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RESEARCH ARTICLE

Tree functional traits across Caribbean island dry forests are remarkably similar

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Abstract

Aim: To examine the climatic and biogeographic drivers of plant trait variation across Caribbean tropical dry forests, a system characterised by high rates of plant endemism despite low moisture availability, high rainfall variability and persistent exposure to hurricanes.

Location: Caribbean tropical dry forests.

Taxon: Woody plants.

Methods: We used a database of 572 woody vegetation plots spanning across the Caribbean, including Florida. We then extracted seed mass, specific leaf area and wood density from global trait databases. We supplemented additional trait data from herbaria collections and calculated phylogenetic imputation of traits. Furthermore, we calculated presence–absence community means and functional diversity and correlated these metrics with bioclimatic variables in addition to island and dry forest area using generalised additive models.

Results: Despite occurring in climatically distinct regions, Caribbean tropical dry forests are functionally similar, and the trait space of many dry forests are nested within the functional space of others. In line with island biogeographic theory, island area, dry forest area and island isolation were correlated with functional diversity. Although temperature and precipitation were important determinants of trait variation and functional diversity, environmental variables differently impacted trait variation and the variance explained was generally low.

Main Conclusions: The high functional overlap among Caribbean dry forests is remarkable given the broad climatic gradient across these islands. High functional overlap suggests that environmental and biogeographic filters constrain plant form and function in these intrinsically fascinating systems. The trait space of these insular dry forest systems points to dispersal-limitation, in addition to high temperature and water limitations, and favouring persistence strategies to withstand high frequency hurricane disturbance.

KEYWORDS
biogeography, Caribbean, islands, plant traits, seasonality, seasonally dry tropical forests

1 | INTRODUCTION

The theory of island biogeography predicts that species diversity on islands will be the result of a dynamic balance between immigration, speciation, and extinction in relation to island isolation, area, and age (MacArthur & Wilson, 2001). According to this theory, isolated, small and young islands are less species rich owing to reduced dispersal probability, influencing the probability of colonisation, while less-isolated, larger and older islands are more species rich owing to the continuous arrival of propagules. This theory, however, assumes all species have equal probabilities to establish or become extinct, irrespective of their ecological strategies. Yet there is increasing evidence that species differ in dispersal and persistence based on functional traits (Burns, 2005; Schrader et al., 2021). As a result, functional island biogeography, the study of ecological and evolutionary processes that shape the structure, diversity and functioning of island assemblages (Schrader et al., 2021) can be used to understand the determinants of island biodiversity.

The Caribbean region is a biodiversity hotspot owing, in part, to the historic and geographical heterogeneity of islands across a broad climatic gradient (Ricklefs & Bermingham, 2008). Caribbean islands are sufficiently isolated to form endemic elements, but sufficiently close to form interactions with nearby continents. Caribbean dry forests are highly representative of this duality—they are characterised by high endemism while sharing species with continental dry forests. The Caribbean and its dry forests are ideal model systems for determining the role of climatic variability on island biogeographic patterns for three reasons. First, the Caribbean Biodiversity Hotspot is one of the hottest hotspots (Myers et al., 2000) with 71% plant endemism (Franklin et al., 2015; Pennington et al., 2009). Second, the Caribbean encompasses a large climatic gradient including a large gradient in climatic variability. Dry forests, in particular, are defined by high variability in precipitation seasonality (Allen et al., 2017). Third, the Caribbean harbours 10% of remaining tropical dry forests in the Americas (Portillo-Quintero & Sánchez-Azofeifa, 2010), yet are understudied compared to mainland dry forests. Consequently, quantifying trait variation across Caribbean dry forests offers a mechanistic and predictive approach for understanding the climatic and biogeographic drivers of dry forest plant diversity.

Recent work showed that remnant Caribbean dry forests are geographically structured and dispersal-limited (Franklin et al., 2018; Pennington et al., 2009). This finding, combined with the high rates of endemism among Caribbean dry forests (upward of 77%, Dryflor et al., 2016), suggests that both biogeographic and environmental filtering are drivers of speciation that shape Caribbean dry forest plant communities. The strong dispersal limitation in tropical dry forests may result in lower species richness and a geographically structured metacommunity (Pennington et al., 2009). Although the theory of island biogeography assumes that all species have the same dispersal ability, dispersal modes and ecological traits will determine what species arrive to island systems (Schrader et al., 2021). Consequently, island functional composition may partly be associated with dispersal modes (e.g. Negoita et al., 2016). Thus, the dominant ecological and evolutionary strategies on islands likely reflect dispersal limitation. Even though evidence for dispersal limitation on islands is well known, island isolation distances did not appear large enough to impose constraints on species' distributions (Burns, 2005). As a result, whether dispersal limitation impacts functional and taxonomic diversity of islands remains unresolved.

In addition, although biogeographic drivers (e.g. isolation, island area and habitat area) are known to underlie patterns of island species diversity, the impacts of area and isolation on functional diversity are less clear. In some studies, functional diversity appears to scale with island or habitat area (e.g. Alirezazadeh et al., 2021; de Camargo et al., 2019; Dias et al., 2020; Karadimou et al., 2016; Mazel et al., 2014; Smith et al., 2013; White et al., 2018; Whittaker et al., 2014) and isolation (e.g. Jacquet et al., 2017; Negoita et al., 2016), suggesting that greater environmental variation encompassed by larger and less isolated areas may be key for determining functional diversity. Yet, in other studies, island or habitat area had only a small effect on functional diversity (Karadimou et al., 2016; Negoita et al., 2016). These contrasting results may partly be explained by differences in life history strategies. For example, island areas differentially impacted non-native and native species depending on their dispersal syndromes and growth forms (Mologni et al., 2022). Similarly, island isolation differentially impacted non-endemic, endemic and non-indigenous species (Hanz et al., 2022). Another study showed that functional diversity of persistence traits was associated with island isolation and area, such that species with specific growth forms and reproductive strategies were likely to survive on small and isolated islands (Conti et al., 2022). Finally, stochastic colonisation and extinctions may override the impacts of area and isolation on trait variation (as shown in Schrader et al., 2023).

In addition to island area and isolation, the environment is an important filter of functional trait strategies (Keddy, 1992; Messier et al., 2010; Violle et al., 2007). For example, because precipitation seasonality defines tropical dry forests, the notable precipitation seasonality gradient across Caribbean dry forests should underlie trait means and variances. Specifically, ecological theory predicts that greater climatic variability should lead to greater trait variation (Janzen, 1967). Indeed, greater precipitation seasonality has been shown to lead to greater variation in specific leaf area, a key plant trait, across continental dry forests (Hulshof et al., 2013). Other research has shown that temperature seasonality was a primary driver of plant functional diversity across broad spatial scales and forest types (Wieczynski et al., 2019), providing further evidence that seasonality plays an important role in structuring plant communities. Alternatively, other research has shown that temperature seasonality constrained functional diversity, whereas precipitation seasonality had the opposite effect (Swenson et al., 2012), suggesting that the relationship between climatic variability and functional diversity is likely more complex. Finally, other studies completely ignore seasonality as a primary factor driving plant functional diversity or argue that precipitation seasonality is less important than temperature seasonality (e.g. Moles et al., 2014), perpetuating uncertainties in our understanding of the relationship between climatic variability and functional diversity. The influence of climatic drivers on trait means and functional diversity, in combination with biogeographic drivers like island area and isolation, is much less understood.

Here, we examine the spatial variation and climatic and biogeographic drivers of three traits across Caribbean dry forests—seed mass, wood density and specific leaf area—representing key axes of life history variation (Díaz et al., 2016). Specifically, we asked: (1) what is the magnitude of variation of trait means and functional diversity across Caribbean dry forests and (2) what are the underlying climatic (e.g. seasonality) and biogeographic (isolation, island area and dry forest area) determinants of trait means and functional diversity? We expected functional diversity to be driven by precipitation variability, with more seasonal climates exhibiting greater functional diversity, as suggested by theoretical and empirical work (Hulshof et al., 2013; Janzen, 1967; Wieczynski et al., 2019). Furthermore, we also expected less isolated and larger islands, as well as larger dry forest area, to encompass greater functional diversity, in light of a main tenant of island biogeography theory (MacArthur & Wilson, 2001; Ottaviani et al., 2020; Schrader et al., 2021). Finally, we expected more isolated and smaller islands to harbour plants with more persistent strategies, such as thicker leaves, larger seed sizes and greater wood density, characteristic of dispersal-limited, frequently disturbed, highly seasonal systems (e.g. Conti et al., 2022; Schrader et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Plot data

The Caribbean has more than 700 islands, delineated by two major island arcs, the Greater Antilles (Cuba, Puerto Rico, Hispaniola and Jamaica, all represented in our analyses) and Lesser Antilles (Virgin Islands, Guadeloupe, Martinique and St. Lucia are included in our sample) (Figure 1a,b). We also included dry forests of the Bahamas (Abaco, Eleuthera, North Andros, Cat, Crooked and San Salvador), part of the Lucayan Archipelago. Additionally, we included Isla de Providencia (Colombia) and Florida (Florida keys and mainland south Florida, USA), which are continental, because they represent the northern and western limits of dry forests in the Caribbean Basin. Thus, in total, our sampling sites were composed of 18 separate islands that can be grouped into 11 sites (islands, archipelagos, or regions), including south Florida, largely representing the Greater and Lesser Antilles (Table S2). The Greater and Lesser Antilles are located on two different interacting tectonic plates, which determine geological, biological and ecological differences among islands and which encompass different biogeographic regions (Franklin et al., 2018). Caribbean dry forests, like other dry forests, are characterised by low and seasonal precipitation. However, unlike their continental counterparts, Caribbean dry forests are persistently exposed to hurricanes and continuous trade winds, which shape forest structure and, likely, species and trait composition. Anthropogenic disturbance also impacts dry forest structure and species and trait composition. Caribbean dry forests have been impacted by land use, driven mainly by urban expansion, tourism, and agriculture (Portillo-Quintero & Sánchez-Azofeifa, 2010).

We used an existing database (Franklin, 2018) of species occurrences (presence–absence matrix) of tropical dry forests (Franklin et al., 2018) spanning the 18 islands (Figure 1a,b). Data consisted of stem diameter measurements for woody taxa ≥5 cm in diameter at breast height, identified to species (in a very few cases to morphospecies, genus or family) in fixed-area plots, most ranging between 100 and 500 m^2 (see Franklin et al. (2018) and Supplementary Materials). In total, we used data from 572 plots, distributed across the 11 sites (islands or archipelagos) including 10 plots from mainland Florida (Table S2), encompassing 616 species, 46,000 stems and 3000 species-by-site occurrences. These plots spanned 13° latitude (>1300 km) and 24° longitude (>2200 km).

2.2 | Environmental and functional trait data

First, to quantify the magnitude of functional diversity across Caribbean dry forests, we followed a two-step process: phylogenetic imputation followed by trait metric calculations. To do this, we appended species level trait data from TRY (Kattge et al., 2020) and BIEN (Maitner et al., 2018). We focused on three plant traits: specific leaf area (SLA, $cm^2\ g^{-1}$), seed mass (SM, mg), and wood density (WD, $g\ cm^{-2}$). In addition to representing key axes of life history variation, these traits play important roles in physiological responses, dispersal, and drought tolerance of dry forest species (Swenson et al., 2020). Species coverage in TRY and BIEN were 33% and 20% for seed mass, 35% and 28% for wood density, and 20% and 12% for specific leaf area, respectively. Additionally, we filled in missing seed mass data using the University of Puerto Rico Rio Piedras (UPRRP) herbarium collection (18.5% species, Table S1). Seed mass was measured on 1–10 undamaged seeds (depending on availability in the collection) from at least one individual per species. We removed *Cocos nucifera* (Arecaceae) from analyses due to its pantropical distribution, unique dispersal and because its seed mass was an extreme outlier (mean: 576,800 g compared to a mean of 415 g for all other species). The values from the three sources (TRY, BIEN and seed mass from UPRRP) were independently averaged per trait and species after standardising units. Then, the values from the three datasets were merged by averaging once more per trait and species to calculate a single species-level value. For any remaining species

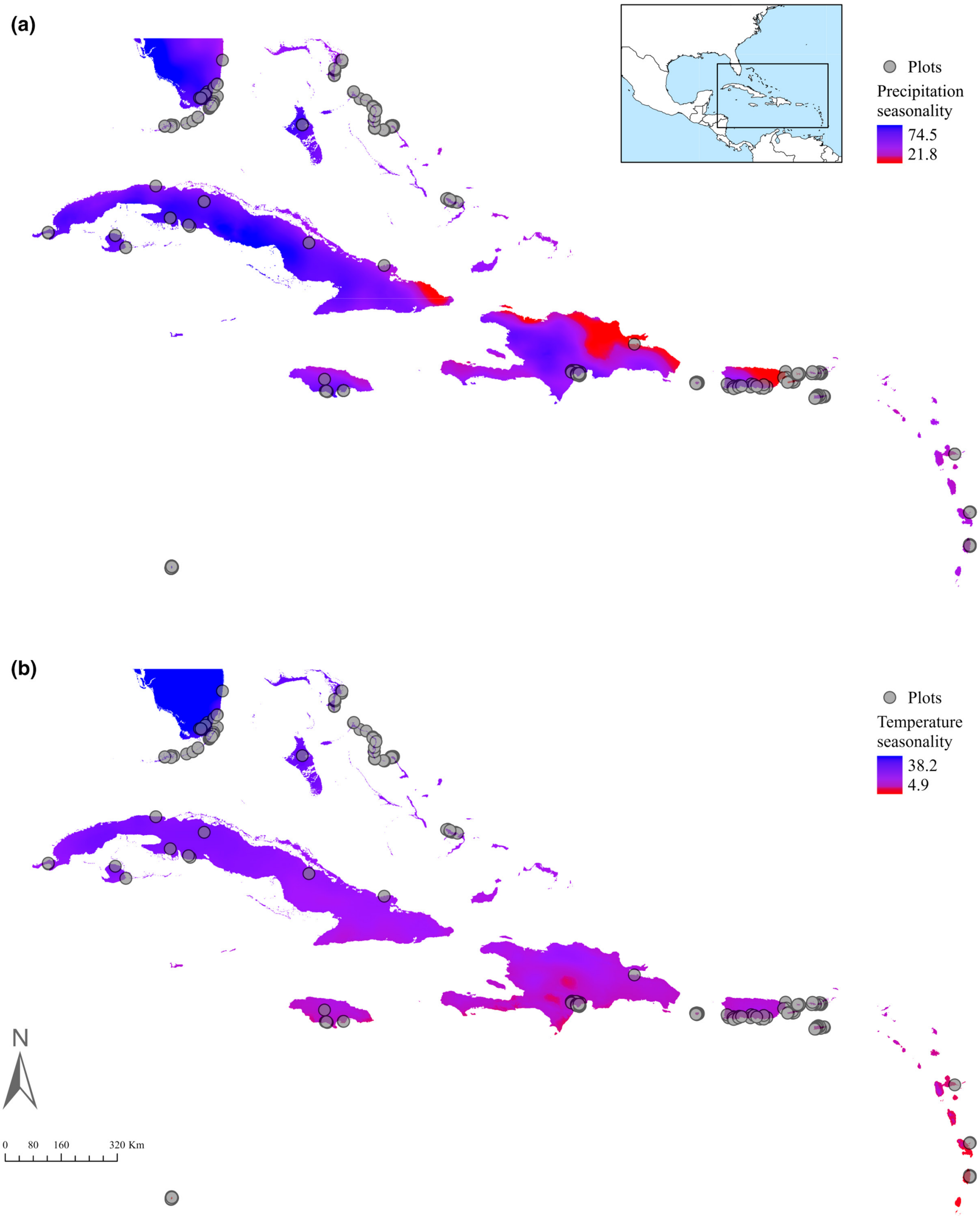

FIGURE 1 Sampling site locations (filled circles) and (a) precipitation seasonality (bio15, CV of mean monthly precipitation; %) and (b) temperature seasonality (bio4, SD of mean monthly temperature °C) across the Caribbean Basin, showing a general northwest to southeast gradient. Red colours indicate lower and blue colours indicate higher precipitation and temperature seasonality.

and trait values, we performed phylogenetic imputation up to 100% of species trait coverage.

Phylogenetic imputation is a tool to predict missing trait data based on phylogenetic relatedness. It is based on the assumption that closely related species have more similar trait values (Penone et al., 2014). While we recognise the limitations of this approach, it facilitates an important first step toward understanding functional diversity across this biodiversity hotspot. We constructed a phylogeny using the function *phylo.maker* in the R package '*V.PhyloMaker2*' 0.1.0 (Jin & Qian, 2022). We then used the function *phylopars* in the R package '*Rphylopars*' 0.3.9 (Goolsby et al., 2017) to impute the species values for any missing species data for any of the three traits and, finally, to obtain a complete trait database using the constructed phylogeny. *Rphylopars* was used as it has been demonstrated to be the most accurate of imputation methods (Johnson et al., 2021). In total, we imputed seed mass values for 49% of all species, wood density values for 64% of all species, and SLA values for 72% of all species (Table S1).

Next, we calculated unweighted community means and functional dispersion per site using the function *dbFD* in the R package '*FD*' 1.0-12.1 (Laliberté & Legendre, 2010). Functional dispersion is the mean distance in multidimensional trait space of individual species to the centroid of all species, and represents the breadth of functional strategies across species. Sites with greater dispersion are composed of species with greater functional dissimilarity and thus greater functional diversity. We chose functional dispersion as a metric of functional diversity because it is, by construction, unaffected by species richness (Anderson, 2006).

Second, to determine the underlying climatic (e.g. seasonality) determinants of functional diversity and trait means (i.e. how means vary across space), we downloaded 19 bioclimatic variables at 1-km resolution across the Caribbean from CHELSA 2.1 (Karger et al., 2017). CHELSA was designed for regions with high topographic complexity, and dry forests are often characterised by complex topography. In addition, CHELSA more accurately represents the climatic variability of dry forests than other climate databases (Ocón et al., 2021). These bioclimatic variables describe seasonal and annual averages of precipitation and averages and extremes of temperature based on long-term monthly means (for the period 1979–2013). As bioclimatic variables tend to be correlated, a subset was selected based on their relevance to dry forests (e.g. seasonality) and their multicollinearity tested using a step-wise variance inflation factor (VIF) with the R package '*usdm*' 1.1-18 (Naimi et al., 2014). The following variables were thus included in the subset: mean annual temperature (bio1) and precipitation (bio12), isothermality (bio3), mean daily maximum temperature of the warmest month (bio5), mean temperature of the driest month (bio9), precipitation of the wettest (bio13) and driest month (bio14), mean monthly precipitation of the warmest quarter (bio18) and temperature (bio4), and precipitation (bio15) seasonality (Table 1), which were standardised to mean zero and unit variance.

In addition to climatic variables, to determine the effect of biogeographic factors (island area, forest area and isolation) on trait means and functional diversity, we calculated island area (km^2) using the Caribbean Island Nations Coastline Boundaries (Williams, 2004). We estimated dry forest extent following Ocón et al. (2021), who showed that the FAO definition of dry forests, which is based on a minimum annual precipitation range of 500–1500 mm and a dry season of 5–8 months with less than 100 mm of precipitation (Sunderland et al., 2015), accurately delineates tropical dry forest cover when combined with CHELSA data (Karger et al., 2017). To determine dry forest area (km^2), we thus merged CHELSA data with the FAO definition of dry forests (Figure S1). Furthermore, we calculated island isolation as the distance to the nearest mainland from each plot (m) using the 'NEAR' tool on ArcGIS Pro 3.0.3 and the World Administrative Division (2021) of the ArcGIS base map. The distances calculated for Florida were zero, as it is located on the mainland. All biogeographic variables were standardised to mean zero and unit variance.

Finally, we examined whether functional dispersion, seed mass, wood density and specific leaf area values per plot were spatially autocorrelated by calculating semi-variograms using the function *variogram*, and the '*gstat*' R package (Gräler et al., 2016; Pebesma, 2004). The variogram lag distances were defined following the default parameters, which set the maximum lag distance as the maximum distance between a pair of points (~2700 km) divided by three (900 km), resulting in an interval of 60 km. The semivariograms showed that functional dispersion and the three trait semi-variances were uncorrelated with distance among sampling sites, at lag distances ranging from 60 to 900 km, indicating that they were not spatially autocorrelated at those scales (Figure S2).

2.3 | Statistical analyses

First, to better understand patterns of functional diversity across Caribbean dry forests, we performed a non-metric multidimensional scaling (NMDS) across sites with the *metaMDS* function of the '*vegan*' 2.6-4 R package. Second, to quantify climatic and biogeographic determinants of trait means and functional diversity, we used generalised additive models (GAMs) using the '*mgcv*' 1.8-41 R package (Wood, 2003, 2011). For each GAM, a thin plate regression

TABLE 1 Bioclimatic variables from CHELSA 2.1 (Karger et al., 2017) based on long-term averages (1979–2013) and their ranges across the 572 plots.

Abbreviation	Variable	Range
MAT (bio1)	Mean annual temperature	21.8–27.5°C
ISOT (bio3)	Isothermality (ratio of mean diurnal range to annual temperature range × 100)	15.8%–58.9%
SD T (bio4)	Temperature seasonality (standard deviation of monthly mean temperatures)	5.29–30.03°C
Twarm (bio5)	Maximum temperature of the warmest month	26.1–30.9°C
Tdry (bio9)	Mean temperature of the driest month	19.8–27.1°C
MAP (bio12)	Mean annual precipitation	628–2365 mm
Pwet (bio13)	Precipitation of the wettest month	101–388 mm
Pdry (bio14)	Precipitation of the driest month	15–102 mm
CV P (bio15)	Precipitation seasonality (coefficient of variation—ratio of the standard deviation of monthly mean precipitation to the mean monthly total precipitation × 100)	27%–64%
Pwarmq (bio18)	Mean monthly precipitation of the warmest quarter	171–870 mm

Note: These variables were standardised to mean zero and unit variance for statistical analysis.

spline was used as the smoothing parameter and an extra penalty was added to each smooth term using the 'select' parameter to identify the explanatory variables that significantly explained the dependent variables. Finally, after selecting the independent variables in each model, those whose effective degrees of freedom (edf) were one, were included in the GAM as linear terms (an edf of one is equivalent to a straight line).

3 | RESULTS

3.1 | Geographic variation of traits across Caribbean dry forests

Despite occurring across a large climatic gradient (Table 1; Figure 1a,b), Caribbean dry forests were functionally similar, and the trait space of most Caribbean dry forests were nested within the functional space of others (Figure 2). According to the NMDS island ellipses, dry forests of Puerto Rico and Providencia encompassed nearly all functional diversity among Caribbean dry forests. Furthermore, this analysis showed that sites primarily differed in wood density and specific leaf area located on the left side of the NMDS biplot, while seed mass showed less variation located closer to the center.

3.2 | Climatic and biogeographic determinants of trait variation

The GAMs showed that, in general, island area, dry forest area and island isolation were correlated with trait means and functional diversity, as well as precipitation which was their strongest climatic determinant (Table 2), in line with expectations. Specifically, seed mass exhibited a negative linear relationship with island area, whereas wood density and functional diversity exhibited non-linear relationships with island isolation, and specific leaf area and functional diversity exhibited negative linear relationships with island isolation and dry forest area, respectively (Figures S3–S6). Furthermore, specific leaf area was negatively correlated with temperature seasonality.

Finally, the trait deviance explained by climatic and biogeographic variables was generally low and varied across traits (Table 2). Specific leaf area exhibited the greatest deviance explained (27%), followed by wood density (13%), functional dispersion (9%) and seed mass (7%).

4 | DISCUSSION

Within the Caribbean biodiversity hotspot, tropical dry forests have a unique biogeographic history which underlies their high taxonomic turnover and geographic structure among islands (Franklin et al., 2018). We aimed to expand on this work by quantifying the spatial variation of functional traits and to determine its underlying climatic and biogeographic drivers. We found that the geographic variation of functional diversity was not consistent with the geographic variation of species diversity across Caribbean dry forests. Although other work has shown that tropical dry forest functional diversity varies markedly across climatic gradients spanning the neotropics (e.g. Lamanna et al., 2014; Swenson et al., 2012; Wieczynski et al., 2019), our results showed that functional similarity is remarkably high among biogeographically distinct islands. The high functional similarity among islands suggests that a strong biogeographic and environmental filter, such as island isolation, island area, and forest area, as well as temperature and precipitation variability, likely select for similar ecological strategies among dry forest species. Interestingly, Puerto Rico and Providencia exhibited the greatest trait variation, despite being smaller in area. This may reflect high habitat heterogeneity, as in Puerto Rico, where dry forests occur on limestone soils on the leeward side with annual rainfall averaging 929 mm, to dry forests on volcanic soils on the windward side with annual rainfall averaging twice that amount (1500–2000 mm) (Birdsey & Weaver, 1982; Lugo et al., 1978). Limestone and volcanic substrates are the two most extensive geologic substrates in Puerto Rico, which differ in water-holding capacity and nutrient availability (Muscarella et al., 2016). Dry forest plots occurred on a single substrate on most of the other islands included in the database (Table S2). High functional diversity, as in Providencia (a continental island), may also reflect relatively high species richness due to continental proximity and a history of forest recovery (Ruiz et al., 2009), as abandoned farmlands have created a mosaic of successional forests (Ruiz et al., 2005).

4.1 | Climatic correlates of trait means

Trait means exhibited significant variation across the large precipitation and temperature gradient as expected, even though the model deviance was generally low. In particular, the models for specific leaf area and wood density exhibited the greatest deviance and this was primarily driven by temperature (temperature seasonality and mean annual temperature, respectively), while the seed mass model exhibited the lowest deviance, supporting the hypothesis that Caribbean dry forests are dispersal-limited systems (Pennington et al., 2009). It is possible that dispersal (not climate) is a strong determinant of Caribbean dry forest species and, perhaps, trait composition, where high zoochory predominates compared to continental dry forests (where wind-dispersal dominates; Gillespie, 2006). Thus, comparisons among Caribbean and continental dry forest species composition and dispersal modes would be an insightful exercise (e.g. Gillespie et al., 2006; Pennington & Dick, 2011; Ray & Brown, 1994; and see Walentowitz et al., 2022). However, the effect of dispersal limitation may be masked by a human-induced loss of isolation caused by ongoing maritime traffic (Walentowitz et al., 2022). Indeed, the regionally introduced, nitrogen-fixing and livestock forage legume *Leucaena leucocephala* is a common element

FIGURE 2 NMDS of Caribbean dry forest trait variation for seed mass (SM), wood density (WD) and specific leaf area (SLA). Islands are represented by ellipses of different colour, spanning all the trait variation across their sampling sites.

across secondary Caribbean dry forests (Colón et al., 2011). This species was present across 5 of the 11 archipelagos. Post-dispersal environmental filters were also important. Specifically, seed mass was positively related to precipitation in the wettest and driest month, consistent with geographic trends showing seed mass increases with mean annual precipitation (Swenson et al., 2012), but contrasting with others showing seed mass increases with temperature (Moles et al., 2014; Murray et al., 2004), which is thought to be due to greater metabolic costs at high temperatures (Lord et al., 1997). Nonetheless, limited water availability may impose greater metabolic costs too, as it determines seed germination and seedling establishment (Quesada et al., 2009) due to a temporal gap between seed dispersal and seed germination in tropical dry forests. In tropical dry forests, although seed dormancy is broken with the onset of the rainy season (Núñez-Cruz et al., 2018), most tropical dry forest species produce fruits in the dry season (Bullock

TABLE 2 Generalised additive models (GAM) for community mean seed mass (SM, mg), wood density (WD, g cm^{-3}), specific leaf area (SLA, cm^2 g^{-1}), functional dispersion (FDis) and, isolation (distance to the nearest mainland; km^2), island area, dry forest area and bioclimatic predictors (abbreviations as in Table 1).

Trait	R^2_adjusted	DE (%)	Factor	edf	*F*-value	*p*-value
SM	0.062	7.23	Island area	−50.170 (Coef)	−2.730 (*t*)	0.007
			Pwet (bio13)	51.06 (Coef)	5.446 (*t*)	1.05E-02
			s(Pdry (bio14))	4.57	3.52	0.002
WD	0.123	13.10	MAT (bio1)	−0.008 (Coef)	−2.863 (*t*)	0.004
			s(Isolation)	4.664	8.873	<2.00E-16
SLA	0.257	27.00	Isolation	−3.687 (Coef)	−2.081 (*t*)	0.038
			SD_T (bio4))	−5.685 (Coef)	−2.787 (*t*)	0.006
			s(Pwet (bio13))	3.443	3.804	0.004
			s(MAP (bio12))	4.862	4.932	1.03E-04
FDis	0.072	8.53	Pwet (bio13)	0.082 (Coef)	2.910 (*t*)	0.004
			Dry forest area	−0.029 (Coef)	−1.656 (*t*)	0.098
			s(Pwarmq (bio18))	2.639	5.146	0.001
			s(Isolation)	3.267	3.535	6.96E-03

Note: Effective degree of freedom (edf), *F*-values, and *p*-values of the nonlinear effects are included. The *t*-values (*t*), *p*-values and coefficients (Coef) of the linear effects are also included. DE is deviance explained by the model. Because an edf of one is equivalent to a straight line, factors with an edf of one were included as linear terms and the coefficient is listed (noted in parentheses as Coef) instead of the edf and the *t*-value instead of the *F*-value (again, noted in parentheses as *t*). The non-linear terms are enclosed in parentheses preceded by an *s* referring to the smoothed terms. The greater the edf of the smoothed terms, the more wiggly or nonlinear the curve.

& Solis-Magallanes, 1990; Singh & Kushwaha, 2006; Valdez-Hernández et al., 2010). Therefore, water availability during both the dry season and the germination period should select for species with traits that confer resistance to long periods of drought.

Specific leaf area and wood density were more driven by temperature. Although seasonality was poorly correlated with trait means as initially expected, specific leaf area was lower in more thermally seasonal environments, suggesting that dry forest trait means are partly constrained by temperature seasonality, a pattern reported at local, regional and global scales (Swenson et al., 2012). Our results also align with the idea that tropical dry forests are composed of species with conservative strategies to avoid high transpiration while maintaining active photosynthesis (e.g. Markesteijn & Poorter, 2009). For example, specific leaf area was positively correlated with precipitation of the wettest month and wood density decreased with increasing mean annual temperature, reflecting greater resistance to cavitation (Hacke et al., 2001; Jacobsen et al., 2007). This is likely because plants must cope with both low and high temperatures over the course of a year while confronting drought conditions (such as in Florida, Bahamas, and Cuba). Likewise, the relationship between wood density and the susceptibility of hydraulic failure during severe drought is correlated with the lack of capacity for maintaining leaf water potential, increasing the probability of embolism (Hoffmann et al., 2011). These conditions constrain plant growth, favouring species with low specific leaf area and wood density. However, the relationship between temperature seasonality and specific leaf area, as well as wood density spatial variation across the Caribbean, could also depend on other environmental factors, such as soil nutrient availability or the frequency and intensity of hurricanes (Muscarella et al., 2016). Plants in dry forests with high temperature seasonality occurring on nutrient-poor limestone soils may have lower specific leaf area due to limited water availability (such as in Florida), while plants in nutrient-rich volcanic soils may have higher specific leaf area regardless of temperature seasonality (e.g. in the US Virgin Islands). That Caribbean dry forests occur across a range of parent materials (Colon & Lugo, 2006) suggests that finer environmental sampling may be necessary to disentangle the underlying drivers of geographic variation of trait means in the region. In relation to wood density, it may also play a key role in resistance to hurricanes (Jimenez-Rodríguez et al., 2018), as it may give a tree higher resistance against rupture of the main trunk or branches (Paz et al., 2018). The greatest occurrence of hurricanes and cyclones, as well as the most energetic hurricanes zones, have been recorded in the northern and western region of the Caribbean (Montoya et al., 2018; Reading, 1990), regions with the greatest wood densities.

4.2 | Biogeographic correlates of trait means

In addition to identifying climatic drivers of trait means and functional diversity, we also found consistent patterns between biogeographic factors and trait means and functional diversity across the Caribbean. Trait means and functional diversity were related to island area, forest area, and island isolation, in line with biogeographic theory and other studies across systems and taxa (e.g. Dias et al., 2020; Karadimou et al., 2016; Mologni et al., 2022; Smith et al., 2013; White et al., 2018), but with some important exceptions because functional diversity did not align with the expected relationship with island area. Specifically, functional diversity was negatively related to island isolation, as predicted by the theory of island biogeography and in line with expectations based on isolation and the continental migration-immigration dynamic of Caribbean islands (Ricklefs & Bermingham, 2008).

Furthermore, we found that functional diversity was negatively related to forest area, in contrast with expectations and other studies that report increased functional diversity with increasing habitat area (Jacquet et al., 2017). Island biogeography theory states that increased habitat area should support greater diversity (MacArthur & Wilson, 2001; Ottaviani et al., 2020; Schrader et al., 2021), yet we found the opposite. This result could be confounded by climate. The largest islands are located in the northern Caribbean Basin at a higher latitude, where mean annual precipitation and temperature are lower and seasonality is greater than in the Lesser Antilles. Consequently, environmental drivers may modify the relationship between biogeographic factors and diversity. In addition, stochastic migration and extinction can mask the island area effect on trait variation (Schrader et al., 2023). However, stochastic migration and extinction would arguably result in decreasing speciation and endemism (Johnson & Raven, 1973). This latter explanation thus does not align with the high rates of endemism found throughout Caribbean dry forests. Another possibility is that the calculated dry forest area is not an accurate representation of dry forest distribution, perhaps because of anthropogenic land use change. Given the high fragmentation and difficulty in defining dry forests (see David et al., 2022), it is possible that the area where dry forests can potentially occur based on climatic conditions overestimates actual dry forest area. However, an estimation of actual dry forest area corrected for land cover, using Hansen et al. (2022), showed a nearly 1:1 relationship (Figure S1), suggesting that the inverse relationship between area and functional diversity is not an artefact of our approach.

Specific leaf area and wood density values were lower on more isolated islands, and seed mass was larger on smaller islands. Together, these results are in line with the idea that smaller and more isolated islands replicate the abiotic conditions of early successional stages. That is, the environment on smaller and more isolated islands favours species with larger seeds (increasing survivorship), lower wood density (favouring greater resprouting capacity), and thicker leaves (increasing water retention)—traits reflecting persistence in harsh, frequently disturbed environments (Burns & Neufeld, 2009; Conti et al., 2022; Kavanagh & Burns, 2014; Ottaviani et al., 2022; Schrader et al., 2023). While these results provide some evidence that biogeographic factors select for certain trait values, that seed mass was unrelated to isolation points to other possible interactions. In a study across Danish islands, a weak relation between isolation and seed mass was observed, likely influenced by centuries of maritime traffic facilitating the dispersal of particular species. (Walentowitz et al., 2022). Although in our study seed mass was unrelated to isolation (perhaps reflecting some human-facilitated dispersal), seed mass was related to precipitation of the wettest month and precipitation of the driest month, suggesting that environmental filtering may affect the isolation-diversity relationship by impacting post-dispersal establishment (Leishman & Westoby, 1994; Moles & Westoby, 2006).

One important caveat—a caveat shared among many trait-based studies—is the source of trait data. We compiled species-level trait values from global databases and assumed more closely related species are functionally more similar—both likely underestimating total trait variation (Kohli & Jarzyna, 2021), and perhaps underlying the low deviance explained by climatic variables. Finer scale trait sampling would likely reveal even stronger relationships than that shown here, though would require confronting additional constraints (e.g. permitting, travel, etc.). On the other hand, Caribbean dry forests exhibit high species dominance (Franklin et al., 2018; Lugo et al., 2006). For example, Colon and Lugo (2006) showed that of 36 species in Puerto Rico dry forests, only 5 accounted for 66% of total basal area and 6 accounted for 66% of total tree density. Thus, high species coverage may not be necessary to accurately estimate trait composition.

In summary, we found Caribbean dry forests were remarkably functionally similar, and environmental variables (temperature and precipitation) differently impacted trait means, though the deviance explained tended to be low. However, the relationship between functional diversity, traits, and the biogeographic and environmental factors pointed to dispersal-limitation, under high temperature and water stress, favouring persistence strategies to cope with high frequency disturbance. This first assessment of Caribbean dry forest functional diversity should encourage future investigations to include additional traits, such as dispersal modes and successional groups, and additional environmental variables, such as land cover or soil type. Furthermore, examining other biogeographical drivers such as elevation, and the area of and distance among surrounding islands (as stepping stones), could further disentangle the role of migration, speciation, and extinction in Caribbean dry forests. Our study begins to address the lack of quantitative understanding of Caribbean dry forest functional diversity and establishes important baseline relationships to examine further. Given that dry forests tend to be functionally more diverse than expected (Swenson et al., 2012), there is an urgent need to expand trait sampling in this intrinsically fascinating (Gentry, 1995) and biodiverse region.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All trait, bioclimatic and biogeographic data will be deposited on Dryad upon manuscript acceptance for publication. A peer-review version is available at: doi: https://doi.org/10.5061/dryad.z08kprrj5, https://datadryad.org/stash/share/aWgeUb65syoP27a6SggjIgcR9wCGC7kBZ-x7JLMIyuU. The aggregated species presence by site data is available on Dryad (Franklin et al., 2018; https://doi.org/10.6086/d1zh32).

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BIOSKETCH

PLB is a tropical ecologist who studies the form and function of tropical dry forests.

Author contributions: CMH and JF conceived the idea. PLB and ARS collected the data. PLB analysed the data. PLB and CMH led the writing, with contributions from all authors.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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