutational multivariate analysis of variance (MANOVA; adonis function with the horn-distance metric; vegan package) to test for differences in species composition among the groups.

We calculated stem density and basal area per hectare, and used Fisher's α index of diversity and the rarefied number of species as measures of species diversity. The number of species was rarefied to 146 individuals, which was the lowest number of individuals found in any one plot. As a measure of dominance, we used the Berger-Parker index that calculates the proportion of individuals in a plot composed of the most-common species.

We compared forest structure (stem density, total basal area, and tree height), species diversity (Fisher's α and rarefied number of species), and species dominance (Berger-Parker) among vegetation groups and regions using analysis of variance (ANOVA). We log-transformed density and basal area, and arcsine-transformed the Berger-Parker index to meet the assumptions of normality of residuals and homogeneity of variance. We calculated the η^2 measure of effect size for each test (eta-squared function; lsr package ver. 0.3.2) to compare the degree to which group or region explained differences in structure or diversity. We examined pairwise differences among the 3 regions using Tukey's honest significant differences (HSD) method.

Results

We identified 85 species in 33 families among the 3589 individual trees ≥10 cm dbh we recorded in the 17 plots. Averaged across all plots, Fisher's α diversity was 10.0, the Berger-Parker index was 0.18, rarefied species richness for 146 individuals was 28, stem density was 844 individuals/ha, basal area was 61.6 cm^2/ha, and tree height was 25.0 m.

Overall, the 10 most common tree species were a mixture of canopy, midstory, and understory trees with a range of distributions from those restricted to 2 islands to widely Neotropical (Table 2). The tree species that were most common differed among plots (Table 3). Some species consistently occurred across plots (e.g., *Tapura latifolia* and *Sterculia caribaea*), whereas others were absent from at least one plot (*D. excelsa*, *A. caribaea*, and *M. mirabilis*) (Table 4). *Amanoa caribaea* had the highest density of any species in any 1 plot (59 individuals in MR in the NW), but it was completely absent from 6 plots (Table 4). *Dacryodes excelsa, Sloanea caribaea*, and *A. caribaea* had the highest basal area overall, contributing 20%, 16%, and 12%, respectively. When examining just trees ≥30 cm dbh, the 5 most common species, in order of decreasing abundance, were *D. excelsa*, *A. caribaea*, *T. latifolia*, *Sterculia caribaea*, and *Sloanea caribaea*.

Vegetation associations

Cluster analysis identified 2 groups (Fig. 2). Group 1 had 5 of the 7 SW plots, 1 of the 4 NW plots, and none of the NE plots. The NMS ordination of plots (Fig. 3) closely matched the hierarchical clustering analysis (Fig. 2). The 2 groups identified were significantly different from each other according to the permutational MANOVA ($F_{1,15}$ = 12.1, P < 0.001). The canopy-tree species with greatest basal area were *Sloanea caribaea* and *Dacryodes excelsa* in Group 1 and *D. excelsa*, *Amanoa caribaea*, and *Sloanea caribaea* in Group 2 (Table 5).

The division between the 2 groups was driven primarily by the abundance of *Amanoa caribaea*, which was the only significant indicator species for Group 2. This species was absent or had only 1 individual in the plots that clustered in Group 1, whereas it was present in all plots in Group 2, except the MT plot (Table 4). *Pouteria pallida* and *Licania ternatensis* had greater basal area and more individuals in Group 2 than Group 1 (Table 5). *Pouteria pallida* ranked 10th of 71 species in basal area in Group 2, but was 53rd out of 69 species in Group 1. Fifteen species were significantly associated with Group 1. In decreasing order of the degree to which a

Table 2. Ten most common tree species ≥10 cm dbh across 17 plots in Dominica, listed in order of decreasing abundance. Tree stratum (C = canopy, M = midstory, U = understory) was determined by field observation, measured tree heights, and descriptions in Howard (1989). Distribution = the geographical distribution as determined from Howard (1989); *n* = the number of individuals ≥10 cm dbh in this study; % of stems = the percent of all individuals across the study composed by the species; and Height = the mean height for the 6 tallest trees ≥30 cm.

Species	Family	Stratum	Distribution	*n*	% of stems	Height (m)
Tapura latifolia	Dichapetalaceae	M	Lesser Antilles	330	15.1	31.5
Dacryodes excelsa	Burseraceae	C	Caribbean	324	14.8	41.5
Amanoa caribaea	Phyllanthaceae	C	Guadeloupe, Dominica	321	14.6	41.8
Sterculia caribaea	Malvaceae	M	Lesser Antilles	258	11.8	35.4
Miconia mirabilis	Melastomataceae	M	Neotropical	243	11.1	25.6
Rudgea citrifolia	Rubiaceae	U	Lesser Antilles	159	7.3	-
Licania ternatensis	Chrysobalanaceae	C	Lesser Antilles	151	6.9	36.8
Sloanea caribaea	Elaeocarpaceae	C	Neotropical	147	6.7	37.8
Gerascanthus reticulatus	Boraginaceae	M	Lesser Antilles	132	6.0	-
Micropholis guyanensis	Sapotaceae	M	Neotropical	127	5.8	29.3

Table 3. Forest-structural and species-diversity attributes of trees ≥10 cm dbh in the seventeen 0.25-ha permanent vegetation plots in sub-montane rain forest of Dominica. Group = the vegetation association as identified in Figure 2, # of trees = number of tree stems per ha, BA = total basal area (m^2) per ha, height = the mean height of trees ≥30 cm dbh, *S* = the number of species in the plot, *E*(146) = the number of species that would be expected to occur among 146 individuals in each plot as determined by rarefaction, and BP = Berger-Parker index and is the proportion of individuals composed by the most common species in the plot. Species-level information is in Appendix 1.

		# of trees/ha		BA	Height		Fisher's			Most common
Plot	Group	≥10 cm	≥30 cm	(cm^2/ha)	(m)	*S*	α	*E*(146)	BP	species
Northeast region										
SH1	2	584	204	56.78	28.9	24	8.17	24	0.16	*Tapura latifolia*
SH2	2	804	232	63.33	23.6	21	5.90	20	0.23	*Amanoa caribaea*
SH3	2	932	312	62.32	25.1	23	6.33	20	0.21	*Amanoa caribaea*
SH4	2	620	168	43.09	31.2	23	7.47	23	0.13	*Rudgea citrifolia*
SH5	2	776	168	48.71	25.9	28	8.98	26	0.16	*Sterculia caribaea*
SH6	2	780	160	39.56	27.0	23	6.78	21	0.24	*Tapura latifolia*
Northwest region										
C	1	872	228	88.08	24.5	35	11.78	31	0.10	*Tapura latifolia*
MR	2	876	248	72.90	27.5	31	9.86	27	0.27	*Amanoa caribaea*
MT	1	600	204	54.59	24.3	29	10.71	29	0.19	*Tapura latifolia*
SBNT	2	708	236	88.34	29.2	24	7.49	22	0.32	*Amanoa caribaea*
Southwest region										
M1	1	1216	160	61.70	18.9	38	11.46	32	0.18	*Miconia mirabilis*
M2	1	1052	188	60.70	22.5	42	14.10	35	0.17	*Miconia mirabilis*
M3	1	924	168	52.15	18.4	37	12.44	32	0.11	*Sterculia caribaea*
S1	1	800	140	58.61	25.7	33	11.25	30	0.12	*Eugenia coffeifolia*
S2	2	868	192	60.17	24.1	37	12.82	34	0.16	*Amanoa caribaea*
S3	1	976	232	61.72	23.0	41	14.10	35	0.13	*Miconia mirabilis*
S4	2	964	268	75.22	24.1	33	10.34	27	0.15	*Dacryodes excelsa*

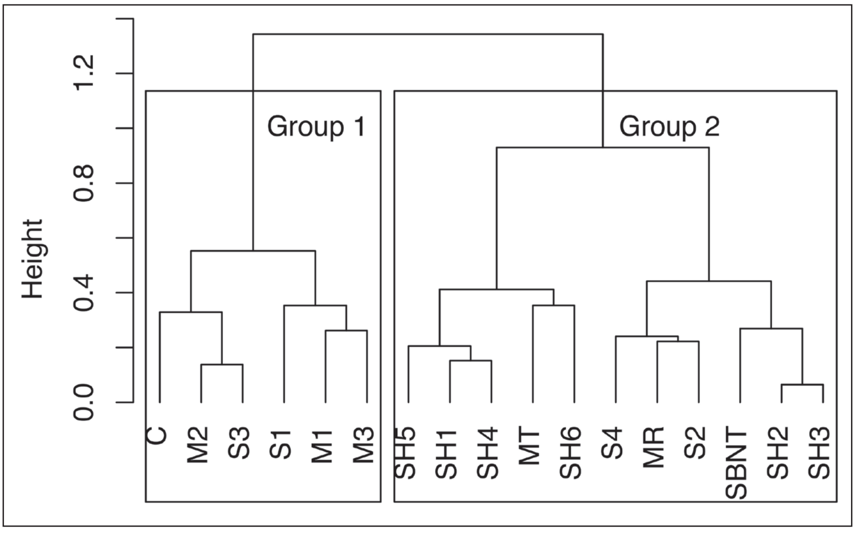

Figure 2. Cluster dendrogram of the 17 vegetation plots in sub-montane rain forests of Dominica based on trees ≥10 cm. The boxes denote the 2 groups identified in the analysis.

Table 4. Number of stems ≥10 cm dbh and percentage of individuals per plot for 8 tree species. *Amanoa caribaea* (*A. c.*), *Dacryodes excelsa* (*D. e.*), *Licania ternatensis* (*L. t.*), *Sloanea caribaea* (*Sl. c.*), *Sterculia caribaea* (*St. c.*), and *Tapura latifolia* (*T. l.*) were among the 10 most common tree species found across Dominica (Table 2). *Amanoa caribaea* was an indicator species for Group 2; *Eugenia coffeifolia* (*E. c.*) and *Miconia mirabilis* (*M. m.*) were indicator species for Group 1.

		A. c.		*D. e.*		*E. c.*		*L. t.*		*M. m.*		*Sl. c.*		*St. c.*		*T. l.*	
Plot	Group	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Northeast region																	
SH1	2	16	11	16	11	2	1	9	6	1	1	2	1	12	8	23	16
SH2	2	47	23	19	9	0	0	25	12	2	1	9	4	9	4	24	12
SH3	2	49	21	29	12	1	0	47	20	0	0	1	0	2	1	22	9
SH4	2	12	8	13	8	1	1	0	0	0	0	5	3	17	11	18	12
SH5	2	11	6	19	10	5	3	8	4	7	4	7	4	32	16	13	7
SH6	2	1	1	44	23	0	0	4	2	0	0	0	0	9	5	47	24
Northwest region																	
C	1	1	0	21	10	1	0	2	1	14	6	13	6	7	3	22	10
MR	2	59	27	25	11	0	0	0	0	27	12	6	3	13	6	2	1
MT	2	0	0	11	7	0	0	0	0	0	0	16	11	25	17	28	19
SBNT	2	57	32	21	12	0	0	3	2	1	1	4	2	4	2	49	28
Southwest region																	
M1	1	0	0	6	2	6	2	3	1	55	18	14	5	34	11	5	2
M2	1	0	0	13	5	12	5	11	4	44	17	9	3	19	7	12	5
M3	1	0	0	0	0	8	3	0	0	17	7	12	5	24	10	16	7
S1	1	0	0	4	2	23	12	0	0	15	8	18	9	16	8	9	5
S2	2	34	16	15	7	0	0	17	8	15	7	7	3	7	3	8	4
S3	1	0	0	31	13	11	5	14	6	32	13	8	3	14	6	9	4
S4	2	34	14	37	15	7	3	8	3	13	5	16	7	14	6	23	10

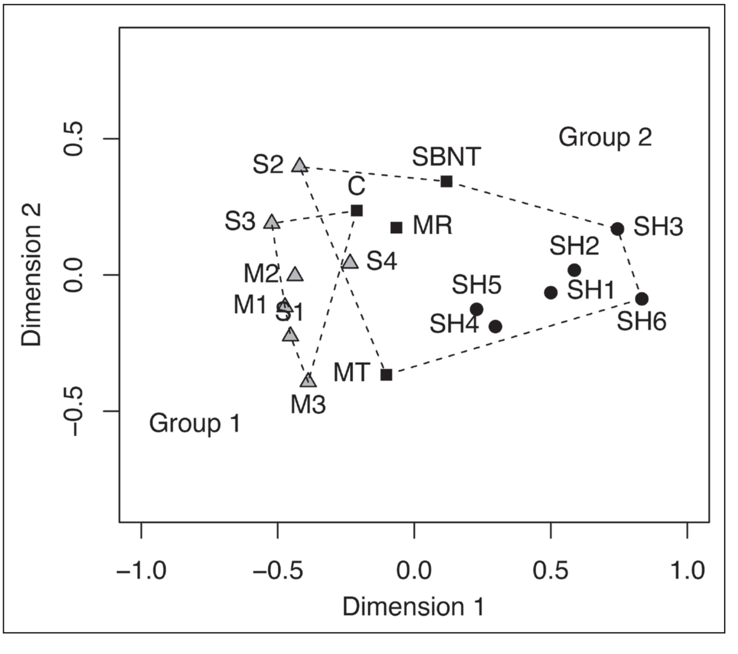

Figure 3. Non-metric multidimensional scaling ordination of seventeen 0.25-ha plots on the island of Dominica based on their similarity in species composition of trees ≥10 cm dbh. Plot codes correspond to those given in Table 1. Plots are labeled with black-filled circles in the NE region, black-filled squares in the NW, and gray-filled triangles in the SW. Dashed lines intersect or enclose plots that were grouped into 1 of 2 groups shown in Figure 2. The stress was 12.6.

species was found only in plots assigned to Group 1, they were the following: *Eugenia coffeifolia*, *Endlicheria sericea*, *Myrcia deflexa*, *Acinodendron trichotomum*, *Prestoea acuminata*, *Miconia mirabilis*, *Inga ingoides*, *Micropholis guyanensis*, *Symplocos martinicensis*, *Guarea glabra*, *Nectandra membranacea*, *Abarema jupunba*, *Myrcia fallax*, *Cyathea arborea*, and *Rauvolfia biauriculata*.

Forest structure and species diversity

The 2 vegetation groups differed significantly in forest structure and species diversity (Table 6). The group without *A. caribaea* and with more of the pioneer tree *M. mirabilis* (Group 1) had more individuals, lower tree height, greater Fisher's α diversity and rarefied species richness, and lower dominance (Fig. 4).

The geographic regions differed significantly in the number of individuals, basal area, Fisher's α, tree height, and rarefied species richness (Table 6). SW plots had more individuals and lower tree height than the northern plots. Both SW and NW regions had higher diversity (Fisher's α and rarefied species richness) than the NE plots. The NW plots had greater basal area than the NE plots (Fig. 5).

Table 5. Percentage of basal area (% of BA) and individuals (% of stems) composed by dominant tree species ≥10 cm dbh found in each of the 2 groups identified by the hierarchical clustering. * denotes canopy species (see Appendix 1) and A denotes species classified as indicator species for those particular groups. Group 1 corresponds to the *Dacryodes*-*Sloanea* association of Beard (1949), while Group 2 corresponds to a variant of this association with *Amanoa*. The species are listed in order of decreasing basal area.

Group 1			Group 2		
Species	% of BA	% of stems	Species	% of BA	% of stems
*Sloanea caribaea**	24.69	5.07	*Dacryodes excelsa**	23.26	11.70
*Dacryodes excelsa**	14.48	5.14	*Amanoa caribaea**,A	19.07	15.08
Sterculia caribaea	9.54	7.81	*Sloanea caribaea**	11.44	3.43
Tapura latifolia	7.13	5.00	*Tapura latifolia*	9.86	12.07
*Miconia mirabilis*A	6.97	12.12	*Licania ternatensis**	6.15	5.68
*Sloanea dentata**	5.65	1.58	*Sterculia caribaea*	5.77	6.76
*Byrsonima trinitensis**	5.02	3.84	*Cananga caribaea**	2.90	2.44
*Micropholis guyanensis*A	3.55	5.00	*Byrsonima trinitensis**	2.28	3.10
*Licania ternatensis**	2.16	2.05	*Sloanea dentata**	2.15	1.41
Swartzia caribaea	1.54	2.12	*Pouteria pallida**	2.05	1.60

Table 6. Results from an analysis of variance to test for differences among the 2 groups and 3 geographical regions for 3 forest structural and 3 diversity variables. An estimate of the variance explained (η^2) is also provided.

	Groups			Regions		
Variable	$F_{1,15}$	P	η^2	$F_{2,14}$	P	η^2
Number of individuals ≥10 cm/ha	7.6	0.01	0.34	5.3	0.02	0.43
Basal area (m^2/ha)	0.4	0.56	0.02	5.6	0.02	0.44
Height	10.0	0.01	0.40	5.5	0.02	0.44
Fisher's α	16.5	0.001	0.52	20.1	<0.001	0.74
E(146)	17.1	<0.001	0.53	20.1	<0.001	0.74
Berger-Parker	7.4	0.02	0.33	2.3	0.14	0.25

For the variables that significantly differed between groups and among regions, the effect size was greater for regions (Table 6). In statistical models that incorporated both region and group, region explained more of the variation for Fisher's α, rarefied species richness, basal area, and number of individuals (data not shown). The only variable that differed significantly among groups but not regions was the Berger-Parker index of dominance. The high dominance of *Amanoa caribaea* in most plots that were categorized as Group 2 (range = 0.00–0.32, average = 0.14) likely contributed to this difference.

Discussion

Vegetation associations

We found at least one vegetation association within the sub-montane rain forests we studied in Dominica, and it corresponded with the *Dacryodes*-*Sloanea*

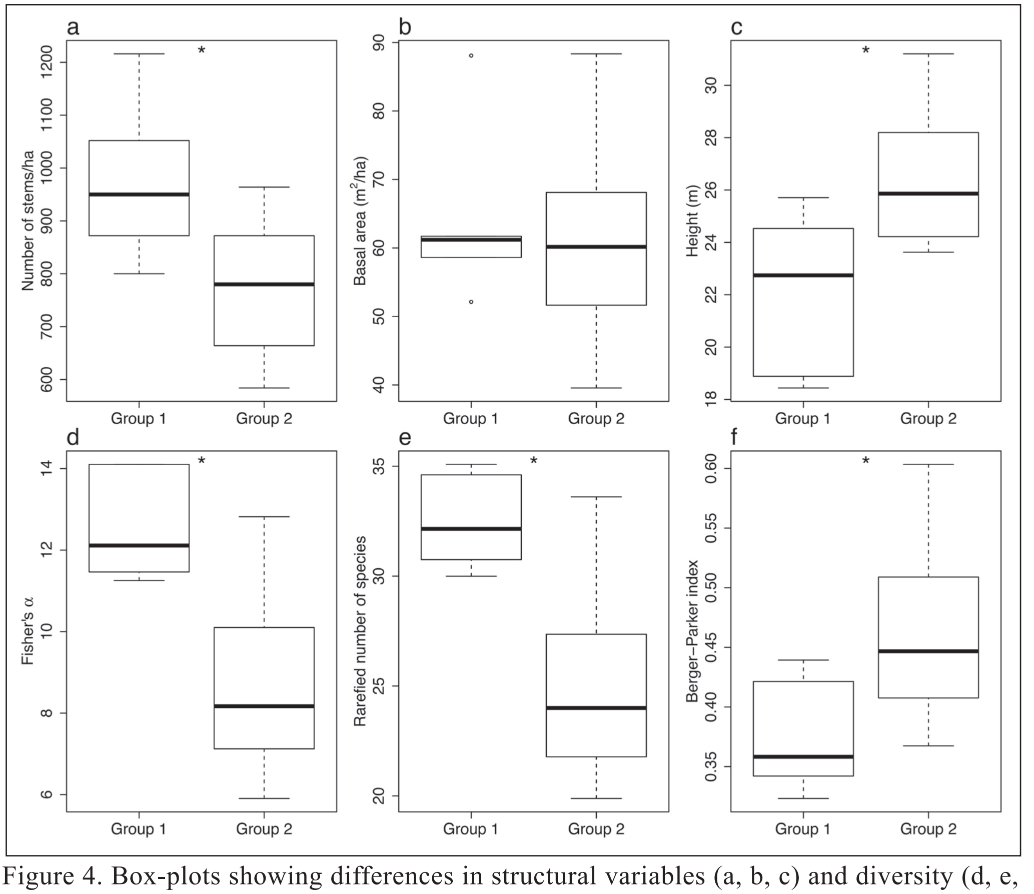

Figure 4. Box-plots showing differences in structural variables (a, b, c) and diversity (d, e, f) for the 2 vegetation groups. The bold line is the median; the upper and lower parts of the box are the upper and lower quartiles, respectively; the whiskers show the maximum and minimum values, excluding outliers; the points show outliers. Height was based on trees ≥30 cm dbh; all other structural and diversity variables were based on trees ≥10 cm dbh. Both groups are a *Dacryodes–Sloanea* association, with Group 2 also containing *Amanoa caribaea*. Significant differences between the groups (Table 5) are shown with an asterisk.

association that is found across the Lesser Antilles. Unlike Beard (1949), we did not find any forests that had a high density of *Licania ternatensis* and *Pouteria pallida*, which would have corresponded to his *Licania–Pouteria* association. We found a variant of the *Dacryodes*-*Sloanea* association that had a higher density of *A. caribaea*, higher abundance of *Licania ternatensis* and *Pouteria pallida*, and lower abundance of *M. mirabilis* (i.e., Group 2) than the typical association. However, we hesitate to call Group 2 a different association than Group 1 for several reasons.

First, the distribution of *A. caribaea* appears to be determined more by dispersal limitation than edaphic conditions. *Amanoa caribaea* was either almost absent or very common; 8 plots had 0 or only 1 individual ≥10 cm dbh, while the other 9 plots had between 11 and 59 individuals. Even plots relatively close to each other (e.g., S2 and S3; SBNT and MT) either had *A. caribaea* (S2, SBNT) or did not (S3, MT). *Amanoa caribaea* has dry, dehiscent fruit (Howard 1989), which seems

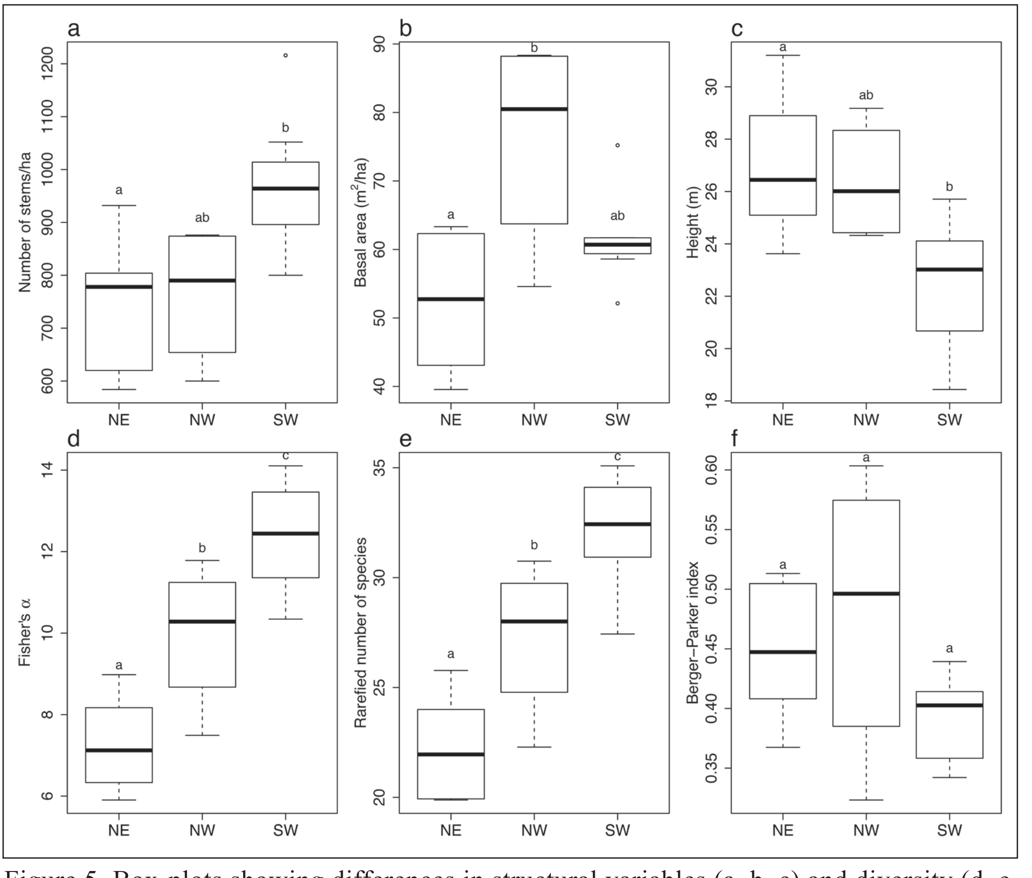

Figure 5. Box-plots showing differences in structural variables (a, b, c) and diversity (d, e, f) for the three regions (NE = northeast, NW = northwest, and SW = southwest Dominica). The bold line is the median; the upper and lower parts of the box are the upper and lower quartiles, respectively; the whiskers show the maximum and minimum values, excluding outliers; the points show outliers. Height was based on trees ≥30 cm dbh; all other structural and diversity variables were based on trees ≥10 cm dbh. Significant differences among regions based on Tukey's HSD test are noted with different letters.

likely to result in substantial dispersal limitation and therefore seedling recruitment primarily near maternal trees. As with adults, seedlings of *A. caribaea* were high in abundance in some plots, but were completely absent in others (DeWalt et al. 2015). All of this evidence points to dispersal limitation in this species.

Second, *Dacryodes excelsa* and *Sloanea caribaea* are co-dominant within the forests where *A. caribaea* occurs. The only plot in which *D. excelsa* was absent was the M3 plot in the SW, which is adjacent to a *Symphonia globulifera* (Clusiaceae) swamp, is flat, has impeded drainage, and has low canopy height. *Sloanea caribaea* was not as abundant as *D. excelsa* across plots, but the massive diameters of trees of this species contributed to its dominance in terms of basal area.

Third, vegetation group explained some forest structure and diversity variation among plots, but region tended to explain more of those differences, suggesting that the forests with *A. caribaea* do not differ just because *A. caribaea* is a co-dominant. The NE plots differed from the NW and SW in diversity and from the NW in terms of basal area. Because all 6 of the plots in the NE were classified in Group 2, they tended to drive any differences detected among the groups. The NE plots were all at lower elevation than the NW or SW plots (Table 1) and therefore likely have lower mean annual rainfall. The lower species-diversity in the NE plots may result from a number of factors, including lower rainfall, and likely are not due to the presence of *A. caribaea*.

Thus, it appears that on sites where *A. caribaea* gets established, a forest co-dominated by *Amanoa, Dacryodes*, and *Sloanea* arises. It will be very interesting to compare the forest structure and diversity of our plots to those in Guadeloupe, the only other island on which *A. caribaea* occurs and where it is also a canopy dominant (Beard 1949).

Although our results suggest that there is only one forest type in the rain forests of Dominica, we cannot rule out the possibility that we simply did not sample in areas that might be more heavily dominated by *Licania ternatensis* and *Pouteria pallida*. Beard (1949) did not specify his survey locations on Dominica, but they may have been in the east-central section of Dominica and at lower elevations of the NE, where we did not have any plots. His vegetation map of Dominica shows a large section of forest in the east-central area where this type of forest might be found. Surveys in the Central Forest Reserve or at lower elevations in the NE would help determine whether a separate association really exists or whether *Dacryodes excelsa* and *Sloanea caribaea* are always among the forest dominants.

Our results corroborate those of the Caribbean Vegetation Ecology Working Group, who identified only one forest alliance in sub-montane rain forests in the Lesser Antilles (Areces-Mallea et al. 1999). However, we recommend that the name be changed from *Dacryodes excelsa–Sloanea truncata* forest alliance to *Dacryodes–Sloanea* forest alliance to reflect the fact that *Sloanea caribaea* appears to be the most common *Sloanea* species on Dominica, St. Lucia, St. Vincent, and Grenada (Beard 1949). Even if *S. truncata* is the more common species on Martinique (Fiard 1994), there would likely be better region-wide communication and ability to compare various datasets if the dominant species of *Sloanea* is not specified.

Effect of hurricanes

The effects of hurricanes were still evident both in the structure and species composition of our plots. Disturbance effects partially explained some of the clustering of plots, although the abundance of *A. caribaea* was the primary determinant (see above). The main legacy of the hurricanes, and possibly primarily of Hurricane David, which affected the southern half of the island more than the northern half (Lugo et al. 1983), could be seen in the number of pioneer trees, particularly of *Miconia mirabilis*. The density of *M. mirabilis* was highest in the SW for trees ≥10 cm (Table 4). The association of *M. mirabilis* with Group 1 may indicate that most of the plots in this group (5 of the 7 in the SW and 1 of the northern plots) were more recently disturbed than most of the plots in Group 2 (all of the NE plots, 3 of the NW plots, and 2 in the SW). *Miconia mirabilis* was also common in one NW plot in Group 2 (Morne Rachette), which along with the Carholm plot (Group 1), may have been affected as much as the SW plots by Hurricane David. *Cecropia schreberiana*, a shorter-lived pioneer than *M. mirabilis*, was not very common (14 stems ≥10 cm total) and was only found in the SW. In addition, all *C. schreberiana* were moribund during the initial census, and 10 out of 14 had died within a year (S.J. DeWalt and K Ickes, unpubl. data), suggesting that we missed the main period when this species was common in the hurricane-disturbed plots.

In addition to having more pioneer trees, the structure of SW plots also differed from those in the NW and NE, in that the SW plots tended to have higher stem density and lower tree height, as might be expected from a forest recovering slowly from a hurricane. However, based on work in Puerto Rico (Lugo 2008), we would have expected density and basal area to increase rapidly and peak within 15 years. Even though Hurricane David struck the island 27 years before our study, density and basal area may not have returned to peak levels in our Dominica plots by the time of our 2006–2007 census because 2 additional storms, Hurricane Hugo in 1989 and Marilyn in 1995, also hit the island and presumably disturbed the rain forests where our plots were subsequently located. Alternatively, factors other than hurricane disturbance may promote higher stem density and lower tree height in the SW.

Species diversity of plots in the SW was higher than those in the northern plots, particularly the ones in NE. This higher diversity was not an effect of the higher stem density because Fisher's α and rarefied species richness are not affected by stem density. The hurricanes that passed over Dominica may have promoted species diversity, as has been found following hurricanes in Nicaragua (Vandermeer et al. 2000) and Puerto Rico (Heartsill Scalley et al. 2010). Equally likely, however, is that the lower elevation and possibly drier plots in the NE simply have lower species diversity for reasons unrelated to hurricane disturbance.

Dominican wet forest compared to others in the Caribbean

Data from only a few studies of structure, diversity, and species composition are available from plots in the Caribbean region, and just a small subset of those were conducted in the Lesser Antilles. Here we compare our results with studies of trees ≥10 cm dbh in the Luquillo Long-Term Ecological Research 16-ha plot in Puerto

Rico, part of the Greater Antilles. The Luquillo Plot is a *Dacryodes*-*Sloanea* rain forest similar to this association in the Lesser Antilles (Beard 1949).

Tree diversity was remarkably similar between forests in Dominica and the Luquillo plot. Mean Fisher's α per 1 ha at Luquillo was 9.27 (Thompson et al. 2004), compared with 10.0 per plot in Dominica. Eighty-five tree, palm, and fern species were enumerated across the 17 plots in Dominica (4.25 ha), compared to 89 and 86 species found in the censuses completed in 1993 and 1996, respectively, in the 16-ha Luquillo plot. The rain forests of Puerto Rico and Dominica are both co-dominated by *Dacryodes excelsa*. In 1990 in the Luquillo plot, *D. excelsa* made up 8% of the stems and 12% of the basal area on average for stems ≥10 cm (Thompson et al. 2002). This species had an even higher relative abundance across the plots in Dominica: 9% of stems and 20% of the basal area (Appendix 1).

Aside from sharing this co-dominant tree species and similar level of diversity, however, overall tree-species composition was quite different between the Dominica and Luquillo plots—only 18 of the 85 species from Dominica occurred in Luquillo. Furthermore, of the 10 most common trees in Dominica, only *D. excelsa* was among the 10 most common in Luquillo. Another dramatic difference between the Dominican plots and those in Puerto Rico was the relative abundance of the palm *Prestoea acuminata* var. *montana*. This species composed 32% of the stems and 13% of the basal area on average in Luquillo (Thompson et al. 2002) but only 1.7% of the stems and <0.5% of basal area in Dominica. In Puerto Rico, this palm species is an important component of disturbed rain forest, and its abundance in the Luquillo plot was likely due, at least in part, to logging and other anthropogenic disturbance (Thompson et al. 2002). *Prestoea acuminata* var. *montana* is more common at elevations above where our plots were located, and it may be an indicator of disturbance at these higher elevations (A. James, pers. observ.).

Basal-area estimates for our plots in Dominica were much higher (61.6 m^2/ha) than those reported for Luquillo (34.4 m^2/ha). Similarly, Thompson et al. (2002) and Soriano-Ressy et al. (1970) noted that basal area and tree size on Dominica were almost double that in the least-disturbed forest at Luquillo. Soriano-Ressy et al. (1970) found that the ages of the trees were relatively similar and instead attributed the differences to higher rainfall or fertility of soils in Dominica. In contrast to basal area, stem density of trees ≥10 cm was similar between Luquillo (876 individuals/ha) and Dominica (844 individuals/ha). Thus, on average the size of trees is greater in Dominica, which leads to greater stand basal area. It would be highly informative to examine differences in soil fertility among these sites.

Dominica's sub-montane rain forests are among the most intact forests in the Lesser Antilles. In addition, they are characterized by high basal area, and presumably biomass, as well as high species-diversity. Beard (1949) noted that the *Dacryodes*-*Sloanea* stands in Dominica had the highest tree-species richness of those sampled in the Lesser Antilles. Thus, our detailed measurements of trees, palms, and lianas in 17 plots across 3 regions of Dominica provide an important baseline dataset to examine the dynamics of these high-diversity, high-biomass forests over time. In addition, the preliminary comparison to structure and composition of Puerto Rican forests demonstrates similarities, and distinct differences between the Puerto Rican and Lesser Antillean versions of *Dacryodes*-*Sloanea* forests. Whether diversity, forest structure, and species composition of Dominican plots are similar to those on surrounding islands (i.e., Guadeloupe and Martinique) and farther north and south in the Lesser Antilles remains to be determined by careful comparisons of plot-based data. So far, we know that *Dacryodes excelsa*, *Tapura latifolia*, and *Amanoa caribaea* are the dominant tree species in the rain forests of Guadeloupe (Imbert et al. 1996, 1998; Rousteau 1993), and rain forests in Martinique appear to be dominated by *Dacryodes excelsa, Tapura latifolia,* and *Sloanea truncata* and to lack *A. caribaea* (Fiard 1994). A Caribbean Plot Network, similar to the network managed by the Center for Tropical Forest Science, would facilitate more detailed comparisons of stand structure, diversity, and composition as well as allow for studies of post-hurricane dynamics, as has been possible with the Luquillo plot in Puerto Rico. The Caribbean Foresters Information Sharing Platform will facilitate this work (Heartsill Scalley et al. 2016 [this issue]).

Acknowledgments

We thank L. Burgess, J. Jones, A. Martin, B. McGill, C. Riley, B. Taylor, C. Woods, D. Zoellner-Kelly, and particularly E. Stedman for help with field work; F. Axelrod and R. Graveson for assistance in identifying species; R. Charles and S. Durand for aid with obtaining permits, locating sites for plots, and sharing information on the natural history of Dominica; the Forestry, Wildlife, and Parks Division of Dominica for permits; E. Helmer for helping calculate forest-cover values; N. Osler and the Archbold Tropical Research and Education Center for substantial logistical assistance; and anonymous reviewers and Inés Sastre-de Jesús for helpful comments on the manuscript. Funding for the project was provided by Clemson University and gifts from the Bay and Paul Foundations and the SeaWorld and Busch Gardens Conservation Fund.

Literature Cited

Areces-Mallea, A., A.S. Weakley, X. Li, R.G. Sayre, J.D. Parrish, C.V. Tipton, and T. Boucher. N. Panagopoulos (Ed.). 1999. A Guide to Caribbean Vegetation Types: Preliminary Classification Systems and Descriptions. The Nature Conservancy, Arlington, VA, USA. 166 pp.

Beard, J.S. 1949. The Natural Vegetation of the Windward and Leeward Islands. Clarendon Press, Oxford, UK. 192 pp.

Boyle, B., N. Hopkins, Z. Lu, J.A. Raygoza Garay, D. Mozzherin, T. Rees, N. Matasci, M. Narro, W. Piel, S. Mckay, S. Lowry, C. Freeland, R. Peet, and B. Enquist. 2013. The taxonomic name-resolution service: An online tool for automated standardization of plant names. BMC Bioinformatics 14:16.

Chao, A., R.L. Chazdon, R.K. Colwell, and T.-J. Shen. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8:148–159.

Chao, A., R.L. Chazdon, R.K. Colwell, and T.-J. Shen. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. Biometrics 62:361–371.

Coan, M.J., E.C. Wood, and P.R. Reillo. 2007. Forest formation and land-cover map series: Dominica. Available online at http://lca.usgs.gov/lca/carland/data/dominica/dominica_lulc_final.tif.htm. Accessed 15 May 2015.

Condit, R. 1998. Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots. Springer, Berlin, Germany. 221 pp.

DeWalt, S.J., B.N. Taylor, and K. Ickes. 2015. Density-dependent survival in seedlings differs among woody life-forms in tropical wet forests of a Caribbean island. Biotropica 47:310–319.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436:686–688.

Evans, P.G.H. 1986. Dominica multiple land-use project. Ambio 15:82–89.

Evans, P.G.H. 1991. Status and conservation of Imperial and Red-necked Parrots *Amazona imperalis* and *A. arausiaca* on Dominica. Bird Conservation International 1:11–32.

Fiard, J.-P. 1994. Les forêts du nord de la Montagne pelée et des édifices volcaniques du Piton du Mont Conil et du Morne Sibérie, Martinique. Université Antilles Guyane, Sainte-Claude, Guadeloupe.

Fournier, N., F. Witham, M. Moreau-Fournier, and L. Bardou. 2009. Boiling Lake of Dominica, West Indies: High-temperature volcanic crater-lake dynamics. Journal of Geophysical Research: Solid Earth 114:B02203.

Gregoire, F.W. 1981. The dilemma of the *Amazona imperialis* and *Amazona arausiaca* parrots in Dominica following Hurricane David in 1979. Pp. 161–167, *In* R.F. Pasquier (Ed.). Conservation of New World Parrots. Smithsonian Institution Press for the International Council for Bird Preservation, Washington, DC, USA. 485 pp.

Heartsill Scalley, T., F.N. Scatena, A.E. Lugo, S. Moya, and C.R.E. Ruiz. 2010. Changes in structure, composition, and nutrients during 15 yr of hurricane-induced succession in a subtropical wet forest in Puerto Rico. Biotropica 42:455–463.

Heartsill Scalley, T., S. DeWalt, F. Korysko, G. Van Laere, K. Jacobs, S. Panka, and J. Torres. 2016. Communication from the Information Sharing Working Group: Agreement for data sharing among Caribbean Foresters. Caribbean Naturalist Special Issue 1:30–34.

Hodge, W.H. 1943. Vegetation of Dominica. Geographical Review 33:349–375.

Howard, R.A. 1989. Flora of the Lesser Antilles, Volume 5. Arnold Arboretum of Harvard University, Jamaica Plain, MA, USA. 604 pp.

Imbert, D., P. Labbe, and A. Rousteau. 1996. Hurricane damage and forest structure in Guadeloupe, French West Indies. Journal of Tropical Ecology 12:663–680.

Imbert, D., A. Roustéau, and P. Labbé. 1998. Ouragans et diversité biologique dans les forêts tropicales. L'exemple de la Guadeloupe. Acta Oecologica 19:251–262.

Lugo, A.E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: An international review. Austral Ecology 33:368–398.

Lugo, A.E., M. Applefield, D. Pool, and R.B. McDonald. 1983. The impact of Hurricane David on the forests of Dominica. Canadian Journal of Forest Research 13:201–211.

Mittermeier, R.A., R.R. Gil, M. Hoffman, J. Pilgrim, T. Brooks, C.G. Mittermeier, J. Lamoreux, and G.A.B. da Fonseca (Eds.). 2004. Hotspots revisted: Earth's biologically richest and most-threatened terrestrial ecoregions. CEMEX, Mexico, DF.

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rousteau, A. 1993. Structures, flores, dynamiques: Reponses des forests pluviales des petites antilles aux milieux montagnards. Pp. 308–321, *In* J.-L. Guillaumet, M. Belin, and H. Puig (Eds.). Phytogéographie tropicale Réalités et perspectives. ORSTOM, Paris, France. 386 pp..

Santiago-Valentin, E., and R.G. Olmstead. 2004. Historical biogeography of Caribbean plants: Introduction to current knowledge and possibilities from a phylogenetic perspective. Taxon 53:299–319.

Soriano-Ressy, M., A.P. Desmarais, and J.W. Perez. 1970. A comparison of environments of rain forests in Dominica, British West Indies, and Puerto Rico. B329–B346, *In* H.T. Odum and R.F. Pigeon (Eds.). A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico. United States Atomic Energy Commission Division of Technical Information Extension, Oak Ridge, TN, USA. 1600 pp.

Stehlé, H. 1935. Flora de la Guadeloupe et dépendances. Tome 1. Essai d'écologie et de géographie botanique. L'Imprimerie catholique, Basse Terre, Guadeloupe.

Stehlé, H. 1945. Forest types of the Caribbean Islands. Caribbean Forester (Supplement) 6:273–408.

Tanner, E.V.J., and P.J. Bellingham. 2006. Less-diverse forest is more resistant to hurricane disturbance: Evidence from montane rain forests in Jamaica. Journal of Ecology 94:1003–1010.

Tanner, E.V.J., V. Kapos, and J.R. Healey. 1991. Hurricane effects on forest ecosystems in the Caribbean. Biotropica 23:513–521.

Thompson, J., N. Brokaw, J.K. Zimmerman, R.B. Waide, E.M. Everham III, D.J. Lodge, C.M. Taylor, D.C. García-Montiel, and M. Fluet. 2002. Land-use history, environment, and tree composition in a tropical forest. Ecological Applications 12:1344–1363.

Thompson, J., N. Brokaw, J.K. Zimmerman, R.B. Waide, E.M. Everham, III, and D.A. Schaefer. 2004. Luquillo Forest Dynamics Plot, Puerto Rico, United States. Pp. 540–550, *In* E.C. Losos and E.G. Leigh Jr. (Eds.). Tropical Forest Diversity and Dynamism: Findings From a Large-scale Plot Network. University of Chicago Press, Chicago, IL, USA. 688 pp.

Vandermeer, J., I. Granzow de la Cerda, D. Boucher, I. Perfecto, and J. Ruiz. 2000. Hurricane disturbance and tropical tree-species diversity. Science 290:788–791.

Webster, P.J., G.J. Holland, J.A. Curry, and H.-R. Chang. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. Science 309:1844–1846.

Wiley, J.W., R.S. Gnam, S.E. Koenig, A. Dornelly, X. Gálvez, P.E. Bradley, T. White, M. Zamore, P.R. Reillo, and D. Anthony. 2004. Status and conservation of the family Psittacidae in the West Indies. Journal of Caribbean Ornithology 17:94–154.

Appendix 1. Species, family, life-form, number of stems, number of plots, and basal area of trees ≥10 cm dbh found across the 17 permanent plots on the island of Dominica. In addition, we include the mean diameter of the largest trees ≥10 cm dbh and mean height of the 6 tallest trees ≥30 cm dbh for species that were represented by at least 5 individuals. We recorded a total of 3589 stems across the 4.25 ha. Life-form designations are based on field observations (C = canopy tree, M = midstory tree, U = understory tree, F = fern, P = palm).

Species	Family	Life-form	# of stems	# of plots	Basal area (m^2)	Diameter (cm)	Height (m)
Abarema jupunba (Willd.) Britton & Killip	Fabaceae	C	7	5	0.20	18.2	-
Acinodendron trichotomum (Desr.) Kuntze	Melastomataceae	U	38	11	0.42	11.2	-
Alsophila imrayana (Hook.) D.S. Conant	Cyatheaceae	F	89	12	1.29	11.5	-
Amanoa caribaea Krug & Urb.	Phyllanthaceae	C	322	11	31.79	28.6	41.8
Aniba bracteata (Nees) Mez	Lauraceae	M	10	2	0.22	13.1	-
Aniba ramageana Mez	Lauraceae	M	1	1	0.95	-	-
Antirhea coriacea (Vahl) Urb.	Rubiaceae	M	9	2	0.23	16.4	-
Bunchosia polystachia (Andrews) DC.	Malpighiaceae	U	39	12	0.65	14.4	-
Byrsonima trinitensis A. Juss.	Malpighiaceae	C	122	14	8.59	20.8	32.8
Calyptranthes forsteri O. Berg	Myrtaceae	M	3	2	0.11	-	-
Cananga caribaea (Urb.) Britton	Annonaceae	C	52	6	4.82	34.8	30.3
Cecropia schreberiana Miq.	Moraceae	M	14	4	0.28	15.7	-
Chimarrhis cymosa Jacq.	Rubiaceae	C	36	7	1.66	21.6	22.4
Chrysobalanus cuspidatus Griseb. ex Duss	Chrysobalanaceae	U	2	1	0.04	-	-
Chrysophyllum argenteum Jacq.	Sapotaceae	C	1	1	0.09	-	-
Cordia sulcata A. DC.	Boraginaceae	M	2	2	0.02	-	-
Cyathea arborea (L.) Sm.	Cyatheaceae	F	12	3	0.21	14.4	-
Cybianthus rostratus (Hassk.) G. Agostini	Myrsinaceae	U	5	3	0.06	12.3	-
Dacryodes excelsa Vahl	Burseraceae	C	324	16	52.51	54.2	41.5
Drypetes glauca Vahl	Putranjivaceae	M	5	2	0.16	17.9	-
Dussia martinicensis Krug & Urb. ex Taub.	Fabaceae	C	2	2	0.21	-	-
Endlicheria sericea Nees	Lauraceae	M	50	11	0.97	13.8	-
Erythroxylum squamatum Sw.	Erythroxylaceae	U	3	2	0.08	-	-
Eugenia albicans (O. Berg) Urb.	Myrtaceae	M	3	2	0.04	-	-

Species	Family	Life-form	# of stems	# of plots	Basal area (m^2)	Diameter (cm)	Height (m)
Eugenia coffeifolia DC.	Myrtaceae	U	77	11	1.06	13.5	-
Eugenia duchassaingiana O. Berg	Myrtaceae	M	1	1	0.03	-	-
Eugenia lambertiana DC.	Myrtaceae	U	3	2	0.03	10.8	-
Euterpe broadwayi Becc. ex Broadway	Arecaceae	P	37	8	1.07	24.0	-
Faramea occidentalis (L.) A. Rich.	Rubiaceae	U	56	14	0.64	11.5	-
Ficus americana Aubl.	Moraceae	H	1	1	0.03	-	-
Gerascanthus reticulatus (Vahl) Borhidi	Boraginaceae	M	132	17	2.66	13.5	-
Graffenrieda latifolia (Naudin) Triana	Melastomataceae	U	15	4	0.19	13.3	-
Guapira fragrans (Dum. Cours.) Little	Nyctaginaceae	M	11	7	1.18	13.4	-
Guarea glabra Vahl	Meliaceae	U	10	5	0.15	13.6	-
Heisteria coccinea Jacq.	Olacaceae	U	8	2	0.09	10.9	-
Hemitelia muricata (Willd.) Fée	Cyatheaceae	F	1	1	0.01	-	-
Ilex sideroxyloides (Sw.) Griseb.	Aquifoliaceae	C	1	1	0.01	-	-
Inga dominicensis Benth.	Fabaceae	M	3	1	0.03	-	-
Inga ingoides (Rich.) Willd.	Fabaceae	M	53	8	1.33	19.7	-
Ixora ferrea (Jacq.) Benth.	Rubiaceae	U	29	11	0.36	12.0	-
Licania ternatensis Hook. f. ex Duss	Chrysobalanaceae	C	151	12	12.29	29.0	36.8
Magnolia dodecapetala (Lam.) Govaerts	Magnoliaceae	C	14	6	1.84	41.6	27.3
Marila racemosa Sw.	Calophyllaceae	U	21	8	0.42	17.2	-
Meliosma herbertii Rolfe	Sabiaceae	C	15	6	0.69	23.7	-
Miconia mirabilis (Aubl.) L.O. Williams	Melastomataceae	M	243	13	8.70	20.9	25.6
Micropholis guyanensis (A. DC.) Pierre	Sapotaceae	M	127	12	5.98	21.7	29.3
Myrcia amazonica DC.	Myrtaceae	U	1	1	0.05	-	-
Myrcia antillana McVaugh	Myrtaceae	M	4	2	0.08	-	-
Myrcia deflexa (Poir.) DC.	Myrtaceae	M	26	10	0.76	18.0	-
Myrcia fallax (Rich.) DC.	Myrtaceae	M	16	8	0.35	17.9	-
Myrcia splendens (Sw.) DC.	Myrtaceae	U	1	1	0.03	-	-
Nectandra membranacea (Sw.) Griseb.	Lauraceae	M	34	6	0.58	14.3	-
Ocotea cernua (Nees) Mez	Lauraceae	M	1	1	0.01	-	-

Species	Family	Life-form	# of stems	# of plots	Basal area (m^2)	Diameter (cm)	Height (m)
Ormosia monosperma (Sw.) Urb.	Fabaceae	M	2	1	0.17	-	-
Pouteria multiflora (A. DC.) Eyma	Sapotaceae	C	2	2	0.31	-	-
Pouteria pallida (C.F. Gaertn.) Baehni	Sapotaceae	C	36	7	3.46	20.3	34.7
Pouteria semecarpifolia (Pierre ex Duss) Pierre	Sapotaceae	M	1	1	0.05	-	-
Prestoea acuminata (Willd.) H.E. Moore var. *montana* (Graham) A.J. Hend. & Galeano	Arecaceae	P	62	10	1.13	15.4	-
Psychotria mapourioides DC.	Rubiaceae	U	1	1	0.01	-	-
Rauvolfia biauriculata Muell. Arg.	Apocynaceae	U	16	4	0.49	19.4	-
Richeria grandis Vahl	Phyllanthaceae	M	23	9	1.72	23.6	20.6
Rondeletia parviflora Poir.	Rubiaceae	U	1	1	0.03	-	-
Rudgea citrifolia (Sw.) K. Schum.	Rubiaceae	U	159	17	2.59	16.2	-
Sapium glandulosum (L.) Morong	Euphorbiaceae	C	6	4	0.59	30.9	-
Simarouba amara Aubl.	Simaroubaceae	C	36	12	1.04	21.5	-
Sloanea berteriana Choisy ex DC.	Elaeocarpaceae	C	8	5	1.19	33.7	-
Sloanea caribaea Krug & Urb. ex Duss.	Elaeocarpaceae	C	147	16	42.63	78.6	37.8
Sloanea dentata L.	Elaeocarpaceae	C	53	13	8.98	50.9	29.9
Sloanea truncata Urb.	Elaeocarpaceae	C	14	8	2.92	51.1	35.9
Sterculia caribaea R. Br.	Malvaceae	M	258	17	18.72	23.3	35.4
Stylogyne lateriflora (Sw.) Mez	Myrsinaceae	U	3	2	0.03	-	-
Swartzia caribaea Griseb.	Fabaceae	M	52	12	2.67	17.8	26.4
Symphonia globulifera L. f.	Clusiaceae	C	10	4	0.32	13.5	-
Symplocos martinicensis Jacq.	Symplocaceae	M	18	7	0.69	27.2	-
Tapura latifolia Benth.	Dichapetalaceae	M	330	17	23.22	32.8	31.5
Tovomita plumieri Griseb.	Clusiaceae	M	15	6	0.36	18.6	-
Trichilia pallida Sw.	Meliaceae	U	1	1	0.01	-	-
Trichilia septentrionalis C. DC.	Meliaceae	M	19	10	0.38	14.8	-
Unknown Laurac1	Lauraceae	M	10	4	0.23	18.2	-
Unknown Laurac2	Lauraceae	M	8	5	0.22	15.5	-
Unknown Laurac3	Lauraceae	M	1	1	0.01	-	-

Species	Family	Life-form	# of stems	# of plots	Basal area (m^2)	Diameter (cm)	Height (m)
Unknown Myrtac1	Myrtaceae	M	33	4	0.51	16.0	-
Unknown Myrtac2	Myrtaceae	M	10	2	0.34	20.7	-
Unknown Myrtac3	Myrtaceae	U	1	1	0.11	-	-
Wercklea tulipiflora (Hook.) Fryxell	Malvaceae	M	10	4	0.56	25.8	-

Synonymous species names: *Abarema jupunba* = *Pithecellobium jupunba*, *Acinodendron trichotomum* = *Miconia trichotoma*, *Alsophila imrayana* = *Cyathea imrayana, Byrsonima trinitensis* = *Byrsonima martinicensis*, *Cananga caribaea* = *Guatteria caribaea*, *Gerascanthus reticulatus* = *Cordia reticulata*, *Guapira fragrans* = *Pisonia fragrans*, *Magnolia dodecapetala* = *Talauma dodecapetala*, *Miconia mirabilis* = *Miconia guianensis*, *Micropholis guyanensis* = *Micropholis chrysophylloides*, *Myrcia amazonica* = *Myrcia leptoclada*, *Pouteria pallida* = *Oxythece pallida*, *Prestoea acuminata* var. *montana* = *Euterpe globosa*, *Sapium glandulosum* = *Sapium caribaeum*, *Sloanea truncata* = *Sloanea massoni*, *Tapura latifolia* = *Tapura antillana*