



Geographical ecology of dry forest tree communities in the West Indies

Janet Franklin¹ | Riley Andrade¹ | Mark L. Daniels² | Patrick Fairbairn³ | Maria C. Fandino⁴ | Thomas W. Gillespie⁵ | Grizelle González⁶ | Otto Gonzalez⁷ | Daniel Imbert⁸ | Valerie Kapos⁹ | Daniel L. Kelly¹⁰ | Humfredo Marciano-Vega¹¹ | Elvia J. Meléndez-Ackerman¹² | Kurt P. McLaren¹³ | Morag A. McDonald¹⁴ | Julie Ripplinger¹ | Julissa Rojas-Sandoval¹⁵ | Michael S. Ross¹⁶ | Jorge Ruiz¹⁷ | David W. Steadman¹⁸ | Edmund V. J. Tanner¹⁹ | Inge Terrill²⁰ | Michel Vennetier²¹

¹School of Geographical Sciences and Urban Planning, Arizona State University, Tempe, AZ, USA

²The Bahamas National Trust, The Retreat, Nassau, The Bahamas

³Natural Resource Conservation Department, Government of Jamaica, Kingston, Jamaica

⁴Patrimonio Natural Fondo para la Biodiversidad y Áreas Protegidas, Bogotá D. C., Colombia

⁵Department of Geography, University of California, Los Angeles, CA, USA

⁶USDA-Forest Service, International Institute of Tropical Forestry, Río Piedras, Puerto Rico

⁷National Institute of Food and Agriculture, U.S. Department of Agriculture, Washington, DC, USA

⁸Laboratoire de Biologie Végétale, UMR EcoFoG, Université des Antilles, Pointe-à-Pitre, Guadeloupe

⁹UN Environment World Conservation Monitoring Centre (UNEP-WCMC), Cambridge, UK

¹⁰Department of Botany, School of Natural Sciences, Trinity College, The University of Dublin, Dublin 2, Ireland

¹¹USDA Forest Service, Southern Research Station, San Juan, Puerto Rico

¹²Environmental Sciences, College of Natural Sciences, University of Puerto Rico, Río Piedras, Puerto Rico

¹³Department of Life Sciences, University of the West Indies, Mona, Kingston 7, Jamaica

¹⁴School of Environment, Natural Resources and Geography, Bangor University, Bangor, UK

¹⁵Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

¹⁶Department of Earth & Environment, Florida International University, Miami, FL, USA

¹⁷Grupo de Investigación Caldas, School of Social Sciences, Universidad Pedagógica y Tecnológica de Colombia, Tunja, Colombia

¹⁸Florida Museum of Natural History, University of Florida, Gainesville, FL, USA

¹⁹Department of Plant Sciences, University of Cambridge, Cambridge, UK

²⁰Turtle Spring Farm, Ferrum, VA, USA

²¹Irstea, UR RECOVER, Aix-en-Provence, France

Correspondence

Janet Franklin, Department of Botany and Plant Sciences, University of California, Riverside CA, USA.
Email: janet.franklin@ucr.edu

Present address

Janet Franklin and Julie Ripplinger, Department of Botany and Plant Sciences, University of California, Riverside, CA, USA.

Abstract

Aim: Seasonally dry tropical forest (SDTF) of the Caribbean Islands (primarily West Indies) is floristically distinct from Neotropical SDTF in Central and South America. We evaluate whether tree species composition was associated with climatic gradients or geographical distance. Turnover (dissimilarity) in species composition of different islands or among more distant sites would suggest communities structured by

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2018 The Authors. *Journal of Biogeography* Published by John Wiley & Sons Ltd

**Funding information**

Departamento Administrativo de Ciencia, Tecnología e Innovación, Grant/Award Number: 1243-13-16640; National Science Foundation, Grant/Award Number: BCS-1118340, BCS-1118369, DEB-0218039, DEB-1239764, GSS-1461496; United Nations Environmental Program, Grant/Award Number: FP/0409-76-01; USFS-Southern Research Station; Luquillo LCZO, Grant/Award Number: EAR-1331841

Editor: Ole R. Vetaas

speciation and dispersal limitations. A nested pattern would be consistent with a steep resource gradient. Correlation of species composition with climatic variation would suggest communities structured by broad-scale environmental filtering.

Location: The West Indies (The Bahamas, Cuba, Hispaniola, Jamaica, Puerto Rico, US Virgin Islands, Guadeloupe, Martinique, St. Lucia), Providencia (Colombia), south Florida (USA) and Florida Keys (USA).

Taxon: Seed plants—woody taxa (primarily trees).

Methods: We compiled 572 plots from 23 surveys conducted between 1969 and 2016. Hierarchical clustering of species in plots, and indicator species analysis for the resulting groups of sites, identified geographical patterns of turnover in species composition. Nonparametric analysis of variance, applied to principal components of bioclimatic variables, determined the degree of covariation in climate with location. Nestedness versus turnover in species composition was evaluated using beta diversity partitioning. Generalized dissimilarity modelling partitioned the effect of climate versus geographical distance on species composition.

Results: Despite a set of commonly occurring species, SDTF tree community composition was distinct among islands and was characterized by spatial turnover on climatic gradients that covaried with geographical gradients. Greater Antillean islands were characterized by endemic indicator species. Northern subtropical areas supported distinct, rather than nested, SDTF communities in spite of low levels of endemism.

Main conclusions: The SDTF species composition was correlated with climatic variation. SDTF on large Greater Antillean islands (Hispaniola, Jamaica and Cuba) was characterized by endemic species, consistent with their geological history and the biogeography of plant lineages. These results suggest that both environmental filtering and speciation shape Caribbean SDTF tree communities.

KEYWORDS

beta diversity, Caribbean, community composition, seasonally dry tropical forest, species turnover, tropical dry forest, West Indies

1 | INTRODUCTION

The West Indies, the islands of the Caribbean Basin, share a fascinating geological and biogeographical history that has resulted in complex distributions of terrestrial organisms (Iturralde-Vinent & MacPhee, 1999; Santiago-Valentin & Olmstead, 2004). These islands constitute a global biodiversity hotspot (Maunder et al., 2008), and have experienced major prehistoric (e.g. Steadman et al., 2005, 2015) and historic (Dixon, Hamilton, Pagiola, & Segnestam, 2001) human impacts on that biodiversity. Terrestrial plant communities in the West Indies include most major tropical habitats, from mangrove to cloud forest (Dinerstein et al., 1995). The West Indian terrestrial vegetation comprises a seed plant flora with 71% endemism (Acevedo-Rodríguez & Strong, 2008, 2012), a value that increases to 77% for woody species in its dry forests (DRYFLOR et al., 2016).

We focus on seasonally dry tropical forest (SDTF), also known as tropical dry forest. SDTF has been called the most threatened

tropical forest community, both globally (Gillespie et al., 2012; Miles et al., 2006) and in the West Indies (Banda-R, Weintritt, & Pennington, 2016), owing to its history of extensive human disturbance (Murphy & Lugo, 1986). We define SDTF as closed-canopy tropical and subtropical forests typically found in frost-free areas characterized by low and seasonal availability of moisture, where annual rainfall is less than ca. 1800 mm with a 3–6-month dry season receiving <100 mm per month (Lugo, Medina, Trejo-Torres, & Helmer, 2006). SDTF is distinguished from tropical savanna by its closed tree canopy and lack of fire, and from tropical rain forest, with which it shares few species, by its deciduous to semi-deciduous canopy, shorter stature, and lesser vertical complexity. SDTF is often found on fertile soils, and in the West Indies it is usually found at low elevation on the lee side of mountainous islands or in coastal zones (DRYFLOR et al., 2016).

The tree flora of the SDTF biome in the Neotropics has a shared evolutionary and biogeographical history (Dexter et al., 2015). In a

recent study evaluating SDTF diversity across the entire Neotropics, the West Indian ("Antillean") subregion was identified as floristically distinct (DRYFLOR et al., 2016). Subregional patterns have previously been identified in continental Neotropical SDTF (Neves, Dexter, Pennington, Bueno, & Oliveira Filho, 2015). A better understanding of variation in SDTF species composition and its drivers within the West Indies may further identify floristically distinct subregions—patterns of diversity useful for understanding biogeographical processes and setting regional conservation targets.

An analysis of SDTF tree species composition in just three Caribbean archipelagos (Bahamas, Puerto Rico, US Virgin Islands) suggested similarity in dominant species composition across that portion of the West Indies in spite of the differences in geological history (Franklin, Ripplinger, Marcano-Vega, Freid, & Steadman, 2015), leaving open the question of whether SDTF shows distinct subregional composition within the islands of the Caribbean Basin. Using data compiled from almost 600 forest inventory plots or relevés, recording over 650 woody plant taxa from 11 countries (22 individual islands) across the West Indies, we addressed the following research questions:

1. What are the patterns of tree species composition in Caribbean SDTF?

We expected that composition would be the least distinctive (would consist of a nested subset of species found elsewhere) in low elevation areas, young islands and areas at the climatic margins of the tropics (northern Bahamas, Florida), and most distinctive (greater species turnover among locations) in geologically old and complex, large islands of the Greater Antilles where 30–50% of plant species are island endemics. Nestedness is expected when there is a steep gradient in resource supply with strong environmental filtering at one end of the gradient (Chase & Leibold, 2003) and has also been attributed to dispersal limitations in archipelagos (Lomolino, 1996). Alternatively, a non-nested pattern dominated by turnover in species composition among all sites across space would occur if dispersal limitation, as well as speciation, was important and therefore the "local" (subregional) species pool contributed strongly to the community. This integrated time-area effect, with larger, older areas having accumulated more species (Fine & Ree, 2006), could be manifested as distinct SDTF composition in the three subregions with different geological histories (Greater Antilles, Lesser Antilles, Bahamian Archipelago).

2. How much variation in species composition among sites (species turnover across space) is related to geographical distance among sites, environmental gradients (Austin, 1985), or both?

Ecological communities are assembled from a regional species pool through the processes of speciation, biotic and abiotic filtering (selection), and dispersal (Vellend, 2010; Zobel, 1997). We expected variation to be related to geographical distance if community composition has been strongly affected by dispersal limitations and

speciation (island endemism) (e.g. Gillespie et al., 2013; Ibanez et al., 2018; Pennington, Lavin, & Oliveira-Filho, 2009), especially within large, old islands in the Greater Antilles. Alternatively, the amount of environmental variation across the study region suggests that compositional variation may also be related to environmental filtering (Franklin et al., 2013; Toledo et al., 2012). If there is environmental filtering of a region-wide species pool, for example, for species that can tolerate a strong dry season (Markestijn, Poorter, Bongers, Paz, & Sack, 2011), and poor dispersal has not been a factor limiting distributions, then species composition would be weakly structured by geographical distance. Here, we pursue both research questions by synthesizing data from 23 studies of SDTF throughout the West Indies.

2 | MATERIALS AND METHODS

2.1 | Study area and species composition data

Caribbean SDTF occurs most often on limestone (carbonate) substrates. From a tectonic perspective, Cuba and the Bahamian Archipelago lie on the North American plate, whereas all other sampled islands lie on the Caribbean plate, which is moving eastward relative to the adjoining North and South American plates (Meschede & Frisch, 1998). The Puerto Rico Archipelago and the Virgin Islands are found on the same microplate that moves somewhat independently (Hippolyte, Mann, & Grindlay, 2005) and they share biogeographical affinities (Acevedo-Rodríguez & Strong, 2008). Complex interactions during the Cenozoic (mostly large-scale strike-slip faulting) at both the northern and southern boundaries of the Caribbean plate have deformed the diverse bedrock formations on the Greater Antillean islands (Cuba, Hispaniola, Jamaica and Puerto Rico + Virgin Islands, Keppie, 2014). In contrast, the Bahamian islands and southern Florida are tectonically stable, geologically very young and consist exclusively of carbonate bedrock (Mylroie & Mylroie, 2013; Randazzo & Jones, 1997). The Lesser Antillean island arc, represented in our dataset by Guadeloupe, Martinique and St. Lucia, is the result of late Cenozoic subduction of Atlantic Ocean crust at the eastern margin of the Caribbean plate (Meschede & Frisch, 1998).

Species occurrences or abundances within sampled locations (sites) were compiled from 23 published and unpublished datasets (Table 1; Supporting Information Appendix S1 Table S1) spanning 11 regions— islands or archipelagos—across the West Indies (Figure 1a). One region is continental—the south Florida peninsula—but we will refer to islands or archipelagos for simplicity. We include data from Florida (USA) and Providencia (Colombia) because, although not considered biogeographically part of the West Indies (Acevedo-Rodríguez & Strong, 2012), they represent the northern and western limits of SDTF in the Caribbean Basin and allow us to build a region-wide understanding of species composition. Furthermore, south Florida and the Keys are part of the Caribbean Biodiversity Hotspot (Mauder et al., 2008). Sites were located from 13° to 26° N and 61° to 85° W. Elevations ranged from sea level to 884 m and median site elevation was 38 m.

**TABLE 1** Summary of community composition data sources for woody taxa in Caribbean Seasonally Dry Tropical Forest (STDF)

Region	Archipelago	Island/Location	# stems ≥ 5 cm	Sites	Citation
Bahamian Archipelago	Bahamas	Abaco, Eleuthera	4220	42	(Franklin et al., 2015)
Bahamian Archipelago	Bahamas	N. Andros	3203	12	(I. K. Smith & Vankat, 1992)
Bahamian Archipelago	Bahamas	Cat, Eleuthera, San Salvador	6061	71	(Daniels, 2016)
Bahamian Archipelago	Bahamas	Crooked Island	1739	17	J. Franklin, unpublished
Greater Antilles	Cuba	Dry forest	sXp 1339	31	(Borhidi, 1991)
Greater Antilles	Hispaniola	Los Haitises	105	1	Gentry plot (mobot.org)
Greater Antilles	Hispaniola	Sierra Martin Garcia	sXp 1130	35	(García et al., 2007)
Greater Antilles	Hispaniola	Sierra Martin Garcia	644	11	J. Franklin, unpublished
Greater Antilles	Jamaica	Bossue	27	2	D. Kelly, unpublished
Greater Antilles	Jamaica	Broom Hall, Round Hill	1257	4	(Kelly et al., 1988)
Greater Antilles	Jamaica	Hellshire Hills	684	12	(McLaren, McDonald, Hall, & Healey, 2005)
Greater Antilles	Puerto Rico	Mona Island	310	8	(Rojas-Sandoval et al., 2014)
Greater Antilles	Puerto Rico	Mona Island	sXp 660	46	(Melendez-Ackerman et al., 2016)
Greater Antilles	Puerto Rico	Northeast Puerto Rico	306	3	(Gould, González, & Carrero Rivera, 2006)
Greater Antilles	Puerto Rico	Dry forest	1369	113	FIA; (Franklin et al., 2015)
Lesser Antilles	Guadeloupe	Grand-Terre	642	6	(Imbert & Portecop, 2008)
Lesser Antilles	Martinique	Martinique	257	16	(Vennetier, 2015)
Lesser Antilles	St Lucia	St Lucia	826	21	(Gonzalez & Zak, 1996)
Lesser Antilles	US Virgin Islands	Dry forest	1077	90	FIA; (Franklin et al., 2015)
South Florida and Keys	Florida	Florida Keys	1773	9	(Ross, O'Brien, & Flynn, 1992)
South Florida and Keys	Florida	Key Largo, Florida Keys	1632	23	(Ross, Carrington, Flynn, & Ruiz, 2001)
South Florida and Keys	Florida	South Florida and Keys	2995	23	(Gillespie, 2005)
SW Caribbean	San Andrés, Providencia and Santa Catalina	Providencia	1155	60	(J. Ruiz et al., 2005)

Sites correspond to the number of sites used in the present study. # stems ≥ 5 cm is the number of tree stems ≥ 5 cm diameter at a standard height (1.3–1.45 m) included in the present study. sXp indicated species in plot abundance or presence data (rather than individual stem measurements). FIA = data from US Forest Service Forest Inventory and Analysis (Gray et al., 2012; O'Connell et al., 2014). For more details see Table S1.

Data were from ecological surveys or forest inventories between 1969 and 2016, and most consisted of stem diameter measurements at a standard height (1.3–1.45 m) for woody or arboreal taxa of seed plants identified to species level (in a very few cases to morphospecies, genus or family) in fixed-area plots. For multi-stemmed individuals, all stems above the diameter threshold were measured and each stem was treated as an observation in our study. Two studies recorded cover or Braun-Blanquet importance values for different height strata, and one recorded species presence/absence (Table 1). Plot size ranged from 28 to 1000 m², with most falling between 100 and 500 m². In total, measurements of almost 46,000 stems and 3,000 species-in-sites (abundance or occurrence) were compiled, and then stem diameter data were filtered to about 35,000 individuals ≥ 5 cm (corresponding to the largest minimum diameter in all but one of the datasets; Table S1, Table 1). While we refer to tree species for simplicity in this paper, the data include palms (Arecaceae), arboreal cacti (Cactaceae) and woody taxa typically taking a shrubby form if they had at least one stem ≥ 5 cm in diameter.

Multivariate analyses were conducted using both species relative abundance (Importance Value calculated from averaging relative

basal area and relative stem density, or from cover or Braun-Blanquet values) and the presence/absence. The results were very similar and so we emphasize results based on the presence/absence, allowing an additional dataset from Hispaniola and a total of 637 sites to be potentially included for the analysis. After sites with zero compositional Jaccard distance were eliminated (required for multivariate ordination based on a dissimilarity matrix), 572 sites remained. Most (54) of the eliminated sites were monospecific plots from the large US Forest Service's Forest Inventory and Analysis (FIA) (Gray, Brandeis, Shaw, McWilliams, & Miles, 2012) dataset for Puerto Rico and the US Virgin Islands, and their removal helped to improve the evenness of sampling across the region.

Most data were collected during the last two decades and their site locations were recorded using a hand-held global positioning system (GPS) in the field (Table S1). For datasets acquired in earlier decades, geographical coordinates were assigned from site maps and descriptions using Google Earth (Table S1). Our environmental variables consist primarily of 1-km resolution climate data that are spatially autocorrelated over long distances. For the Cuba data, only a general description of the sample location was given and these have

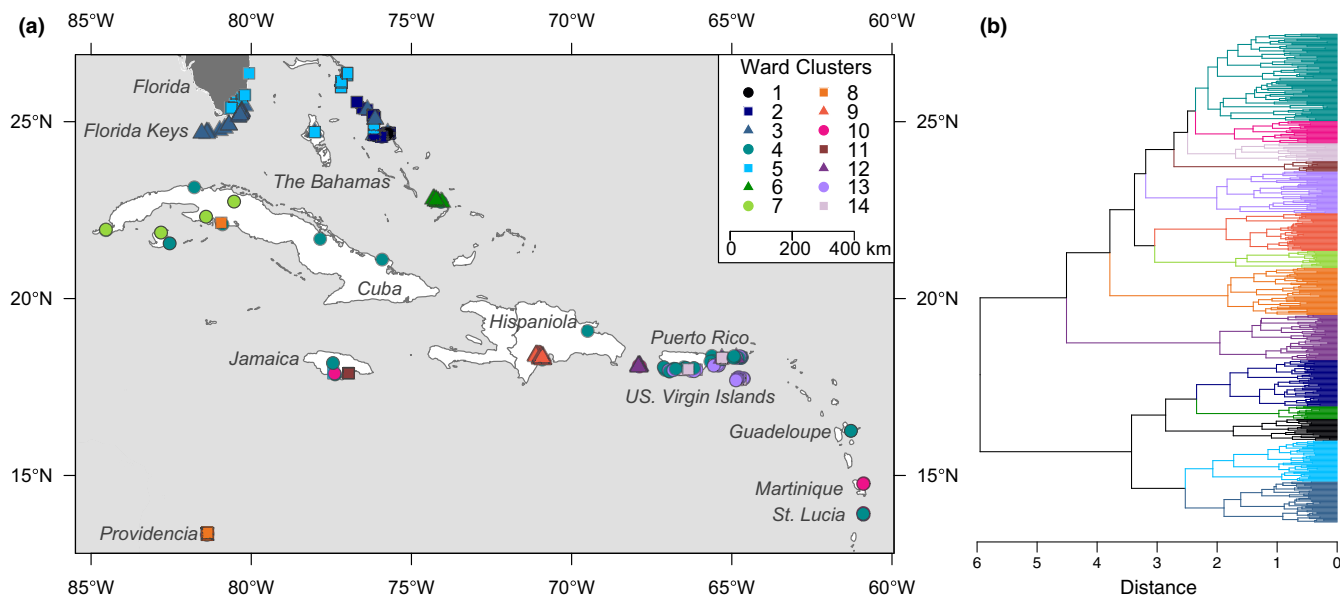


FIGURE 1 a) Map of site locations showing group membership and b) cluster dendrogram resulting from Ward's hierarchical clustering of Jaccard distance matrix among 554 sites based on the species presence/absence showing relationships among groups (using the same colour scheme for group as in (a)). Note that in (a), at this map scale individual sites are not always visible and one symbol may represent tens of nearby sites (see Tables 1 and S2) [Colour figure can be viewed at wileyonlinelibrary.com]

the lowest precision (we estimate 10 km), introducing some noise to the analysis.

2.2 | Environmental data

Bioclimatic ("Bioclim") variables (Nix & Busby, 1986) at 1-km spatial resolution were acquired from worldclim.org (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). These data only cover terrestrial areas and thus excluded the small island of Providencia, where we calculated bioclimatic variables (one value for all sites) using local climate records that featured average but not maximum and minimum monthly temperatures (Jorge Ruiz & Molano-González, 2017).

The 19 bioclimatic variables provided by worldclim.org describe seasonal and annual averages of precipitation and averages and extremes of temperature based on long-term means of monthly values. They tend to be correlated, and a subset was initially selected based on their relevance to SDTF distribution (DRYFLOR et al., 2016; Murphy & Lugo, 1986) and our ability to calculate them for Providencia. We selected annual mean temperature and precipitation, mean temperature of the warmest and coldest quarters, temperature seasonality and precipitation of the wettest and driest months (Table 2). These were further examined for multicollinearity, which led to precipitation of the wettest month being eliminated from some analyses (Table 2).

Elevation values were extracted from NASA's Shuttle Radar Topography Mission (STRM) 90-m resolution data. Elevation is considered an indirect gradient (Austin, 2002), strongly related to temperature (via the lapse rate), and precipitation (orography), but we included it because it can serve as a proxy for finer scale climate variation than is available from the Bioclim 1-km data.

2.3 | Analyses

Hierarchical agglomerative clustering using Jaccard distance and Ward's linkage (Peet & Roberts, 2013) was applied to species presence/absence data for 572 sites and 649 taxa to identify patterns of tree species composition in Caribbean SDTF (question 1). Differences among clusters were tested using analysis of variance based on 999 permutations (PERMANOVA, Anderson, 2001). Patterns of similarities and differences among groups identified by clustering, and their distribution with respect to environmental gradients, were visualized using indirect ordination based on non-metric multidimensional scaling (NMDS, Clarke, 1993). Indicator species analysis (Dufrêne & Legendre, 1997) identified species characteristic of the groups of sites identified by hierarchical clustering. The multivariate vegetation analyses used are robust to variations in forest plot sizes ranging from 50 to 1000 m² (Otyková & Chytrý, 2006), encompassing most of the range found in this study. We were able to use Importance Value (IV) and stem density (from the plots where those were measured) to evaluate patterns of species frequency versus abundance within and among groups defined in the multivariate analyses.

The degree of correlation between climate predictor variables and geographical coordinates was calculated. Principal components analysis was applied to the bioclimatic variables for the sites and then analysis of variance was used to evaluate whether climatic differences were due to sites belonging to different islands/archipelagos. Beta diversity (compositional dissimilarity among sites) was partitioned into nested and turnover components (question 1) using the R package 'betapart' (Baselga & Orme, 2012). We assessed the importance of climate versus geographical distances between sites



TABLE 2 Bioclimatic and geographical variables analysed and their ranges of values for the 572 West Indian sites analysed

Abbreviation (bio)	Variable	Range
MAT (bio1)*	Annual Mean Temperature	21.0–27.4°C
CV_T (bio4)*	Temperature Seasonality (Coefficient of Variation)	7.8–33.1
Twarm (bio10)*	Mean Temperature of Warmest Quarter	22.1–28.6°C
Tcold (bio11)*	Mean Temperature of Coldest Quarter	19.2–25.0°C
MAP (bio12)*	Annual Precipitation	164–2026 mm
Pwet (bio13)	Precipitation of Wettest Period (month)	33–336 mm
Pdry (bio14)*	Precipitation of Driest Period (month)	2–98 mm
alt	'Altitude' (elevation above sea level)	0–884 m
lat	Latitude	13.3° to 26.4°N
long	Longitude	60.9° to 84.5°W

bio# is the Bioclim variable name (used in worldclim.org).

*Predictors used in generalized dissimilarity modelling (GDM). Bioclimatic variables were from worldclim.org. Elevation from NASA Shuttle Radar Topography Mission (STRM) 90 m data downloaded using the `getData()` function in the R package `raster`. Latitude and longitude were from GPS data recorded for each site or, if not available, approximated using methods described in Table S1.

in explaining dissimilarity in species composition (question 2) using generalized dissimilarity modelling (GDM, Ferrier, Manion, Elith, & Richardson, 2007) applied to the same Jaccard community distance matrix (appropriate for beta diversity studies, Legendre & Cáceres, 2013) used in our clustering and ordination analyses. A reduced set of bioclimatic predictors (Table 2) was used; because elevation represents an indirect gradient, and precipitation of the wettest month (Pwet, bio13) was correlated with mean annual precipitation (MAP, bio12; $r = .89$), we dropped these two variables from the GDM. GDM was implemented using the R package “`gdm`” (Manion, Lisk, Ferrier, Nieto-Lugilde, & Fitzpatrick, 2016). We compared the variance explained by different models computed with both climate and geographical distance as predictors versus models with only climate or only geographical distances as predictors (Legendre, 2008). The importance of each variable in driving compositional dissimilarity was calculated from the curves produced by GDM (functions showing how beta diversity varies with each environmental and geographical predictor while holding all other variables constant) by summing the coefficients of the partial regressions (Fitzpatrick et al., 2013).

Analyses (clustering, NMDS, analysis of variance, GDM, variance partitioning) were repeated aggregating taxa to the genus level as a first-order approximation of the functional, rather than taxonomic, similarity of sites, assuming that plant species in the same genus share similar traits and ecological requirements, and play similar roles

in the community. Detrended correspondence analysis (DCA, Hill & Gauch, 1980), a form of indirect ordination, was also performed for both species and genus data in order to compare their relative amount of turnover (compositional dissimilarity) in terms of ordination axis length (in units of standard deviation of species turnover). We expected that less turnover of genera would reflect greater functional similarity of TDF throughout the West Indies as compared to the species-level analysis which reflects more local patterns of speciation and endemism. Multivariate community analyses were performed using the R packages ‘`vegan`’ (Oksanen et al., 2011) and `labdsv` (Roberts, 2012). All analyses were done using R 3.3.3 (R Core Team, 2017) (script provided in Supporting Information Appendix S2).

3 | RESULTS

3.1 | Biogeography of community composition

Clustering based on Jaccard distance calculated from the presence/absence of species, cut at a multivariate Ward's distance of 2, yielded 14 groups of sites (Figure 1b) that were significantly different ($R^2 = .41$; $F = 29.9$; $p = .001$). Clusters consisted primarily of sites within archipelagos or nearby archipelagos (Figure 1; Figure 2 vs. 3; Table S2), although some clusters overlapped (Fig. S1). The most distinct was cluster 8 (most sites from Providencia). Island/archipelago explained 30% of the variation in the community distance matrix (PERMANOVA; $F = 24.2$, $p = .001$).

The SDTF in the West Indies is characterized by several species-rich plant families including Fabaceae, Myrtaceae (see also Acevedo-Rodríguez & Strong, 2012), Polygonaceae, Rhamnaceae and Sapindaceae (Table 3). Indicator species analysis (Table 3; Table S3) revealed the following patterns: Northern Caribbean groups 1, 2 (Cat, Eleuthera, and San Salvador islands), and 6 (Crooked Island) are clusters of Bahamian sites characterized by *Coccothrinax argentata*, *Vachellia choriophylla* and *Bursera inaguensis* respectively. Northern Caribbean group 3 (Florida Keys and Bahamas) has *Piscidia piscipula*, *Metopium toxiferum* and *Coccoloba diversifolia* as indicator species, while group 5 (Abaco, Andros and Eleuthera in the Bahamas, Florida peninsula, Florida Keys, Jamaica) is characterized by *Exothea paniculata*, *Sideroxylon salicifolium* and *Lysiloma sambicu*. Indicator species for Northern Caribbean groups include few endemics (Table S3).

Group 4 includes 102 sites from throughout the region (47 from Puerto Rico but others from Cuba, Guadeloupe, Jamaica, Providencia, Crooked Island) with *Maytenus laevigata* and *Pictetia aculeata* (West Indian endemics) as characteristic species, although neither Indicator Values nor p -values are strong (i.e. not $>.1$ or $<.01$ respectively) for species associated with this group (Tables 3, S3). Lesser Antillean group 10 (Martinique, St. Lucia, with a few sites from the Greater Antilles) had Lesser Antillean (*Tabebuia pallida*) and West Indian (*Coccoloba pubescens*) endemics as indicator species. Group 8 includes 53 of 58 sites from Providencia (and two sites from the Greater Antilles), with *Vachellia collinsii* and *Campomanesia* sp. as indicators.

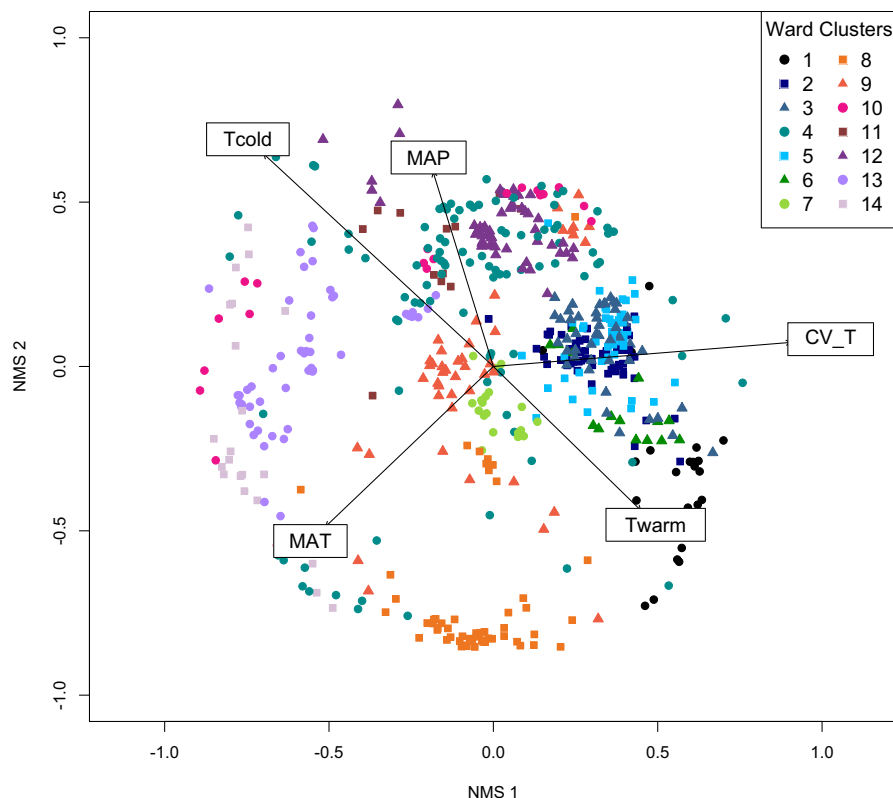


FIGURE 2 Sites arrayed in two dimensions based on indirect ordination, non-metric multidimensional scaling (NMS), applied to a Jaccard distance matrix calculated from the presence/absence of species in sites, labelled by cluster number (clustered using Ward's distance). Vector length indicates degree of correlation of environmental variables with ordination axes (bioclimatic and geographical abbreviations as in Table 2) [Colour figure can be viewed at wileyonlinelibrary.com]

Large Greater Antillean islands tend to be distinctive in their composition. Group 7 includes 20 of the 30 sites from Cuba, group 11 includes 12 of the 16 sites from Jamaica, and Group 9 includes 44 of 46 sites from Hispaniola, each characterized by many high indicator value species, including endemics (Table 3; Table S3). Group 12 comprises sites from Mona (in the Puerto Rico Archipelago) and the main island of Puerto Rico with *Coccoloba microstachya* and other West Indian endemics as indicators. Two groups (13, 14) that characterize “novel ecosystems” sampled mainly in Puerto Rico and the US Virgin Islands (Table S2), were dominated by non-native and invasive tree species—*Leucaena leucocephala* (Wolfe & Van Bloem, 2012) and *Melicoccus bijugatus* in group 13, and *Vachellia farnesiana* and *Prosopis pallida* in group 14.

Twelve of the 20 most frequently recorded native species occurred in eight or more of the 14 groups (Table S4). Dry forest specialist *Bursera simaruba* was the most widespread species, and was often abundant (as measured by IV or stem density) or even dominant in sites where it was recorded (see also Lugo et al., 2006). *Bourreria baccata*, *Krugiodendron ferreum*, *Amyris elemifera* and *Eugenia axillaris* also were widespread and moderately abundant (occurring in 9–12 groups, 17–26% of sites, with 0.01–0.09 average IV). *Coccoloba diversifolia*, *Metopium toxiferum*, *Swietenia mahagoni* and *Lysiloma latisiliquum* were moderately widespread and abundant (7–8 groups, 11–20% of sites, 0.09–0.16 IV; Table S4).

At the genus level (298 taxa in 569 sites), there was less overall turnover and greater overlap among sites from different islands or

archipelagos. For example, a detrended correspondence analysis (DCA) based on species data had greater eigenvalues and axis lengths (in units of standard deviation of species turnover) than a DCA of genera. DCA axis 1 length for species data was 7.6, while for genus data it was 3.9 (eigenvalues 0.71 and 0.42 respectively). In GDM there was less total variance explained in the genus-level distance matrix (34%) than at the species level (40%), and less overlap of climate and geographical distance (27% for species, 14% for genera). The general pattern of proportions variance explained by environment versus geographical space is similar—10% climate, 1% geographical distance, 14% combined at the genus level. At the aggregated taxonomic level, however, the Lesser Antillean sites (St. Lucia, Martinique) clustered with those from Puerto Rico and USVI, and from other Greater Antillean islands (Table S5). Also, the Northern Caribbean clusters were more central to the ordination, sharing many genera with the other groups (Fig. S2).

Almost all variation in site environmental data (bioclimatic variables and elevation, Table 2) was explained by archipelago membership (999 permutations; $R^2 = .95$; $F = 1082$; $p = .001$). Higher latitude Florida and Bahamas have greater temperature seasonality, higher average temperature of the warmest quarter, and lower average temperature of the coolest quarter. Lower latitude Providencia and St. Lucia have higher mean annual temperature and lower mean annual precipitation. Easterly (less negative) longitude Puerto Rico and the US Virgin Islands have higher average temperature of the coldest quarter, lower temperature of the warmest quarter and lower temperature seasonality. Hispaniola, Puerto Rico and US Virgin

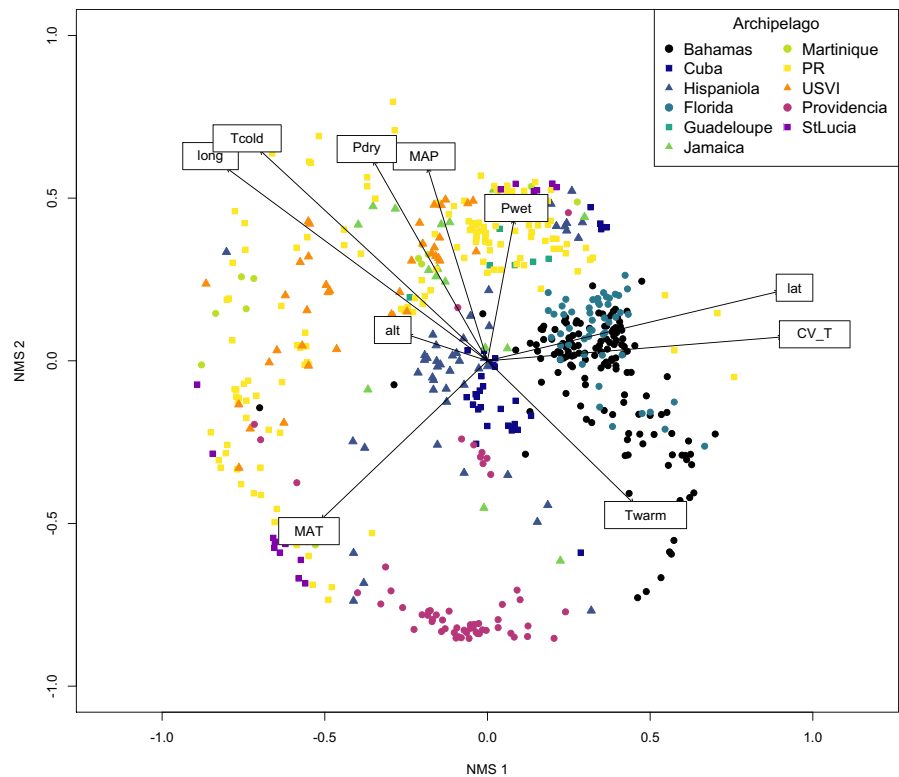


FIGURE 3 Sites arrayed in two dimensions based on indirect ordination, non-metric multidimensional scaling (NMS2), applied to a Jaccard distance matrix calculated from the presence/absence of species in sites, labelled by archipelago. Vectors indicate correlation of environmental (bioclimatic and geographical abbreviations as in Table 2) variables with ordination axes. PR = Puerto Rico. USVI = US Virgin Islands elevation [Colour figure can be viewed at wileyonlinelibrary.com]

Islands include higher elevation SDTF sites (Figure 3; Fig. S3), the highest being 884 m on the leeward side of Sierra Martín García, Dominican Republic.

3.2 | Geographical and bioclimatic gradients

Essentially all variance in the compositional dissimilarity matrix was attributed to species turnover among sites (99.6%) rather than nested patterns of species composition in sites (Jaccard dissimilarity based on the presence/absence) by beta partitioning. Most explained variance in the dissimilarity matrix was explained by climatic dissimilarity (12%), or shared geographical distance and climate (27%) and very little by distance alone (1%; Figure 4). Climate was strongly geographically structured (Figure 3, Fig. S3). Precipitation of the driest month and average temperature of the coldest quarter were the climate variables most important in explaining variance in the dissimilarity matrix (Table 4).

4 | DISCUSSION

A recent study of SDTF throughout the Western Hemisphere placed Caribbean (Antillean) SDTF as distinct from dry forest in the continental Neotropics, characterized by a high proportion of endemic tree species (DRYFLOR et al., 2016). We have further demonstrated intraregional patterns of species composition in West Indian dry forests, characterized by species turnover among archipelagos and islands (e.g. Franklin et al., 2013; Ibanez et al., 2018). Turnover is

correlated with climatic variation, which in turn is strongly geographically structured (T. W. Smith & Lundholm, 2010) such that most variation in climate is explained by archipelago.

Climate and climate + distance accounted for most of the (explained) variance in site compositional dissimilarity. A strong climate signal would be expected if comparing wet and seasonally dry tropical forests in the region, as has been shown globally (Guan et al., 2015). However, our study, like Neves et al. (2015), identified climate variation associated with SDTF variation within a Neotropical subregion. Inter-site geographical distance explains very little additional variance. In other words, nearby SDTF sites on well-sampled islands could be quite dissimilar owing to fine-scale environmental heterogeneity. Spatial vegetation heterogeneity is not uncommon in water-stressed environments including SDTF (Gerhardt & Hytteborn, 1992), especially in karstic settings (Zhang, Hu, & Hu, 2014). Within our study region, for example, on Mona island the abundance of tree species is associated with fine-scale soil nutrient variation (Meléndez-Ackerman et al., 2016). Furthermore, there are functional physiological differences among species that are associated with soil conditions including available moisture (Medina, Cuevas, Marcano-Vega, Meléndez-Ackerman, & Helmer, 2017).

While we found very little effect of distance alone on composition, suggesting that dispersal limitation is not important in shaping SDTF composition, species composition differed among archipelagos, a pattern that could be consistent with dispersal limitation (Franklin et al., 2013). We are not able to completely isolate climate versus distance effects in our study given the strongly geographically structured climate.



TABLE 3 Indicator taxa for 14 vegetation groups in the West Indies established by clustering, and islands. Top five species with indicator values (IV) >0.5 or, if none >0.5, the top three values are shown

Cluster	Islands	Species (Family)	IV	Probability
1	Cat, Eleuthera, San Salvador (Bahamas)	<i>Coccothrinax argentata</i> (Arecaceae)	0.47	0.001
		<i>Casuarina equisetifolia</i> * (Casuarinaceae)	0.35	0.001
		<i>Sabal palmetto</i> (Arecaceae)	0.17	0.001
2	Cat, Eleuthera, San Salvador (Bahamas)	<i>Vachellia choriophylla</i> ^W (Fabaceae)	0.37	0.001
		<i>Reynosa septentrionalis</i> (Rhamnaceae)	0.24	0.001
3	Florida Keys, Eleuthera, Andros, Cat (Bahamas)	<i>Piscidia piscipula</i> (Fabaceae)	0.42	0.001
		<i>Metopium toxiferum</i> (Anacardiaceae)	0.24	0.001
		<i>Coccoloba diversifolia</i> (Polygonaceae)	0.22	0.001
4	Puerto Rico; USVI; Cuba; Guadeloupe; Jamaica; Providencia; Crooked (Bahamas)	<i>Maytenus laevigata</i> ^W (Celastraceae)	0.09	0.009
		<i>Pictetia aculeata</i> ^{GA} (Fabaceae)	0.05	0.042
		<i>Myrciaria floribunda</i> (Myrtaceae)	0.05	0.042
5	Abaco, Andros, Eleuthera (Bahamas); Florida; Florida Keys; Jamaica	<i>Exothea paniculata</i> (Sapindaceae)	0.34	0.001
		<i>Sideroxylon salicifolium</i> (Sapotaceae)	0.25	0.001
		<i>Lysiloma sabicu</i> (Fabaceae)	0.21	0.001
		<i>Myrsine floridana</i> (Primulaceae)	0.05	0.042
6	Crooked (Bahamas)	<i>Bursera inaguensis</i> ^W (Burseraceae)	0.91	0.001
		<i>Guapira obtusata</i> (Nyctaginaceae)	0.52	0.001
		<i>Thouinia discolor</i> ^B (Sapindaceae)	0.51	0.001
7	Cuba	<i>Oxandra lanceolata</i> ^{GA} (Annonaceae)	0.89	0.001
		<i>Zuelania guidonia</i> (Salicaceae)	0.84	0.001
		<i>Cecropia peltata</i> (Urticaceae)	0.77	0.001
		<i>Amyris balsamifera</i> (Rutaceae)	0.77	0.001
		<i>Cedrela odorata</i> (Meliaceae)	0.77	0.001
8	Providencia; Puerto Rico; Cuba	<i>Vachellia collinsii</i> (Fabaceae)	0.71	0.001
		<i>Campomanesia</i> sp. (Myrtaceae)	0.40	0.001
		<i>Euphorbia cotinifolia</i> (Euphorbiaceae)	0.36	0.001
9	Hispaniola	<i>Senna atomaria</i> (Fabaceae)	0.66	0.001
		<i>Pilosocereus polygonus</i> (Cactaceae)	0.57	0.001
		<i>Guaiacum officinale</i> (Zygophyllaceae)	0.49	0.001
10	Martinique; St. Lucia; Jamaica	<i>Tabebuia pallida</i> ^{LA} (Bignoniaceae)	0.52	0.001
		<i>Coccoloba pubescens</i> ^W (Polygonaceae)	0.42	0.001
		<i>Lonchocarpus punctatus</i> (Fabaceae)	0.18	0.001
11	Jamaica	<i>Comocladia velutina</i> ^J (Anacardiaceae)	1.00	0.001
		<i>Linociera</i> sp. (Oleaceae)	0.98	0.001
		<i>Bauhinia divaricata</i> ^H (Fabaceae)	0.76	0.001
		<i>Casearia sylvestris</i> (Salicaceae)	0.76	0.001
		<i>Sarcomphalus laurinus</i> ^J (Rhamnaceae)	0.74	0.001
12	Mona, Puerto Rico	<i>Coccoloba microstachya</i> ^W (Polygonaceae)	0.69	0.001
		<i>Reynosa uncinata</i> ^W (Rhamnaceae)	0.46	0.001
		<i>Stenostomum acutatum</i> ^W (Rubiaceae)	0.35	0.001
13	Puerto Rico; USVI; Mona; Providencia	<i>Leucaena leucocephala</i> * (Fabaceae)	0.29	0.001
		<i>Trema micrantha</i> (Cannabaceae)	0.09	0.01
		<i>Melicoccus bijugatus</i> * (Sapindaceae)	0.08	0.01
14	Puerto Rico; USVI	<i>Vachellia farnesiana</i> * (Fabaceae)	0.50	0.001
		<i>Prosopis pallida</i> * (Fabaceae)	0.34	0.001
		<i>Pithecellobium dulce</i> (Fabaceae)	0.17	0.001

Endemic to ^B = Bahamas; ^C = Cuba; ^{GA} = Greater Antilles; ^H = Hispaniola; ^{LA} = Lesser Antilles; ^P = Puerto Rican Bank; ^J = Jamaica; ^W = West Indies; * = non-native, USVI = U.S. Virgin Islands.

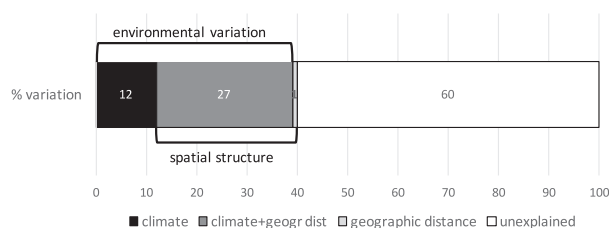


FIGURE 4 Proportion of variance (% variation) in compositional dissimilarity between sites (turnover or beta diversity) explained by climate variables, geographical distance (1%), their shared variation (27%), and unexplained variation, based on generalized dissimilarity modelling (GDM) of Jaccard distance matrix from presence/absence data

Floristic distinctions within the West Indies are enhanced by endemism in the three largest islands. One third to one half of the seed plant species found there are endemic to Jamaica (32%), Hispaniola (42%) and Cuba (51%), compared to the Lesser Antilles (14%), Puerto Rico and the Virgin Islands (14%), and the Bahamian Archipelago (9%) (Acevedo-Rodríguez & Strong, 2012). These patterns are reflected in the tree communities of the SDTF where we found similarities between the Bahamas and Florida, between the Puerto Rican Bank (Puerto Rico + Virgin Islands) and the Lesser Antilles, and even between these northern and southeastern subregions (see also Franklin et al., 2015). The most distinctive floristic expressions of SDTF, characterized by endemic indicator species, were found on Hispaniola, Jamaica and Cuba. Providencia, far from the other sampled islands, also supported distinct SDTF, although, as previously shown, it has greater floristic affinities with the West Indies than with Central America (J. Ruiz & Fandiño, 2010; J. Ruiz, Fandiño, & Chazdon, 2005).

The subregional patterns found in this study are consistent with the geological and biogeographical history of the West Indies. Much of the current Greater Antilles has been continuously above water since the Middle Eocene (Iturralde-Vinent & MacPhee, 1999), and so is much older than the Lesser Antilles and the Bahamian Archipelago. The Greater Antilles share part of their biogeographical history with southern Mexico and Central America where cooling and drying may have begun to shape modern plant communities in the Miocene and Pliocene (reviewed in Santiago-Valentin & Olmstead, 2004). Indeed,

TABLE 4 Predictor variable relative importance (Importance) in generalized dissimilarity model (GDM) based on Jaccard distance matrix from species-in-sites presence/absence data. Variables as in Table 2

Environmental variables	Importance
Precipitation of Driest Period (Pdry)	0.14
Mean Temperature of Coldest Quarter (Tcold)	0.09
Mean Temperature of Warmest Quarter (Twarm)	0.05
Annual Mean Temperature (MAT)	0.03
Annual Precipitation (MAP)	0.03
Geographical (lat/long)	0.03
Temperature Seasonality (CV_T)	0.02

Pliocene climatic changes are thought to have shaped the biogeography and distribution of SDTF plants throughout the Neotropics (Linares-Palomino, Oliveira-Filho, & Pennington, 2011).

Biogeographical patterns based on plant phylogenies suggest that many West Indian lineages have origins in Mexico and Central America, whereas others originated within the Caribbean region (Santiago-Valentin & Olmstead, 2004). Overwater dispersal played an important role in interchanges of plant taxa both between the continents and among other land masses in the Caribbean Basin (Pennington & Dick, 2010), predating the late Pliocene Central American isthmian connection (O'Dea et al., 2016). Contemporary West Indian (Antillean) dry forests also share the greatest number of species with dry forests in Mexico and Central America/northern South America (DRYFLOR et al., 2016; Linares-Palomino et al., 2011). When analysed at a higher taxonomic level, we found Lesser Antillean SDTF to be similar to Greater Antillean, reflecting that the Lesser Antilles are geologically young (lack of genus-level endemism) and that their flora is largely Antillean rather than South American in origin (Acevedo-Rodríguez & Strong, 2012).

Contrary to our first prediction, we did not find that subtropical northern Bahamas and Florida supported a depauperate (nested) subset of Caribbean SDTF diversity. This is in contrast to nested patterns found over smaller spatial extents in response to habitat fragmentation (Ross, Sah, Ruiz, Spitzig, & Subedi, 2016). While the Bahamian archipelago is geologically young and does not support high levels of seed plant endemism (Acevedo-Rodríguez & Strong, 2012), we found that SDTF composition in this northern subregion is distinct within the Caribbean Basin (Franklin et al., 2015), consistent with the climatic differences found there (Figure 3; Fig. S3). West Indian SDTF tree species that characterize this subregion may be widely distributed but are not typical (indicators) of other subregions (Table 3), suggesting environmental sorting on the climatic gradient represented in our study (e.g. Table S3).

The high species turnover found in this study is driven by the many less common species that are important within and restricted to archipelagos or subregions. In contrast to broader scale Neotropical patterns (DRYFLOR et al., 2016), however, some widespread species also are found frequently (in many sites) and across many archipelagos or groups in the West Indies. These widespread "generalist" species may be those that are best adapted to recover from hurricane disturbance by coppicing, withstand seasonal drought and/or tolerate edaphic extremes (Murphy & Lugo, 1986; Rojas-Sandoval et al., 2014; Van Bloem, Murphy, & Lugo, 2003).

Future work is needed to better understand the effects of both natural and human disturbance on patterns of Caribbean SDTF composition. Hurricanes are an important natural disturbance in the Caribbean (Mumby, Vitolo, & Stephenson, 2011) driving forest dynamics (Gannon & Martin, 2014; Tanner, Rodríguez-Sánchez, Healey, Holdaway, & Bellingham, 2014), whereas continental Neotropical SDTF experiences fewer hurricanes on average (Bullock, Mooney, & Medina, 1995). Human disturbance includes forest clearing (Chazdon, 2014) and selective tree removal (Murphy & Lugo, 1986). Prehistorically and historically, humans have greatly reduced populations of



birds and other vertebrate dispersers of SDTF seeds on islands (e.g. Steadman, 2006; Steadman et al., 2005). In contrast with continental SDTF where wind dispersal of seeds is common (Bullock, 1995; Pennington, Prado, & Pendry, 2000), bird dispersal dominates Caribbean SDTF (Ray & Brown, 1994). Disturbance history is undoubtedly an important factor affecting site composition in our study but knowledge of the disturbance history of sites included in our study was very uneven among datasets and therefore, we could not directly analyse disturbance as factor. We did identify some West Indian SDTF tree communities that were dominated by non-native and invasive species (see also Franklin et al., 2015).

Low similarity and high turnover across space in this study suggest that conservation areas should range across West Indian countries and subregions in order to protect SDTF diversity (DRYFLOR et al., 2016). Our study provides unprecedented detail on the biogeography of woody SDTF species in the West Indies, supporting conservation and restoration decision-making in the region, but also highlighting data gaps. At the 2013 Caribbean Foresters Meeting, the National Forests Inventories Working Group noted that their most recent forest inventories were over 20 years old, and some Caribbean islands have never conducted a national forest inventory (Marcano-Vega et al., 2016). SDTF in the West Indies is in a critical state (Banda-R et al., 2016) and there is an urgent need for regionally coordinated forest inventories and monitoring.

ACKNOWLEDGEMENTS

Funding from the US National Science Foundation (BCS-1118340, BCS-1118369, and GSS-1461496) to JF and DWS supported their data collection in The Bahamas and Dominican Republic, the latter work also funded by the Florida Museum of Natural History Biodiversity Seed Fund. Funding from COLCIENCIAS (grant number 1243-13-16640), supported JR for data collection in Providencia, Colombia. Data collected by GG was supported by grants DEB-0218039 and 1239764 from the National Science Foundation to the Institute of Tropical Ecosystem Studies, University of Puerto Rico, and the United States Department of Agriculture (USDA) Forest Service (USFS), International Institute of Tropical Forestry (IITF) as part of the Luquillo Experimental Forest Long-Term Ecological Research Program. Additional support was provided by the Luquillo LCZO grant (EAR-1331841). The USFS FIA program for Puerto Rico and the US Virgin Islands is jointly funded and conducted by the USFS-Southern Research Station-FIA and the USFS IITF. Fieldwork in Bosue, Jamaica was supported by UNEP Project No. FP/0409-76-01. C. M. Hulshof, T. Heartsill and E. Helmer provided information, suggestions and contacts. T. Ibanez shared advice and R code for data analysis. DryFlor.org (T. Pennington, K. Banda-R) shared a digital version of published data from Hispaniola. JF and DWS thank Y. Encarnación Piñero, T. Clase, L. Majure and D. Soltis for assistance in the field in the Dominican Republic. We thank K. Dexter, R. T. Pennington, O. Vetaas and an anonymous reviewer for comments that greatly improved the manuscript.

DATA ACCESSIBILITY

In support of reproducible science, the aggregated species presence/absence in sites, species list and environment by site data used in this study are deposited in the University of California—Riverside DASH repository (<https://doi.org/10.6086/d1zh32>).

ORCID

Janet Franklin  <http://orcid.org/0000-0003-0314-4598>

Riley Andrade  <http://orcid.org/0000-0003-3640-6013>

Julie Ripplinger  <http://orcid.org/0000-0002-2771-6637>

REFERENCES

- Acevedo-Rodríguez, P., & Strong, M. T. (2008). Floristic richness and affinities in the West Indies. *The Botanical Review*, 74(1), 5–36.
- Acevedo-Rodríguez, P., & Strong, M. T. (2012). Catalogue of seed plants of the West Indies. *Smithsonian Contributions to Botany*, 98, 1–1192.
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26(1), 32–46.
- Austin, M. P. (1985). Continuum concept, ordination methods, and niche theory. *Annual Review of Ecology and Systematics*, 16, 39–61.
- Austin, M. P. (2002). Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. *Ecological Modelling*, 157, 101–118.
- Banda-R, K., Weintritt, J., & Pennington, R. T. (2016). Caribbean dry forest networking: An opportunity for conservation. *Caribbean Naturalist*, 1, 63–72.
- Baselga, A., & Orme, C. D. L. (2012). betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), 808–812.
- Borhidi, A. (1991). *Phytogeography and vegetation ecology of Cuba*. Budapest: Akademiai Kiado.
- Bullock, S. H. (1995). Plant reproduction in neotropical dry forests. In S. H. Bullock, H. A. Mooney, & E. Medina (Eds), *Seasonally dry tropical forests* (pp. 277–303). Cambridge, UK: Cambridge University Press.
- Bullock, S. H., Mooney, H. A., & Medina, E. (1995). *Seasonally dry tropical forests*. Cambridge, UK: Cambridge University Press.
- Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: Linking classical and contemporary approaches*. Chicago, IL: University of Chicago Press.
- Chazdon, R. L. (2014). *Second growth: The promise of tropical forest regeneration in an age of deforestation*. Chicago, IL: University of Chicago Press.
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Journal of Ecology*, 18, 117–143.
- Daniels, M. L. (2016). *A floristic study of a former land bridge in The Bahama Archipelago*. (Master of Science in Botany Masters Thesis), Miami University, Oxford, OH. Retrieved from https://etd.ohiolink.edu/pg_10?0::NO:10:P10_ACCESSION_NUM:miami1470149291
- Dexter, K., Smart, B., Baldauf, C., Baker, T., Balinga, M. B., Brienen, R., & Ilunga Muledi, J. (2015). Floristics and biogeography of vegetation in seasonally dry tropical regions. *International Forestry Review*, 17(S2), 10–32.
- Dinerstein, E., Olson, D. M., Graham, D. J., Webster, A. L., Primm, S. A., Bookbinder, M. P., & Ledec, G. (1995). *A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean*. Washington, D.C.: World Bank.
- Dixon, J., Hamilton, K., Pagiola, S., & Segnestam, L. (2001). *Tourism and the environment in the Caribbean: an economic framework*. In: Environmental Economics Series, Environmental Department Papers. The World Bank, New York.



- DRYFLOR, Banda-R, K., Delgado-Salinas, A., Dexter, K. G., Linares-Palomino, R., Oliveira-Filho, A., ... Pennington, R. T. (2016). Plant diversity patterns in neotropical dry forests and their conservation implications. *Science*, 353(6306), 1383–1387. <https://doi.org/10.1126/science.aaf5080>
- Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366.
- Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity And Distributions*, 13(3), 252–264.
- Fine, P. V., & Ree, R. H. (2006). Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *The American Naturalist*, 168(6), 796–804.
- Fitzpatrick, M. C., Sanders, N. J., Normand, S., Svenning, J.-C., Ferrier, S., Gove, A. D., & Dunn, R. R. (2013). Environmental and historical imprints on beta diversity: Insights from variation in rates of species turnover along gradients. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1768), 20131201.
- Franklin, J., Keppel, G., Webb, E. L., Rey, S. J., Seamon, J. O., Wiser, S. K., & Steadman, D. W. (2013). Dispersal limitations, speciation, environmental filtering and niche differentiation influence forest tree communities in West Polynesia. *Journal of Biogeography*, 40, 988–999. <https://doi.org/10.1111/jbi.12038>
- Franklin, J., Ripplinger, J., Marciano-Vega, H., Freid, E., & Steadman, D. W. (2015). Regional variation in Caribbean dry forest tree species composition. *Plant Ecology*, 216, 873–886. <https://doi.org/10.1007/s11258-015-0474-8>
- Gannon, B. M., & Martin, P. H. (2014). Reconstructing hurricane disturbance in a tropical montane forest landscape in the Cordillera Central, Dominican Republic: Implications for vegetation patterns and dynamics. *Arctic, Antarctic, and Alpine Research*, 46(4), 767–776.
- García, R., Peguero, B., Clase, T., Veloz, A., Jiménez, F., & Mejías, M. (2007). Flora y vegetación de las zonas áridas de la Sierra Martín García, República Dominicana. *Moscosoa*, 15, 5–60.
- Gerhardt, K., & Hytteborn, H. (1992). Natural dynamics and regeneration methods in tropical dry forests: An introduction. *Journal of Vegetation Science*, 3(3), 361–364.
- Gillespie, T. W. (2005). Predicting woody-plant species richness in tropical dry forests: A case study from south Florida, USA. *Ecological Applications*, 15(1), 27–37.
- Gillespie, T. W., Keppel, G., Pau, S., Price, J. P., Jaffré, T., & O'Neill, K. (2013). Scaling species richness and endemism of tropical dry forests on oceanic islands. *Diversity and Distributions*, 19(8), 896–906.
- Gillespie, T. W., Lipkin, B., Sullivan, L., Benowitz, D. R., Pau, S., & Keppel, G. (2012). The rarest and least protected forests in biodiversity hotspots. *Biodiversity and Conservation*, 21(14), 3597–3611.
- Gonzalez, O. J., & Zak, D. R. (1996). Tropical dry forests of St. Lucia, West Indies: Vegetation and soil properties. *Biotropica*, 28, 618–626.
- Gould, W., González, G., & Carrero Rivera, G. (2006). Structure and composition of vegetation along an elevational gradient in Puerto Rico. *Journal of Vegetation Science*, 17(5), 653–664.
- Gray, A. N., Brandeis, T. J., Shaw, J. D., McWilliams, W. H., & Miles, P. D. (2012). Forest Inventory and Analysis database of the United States of America (FIA). *Vegetation databases for the 21st century. Biodiversity & Ecology*, 4, 255–264.
- Guan, K., Pan, M., Li, H., Wolf, A., Wu, J., Medvigy, D., & Malhi, Y. (2015). Photosynthetic seasonality of global tropical forests constrained by hydroclimate. *Nature Geoscience*, 8(4), 284–289.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978. <https://doi.org/DOI: 10.1002/joc.1276>
- Hill, M. O., & Gauch, H. G. (1980). Detrended correspondence analysis, an improved ordination technique. *Vegetatio*, 42, 47–58.
- Hippolyte, J.-C., Mann, P., & Grindlay, N. R. (2005). Geologic evidence for the prolongation of active normal faults of the Mona rift into northwestern Puerto Rico. *Geological Society of America Special Papers*, 385, 161–171.
- Ibanez, T., Keppel, G., Baider, C., Birkinshaw, C., Culmsee, H., Cordell, S., & ... Birnbaum, P. (2018). Regional forcing explains local species diversity and turnover on tropical islands. *Global Ecology & Biogeography*. <https://doi.org/10.1111/geb.12712>
- Imbert, D., & Portecop, J. (2008). Hurricane disturbance and forest resilience: Assessing structural vs. functional changes in a Caribbean dry forest. *Forest Ecology and Management*, 255(8), 3494–3501.
- Iturralde-Vinent, M. A., & MacPhee, R. D. E. (1999). Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, 238, 1–95.
- Kelly, D. L., Tanner, E. V. J., Kapos, V., Dickinson, T. A., Goodfriend, G. A., & Fairbairn, P. (1988). Jamaican limestone forests: Floristics, structure and environment of three examples along a rainfall gradient. *Journal of Tropical Ecology*, 4(2), 121–156.
- Keppie, D. (2014). *The analysis of diffuse triple junction zones in plate tectonics and the Pirate Model of Western Caribbean tectonics*. Berlin/Heidelberg, Germany: Springer Science & Business Media.
- Legendre, P. (2008). Studying beta diversity: Ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology*, 1(1), 3–8.
- Legendre, P., & Cáceres, M. (2013). Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters*, 16(8), 951–963.
- Linares-Palomino, R., Oliveira-Filho, A. T., & Pennington, R. T. (2011). Neotropical seasonally dry forests: Diversity, endemism, and biogeography of woody plants. In R. Dirzo, H. S. Young, H. A. Mooney & G. Ceballos (Eds), *Seasonally dry tropical forests* (pp. 3–21). Washington, D.C.: Island Press.
- Lomolino, M. V. (1996). Investigating causality of nestedness of insular communities: Selective immigrations or extinctions? *Journal of Biogeography*, 23(5), 699–703.
- Lugo, A. E., Medina, E., Trejo-Torres, J. C., & Helmer, E. (2006). Botanical and ecological basis for the resilience of Antillean Dry Forests. In R. T. Pennington, G. P. Lewis & J. A. Ratter (Eds), *Neotropical savannas and seasonally dry forests* (Vol. Systematics Association special volume (69), pp. 359–381). Boca Raton, FL: CRC Press.
- Manion, G., Lisk, M., Ferrier, S., Nieto-Lugilde, D., & Fitzpatrick, M. (2016). GDM: Functions for Generalized Dissimilarity Modeling; R Package Version 1.2. 3. Available online: <http://cran.r-project.org/package= gdm> (accessed on 18 January 2017).
- Marciano-Vega, H., Roberts, C., Valles, H., Andre, J., Boswell, K., Lemen, D., ... López, C. (2016). Communication from the National Forest Inventories Working Group of the 16th Caribbean Foresters Meeting: Proposal for a regional workshop. *Caribbean Naturalist* (1), 25–29.
- Markestijn, L., Poorter, L., Bongers, F., Paz, H., & Sack, L. (2011). Hydraulics and life history of tropical dry forest tree species: Coordination of species' drought and shade tolerance. *New Phytologist*, 191(2), 480–495.
- Mauder, M., Leiva, A., Santiago-Valentin, E., Stevenson, D. W., Acevedo-Rodríguez, P., Meerow, A. W., & Francisco-Ortega, J. (2008). Plant conservation in the Caribbean Island biodiversity hotspot. *The Botanical Review*, 74(1), 197–207.
- McLaren, K., McDonald, M., Hall, J., & Healey, J. (2005). Predicting species response to disturbance from size class distributions of adults and saplings in a Jamaican tropical dry forest. *Plant Ecology*, 181(1), 69–84.
- Medina, E., Cuevas, E., Marciano-Vega, H., Meléndez-Ackerman, E., & Helmer, E. (2017). Biogeochemical relationships of a subtropical dry forest on Karst. *Caribbean Naturalist*, 13, 1–15.

- Melendez-Ackerman, E. M., Rojas-Sandoval, J., Fernandez, D. S., González, G., Lopez, H., Sustache, J., & Aragón, S. (2016). Associations between soil variables and vegetation structure and composition of Caribbean dry forests. *Caribbean Naturalist*, 2016(1), 176–198.
- Meschede, M., & Frisch, W. (1998). A plate-tectonic model for the Mesozoic and Early Cenozoic history of the Caribbean plate. *Tectonophysics*, 296(3), 269–291.
- Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., & Gordon, J. E. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, 33(3), 491–505.
- Mumby, P. J., Vitolo, R., & Stephenson, D. B. (2011). Temporal clustering of tropical cyclones and its ecosystem impacts. *Proceedings of the National Academy of Sciences*, 108(43), 17626–17630.
- Murphy, P. F., & Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, 17, 67–88.
- Mylroie, J. E., & Mylroie, J. R. (2013). Caves and karst of the Bahama Islands. In M. J. Lace, & J. E. Mylroie (Eds), *Coastal karst landforms* (pp. 147–176). Dordrecht: Springer.
- Neves, D. M., Dexter, K. G., Pennington, R. T., Bueno, M. L., & Oliveira Filho, A. T. (2015). Environmental and historical controls of floristic composition across the South American Dry Diagonal. *Journal of Biogeography*, 42(8), 1566–1576.
- Nix, H., & Busby, J. (1986). *BIOCLIM, a bioclimatic analysis and prediction system*. Canberra: CSIRO Division of Water and Land Resources.
- O'Connell, B. M., LaPoint, E. B., Turner, J. A., Ridley, T., Pugh, S. A., Wilson, A. M., ... Conkling, B. L. (2014). *The Forest Inventory and Analysis Database: Database Description and User Guide Version 6.0 for Phase 2*. Retrieved from Raleigh, NC.
- O'Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A. L., & Norris, R. D. (2016). Formation of the Isthmus of Panama. *Science Advances*, 2(8), e1600883.
- Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., O'Hara, R. B., Simpson, G. L., ... Wagner, H. (2011). *vegan: Community Ecology Package*. R package version 1.17-11. <http://cran.r-project.org/package=vegan> (Version R package version 1.17-11). Retrieved from <http://cran.r-project.org/package=vegan>
- Otypková, Z., & Chytrý, M. (2006). Effects of plot size on the ordination of vegetation samples. *Journal of Vegetation Science*, 17(4), 465–472.
- Peet, R. K., & Roberts, D. W. (2013). Classification of natural and semi-natural vegetation. In E. van der Maarel, & J. Franklin (Eds), *Vegetation ecology*, 2nd ed. (pp. 28–70). Chichester, UK: Wiley-Blackwell.
- Pennington, R. T., & Dick, C. W. (2010). Diversification of the Amazonian flora and its relation to key geological and environmental events: A molecular perspective. In C. Hoorn, & F. P. Wesselingh (Eds), *Amazonia, landscape and species evolution* (pp. 373–385). Oxford, UK: Blackwell Publishing.
- Pennington, R. T., Lavin, M., & Oliveira-Filho, A. (2009). Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution, and Systematics*, 40, 437–457.
- Pennington, R. T., Prado, D. E., & Peadar, C. A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography*, 27(2), 261–273.
- R Core Team. (2017). *R: A language and environment for statistical computing*. <http://www.r-project.org/>. Vienna, Austria: R Foundation for Statistical Computing.
- Randazzo, A. F., & Jones, D. S. (1997). *The geology of Florida*. Gainesville, FL, USA: University Press of Florida.
- Ray, G. J., & Brown, B. J. (1994). Seed ecology of woody species in a Caribbean dry forest. *Restoration Ecology*, 2(3), 156–163.
- Roberts, D. W. (2012). *labdsv: Ordination and Multivariate Analysis for Ecology*. R package version 1.5-0. <http://cran.r-project.org/package=labdsv>.
- Rojas-Sandoval, J., Meléndez-Ackerman, E. J., Fumero-Cabán, J., García-Bermúdez, M. A., Sustache, J., Aragón, S., & Fernández, D. S. (2014). Effects of hurricane disturbance and feral goat herbivory on the structure of a Caribbean dry forest. *Journal of Vegetation Science*, 25(4), 1069–1077.
- Ross, M. S., Carrington, M., Flynn, L. J., & Ruiz, P. L. (2001). Forest succession in tropical hardwood hammocks of the Florida Keys: Effects of direct mortality from Hurricane Andrew 1. *Biotropica*, 33(1), 23–33.
- Ross, M. S., O'Brien, J. J., & Flynn, L. J. (1992). Ecological site classification of Florida Keys terrestrial habitats. *Biotropica*, 24, 488–502.
- Ross, M. S., Sah, J. P., Ruiz, P. L., Spitzig, A. A., & Subedi, S. C. (2016). Inferring implications of climate change in south Florida hardwood hammocks through analysis of metacommunity structure. *Diversity and Distributions*, 22(7), 783–796.
- Ruiz, J., & Fandiño, M. C. (2010). The impact of hurricane Beta on the forests of Providencia Island, Colombia, Southwest Caribbean. *Caldasia*, 32, 425–434.
- Ruiz, J., Fandiño, M. C., & Chazdon, R. L. (2005). Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia 1. *Biotropica*, 37(4), 520–530.
- Ruiz, J., & Molano-González, N. (2017). Dinámica de la precipitación, la temperatura y la razón de aridez (1973–2011) en un escenario de cambio global en la isla de la vieja Providencia, Colombia: ¿qué está cambiando? *Cuadernos de Geografía-Revista Colombiana de Geografía*, 26(1).
- Santiago-Valentin, E., & Olmstead, R. G. (2004). Historical biogeography of Caribbean plants: Introduction to current knowledge and possibilities from a phylogenetic perspective. *Taxon*, 53(2), 299–319.
- Smith, T. W., & Lundholm, J. T. (2010). Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography*, 33(4), 648–655.
- Smith, I. K., & Vankat, J. L. (1992). Dry evergreen forest (coppice) communities of North Andros Island, Bahamas. *Bulletin of the Torrey Botanical Club*, 119(2), 181–191.
- Steadman, D. W. (2006). *Extinction and biogeography of tropical Pacific birds*. Chicago: University of Chicago Press.
- Steadman, D. W., Albury, N. A., Kakuk, B., Mead, J. I., Soto-Centeno, J. A., Singleton, H. M., & Franklin, J. (2015). Vertebrate community on an ice-age Caribbean island. *Proceedings of the National Academy of Science, USA*, 112(44), E5963–E5971. <https://doi.org/10.1073/pnas.1516490112>
- Steadman, D. W., Martin, P. S., MacPhee, R. D. E., Jull, A. J. T., McDonald, H. G., Woods, C. A., & Hodgins, G. W. L. (2005). Asynchronous extinction of late Quaternary sloths on continents and islands. *Proceedings of the National Academy of Science, USA*, 102(33), 11763–11768. <https://doi.org/10.1073/pnas.0502777102>
- Tanner, E. V. J., Rodríguez-Sánchez, F., Healey, J. R., Holdaway, R. J., & Bellingham, P. J. (2014). Long-term hurricane damage effects on tropical forest tree growth and mortality. *Ecology*, 95(10), 2974–2983.
- Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuviña, J., & Poorter, L. (2012). Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology*, 100(1), 253–263.
- Van Bloem, S. J., Murphy, P. G., & Lugo, A. E. (2003). Subtropical dry forest trees with no apparent damage sprout following a hurricane. *Tropical Ecology*, 44(2), 137–146.
- Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, 85(2), 183–206.
- Vennetier, M. (2015). *Reserve Naturelle de la Caravelle (Martinique): Inventaire 2015 des placettes permanentes, évolution des unités écologiques*. Synthèse des travaux réalisés de 1990 à 2015. Retrieved from Aix-en-Provence Cedex FRANCE:
- Wolfe, B. T., & Van Bloem, S. J. (2012). Subtropical dry forest regeneration in grass-invaded areas of Puerto Rico: Understanding why *Leucaena leucocephala* dominates and native species fail. *Forest Ecology and Management*, 267, 253–261.



- Zhang, Z., Hu, B., & Hu, G. (2014). Spatial heterogeneity of soil chemical properties in a subtropical karst forest, southwest China. *The Scientific World Journal*, 2014, 9.
- Zobel, M. (1997). The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? *Trends in Ecology & Evolution*, 12(7), 266–269.

BIOSKETCH

Janet Franklin is a biogeographer who uses geospatial data and spatial analytical tools to study the past, present and future distributions of biodiversity and ecosystems in relation to the physical environment, evolutionary and ecological processes, and human impacts, focusing on patterns and dynamics of terrestrial plant communities.

Author contributions: J.F. initiated the research and wrote the manuscript; J.F., R.A. and J.R. compiled and analysed the data; all other authors are experts on seasonally dry tropical forest in the Caribbean and provided data and contributed to the study design, interpretation of results and manuscript writing.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Franklin J, Andrade R, Daniels ML, et al. Geographical ecology of dry forest tree communities in the West Indies. *J Biogeogr.* 2018;45:1168–1181.

<https://doi.org/10.1111/jbi.13198>