

Frugivore distributions are associated with plant dispersal syndrome diversity in the Caribbean archipelagos

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Abstract

Aim: Many plants rely on interactions with frugivores for dispersal, suggesting that animal communities may affect plant occupancy and diversity. However, the contribution of these interaction-led biotic variables on plant diversity is poorly understood, especially in archipelagic hotspots such as the Caribbean. In island ecosystems, biogeographic theories suggest that island configurations drive colonization-extinction dynamics, while macroecology argues for the importance of climatic drivers of biodiversity. Within this context, we examine how frugivore-driven biotic factors are associated with fruiting plant species richness in relation to abiotic (climatic and geologic) and island configuration characteristics.

Location: Caribbean archipelagos.

Methods: We compiled a review of the diversity and distributions of 6039 plants and 326 vertebrate frugivores across 105 islands within the Caribbean. We then identified characteristics related to plant-frugivore interactions and assigned each species as having either abiotic (wind, water, etc.) or zoochoric (frugivory-dependent) dispersal syndromes. We related plant richness and dispersal syndromes to the regional diversity and characteristics of frugivorous animals, abiotic environments and island configuration characteristics through stepwise multivariate regression with generalized linear models and model selection.

Results: We found that 44.6% of Caribbean plants are dispersed through frugivory (endozoochory). Frugivore-related characteristics, namely accumulated body mass of island bird assemblages, were the best predictors of the diversity of seed dispersal syndromes. To a lesser degree, reptile richness and soil variety were also considered important predictors for zoochoric plant distribution, while island areas affected abiotically-dispersed plants.

Main conclusion: We found that biotic characteristics of frugivore communities are important predictors of plant diversity in the Caribbean archipelagos. However, this may also be influenced by climate and colonization history. Given the importance of biotic metrics in explaining plant diversity, we suggest that fruit-frugivore interactions are important components of island biogeography and that frugivorous communities should be accounted for plant biodiversity predictions and forecast models.

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KEYWORDS

Antilles, Bahamas, Caribbean, Cuba, frugivory, island biogeography, Jamaica, plant diversity, plant-animal interactions, Puerto Rico

1 | INTRODUCTION

Despite amounting to just 5% of the global landmass (Weigelt et al., 2013), islands hold more than 25% of the world's plant diversity (Kier et al., 2009). Islands can host a disproportionate amount of the world's biodiversity due to the high level of species endemism and the often-accelerated evolution experienced by the organisms insulated within islands (Kier et al., 2009; Millien, 2006). However, insular ecosystems are particularly vulnerable to anthropogenic disturbances such as habitat loss and biological invasions, which often lead to biodiversity decline (Buckley & Jetz, 2007; Pyšek & Richardson, 2006; Russell & Kueffer, 2019). Therefore, understanding the mechanisms that drive the high species richness present in islands (Cronk, 1997; Weigelt et al., 2015) could be important for identifying biodiversity hotspots and planning conservation efforts (Kueffer & Kinney, 2017). Abiotic characteristics, such as climate, geology, and topography, are known to be important predictors of island biodiversity and endemism (Irl et al., 2015), as are the effects of island biogeography (MacArthur & Wilson, 1967; Ottaviani et al., 2020; Rojas-Sandoval et al., 2020) particularly through the determination of dispersal potential between neighbouring islands (Cowie & Holland, 2006). However, biotic factors, particularly frugivorous seed dispersers, may also be important in structuring plant diversity by facilitating plant recruitment (Rey & Alcántara, 2000) and connecting local plant communities to the regional species pool (Plue & Cousins, 2018).

Frugivore-driven biotic factors may have especially strong associations with the diversity and distributions of plants with zoochoric dispersal syndromes because these plants possess fleshy fruits and depend on plant-frugivore mutualistic interactions for dispersal and recruitment (Figure 1; Nogales et al., 2017; Valenta & Nevo, 2020; van Leeuwen et al., 2020). Such interaction-driven propagation could have important implications for shaping plant distribution and speciation in islands (Lim et al., 2020; Onstein et al., 2017). As these plants support biodiversity in ecosystems through providing habitat (Maruyama et al., 2019) and sources of food (Walther et al., 2018), examining the associations between their distribution and diversity is not only important for plant species conservation but also the biotic interactions that they take part in.

The Caribbean archipelagos are a particularly interesting study system, holding about 13,000 native vascular plants and 2.3% of the Earth's flora (Myers et al., 2000; Torres-Santana et al., 2010). This archipelago can be divided broadly into three main regions: the Lucayan archipelago (Bahamas and Turks and Caicos), the Greater Antilles (Cuba, Hispaniola, Jamaica, Puerto Rico, and adjacent islands), and the Lesser Antilles (comprised of 8 independent countries and 12 territories). These formations have diverse geologic histories ranging from the recently emerged limestone islands of the Lucayan archipelago, the land-bridge islands of the Greater Antilles, and the volcanic islands of the Lesser Antilles (Graham, 2003). The

combination of varying island sizes, ages, and isolation has contributed to creating one of the most biodiverse ecosystems in the world (Maunder et al., 2008; Nieto-Blázquez et al., 2017; Shi et al., 2005). Featuring elevated endemism and high levels of habitat loss (Brooks et al., 2002), it is widely considered to be a biological hotspot and is of great priority for conservation (Shi et al., 2005; Williams, 2011). Understanding the determinants of the region's plant biodiversity could, therefore, provide useful insight into the associations that could form and predict island diversity. Island biogeography has been clearly associated with native plant diversity in the region (Rojas-Sandoval et al., 2020), as has climatic (Mendoza et al., 2017), geologic (Barthlott et al., 2005), and topographic characteristics (Carrington et al., 2018). However, there is little research done on examining the covariation between interaction-led biotic characteristics with plant diversity in the Caribbean archipelago, particularly at a regional scale.

In this study, we aim to broaden our understanding of the important predictors of plant diversity and distribution in the Caribbean archipelago by incorporating abiotic, biotic and island configuration elements. We focus our approach on addressing the following questions: (1) What is the relative importance of frugivore-driven biotic factors in predicting the richness of plants with different dispersal syndromes in the Caribbean compared to abiotic (climatic and geologic) factors and island configuration? (2) Do the relative strengths of non-biotic characteristics differ between plants with abiotic and zoochoric dispersal syndromes? To investigate these questions, we characterized the islands' frugivorous community, and the composition of fruiting plants, with abiotic fruits, characterized as dry fruits that disperse through abiotic factors such as wind and water, and zoochoric fruits characterized as fleshy fruits that depend on frugivory for dispersal (van der Pijl, 1972). Additionally, we gridded spatial files on climate, topography, and soil characteristics, as well as island configuration metrics describing the level of isolation and size of the study islands. Using these variables, we applied model selection and measured the relative importance of each variable to rank the strengths of each factor for plants with either abiotic or zoochoric dispersal syndromes. Given that zoochoric, fleshy fruits depend heavily on plant-frugivore interactions (van Leeuwen et al., 2020), we expect to find that biotic characteristics are more important in predicting distributions of plants with zoochoric dispersal syndromes than those with abiotic dispersal syndromes.

2 | METHODS

2.1 | Study system

The Caribbean archipelagos are geologically and biologically diverse. Geologically, the region was formed through a combination

FIGURE 1 (a) *Swietenia mahogoni* (Caribbean mahogany): an example of a plant with abiotic dispersal syndromes (photo credit 1). (b) *Guaiaecum sanctum* (Holywood lignum-vitae): an example of a plant with zoochoric dispersal syndromes (photo credit 1). Plants with zoochoric dispersal syndromes can interact with frugivorous birds (c: *Patagioenas leucocephala*—White crowned pigeon; photo credit 1) or reptiles (d: *Cyclura cychlura*—Northern Bahamian rock iguana—photo credit 2). Mauro Galetti (photo credit 1) and Laís Lautenschlager Rodrigues (photo credit 2)



of volcanism (Lesser Antilles) and tectonic activity and uplift (Greater Antilles and the Lucayan archipelago), which exposed dry land for colonization by terrestrial organisms (Graham, 2003). Climatically, while the Caribbean archipelagos are primarily tropical, rainfall can be highly variable (529–2897 mm/year), with islands such as the Great Inagua Island and parts of Hispaniola having arid conditions (Beck et al., 2018; Fick & Hijmans, 2017). Overall, six ecoregions—tropical/subtropical moist broadleaf forests, tropical/subtropical dry broadleaf forests, tropical/subtropical coniferous forests, flooded grasslands/savannas, deserts/xeric shrublands, mangrove—are recognized in the Caribbean islands (Clark et al., 2021).

For our study, we selected all islands within the Antillean biogeographic dominion. This biogeographically similar region encompasses the Greater and Lesser Antilles and the Lucayan archipelago (Bahamas and Turks and Caicos) and is determined through a cladistic biogeographical analysis based on the correspondence between phylogenetic and area relationships (Morrone, 2014). As shapefiles for smaller islands were not readily available, we focused on islands with areas greater than 20 km² for a total of 105 islands. Our largest island was Cuba with 107,494 km², while our

smallest was Cayo Blanquial with 20 km² (Supporting Information Table S1).

2.2 | Plant dispersal syndromes and distribution

To determine the distributions of plant diversity and dispersal syndromes within our study system, we used a comprehensive database of seed plants in the Caribbean developed by Acevedo-Rodríguez and Strong (2012). This database included 11,619 plants occurring in the Caribbean. To avoid any potential artificial drivers of plant distributions, we focused only on native plant species within this list and then classified each species as having either abiotic or zoochoric dispersal syndromes by their fruit characteristics (dry vs. fleshy; van der Pijl, 1972). We pooled all plants with fruits eaten and dispersed by vertebrate frugivory as having zoochoric dispersal syndromes, while plants that do not involve frugivory for dispersal were pooled as having abiotic dispersal syndromes.

We searched for plant distributions from the Botanical Information and Ecology Network (BIEN) database, which provides range maps for hundreds of thousands of plant species (Maitner

et al., 2018). For any plants that were absent from BIEN, we searched for occurrence record data from the Global Biodiversity Information Facility (GBIF: GBIF, 2020), iNaturalist (2021), and Biodiversity Information Serving Our Nation (BISON: Chamberlain, 2020) databases, using the “spocc” package in R (Chamberlain, 2021) (See Supporting Information Table S2 for the full list of plants).

To calculate plant species richness per island, we considered all species that have been recorded at least once on each island. To account for minor GPS errors, we created 10-km buffers around each point datum. For those data obtained in polygon format from BIEN, we overlaid the polygons over the study island shapefile. Then, using the “Select Layer by Location” ArcGIS tool with “Copy Features”, we determined which islands overlapped species distribution polygons and masked the resulting data to the shape of the islands. These island polygons were then transformed into raster files and then summed using the “Mosaic to New Raster” ArcGIS tool to determine the alpha diversity of plants for each of the study islands.

A potential weakness of broad distribution databases such as those from BIEN is their relative coarseness and their reliance on estimations based not only on occurrence records but also environmental predictors (Maitner et al., 2018). Given these characteristics and to avoid any correlations with our own environmental predictors, we considered using just occurrence record data. However, an assessment of this method showed that some smaller islands had suspiciously low species richness (example: only 24 seeded plant species for Montserrat; Supporting Information Table S1). A comparison of these results with biodiversity surveys and assessments done for select islands (Eshbaugh, 2014; Vincent & Kwit, 2007; Young, 2008) showed that purely occurrence record-focused predictions of island species richness were not representative for certain islands, particularly smaller, less-populated islands—likely due to lack of sampling effort.

2.3 | Abiotic information

To characterize the climatic conditions for each island, we included four variables: Köppen-Geiger Climate Classes (KGCC), average annual minimum/maximum temperatures, and annual precipitation. These variables are strongly correlated with plant distributions and have been used in potential distribution modelling exercises of plants (Magarey et al., 2018). KGCC is an overall representation of an area's climate. This system, based on data between 1980 and 2016, classifies climate into 30 categories by the seasonality of monthly air temperature and precipitation (Beck et al., 2018). Meanwhile, average annual minimum/maximum temperatures are associated with plant temperature tolerance (Daly et al., 2012; Takeuchi et al., 2018), while precipitation levels are associated with a plant's water tolerance (Craine et al., 2013). We obtained average monthly data for both minimum/maximum temperature and precipitation between 1970 and 2000 from WorldClim 2.1 (Fick & Hijmans, 2017). We then used the ‘Mosaic to New Raster’ tool in ArcGIS Pro 2.7.0 (2020) to

create a raster of annual minimum/maximum temperatures and precipitations throughout the region.

In addition to the climatic conditions of each island, we also considered elevation and soil characteristics. Elevation is known to influence climatic and hydrologic conditions (Kenward et al., 2000) and have been highly correlated with plant species distributions (Oke & Thompson, 2015). Meanwhile, soil conditions influence plant development, acting as an important indicator of soil microbial diversity (Xue et al., 2020), nutrient availability (Vejre et al., 2003), and water retention (Leão et al., 2020). For elevation, we obtained 30m resolution data from the Advanced Land Observing Satellite (ALOS) World 3D (Takaku et al., 2014; Todono et al., 2014). For soils characteristics, spatial information was developed by the United States Department of Agriculture (USDA) and is classified into soil types according to their mineral and historical characteristics (Soil Surveys Staff, 2014). We used the Global Soil Regions Map data provided by the USDA, which shows the distribution of 12 soil orders according to soil taxonomy (United States Department of Agriculture, 2005).

The climatic, topographic and soil variables were all in raster format. We used the “Extract by Mask” ArcGIS tool over the study islands and then the “Zonal Statistics as Table” tool to determine the statistics for each island for each of those variables. KGCC and soil order were considered categorical variables. Therefore, for these variables, we determined both the “mode”, the most common classification within an island, and the “variety”, the number of discrete classifications present within an island. For all continuous variables (elevation, minimum temperature, and precipitation), we obtained the means and ranges of each variable within each island.

2.4 | Biotic factors

To survey the richness of frugivorous vertebrate species in the Caribbean, we first consulted an overview of birds, mammals, and reptiles in the study region (birds: Gerbracht & Levesque, 2019; mammals: Turvey et al., 2017; reptiles: Valido & Olesen, 2019). We supplemented the species list from these reviews by searching for a list of available species from each major Caribbean region. We did so using the region (Greater Antilles, Lesser Antilles, Lucayan/Bahamas/Turks and Caicos) and either bird/reptile/mammal diversity as key words within our search. Then to only select frugivorous animals, defined as any animals that consume >10% of its diet as fruits (Kissling et al., 2007), we used the species' scientific name and “diet” as key words to search for that species' diet. If reliable species-specific diet information was not available, we referred to the diet patterns at the genus level. Finally, we considered each species' body mass, which is known to be important in frugivory and plant-animal interactions, particularly seed dispersal (Wotton & Kelly, 2012). To represent body mass, we obtained the average mass of each species in our study by using the species' scientific name and “mass” within our search. All searches were done through a combination of Google Scholar, Google and Ecosia (See Supporting Information Table S3 for the full list of frugivores and their masses).

For each species selected for our study, we searched for its distribution within either BirdLife (for birds) or the International Union for Conservation of Nature (IUCN) databases (for reptiles and mammals). If a species' distribution was not available from these databases, we searched GBIF, iNaturalist, BISON and VertNet (Constable et al., 2010) from the 'spocc' package in R for point data (Chamberlain, 2021). Frugivore animal species richness calculations for each island followed the same procedure as that for plants. In addition to species richness, we calculated the "accumulated biomass" of the frugivore community within each island per taxa as a representation of each island's frugivorous community's collective body mass. This was done by taking the sum of the average masses of all species from specified taxa (i.e., mammals, birds and reptiles) present within each island. This metric would be more representative of the capacity of the larger and heavier frugivores in interacting with plants than a metric that averages the body masses of species present in an island, as averages would be heavily skewed by the more numerous, smaller frugivores thus failing to emphasize the important role that larger frugivores have on frugivory interactions.

2.5 | Island biogeography

Island biogeography considers the area of an island and the characteristics of its nearest neighbours to explain spatial patterns of diversity and community composition (Simberloff & Abele, 1976). According to classical island biogeography rules (e.g., MacArthur & Wilson, 1967), island biodiversity patterns are mostly driven by extinction and colonization events that rely on island size and connectivity/proximity to major landmasses or continents. These island features affect fundamental biogeographical processes, such as speciation, immigration and extinction. We acknowledge, however, that classical models are known to be less successful in predicting island biodiversity patterns when systems and processes operating on evolutionary and geological timescales are considered (Whittaker et al., 2008), such as the rise and fall of volcanic islands (Whittaker et al., 2009). Here, we ignore the particularities of historical narratives to search for the emergent patterns that relate to island configuration in the context of biotic vs abiotic drivers of the diversity of plants with varying dispersal syndromes.

We used island area as the metric related to island size, and three metrics related to connectivity: distance to the nearest neighbour, number of close neighbours, and mass effect (explained below). The area of each island was calculated directly from the polygon shapefile of the study islands through the "Calculate Geometry Attributes" tool in ArcGIS Pro. *Distance to the nearest neighbour* was considered as the distance between the target island and its nearest neighbour. For the *number of close neighbours*, we buffered each island by 100km and counted the number of neighbouring islands within this zone. This distance was chosen as previous studies on nearest neighbour metrics in both marine (Manel et al., 2019; Mellin et al., 2010) and terrestrial (Honorio Coronado et al., 2020; Marrotte et al., 2020) ecosystems used 100 km as a metric of determining independence

between populations. Then, using these neighbours' areas and distances to the target island, we estimated the effect of neighbour sizes on an island in relation to its level of isolation. Focusing on a target island, this "mass effect" variable considered that the strength of propagule donation is stronger for larger and closer neighbour islands. Therefore, this index is a simple weighted average and considers only two parameters: the distance and the area of each neighbour island to the target island. Because the effect of one island over another diminishes with the distance between them, we assumed an inverse relationship (smaller distances lead to larger effects). For each target island, the effect of each neighbouring island (over a 100km buffer) was then summed, according to the equation:

$$\text{Mass effect} = \frac{\sum_i^n \left(\frac{1}{\text{Distance}_n} * \text{Area}_n \right)}{\sum_i^n \left(\frac{1}{\text{Distance}_n} \right)}$$

2.6 | Statistical analysis

To determine how various factors correlate with the diversity of plants of either abiotic or zoochoric dispersal syndromes, we grouped every variable into their respective component of the environment; abiotic (A), biotic (B) and island configuration (I). We then used a correlation matrix of all variables as a reference to select the final group of variables (Supporting Information Table S4). To maintain equal representation between components (i.e., A, B, I), we selected an equal number of variables for each category. To avoid model overfitting, we removed predictors that exhibited high pairwise correlation (cutoff = |0.75|), ending up with a total of four predictors within each component. After carefully checking all the predictors, evaluating their pairwise correlation patterns and log-transforming variables as necessary to reduce correlation and to improve normality, we maintained the following predictors: abiotic (KGCC variety-log-transformed, mean annual precipitation, soil order variety-log-transformed, mean annual minimum temperature), biotic (bird species richness, reptile species richness, accumulated bird mass, accumulated reptile mass) and island configuration (Area-log-transformed, distance nearest neighbour, number of close neighbours, mass effect) (Supporting Information Table S5).

Our hypothesis testing modelling approach relied on the comparison among the ABI components of the environment, to disentangle the main potential predictors of the distribution of plants in the Caribbean. To do so, we used a modified stepwise multiple regression approach, comparing the fit of models containing different combinations of components, but maintaining all the components from a group together. Therefore, we compared models that included the following predictors: (i) A-only; (ii) B-only; (iii) I-only; (iv) A + B; (v) A + I; (vi) B + I; (vii) A + B + I. To fit these seven models, we used generalized linear models (*glms*), which are a type of single summary statistics models with significance testing (McCullagh & Nelder, 2019). The *glms* can handle complex relationships between predictors and the response variables and are able to analyse the simultaneous effects of multiple variables, including both categorical

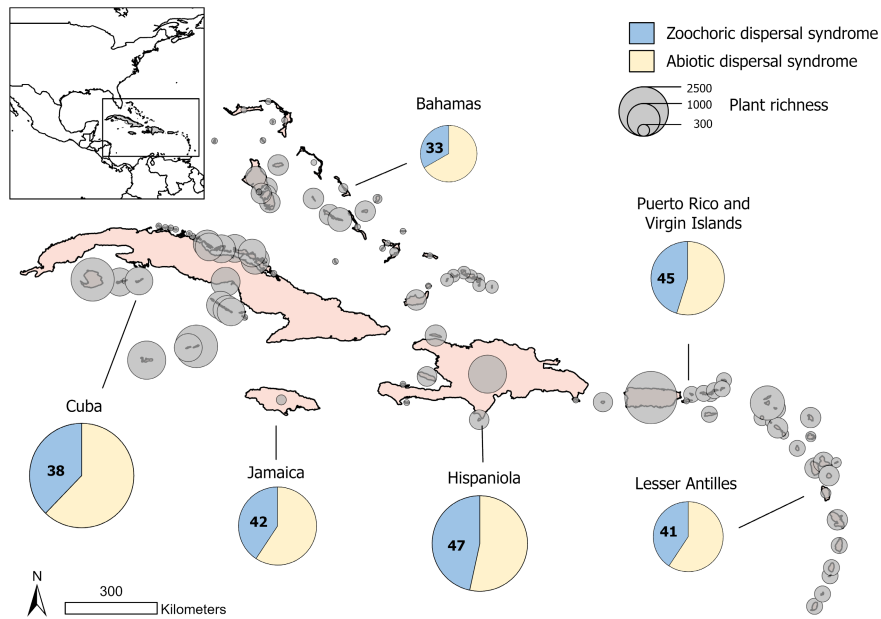


FIGURE 2 Diversity and proportions of abiotic and biotic (zoochoric) seed dispersal syndromes in the Caribbean Islands. The colored pie charts represent the proportion of plant species with zoochoric (blue) and abiotic (yellow) dispersal syndromes for each region and are sized according to their total plant species richness. The percentage of plants with zoochoric dispersal syndromes for each region are shown within each pie chart. Each See Supporting Information Table S1 for the regional designation of each island

TABLE 1 A regional summary of the study area and its plant diversity, ordered by the percentage of plants with biotic dispersal syndromes

| Region | No. of islands | Accumulated area (km ²) | Total abiotic (%) | Total biotic (%) | Total plants |
|------------------------------|----------------|-------------------------------------|-------------------|------------------|--------------|
| Hispaniola | 8 | 76,002 | 1399 (53.42) | 1220 (46.58) | 2619 |
| Puerto Rico + Virgin Islands | 9 | 9668 | 984 (54.85) | 810 (45.15) | 1794 |
| Jamaica | 1 | 11,106 | 1082 (58.11) | 780 (41.89) | 1862 |
| Lesser Antilles | 22 | 6676 | 1027 (59.3) | 705 (40.7) | 1732 |
| Cuba | 29 | 112,784 | 1800 (62.18) | 1095 (37.82) | 2895 |
| Bahamas | 36 | 14,270 | 830 (66.72) | 414 (33.28) | 1244 |

Note: See Supporting Information Table S1 for the regional designation of each island.

and continuous variables and focusing on estimation of model parameters. Although linear models assume normal distribution in the response and errors, *gms* are robust to deviations in these assumptions (McCullagh & Nelder, 2019), so we assumed a gaussian family for our models.

Models were then ranked by their Akaike's Information Criterion (AIC) and their relative weights (Akaike, 1974). Values of AIC within two scores ($\Delta\text{AIC} < 2$) from the top-ranking model indicate similar support (Burnham & Anderson, 2002). After defining the models most supported by the data, we evaluated the relative contribution of each individual predictor. To do so, we calculated the R^2 partitioned by averaging over orders or "lmg scores" (Lindemann et al., 1980), using the previously calculated AIC weights as weighting parameters. The "lmg" index, therefore, is a variance decomposition metric that calculates the relative contribution of each variable to the R^2 . The last procedure was calculated through the "relaimpo" R package (Grömping, 2006) for the best fitting models. To compare the effects of the abiotic, biotic and island configuration on the diversity of dispersal syndromes, we repeated the process three times for total plants, abiotic syndrome plants and zoochoric syndrome plants. All statistical analyses were performed with R platform version 4.0.5 (R Core Team, 2021).

3 | RESULTS

3.1 | Patterns of plant diversity and dispersal syndromes

The distributions of plants obtained from our methods encompassed every island in our study area. Of the 11,619 plants within the catalogue provided by Acevedo-Rodríguez and Strong (2012), we selected 9715 species that were not exotic, naturalized, or cultivated. From this subset, we found that 55.4% (5379) are plants with abiotic dispersal syndromes and 44.6% (4,336) are plants with biotic (zoochoric) dispersal syndromes. From our search, we recovered the distributions of 3313 plants (abiotic: 2085; zoochoric: 1228) from BIEN and 2726 (abiotic: 1417; zoochoric: 1309) from GBIF, iNaturalist, and BISON. Of these, 58% were from abiotic dispersal syndrome plant species and 42% from zoochoric dispersal syndrome plant species (Supporting Information Table S2), although these proportions varied by island (Supporting Information Figure S1).

When grouping islands by geographic neighbours, the highest species richness of plants was from the Cuba region (2895 species), followed by the Hispaniola region (2619) and Jamaica (1862). While the Cuba region also had the highest species richness of plants with

abiotic dispersal syndromes (1800), the Hispaniola region possessed the highest species richness of plants with zoochoric dispersal syndromes (1220). Hispaniola, therefore, had the highest proportion of zoochoric dispersal species at 46.58%, followed by Puerto Rico and the Virgin Islands (45.15%) (Figure 2; Table 1).

3.2 | Patterns of frugivore diversity and accumulated mass

We found 183 bird, 152 reptile and 39 mammal species native to the Caribbean that feed on fleshy fruits and might act as potential seed dispersers. From this list, we obtained the distributions of 151 bird, 140 reptile and 35 mammal species from 26, 6 and 3 families, respectively (Supporting Information Table S3). Our selection of species ranged from species with wide distributions such as *Patagioenas leucocephala* (white-crowned pigeon) and *Tyrannus dominicensis* (gray kingbird), which encompassed nearly our entire study area, and those that were endemic to a single island such as *Anolis bartschi* (west Cuban anole—Cuba) and *Amazona imperialis* (Dominican Amazon - Dominica) (Supporting Information Table S3). While bird distributions encompassed all islands within our study area, reptile distributions were missing from 8 islands and mammal distributions were missing from 37 islands. Overall, Cuba had the greatest diversity of birds (64), and Hispaniola had the highest reptile species richness (61) (Supporting Information Table S1; Supporting Information Figure S2).

Within our selection, the heaviest bird was *Amazona imperialis* with 900g, and the heaviest reptile was *Cyclura nubila* (Cuban ground iguana) with 17.6kg. For birds, 8 parrot (Psittacidae), 6 crow (Corvidae) and 8 pigeon (Columbidae) species made up 49.8% of the total accumulated bird biomass in the region (Supporting Information Figure S3). Meanwhile, for reptiles, iguanas (*Iguanidae*) dominated the weight distribution, with 12 species being attributed with 93% of the accumulated biomass of all reptiles (Supporting Information Figure S3). Cuba had the highest accumulated biomass of birds (4.9 kg), while Puerto Rico had the highest accumulated biomass of reptiles (37.1 kg) (Supporting Information Table S1; Supporting Information Figure S2).

3.3 | Predictors of fruiting plant richness

For all fruiting plants, the model that included just biotic characteristics (model B) best fit the data, with the next most supported model having a Δ AIC of more than two units (Table 2). This pattern, however, changed when examining plants by their dispersal syndromes. For plants that exhibit abiotic dispersal syndrome, the most supported models included both biotic predictors (model B) and biotic predictors + island configuration (model BI). Meanwhile, for plants with zoochoric dispersal syndromes, the model that included abiotic and biotic drivers best explained the distribution (Table 2).

When examining the relative contribution of individual variables, we found that frugivore-related predictors explained most of the variation in the distribution of fruited plants in the Caribbean. *Accumulated bird mass* was the strongest predictor of the distribution of classes of plant dispersal syndrome (Table 3; Total: $\text{Img} = 0.57$ | Abiotic dispersal: $\text{Img} = 0.46$ | Zoochoric: $\text{Img} = 0.30$). *Reptile richness* was the second-best predictor of the distribution of plants with zoochoric dispersal syndrome ($\text{Img} = 0.21$) and that of all plants combined ($\text{Img} = 0.22$), the latter also being strongly affected by *bird richness* ($\text{Img} = 0.12$). However, *island area* was also important for abiotically-dispersed plants ($\text{Img} = 0.13$), while *soil variety* was also considered important for zoochoric plants ($\text{Img} = 0.20$), although both to a lesser extent relative to frugivore-related predictors (Table 3).

4 | DISCUSSION

The mechanisms that drive island biodiversity patterns is a question that has long intrigued natural history scientists (Chase et al., 2019; Kessler & Shnerb, 2015; Russell & Kueffer, 2019). While abiotic characteristics, such as climate, geology and topography, alongside the effects of island configuration and biogeography, have been considered strong drivers of archipelagoes biodiversity (Craine et al., 2013; Daly et al., 2012; Leão et al., 2020; MacArthur & Wilson, 1967; Vejre et al., 2003; Xue et al., 2020), the effect of biotic factors, particularly frugivorous seed dispersers, in structuring plant diversity has been neglected by the literature. Here, we provide the most comprehensive, regional overview on seed plant and frugivore characteristics and distributions in the Caribbean archipelagos. Using this dataset, we examine important predictors associated with seed plant distributions by disentangling abiotic (climatic and geologic), biotic (frugivorous bird and reptile communities), and island configuration characteristics associated with plant species distributions with different dispersal syndromes. Our results indicate that frugivore communities and their distributions explain part of the diversity of plants with both zoochoric and abiotic dispersal syndromes in the Caribbean islands.

As plants with zoochoric dispersal syndromes depend heavily on their mutualistic interactions with frugivores (Valenta & Nevo, 2020; van Leeuwen et al., 2020), we expected them to be heavily associated with biotic characteristics, which was corroborated by our results. We found that the top-ranking models of the distribution of plant diversity included biotic predictors. Namely, *accumulated bird mass* was the predictor with the highest relative importance, alongside *reptile species richness*. The characteristics of bird assemblages were expected to play significant roles in predicting zoochoric plant richness and distributions, as the effect of plant-frugivore interactions on plant dispersal and recruitment potential relies on the functional traits exhibited by frugivore communities (Blake et al., 2009; Hansen & Galetti, 2009; Johnson, 2009). In other words, dispersal-mediated effects of frugivores on plant communities depend on the

TABLE 2 Model selection tables for the analysis of abiotic (KGCC variety, mean minimum temperature, mean precipitation, soil order variety), biotic (bird diversity, reptile diversity, bird mass, reptile mass) and island configuration (Area, distance to nearest neighbour, number of neighbours within 100 km, mass effect) factors for all seed plants (top) and plants with abiotic (middle) and zoochoric (bottom) dispersal syndromes in the Caribbean

| Total seed plants | | | | | | |
|------------------------------|---------|--------|----------------------|----|--------------|--------|
| | Abiotic | Biotic | Island configuration | Df | Δ AIC | Weight |
| Model B | - | X | - | 6 | 0 | 0.744 |
| Model AB | X | X | - | 10 | 2.94 | 0.171 |
| Model BI | - | X | X | 10 | 4.82 | 0.067 |
| Model ABI | X | X | X | 14 | 7.42 | 0.018 |
| Model AI | X | - | X | 10 | 29.03 | 0 |
| Model I | - | - | X | 6 | 32.69 | 0 |
| Model A | X | - | - | 6 | 42.5 | 0 |
| Abiotic dispersal syndrome | | | | | | |
| | Abiotic | Biotic | Island configuration | Df | Δ AIC | Weight |
| Model B | - | X | - | 6 | 0 | 0.447 |
| Model BI | - | X | X | 10 | 0.27 | 0.39 |
| Model ABI | X | X | X | 14 | 2.82 | 0.109 |
| Model AB | X | X | - | 10 | 4.28 | 0.053 |
| Model AI | X | - | X | 10 | 15.65 | 0 |
| Model I | - | - | X | 6 | 17.83 | 0 |
| Model A | X | - | - | 6 | 32.32 | 0 |
| Zoochoric dispersal syndrome | | | | | | |
| | Abiotic | Biotic | Island configuration | Df | Δ AIC | Weight |
| Model AB | X | X | - | 10 | 0 | 0.684 |
| Model BI | - | X | X | 10 | 3.24 | 0.135 |
| Model B | - | X | - | 6 | 4.05 | 0.09 |
| Model ABI | X | X | X | 14 | 4.05 | 0.09 |
| Model AI | X | - | X | 10 | 33.89 | 0 |
| Model A | X | - | - | 6 | 45.46 | 0 |
| Model I | - | - | X | 6 | 49.74 | 0 |

Note: "X" indicates the criterion that was included for the model, with multiple columns selections indicating additive effects. The category of the model is labelled in the first column. " Δ AIC" = difference in Akaike's Information. Criterion score from the best-supported model according to their weight.

composition of functional traits of frugivore assemblages, such as body mass, which affect animal long-distance dispersal rates.

Some studies, however, ignore the important role of reptiles in island ecosystems, (Valido & Olesen, 2019), although many plants are dependent on reptile seed dispersal (Nogales et al., 2017; Pérez-Méndez et al., 2017). Therefore, our findings provide further support for the high relative importance of reptilian plant-frugivore interactions in predicting spatial patterns of overall plant diversity (Nogales et al., 2017; Pérez-Méndez et al., 2017; Valido & Olesen, 2019). This is important as reptiles and birds are thought to have complementary roles in plant dispersal and in promoting plant diversity (Morán-López et al., 2020). Our results, therefore, confirm the assertion that frugivore community characteristics are strongly correlated to the diversity of plant dispersal syndromes, particularly those dispersed

by animals, which has been found by multiple studies (Chanthorn et al., 2018; Kissling et al., 2007; Quitián et al., 2019). However, *soil variety* also featured strongly in zoochoric plant models. Given the energetically intensive requirements from fleshy-fruited plants, it is likely that they develop more often in areas like the wet tropics with abundant abiotic resources such as water, soil nutrients and solar energy (Chen et al., 2017; Ting et al., 2008; Wang et al., 2021). Therefore, our study also corroborates previous studies' findings that soil characteristics may play important roles in shaping the diversity of plants with fleshy fruits (Almeida-Neto et al., 2008; Lotan & Izhaki, 2013).

Variables associated with biotic characteristics were also strongly correlated to the diversity of abiotically dispersed plants. For those plants, top-ranking models included biotic predictors

TABLE 3 Relative importance of each variable for the best fitting models. Results are described for all plants (Total) and those with abiotic and zoochoric dispersal syndromes

| Category | Variables | Total | Plant syndromes | |
|----------------------|-------------------------------|---------------|-----------------|---------------|
| | | | Abiotic | Zoochoric |
| Biotic | Accumulated bird mass | 0.5734 | 0.4586 | 0.2988 |
| Biotic | Reptile species richness | 0.2243 | 0.08609 | 0.2097 |
| Biotic | Bird species richness | 0.12 | 0.09583 | 0.0615 |
| Biotic | Accumulated reptile mass | 0.0813 | 0.05448 | 0.0418 |
| Island configuration | Area (log) | – | 0.1309 | – |
| Island configuration | Number of neighbours | – | 0.08426 | – |
| Island configuration | Mass effect | – | 0.0625 | – |
| Island configuration | Distance to nearest neighbour | – | 0.02731 | – |
| Abiotic | Soil variety (log) | – | – | 0.1978 |
| Abiotic | Mean precipitation | – | – | 0.0946 |
| Abiotic | Mean minimum temperature | – | – | 0.01285 |
| Abiotic | KGCC variety (log) | – | – | 0.083 |

Note: Values refer to the “lmg” index, which measures the relative contribution of each variable to the model R^2 . Bolded numbers are greater than 0.1 and were considered to have high relative importance.

and accumulated body mass was, again, the stronger predictor of plant distribution. We suggest that this result may reflect the potential importance of non-frugivorous interactions in driving plant diversity and dispersal (Nogales et al., 2012). For example, seed predators have been found to play important roles in structuring patterns of plant diversity (Carpenter et al., 2020; Vaz Ferreira et al., 2011) and to contribute to seed dispersal within archipelagos (Ando et al., 2021). In this study, the accumulated bird mass patterns were influenced primarily by species from Psittacidae, Corvidae and Columbidae families, all of which are known to practice seed predation as well as seed dispersal (Galetti & Rodrigues, 1992; Olesen & Valido, 2004; Palmer & Catterall, 2021; Pesendorfer et al., 2018; Tella et al., 2019). Therefore, we suggest that non-frugivorous interactions driven by bird assemblages acting as seed predators could be responsible for driving, at least partially, the distribution patterns of abiotically dispersed plants. To examine this, however, further studies are needed to explicitly explore plant-animal interactions, including non-frugivorous interactions, in these islands.

In addition to biotic characteristics, the *island area* was included among the top-ranking models for plants with abiotic dispersal syndromes. This is unsurprising as the size of an island is associated with the diversity of habitats present (Kohn & Walsh, 1994) and is linked to extinction rates through the determination of the amount of resources present (Simberloff & Abele, 1976). What was surprising, however, was the absence of island area or any of the island configuration metrics in the top-ranking models for plants with zoochoric dispersal syndromes. Given the known important associations of these metrics with biodiversity, this finding likely does not indicate the lack of influence that island configuration has on predicting distributions of plants with zoochoric dispersal syndromes. It may instead hint at the relative strengths of biotic and abiotic characteristics.

We caution, however, that our models cannot be used to infer causal relationships. Instead, they examine covariation between plants and the abiotic, biotic, and island configuration metrics. Therefore, direct links with potential mechanisms behind observed patterns cannot be established. As frugivores and abiotically dispersed plants are not thought to strongly interact, one possibility is that both plant and frugivore communities are highly correlated as they respond similarly to a separate factor, such as abiotic or island configuration characteristics. For instance, it is reasonable to assume that island configuration affects both plants and frugivore communities through colonization-extinction dynamics (Simberloff & Abele, 1976). It is also possible that while frugivore distributions respond directly to plant distributions, plant distributions are more driven by either climate or island configuration metrics. Direct assessments of plant-frugivore interactions and their responses to abiotic or island configuration metrics are needed to tease apart such possibilities and to determine any potential mechanisms behind this pattern.

In conclusion, we highlight the strong associations between biotic characteristics and plant diversity by compiling a comprehensive dataset of native plants and frugivores associated with plant dispersal and controlling for abiotic and island configuration characteristics. Our results support previous studies' assertion of the importance of considering biotic characteristics and interactions in predicting plant diversity and distributions (Kissling et al., 2007; Tripp & Tsai, 2017). Furthermore, we also link reptile species richness with predicting the diversity of plants with zoochoric dispersal syndromes, which may highlight the particular importance of reptile-plant interactions in this region, as found in other island ecosystems (Nogales et al., 2017; Valido & Olesen, 2019). Although this study did not explicitly test the effects of non-fruit diet preferences, the effects of non-frugivorous plant-animal interactions and the historical

ranges of extinct species, the importance of biotic characteristics in explaining plant diversity regardless of their dispersal syndromes suggest that these factors may play important roles in shaping the diversity of plant dispersal syndromes and act as strong predictors for plant distributions (Carpenter et al., 2020; Lim et al., 2020; Nogales et al., 2012). Therefore, further studies that try to elucidate the distribution and diversity of Caribbean plants should explicitly consider the frugivore diversity and consider the interactions they have with plant communities.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest to report.

DATA AVAILABILITY STATEMENT

All data used in this paper and relevant Supporting Informations are available through GitHub (<https://github.com/sxk1332/Caribbean-fruit-frugivore>).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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