Journal of Forestry
https://doi.org/10.1007/s44392-026-00095-8

ORIGINAL PAPER

Developing Species-Specific Height-Diameter Relationship Models for Different Forest Types in Puerto Rico and the US Virgin Islands

Samjhana Wagle[1] · Sheng-I Yang[1] · Thomas J. Brandeis[2] · Humfredo Marcano-Vega[3] · Bronson Bullock[1]

Received: 19 May 2025 / Accepted: 6 April 2026

Abstract

Puerto Rico (PR) and the US Virgin Islands (VI), two archipelagos located in the Caribbean region, possess forest ecosystems with high species diversity, which remain largely underrepresented in forest modeling research compared to temperate forests. Accurately characterizing tree allometry is essential for monitoring forest status over time and predicting tree growth and yield in sustainable forest management. Height-diameter relationship models, denoted as H–D models, are widely used in forestry practice since they effectively reduce the time and cost of field data collection and provide quick estimates of the height of trees based on tree diameter at breast height. For diverse forests, mixed-effects models have often been proposed. In these models, fixed effects provide the predicted H–D curve for the population average (all species) while a calibrated prediction of H–D relationship for each species can be made with the inclusion of both fixed and random effect terms. This study developed species-specific H–D relationship models for different forest types across PR and VI. A total of 25 parametric model candidates published in the literature were examined for each forest type on each archipelago, and the best-fit model in each forest type was selected to build a mixed model for a given forest type and archipelago. The mixed model was then used to generate species-specific predictions of total tree heights. Tree data used were collected from the permanent plots of the USDA Forest Service's Forest Inventory and Analysis (FIA) program. A total of 419 species with 51,166 observations were collected from eight forest types across the two archipelagos. The results highlight variations in H–D relationships across forest types and archipelagos, emphasizing the need for forest type–specific models to capture their unique ecological traits of species. Results show that three-parameter H–D models provide more accurate predictions than two-parameter ones. Carefully examining all possible combinations of placing the random effects when constructing mixed models is suggested, which can improve model predictability for capturing the H–D relationships for diverse species forests.

Extended author information available on the last page of the article

Published online: 04 June 2026

Keywords Caribbean · Random effects · Nonlinear regression · *Spathodea campanulata* · *Leucaena leucocephala*

Introduction

Accurately characterizing tree allometry is essential to monitor forest status over time and predict tree growth and yield in sustainable forest management. Height-diameter relationship models, denoted as H–D models, are widely used in forestry practice since they effectively reduce the time and cost of field data collection, as well as provide quick estimates of the height of trees based on tree diameter at breast height. (Mehtätalo et al. 2015). Over the past decades, various H–D models have been examined and proposed for different species and forest types in the literature (e.g., Fang & Bailey 1998; Huang et al. 1992; Mehtätalo et al. 2015; Ogana 2018; Zhang 1997). Among all H–D models, nonlinear regression is a widely-used statistical method due to the flexibility of the model in capturing variable H–D curves (Arabatzis & Burkhart 1992; El Mamoun et al. 2013; Huang et al. 1992). In contrast to single-species forests, developing species-specific H–D models for diverse-species forests is challenging, due to the small sample sizes of uncommon species in the population. To address this difficulty, several studies have transformed nonlinear regression models into mixed-effects models by adding species as a random effect (Kuehne et al. 2020; Lam et al. 2017; Yang et al. 2022). In mixed-effects modeling, the fixed effects represent the population-average H–D curve across all species, whereas the combination of fixed and random effects provides a calibrated species-specific prediction of the H–D relationship (Calama & Montero 2004; Paulo et al. 2011).

Puerto Rico (PR) and US Virgin Islands (VI), two archipelagos located in the Caribbean region, possess high species-diverse forest ecosystems. The forested lands in both archipelagos are mostly privately owned (85% in PR and 76% in VI) and support a wide array of plant and animal species, including many endemic species to the Caribbean (Brandeis & Turner 2013a, 2013b). These forests were heavily forested prior to European settlement (Wadsworth 1950), but they were continually degraded for timber, fuelwood, charcoal, and agriculture from the 17th until the mid-twentieth century. In 1951, only 6% of PR's total land was covered by forest (Koenig 1953). In the latter half of the twentieth century, widespread abandonment of agricultural lands occurred due to the loss of agricultural export markets and changes in economic development policies (Rudel et al. 2000). The abandonment of agricultural lands in PR and VI along with very limited reforestation and forest land management triggered secondary succession, during which environmental gradients, disturbance regimes and species dispersal (both natural and human-mediated) facilitated the establishment of native and non-native species (Atkinson & Marín-Spiotta 2015; Brandeis et al. 2007; Brandeis & Oswalt 2007; Lugo & Helmer 2004). By 1990, forest cover in PR increased to 32% of the total land area (cite) (Franco et al. 1999) and it was dominated by exotic species (Lugo et al. 2022). In 2009, forest area coverage of PR had increased to 54.7% (Brandeis & Turner 2013a). In the case of VI, forest areas continually decreased from 1990 to 2010 due to increasing

tourism-based economy, high population density and urbanization (Brandeis & Turner 2013b).

Considerable efforts have been made to develop quantitative methods for Caribbean trees (e.g., Brandeis et al. 2006; Brandeis & Randolph 2010; Brandeis & Turner 2013a, 2013b; Yang et al. 2022). With the increasing volume of data from remeasured permanent plots, new opportunities now exist to apply advanced modeling techniques to these expanded datasets and to develop forest type-specific models that better reflect the ecological variation in H–D relationships across forest types and archipelagos (Paulo et al. 2011).

Therefore, the main objective of the study was to develop species-specific H–D relationship models for different forest types in PR and VI. The specific objectives include (1) identifying the best-fit fixed-effects model from 25 parametric candidates published in the literature for each forest type in each archipelago, and (2) building a mixed effects model based on the best-fit, fixed-effects model to provide species-specific predictions of total tree height from tree diameter at breast height. The methodology developed in this study can be used for predicting tree heights of different species present in Caribbean forests, as well as for providing additional insights when constructing mixed effects models for diverse species forest ecosystems.

Materials and Methods

Study Area and Forest Types

Located between 18° 31' and 17° 55' N latitude and 65° 37' and 67° 17' W longitude (Fig. 1), Puerto Rico and the US Virgin Islands were selected for this study because they represent two of the most species-diverse forest ecosystems in the Caribbean, encompassing a wide range of forest types and environmental gradients with relatively small geographic areas (Ewel & Whitmore 1973). Their forests vary significantly over short distances due to rapid changes in moisture, temperature and elevation and exhibit substantial variation in structure, composition and successional stages as a result of differences in climate, topography, geology and land-use history (Brandeis et al. 2009; Ewel & Whitmore 1973). In addition, these island groups have a comprehensive forest inventory and monitoring permanent plot network with over 20 years of data collected (Brandeis et al. 2007; Brandeis & Oswalt 2007).

According to the 2019 forest inventory data published by Marcano-Vega (2023), a total of 289 tree species were recorded in PR, where forests occupy 51.8% of the total land area. Small-diameter stands are predominant in the subtropical dry forests, while larger-diameter stands are more common in the lower montane wet & rain forests. The forests on this archipelago (i.e. the main island, Culebra, Vieques, and Mona) can be categorized into six forest type groups: (1) subtropical dry forest, (2) subtropical moist forest, (3) subtropical wet & rain forest, (4) lower montane wet & rain forest, (5) moist karst forest and (6) intertidal mangrove forest — based on the Holdridge life zone classification (Ewel & Whitmore 1973; Holdridge 1967) and FIA inventory data (Brandeis & Turner 2013a). Detailed forest classification maps of PR are provided in Helmer et al. (2002)

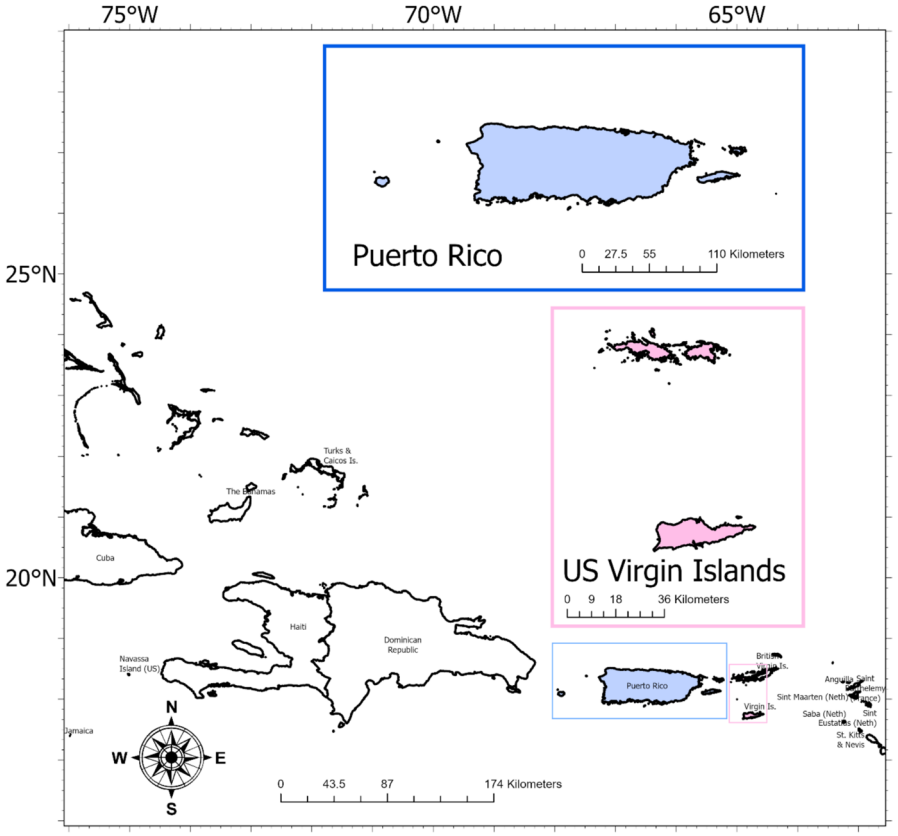


Fig. 1 Map of Puerto Rico and US Virgin Islands

and descriptions of each forest types and their dominant species are given below. More detailed information can be found in Brandeis & Turner (2013a).

(1) Subtropical dry forests: These forests are found in regions receiving 600 mm to 1100 mm of annual precipitation. Major tree species in these forests include *Leucaena leucocephala, Bursera simaruba, Prosopis pallida, Coccoloba microstachya, Bourreria succulenta,* and *Tabebuia heterophylla*.

(2) Subtropical moist forests: This is the most extensive forest type in PR, occurring in areas with annual precipitation of 1000 mm to 2200 mm. This forest type spans a wide range of soil conditions, topography, and land uses, resulting in a diverse mixture of tree species such as *Spathodea campanulata, Guarea guidonia, Andira inermis, Casearia guianensis, Tabebuia heterophylla,* and *Bursera simaruba*.

(3) Subtropical wet & rainforests: These forests are found in areas with annual precipitation of 2000 mm to 4000 mm. The major tree species in this forest

type include *Guarea guidonia, Spathodea campanulata, Prestoea acuminata, Cecropia schreberiana, Inga vera,* and *Syzygium jambos.*

(4) Lower montane wet & rain forests: These forests are located at elevations between 700 and 1000 m. Major forest species include *Prestoea acuminata, Cecropia schreberiana, Micropholis garciniifolia, Henriettea squamulosum, Micropholis guyanensis,* and *Croton poecilanthus*.

(5) Moist karst forests: These forests are located primarily in the northwestern (subtropical moist annual precipitation) part of the main island of PR. The chemical disintegration of the limestone bedrock produces karst landforms, which frequently result in a rugged and dramatic topography. This forest type was inventoried only once, in 2002. The major tree species found in this area are *Spathodea campanulata, Bursera simaruba, Guarea guidonia, Andira inermis, Tabebuia heterophylla,* and *Thouinia striata*.

(6) Intertidal mangrove forests: These forests are found along coastlines and estuaries. They contain less tree species diversity than other forest types and the major species are *Avicennia germinans, Laguncularia racemosa, Rhizophora mangle, Conocarpus erectus* and *Prosopis pallida*.

The VI archipelago is located about 40 miles east of PR in the northeastern Caribbean Sea and consists of St. Thomas, St. John, St. Croix, and several smaller islands. A total of 57.2% of the total area of VI is covered by forest and 121 tree species were recorded in the 2014 forest inventory (Marcano-Vega 2020). Similar to Puerto Rican forests, VI is primarily dominated by secondary forests. Approximately 81% of the forest area is covered by small diameter stands (< 12.7 cm diameter) and the remaining 19% is covered by medium to large diameter stands (> 12.7 cm diameter) (Marcano-Vega 2020). The terrain in VI is less diverse than in PR. The two forest types found in VI and their dominant species are detailed below. For more information see Brandeis & Turner (2013b) and Marcano-Vega (2020).

(1) Subtropical dry forest: This forest is found in areas receiving 600 mm to 1100 mm of annual precipitation. The major tree species are *Leucaena leucocephala, Swietenia mahagoni, Bourreria succulenta, Guapira fragrans, Trema micrantha,* and *Bursera simaruba*.

(2) Subtropical moist forest: This forest is found in areas receiving 1000 mm to 2200 mm of annual precipitation. Some of the major tree species include *Leucaena leucocephala, Guapira fragrans, Bourreria succulenta, Acacia muricata, Maytenus laevigata,* and *Guettarda scabra* (Brandeis & Turner 2013b).

In summary, a total of eight forested regions were examined in this work, including six forest types in PR and two forest types in VI.

Permanent Sample Plots and Tree Data

The data utilized in this research were obtained from the USDA Forest Service, Forest Inventory and Analysis (FIA) program. The first forest inventory in PR was

done by establishing permanent sample plots in 1980 with the primary objective of assessing timber production potential (Birdsey & Weaver 1982). Permanent plots were established along a square systematic grid of 900 ha per square kilometer using the variable radius method with the inclusion of nested regeneration subplots of a fixed radius of 3.6 m (Birdsey & Weaver 1982). In 1990, a re-survey was carried out by using the 1980s' survey method (Franco et al. 1999). In 2001, a new hexagonal sampling grid was generated, the inventory plot design was modified to capture the wide range of diverse forest types and sampling expanded to include all forested areas of PR and VI (Brandeis 2003). The first forest inventory of VI was conducted in 2004 (Brandeis and Turner 2013b). Following the initial inventories under the revised FIA design, permanent plots in PR were remeasured in 2009, 2014, 2019, and 2024, while remeasurements in VI occurred in 2009, 2014, and 2024. This study includes inventory data from PR spanning pre-hexagonal grid surveys (1980, 1990) through 2019, as well as data from the VI inventories conducted in 2004, 2009 and 2014. Data from the 2024 remeasurement cycle was not available at the time of analysis.

According to FIA procedures, forest land is defined as an area of at least 0.4 hectares (1 acre) and 36.6 m (120 feet) in width, with at least 10% tree canopy cover (or potential cover) by live trees of any size, including areas that are regenerating after disturbance (USDA Forest Service 2017). Each permanent plot consists of four 7.3-m (24-ft) fixed radius subplots and four 2.1-m (6.8-ft) nested fixed radius microplots. All trees with a diameter at breast height greater than or equal to 12.7 cm (5 inch) are measured in each subplot and trees from 2.5 to 12.6 cm (1 to 4.9 inch) diameter at breast height are measured in each nested microplot. All permanent plots are revisited and remeasured every five to ten years. Land use, forest type, stand condition, regeneration status, tree density, stand origin, disturbance history and tree condition are recorded in each visit. The details of inventory procedures can be found in Bechtold and Patterson (2005).

For this study, data were compiled from the FIA TREE, COND and PLOT tables, which include information on tree size, height, damage, species identity, forest type, disturbance history, and plot attributes. The final dataset comprised 51,166 tree-level observations from 447 plots across PR and VI including 419 species (Table 1). Trees found with a broken top or missing heights were removed from the dataset. For a given forest type, unknown tree species and species with only one observation were assigned to a single group, denoted as "others". Multiple measurements from the same plots and trees across inventory cycles were retained, with all height-diameter pairs modeled as independent observations, differentiating only by forest type, island and species in the mixed-effects framework. A summary of the data is presented in Table 1.

Model Building

Twenty-five nonlinear H–D models were selected from the published literature (Table 2), including well-established forms based on their frequent use, demonstrated predictive performance in prior research and ability to accommodate

Table 1 Summary of forest inventory data by forest type group in Puerto Rico (PR) and the US Virgin Islands (VI), including number of plots (N_{plot}), number of species (N_{sp}), number of observations (N_{obs}), as well as mean, standard deviation (Std.), minimum (Min.) and maximum (Max.)

Archipelago	Forest type group	N_{plot}	N_{sp}	N_{obs}	D (cm)				H (m)			
					Mean	Std	Min	Max	Mean	Std	Min	Max
PR	Subtropical dry	104	139	6,674	8.5	8.0	2.5	78.0	5.6	2.5	0.9	20.1
PR	Subtropical moist	210	301	20,386	13.8	12.7	2.5	175.0	8.9	4.7	0.3	36.0
PR	Subtropical wet & rain	134	228	14,965	17.6	14.6	2.5	190.2	10.3	5.4	0.9	41.1
PR	Lower montane wet & rain	11	52	1,231	18.0	11.9	2.5	150.6	8.2	4.2	1.5	28.0
PR	Moist karst	35	82	1,041	13.8	11.5	2.5	82.2	9.5	5.4	1.0	30.4
PR	Intertidal mangrove	4	5	387	13.0	9.2	2.5	53.3	8.0	3.2	0.6	20.1
VI	Subtropical dry	70	86	3,971	9.1	7.9	2.5	69.9	6.2	2.4	1.5	17.1
VI	Subtropical moist	31	93	2,511	10.2	9.1	2.5	118.6	6.9	3.1	0.9	36.6

Table 2 List of twenty-five selected model candidates where H is tree height (m), D is tree diameter at breast height (cm) and a, b, c are model parameters

Code	Equation	Reference
M1	$H = \frac{aD}{(1+D)^b}$	Curtis (1967)
M2	$H = \frac{D^2}{(aD+b)^2}$	Näslund (1936) & Peschel (1938)
M3	$H = a\exp(-bD^{-1})$	Schumacher (1939), Michailoff (1943), Curtis (1967) & Burkhart and Strub (1974)
M4	$H = a[1 - \exp(-bD)]$	Meyer (1940) & Curtis (1967)
M5	$H = aD^b$	Stoffels (1953)
M6	$H = \frac{aD}{b+D}$	Menten (1913), Bates and Watts (1980) & Huang et al. (1992),
M7	$H = \exp[a - b(D + 1)]^{-1}$	Wykoff et al. (1982)
M8	$H = a(\frac{D}{1+D})^b$	Huang et al. (2000)
M9	$H = a(1 + \frac{1}{D})^b$	Curtis (1967)
M10	$H = aD\exp(-bD)$	Huang et al. (2000)
M11	$H = \exp(a + \frac{b}{D})$	Staudhammer and LeMay (2000)
M12	$H = a[\log(1 + D)]^b$	El Mamoun et al. (2013)
M13	$H = (a + \frac{b}{D})^{-5}$	El Mamoun et al. (2013)
M14	$H = [(\frac{a}{D})^b]^{-1}$	Ogana (2018)
M15	$H = \frac{D^2}{aD^2+bD+c}$	Strand (1958)
M16	$H = \frac{a}{1+b\exp(-cD)}$	Pearl and Reed (1920) & Huang et al. (1992)
M17	$H = a[1 - \exp(-bD)]^c$	Richards (1959) & Huang et al. (1992)
M18	$H = a[1 - \exp(-bD^c)]$	Weibull (1951) & Huang et al. (1992)
M19	$H = a\exp[-b\exp(-cD)]$	Gompertz (1833) & Huang et al. (1992)
M20	$H = aD^{bD^{-c}}$	Sibbesen (1981) & Huang et al. (1992)
M21	$H = a\exp(-bD^{-c})$	Lundqvist (1957) & Flewelling and Jong (1994)
M22	$H = a\exp(\frac{-b}{D+c})$	Ratkowsky (1990) & Huang et al. (1992)
M23	$H = \frac{a}{1+\frac{1}{bD^c}}$	Peschel (1938)
M24	$H = \frac{a}{1+bD^{-c}}$	Huang et al. (2000)
M25	$H = \exp(a + bD^c)$	Larsen and Hann (1987)

different curve shapes. In all selected models, the total tree height (H, m) is predicted via a nonlinear function $f(D)$ with diameter at breast height (D, cm) as a single predictor due to its ease of measurement and generally high accuracy in field settings. Fourteen model candidates include two parameters (a and b), and the remaining eleven have three parameters (a, b and c). The forms and references of all models are given in Table 2. For a given forest type in an archipelago, models were built in two steps. In the first step, the best-fit, fixed-effects model was selected, which was used for building mixed models in the second step. The best-fit, mixed-effects model was then identified. Specifically,

Step 1.

Selection of the best-fit, fixed-effects model: Twenty-five, fixed-effect model candidates were fitted separately for each forest type using the nlsLM function in R (Elzhov et al. 2016). The best model was selected based on the combined rank of mean bias, root mean square errors and number of parameters. More detailed information about the ranking approach is given in the section "Model evaluation and ranking."

Step 2.

Selection of the best-fit, mixed-effects model: The form of the best model selected in step 1 for each forest type was used to build a mixed-effects model by adding species as a random effect[1]. In each forest type and archipelago, models were fit to all species, with species included as a random effect, allowing predictions across the full species pool. We examined all possible combinations of fixed and random effects and identified the best-fit mixed model using the same ranking approach as described in step 1. For example, model #1 proposed by Curtis (1967) is selected as the best model in step 1. Then, all possible mixed models are built based on the form of model #1. That is,

$$H = \frac{(a + a_{sp})D}{(1 + D)^{b}} \tag{1}$$

$$H = \frac{aD}{(1 + D)^{(b+b_{sp})}} \tag{2}$$

$$H = \frac{(a + a_{sp})D}{(1 + D)^{(b+b_{sp})}} \tag{3}$$

where a_{sp} and b_{sp} are species-specific random effects, which follow a normal distribution with mean zero and variances σ_a^2 and σ_b^2, respectively (i.e., $a_{sp} \sim N(0, \sigma_a^2)$ and $b_{sp} \sim N(0, \sigma_b^2)$). Mixed models were built using the nlme function in R (Pinheiro et al. 2017).

Model Evaluation and Ranking

Three criteria were used in model evaluation, including mean bias (MB), root mean square error (RMSE) and number of parameters. Formulas for computing RMSE and MB are given as:

$$\text{RMSE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(H_i - \hat{H}_i)^2}$$

[1] Notably, if the best fixed-effect model fails to converge in parameter estimation when building mixed models, the next best fixed-effect model will be selected.

$$MB = \frac{1}{n}\sum_{i=1}^{n}(H_i - \hat{H}_i)$$

where n is number of observations, H_i is observed tree height, and $\hat{H}_i$ is predicted tree height.

The number of parameters for fixed-effect models was the total count of parameters in a model. In this study, the fixed-effects models include either two or three parameters. When comparing number of parameters for mixed-effects, both fixed- and random-effects parameters are included in the count. In our previous example, Eqs. 1 and 2 each have three parameters (2 fixed effects and 1 random effect) while Eq. 3 has four parameters (2 fixed effects and 2 random effects).

For a given forest type in an archipelago, models were ranked based on each of three criteria. Lower RMSE, closer to zero MB and fewer number of parameters were considered better. Then, the ranks from all criteria were summed to obtain a cumulative ranking score for each model. The model with the lowest total score was considered the best model which balanced the prediction accuracy and model parsimony.[2]

Results

Observed H–D Relationships

The subtropical moist forests in PR had the highest number of observations (20,386 H–D pairs) and number of species (301 species) followed by subtropical wet & rain forests in PR (Table 1). The tallest tree H is recorded at 41.1 m and the largest tree D is recorded at 190.2 cm in subtropical wet & rain forests. In contrast, subtropical dry forests in PR were characterized by smaller trees with a mean D of 8.5 cm and mean H of 5.6 m (Table 1).

Among all forest types and both archipelagos, H–D relationships are positive and nonlinear, generally increasing at a decreasing rate as diameter at breast height increased (Fig. 2). As shown in Fig. 2, both subtropical moist and subtropical wet & rain forests showed greater variability with increasing tree height than other forest types in PR. When comparing the same forest type between two archipelagos, variation of H–D relationships was less pronounced in VI, where both subtropical dry and subtropical moist forests exhibited more compact H–D patterns (Figure 2).

Selection of Model Candidates Across Forest Types and Archipelagos

The performance of 25 model candidates varied across forest types and archipelagos. As indicated in Table 3, three-parameter models were the top three best models for all

[2] In cases where multiple models had the same total rank, we applied a hierarchical decision rule in model selection. First, we selected the model with the fewest total parameters. If parameter counts were equal, the model with the lowest RMSE was chosen. If RMSEs were also equal, we selected the model with mean bias closest to zero.

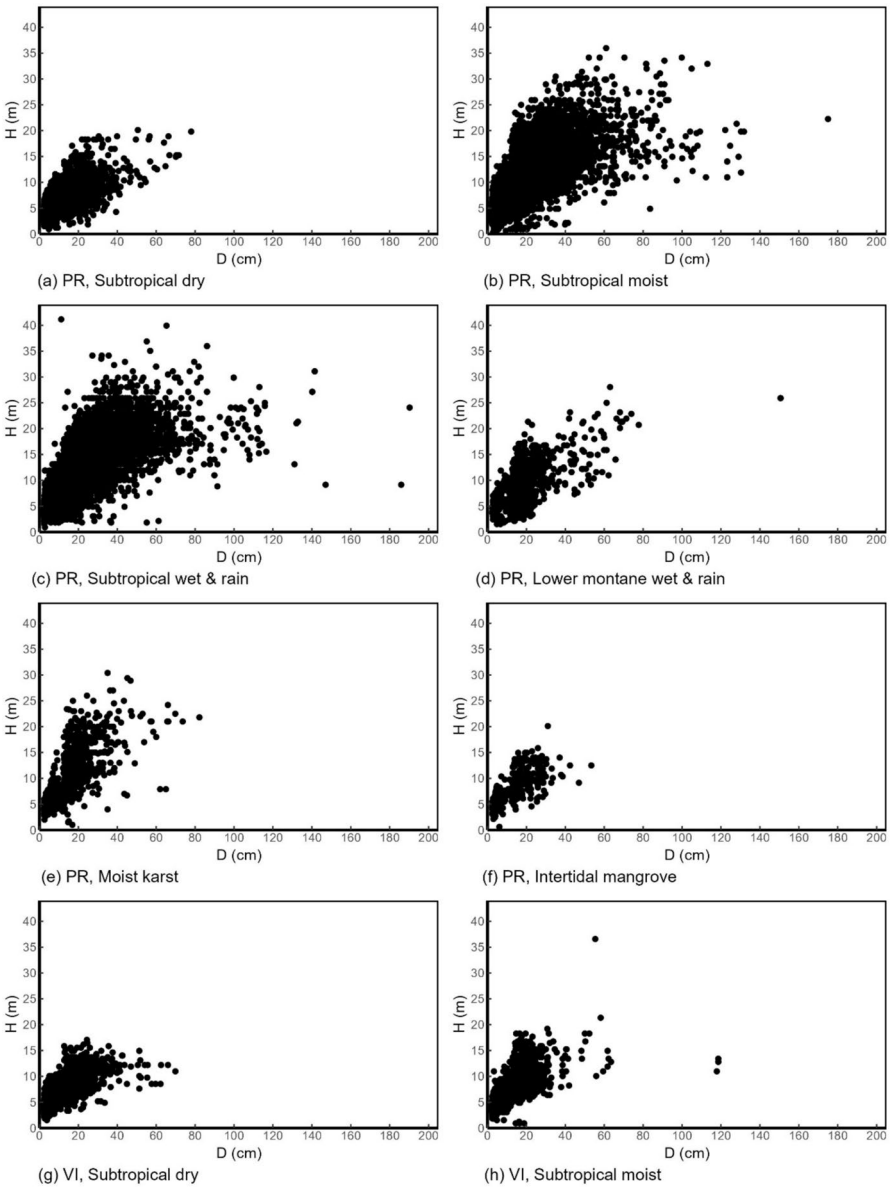


Fig. 2 Observed height-diameter pairs across different forest types in two archipelagos: Puerto Rico (PR) and the US Virgin Islands (VI). H represents tree height (m) and D represents tree diameter at breast height (cm)

forest types and archipelagos, except for subtropical dry forests in PR. Models 19 and 22 ranked the first in four of the six forest type groups in PR: subtropical wet & rain, moist karst, subtropical moist, and lower montane wet & rain forests respectively. In VI, the same three models were selected for both forest types (i.e., Models 17, 18 and 22).

Table 3 The top three best fixed-effects models selected from 25 model candidates across all forest types in Puerto Rico (PR) and the US Virgin Islands (VI). Model performance was ranked based on three criteria: mean bias (MB), root mean square error (RMSE) and number of parameters. The total rank was the sum of ranks across three criteria

Archipelago	Forest type group	Model	RMSE		MB		Parameters		Total rank
			Value	Rank	Value	Rank	Numbers	Rank	
PR	Subtropical dry	M25	1.6520	1	−0.0003	1	3	2	1.3
		M20	1.6520	1	−0.0007	2	3	2	1.7
		M14	1.6520	1	−0.0009	7	2	1	3.0
	Subtropical moist	M22	2.6124	1	0.0000	1	3	2	1.3
		M15	2.6133	2	0.0034	2	3	2	2.0
		M17	2.6139	3	0.0058	5	3	2	3.3
	Subtropical wet & rain	M19	3.0543	1	−0.0048	3	3	2	2.0
		M22	3.0599	2	0.0018	2	3	2	2.0
		M15	3.0629	3	0.0003	1	3	2	2.0
	Lower montane wet & rain	M22	3.1893	1	0.0035	1	3	2	1.3
		M16	3.1926	2	−0.0061	2	3	2	2.0
		M20	3.2193	4	0.0066	3	3	2	3.0
	Moist karst	M19	3.1634	1	−0.0026	2	3	2	1.7
		M22	3.1675	2	0.0025	1	3	2	1.7
		M15	3.1695	3	−0.0077	3	3	2	2.7
	Intertidal mangrove	M16	1.9707	1	−0.0002	3	3	2	2.0
		M19	1.9713	2	0.0002	2	3	2	2.0
		M15	1.9781	6	−0.0002	1	3	2	3.0
VI	Subtropical dry	M22	1.4570	3	−0.0002	1	3	2	2.0
		M17	1.4560	1	0.0005	5	3	2	2.7
		M18	1.4568	2	0.0008	7	3	2	3.7
	Subtropical moist	M17	1.8758	1	0.0011	2	3	2	1.7
		M22	1.8763	2	−0.0001	1	3	2	1.7
		M18	1.8770	3	0.0023	7	3	2	4.0

Specifically, Model 22 ranked highest in subtropical dry forests, while Model 17 was the top model in subtropical moist forests. Among all top models across forest types and archipelagos, RMSE values range from 1.6520 (Model 25 in subtropical dry forests) to 3.1893 m (Model 22 in lower montane wet & rain forests) in PR (Table 3) and range from 1.4570 (Model 22 in subtropical dry forests) to 1.8758 m (Model 17 in subtropical moist forests) in VI. Regarding prediction bias, MB values range from −0.0048 (Model 19 in subtropical wet & rain forests) to 0 m (Model 22 in subtropical moist forests) in PR and range from 0.001 (Model 17 in subtropical moist forests) to −0.0002 m (Model 22 in subtropical dry forests) in VI. Performance of all 25 model candidates across each forest type in both archipelagos are given in supplementary material from Table S1 to Table S8.

Mixed Model Construction

The best-fit, fixed-effect model was used as the base form to construct mixed models. For a given forest type and archipelago, all possible combinations of placing the random effects along with the model parameters were examined. It was found that, when adding random effects to all model parameters for the three parameter models, the parameter estimation failed to converge. Table 4 shows all converged models

Table 4 Fit statistics for mixed effects models across forest types in two archipelagos (Puerto Rico and US Virgin Island). Models differ by random component structure (a, b, c) and are ranked by RMSE, mean bias (MB), and number of parameters. Lower total ranks indicate better overall fit

Archipelago	Forest types	Random Component	RMSE		MB		Parameter		Total rank
			Value	Rank	Value	Rank	Number	Rank	
PR	Subtropical dry	a	1.2530	1	−0.0033	1	4	1	1.0
		b	1.2575	2	−0.0081	2	4	1	1.7
	Subtropical moist	a & b	2.2575	1	−0.0021	2	5	2	1.7
		a & c	2.2658	2	−0.0004	1	5	2	1.7
		a	2.3098	4	0.0031	3	4	1	2.7
		b & c	2.2937	3	−0.0033	4	5	2	3.0
		b	2.3732	5	0.0052	6	4	1	4.0
		c	2.4467	6	0.0044	5	4	1	4.0
	Subtropical wet & rain	a	2.7082	3	−0.0090	1	4	1	1.7
		a & b	2.6602	1	−0.0153	3	5	2	2.0
		c	2.7186	4	−0.0143	2	4	1	2.3
		b & c	2.6913	2	−0.0188	5	5	2	3.0
		b	2.7671	5	−0.0165	4	4	1	3.3
	Lower montane wet & rain	a	2.4115	3	−0.0064	3	4	1	2.3
		b	2.4631	4	−0.0063	2	4	1	2.3
		c	2.5009	5	−0.0001	1	4	1	2.3
		a & b	2.3731	1	−0.0101	5	5	2	2.7
		a & c	2.3985	2	−0.0098	4	5	2	2.7
	Moist karst	a	2.8725	1	−0.0024	1	4	1	1.0
		c	2.9067	2	−0.0222	2	4	1	1.7
		b	3.0549	3	−0.0404	3	4	1	2.3
	Intertidal mangrove	a	1.9225	1	−0.0001	1	4	1	1.0
		c	1.9374	2	−0.0033	3	4	1	2.0
		b	1.9707	3	−0.0002	2	4	1	2.0

Table 4 (continued)

Archipelago	Forest types	Random Component	RMSE		MB		Parameter		Total rank
			Value	Rank	Value	Rank	Number	Rank	
VI	Subtropical dry	a	1.2785	4	−0.0017	3	4	1	2.7
		b	1.2931	5	−0.0016	2	4	1	2.7
		c	1.3233	6	0.0007	1	4	1	2.7
		a & b	1.2520	1	−0.0023	5	5	2	2.7
		a & c	1.2569	2	−0.0017	4	5	2	2.7
		b & c	1.2638	3	−0.0047	6	5	2	3.7
	Subtropical moist	a	1.6084	1	0.0021	3	4	1	1.7
		b	1.6725	2	−0.0011	2	4	1	1.7
		c	1.7466	3	0.0003	1	4	1	1.7

across forest types and archipelagos. The top-ranked model was achieved when the model was fitted with the random parts added along with parameter "*a*" for all forest types in both archipelagos except for subtropical moist forests in PR. Notably, Model 17 ranked highest (Table 3) for subtropical moist forests in VI, but convergence failed during parameter estimation when constructing mixed models. Thus, Model 22, the second-best model, was selected.

Table 5 shows the estimates of variances for mixed models across forest types and archipelagos. The subtropical moist forest in PR exhibited a larger variance in random effects (species) ($\sigma_a^2 = 49.00, \sigma_b^2 = 21.36$). In contrast, the subtropical dry forest in PR showed the lowest model variance $\left(\sigma^2 = 1.60\right)$ and the species-level random effect variance ($\sigma_a^2 = 0.05$). These patterns are supported by the observed versus predicted tree heights in Fig. 3. A strong positive relationship is evident in PR subtropical dry forest and PR lower montane wet & rain forest, where data points fit the 1:1 prediction line more closely than other forest types.

Table 5 Estimates of variances for mixed-effects models among forest type and archipelagos. Variances of species-specific random effects were represented as σ_a^2 and σ_b^2 (see definition in "Model building"), and the random error is denoted as σ^2

Archipelago	Forest type	σ_a^2	σ_b^2	σ^2
PR	Subtropical dry	0.0485	-	1.6004
PR	Subtropical moist	49.0033	21.3648	5.1829
PR	Subtropical wet & rain	7.6138	-	7.4110
PR	Lower montane wet & rain	22.4869	-	6.0279
PR	Moist karst	6.0499	-	8.6232
PR	Intertidal mangrove	0.8519	-	3.7637
VI	Subtropical dry	3.7734	-	1.6646
VI	Subtropical moist	6.0210	-	2.6621

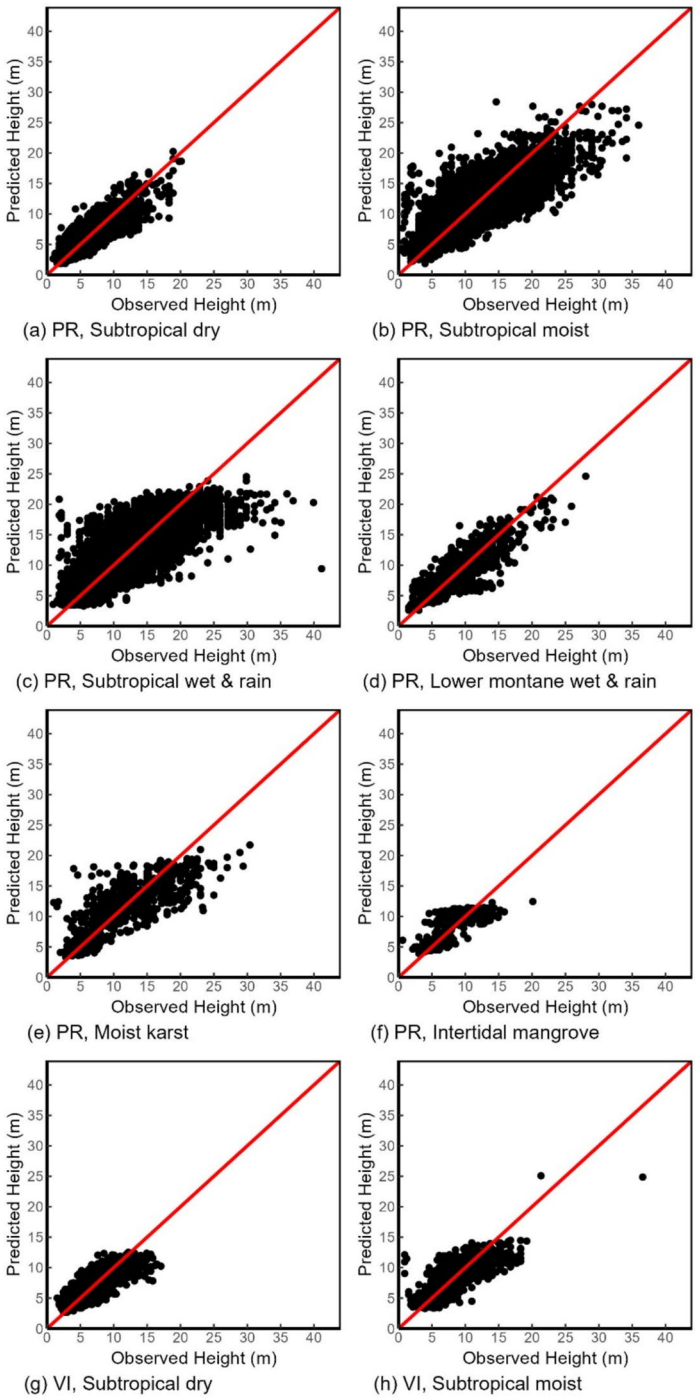


Fig. 3 Observed versus predicted tree heights across various forest types in Puerto Rico and the US Virgin Islands. The red 1:1 line represents the perfect model prediction

Fig. 4 Height–diameter (H–D) relationships across major forest types in Puerto Rico (PR) and the US Virgin Islands (VI) based on nonlinear mixed-effects models. Solid red curves represent H–D relationships predicted from fixed effects, whereas gray curves depict species-specific predictions including species as a random-effects. Gray points denote observed H–D. pairs ▶

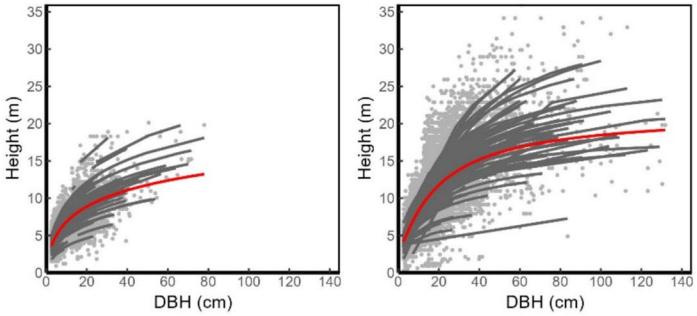
Comparison of Mixed and Fixed-Effects Models

Mixed models with species as a random effect can increase prediction precision compared to fixed models across all forest types (see Tables 3 and Table 4). For example, in the subtropical moist forest of PR, RMSE decreased from 2.6124 (fixed-effects) to 2.2575 (mixed-effects), representing a 13.6% reduction. In addition, by using mixed models, species-specific predictions can be made. As shown in Fig. 4, fixed models can only produce an average H–D curve for a given forest type, while mixed models can be used for capturing the variation of H–D curves among species.

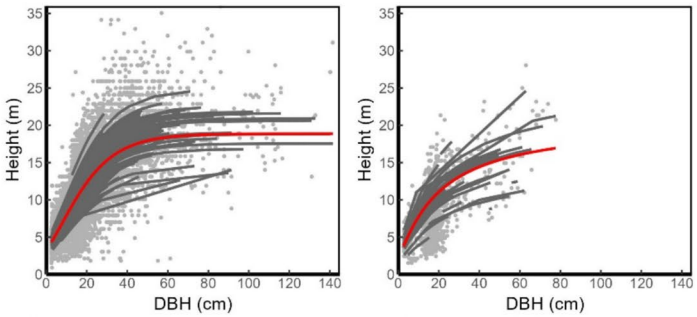
Species-Specific Prediction

For a given forest type and archipelago, species-specific model coefficients for the most abundant species (i.e., the one has the most count of observations) are given in Table 6. Coefficients for all other species are given in supplementary materials from Table S9 to Table S16. As shown in Table 6, *Leucaena leucocephala* accounts for three of the eight combinations (subtropical dry forests in PR and both forest types in VI), followed by *Spathodea campanulata* for two combinations (subtropical moist and moist karst in PR). *Guarea guidonia*, *Prestoea acuminata* and *Avicennia germinans* are found in subtropical wet & rain, lower montane wet & rain and intertidal mangrove, respectively.

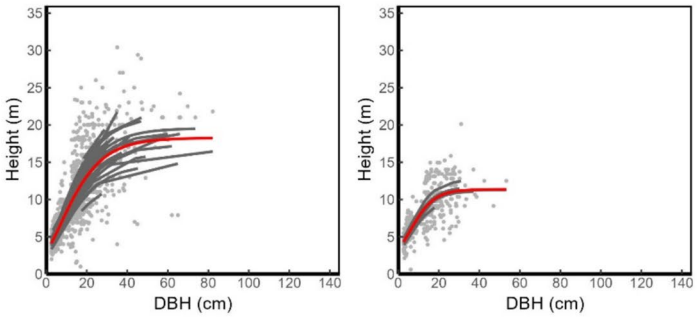
Regarding prediction accuracy, absolute MB values ranged from 0.0025 to 0.0829 m, and RMSE values ranged from 1.0751 to 3.0297 m (Table 6). When comparing species-specific prediction with overall model, bias and precision are dependent on species. Take subtropical dry forests in PR for example. Absolute MB was recorded as 0.0033 m for the overall model, but it increased to 0.0296 m for *Leucaena leucocephala.* However, for subtropical wet & rain forests in PR, absolute MB dropped from 0.0090 m in the overall model to 0.0043 m for *Guarea guidonia.* Similar for prediction precision, RMSE of 1.9225 m was recorded for the overall model, which decreased to 1.6113 m for *Avicennia germinans* for intertidal mangrove in PR. A decline of precision level was found for lower montane wet & rain forests where RMSE of 2.4115 m increased to that of 2.6411 m between the overall model and *Prestoea acuminata*.



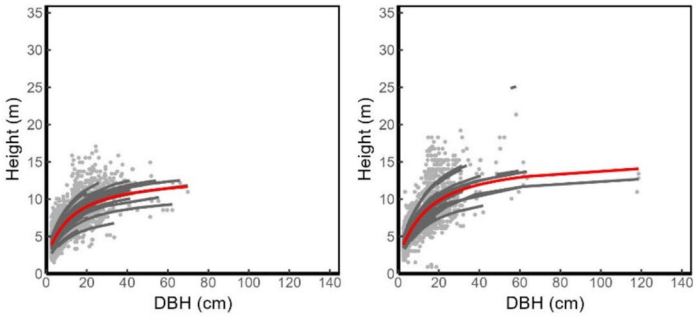
(a) PR Subtropical dry (b) PR Subtropical moist



(c) PR Subtropical wet & rain (d) PR Lower montane wet & rain



(e) PR Moist Karst (f) PR Intertidal mangrove



(g) VI Subtropical dry (h) VI Subtropical moist

Table 6 Statistics and estimated model parameters for the most abundant tree species across forest types in Puerto Rico (PR) and the US Virgin Islands (VI). For each species, sample size (N), root mean square error (RMSE), mean bias (MB), and parameter estimates (*a, b, c*) are given

Archipelago	Forest type	Species	N	RMSE	MB	a	b	c
PR	Subtropical dry	*Leucaena leucocephala*	808	1.0850	0.0296	4.58	−3.65	−0.16
PR	Subtropical moist	*Spathodea campanulata*	2615	3.0297	0.0201	26.78	19.87	7.63
PR	Subtropical wet & rain	*Guarea guidonia*	1710	2.4712	0.0043	18.80	1.76	0.07
PR	Lower montane wet & rain	*Prestoea acuminata*	623	2.6411	−0.0148	13.37	17.37	7.62
PR	Moist karst	*Spathodea campanulata*	165	3.0280	−0.0829	19.55	1.84	0.09
PR	Intertidal mangrove	*Avicennia germinans*	183	1.6113	−0.0155	11.65	2.51	0.17
VI	Subtropical dry	*Leucaena leucocephala*	802	1.1218	−0.0025	14.66	10.08	5.59
VI	Subtropical moist	*Leucaena leucocephala*	302	1.0751	−0.0342	16.57	11.95	6.12

Discussion

Comparison of H–D Relationships Across Forest Types and Archipelagos

The H–D relationship is typically nonlinear with the height curve increasing more rapidly in earlier stage of growth than in the later stages (Huang et al. 1992; Sharma & Yin Zhang 2004). Among both archipelagos and all forest types, H–D relationships exhibited a nonlinear pattern, generally increasing at a decreasing rate as diameter at breast height increased. This trend is consistent with established allometric theory and previous findings in the literature (Mehtätalo et al. 2015). H–D relationships varied notably among forest types in both PR and VI, which could be influenced by species composition, forest structure site conditions and light availability (Yang et al. 2022). Subtropical moist and subtropical wet & rain forests in PR exhibited taller trees and greater H–D variability, possibly due to high species diversity and structural complexity (Brandeis et al. 2007). The dominance of broadleaf evergreen species (e.g., *Guarea guidonia*, *Spathodea campanulata*) adapted to humid environments (Brandeis & Turner 2013b) showed wider height ranges and more dispersed H–D patterns. In contrast, intertidal mangrove and subtropical dry forests showed more concentrated H–D patterns maybe due to lower species diversity and similar diameters and heights among individuals (see lower standard deviations of H and D compared to other forest types in PR in Table 1). Prediction accuracy of the final model is lower in moist karst forest and subtropical wet & rain forest than other forest types. It may be because of the strong variation in soil depth, water retention and exposure in the moist karst forest area and the high environmental diversity

(microclimatic effect) and shallow soil depth in lower montane wet & rain forest (Brandeis & Turner 2013a).

As noted in the "Results" section, variation of H–D relationships in VI was less than PR, where both VI subtropical dry and subtropical moist forests exhibited more compact H–D patterns. It's likely due to more complex forest structure and broader ecological gradients in PR (Brandeis & Turner 2013a; Yang et al. 2025). Another reason may be due to the higher site productivity and broader forest recovery in PR after agricultural decline (Lugo et al. 2022; Rudel et al. 2000). These variations in H–D relationships highlight the importance of developing forest-type-specific models that can effectively capture the unique ecological characteristics of species within each forest type and archipelago.

Comparison of 25 Model Candidates for Characterizing H–D Relationships

Among 25 model candidates evaluated, Models 22 (Ratkowsky 1990) and Model 19 (Gompertz 1833) consistently delivered the most accurate predictions across multiple forest types. These models performed well likely due to their flexibility to capture the asymptotic nature of tree growth, particularly in forests where tree heights tend to level off at larger diameters. These models can capture the sigmoidal or exponential saturation patterns found in tropical and subtropical forests and it makes them good choices for modelling forest allometry (Mehtätalo et al. 2015). As reported by Huang et al. (1992), Model 22 was particularly well suited to predict tree heights of deciduous tree species. We extended this work to evergreen subtropical forests (Brandeis & Turner 2013a, 2013b) and it performed well in most of the forest types.

Selecting an appropriate model is critical and should be based on ecological conditions, data quality and forest structure (Mehtätalo et al. 2015). Generally, three-parameter models provide more accurate predictions for all forest types due to their added flexibility in capturing diverse growth patterns. While some researchers prefer two-parameter models for their simplicity and better convergence properties (Mehtätalo et al. 2015), three-parameter models offer greater flexibility and allow for a more comprehensive representation of the underlying relationships (Lebedev & Kuzmichev 2020). Based on the results, these models are recommended as a first attempt for fitting H–D relationships.

Species-Specific Predictions Using Mixed-Effects Models

Species often demonstrate different allometric responses depending on forest type, suggesting the need for further refinement, either by modeling forest type as an additional random effect or by fitting species specific models within each forest type (Paulo et al. 2011). We chose to fit species-specific models within each forest type to better capture unique growth patterns and avoid pooling across ecologically distinct forest types, which could mask important differences. This would more accurately reflect how environmental factors and species traits interact.

Substantial species variation was observed across forest types and island groups highlighting the importance of considering ecological context during modeling. For example, *Leucaena leucocephala* is found in subtropical dry forests of PR and VI, but with different growth patterns and model coefficients. This indicates that species performance is influenced by site specific environmental factors, emphasizing the need for context specific modeling approach (Kuehne et al. 2020). The use of nonlinear mixed effects models allows for species-level predictions by using species as a random effect, which is particularly effective in ecosystems with higher species richness where fixed effects models fail to capture interspecific variation (Calama & Montero 2004; Kuehne et al. 2020; Temesgen et al. 2008). Notably, a key limitation of using mixed models is that pooling data from all species may not produce the optimal predictions for each species (Yang et al. 2025). However, by pooling data, mixed-effects models are advantageous for characterizing H–D relationships for rare species by leveraging data from others (Gelman & Hill 2007; Mehtätalo et al. 2015).

We used only diameter at breast height to predict tree height, as it is easier to measure and typically provides the highest accuracy during field measurements. To increase prediction accuracy, some researchers have included environmental variables (Yang et al. 2022), competition index (Jha et al. 2023), structural variables (e.g. stand density, canopy structure) (Ratcliffe et al. 2016), stand and site attributes (e.g. elevation, stand age, site index) (Temesgen et al. 2015) in the model. Incorporating these additional variables into future mixed effects models may improve the prediction accuracy in complex and diverse forest ecosystems. Lastly, species was used as a single variable when constructing the random effects. Further studies may consider adding more variables (e.g., forest type, functional trait) in random effects or constructing a nested structure of random effects (e.g., species under forest type) (Paulo et al. 2011) but increasing model complexity may increase the risk of overfitting and reduce model generalizability.

In this study, a mixed modeling approach was used to provide calibrated predictions of H–D relationships for species in a given forest type and archipelago. A list of estimated coefficients by species among forest types and archipelagos can be found in "Supplementary Material". In practice, the proposed method can be applied to build H–D models for diverse species populations, or practitioners can use the species-specific coefficients provided in this study when predicting tree heights is needed. As mentioned previously, with the inclusion of random effects, this technique allows users to model diverse species populations, especially for species with only a few observations. Technically, species-specific coefficients can be estimated for species with only one observation, but the estimates may not be reliable. Thus, we grouped species with less than two observations into a single category, named "others". The coefficients for this group can be used for rare species or previously unobserved species[3]. When using the coefficients of this group, practitioners should

[3] The H–D relationships of the unobserved species can also be predicted using only fixed effects.

interpret such predictions cautiously and consider collecting additional data for underrepresented species when possible. In addition, the predefined threshold was set to provide the maximum number of species for species-specific calibration. An alternative way to select a threshold for species grouping is to select the value with the least prediction bias and greatest precision by evaluating all possible thresholds, which is suggested for a next step of this study.

Lastly, model evaluation was conducted using the same dataset employed for model fitting. The absence of an independent validation dataset should be considered when interpreting the results. Future studies could address this limitation by applying the model to independent datasets to better assess model robustness. In addition, the potential temporal autocorrelation of the repeated measurements could be handled via a bootstrap resampling technique to strengthen model inference. Cluster bootstrapping is advantageous to handle correlated data structure (Yang et al. 2022).

Conclusion

This study developed species-specific H–D relationship models for different forest types across PR and VI, which is crucial for improving forest management and growth predictions in the Caribbean region. Our findings demonstrate that well-established models from literature can be effectively adapted for use in these unique ecosystems, offering more accurate predictions of tree height by accounting for both fixed and random effects. These models serve as valuable tools for forest management in the structurally complex and species-rich tropical and subtropical forests of the Caribbean region, which remain largely underrepresented in forest modeling research. Moreover, the species-specific models developed here can be applied beyond the study area to predict tree heights for species within similar forest types. Expanding these models could improve their accuracy and applicability to different ecological contexts across the region.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s44392-026-00095-8.

Acknowledgements Supports from the USDA Forest Service (project # 24-JV-11330145-057) and the Warnell School of Forestry and Natural Resources, University of Georgia are greatly appreciated.

Author's Contributions Conceptualization – S. Wagle, S. Yang; Data curation – S. Yang;
Methodology – S. Wagle, S. Yang;
Writing—original draft – S. Wagle, S. Yang;
Writing—review & editing – T.J. Brandeis, H. Marcano-Vega, B. Bullock.

Data Availability The FIA data can be found at https://research.fs.usda.gov/products/dataandtools/fia-datamart

Declarations

Competing interests ☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests.

References

Arabatzis, A. A., and H. E. Burkhart. 1992. An evaluation of sampling methods and model forms for estimating height-diameter relationships in loblolly pine plantations. *Forest Science* 38 (1): 192–198.

Atkinson, E. E., and E. Marín-Spiotta. 2015. Land use legacy effects on structure and composition of subtropical dry forests in St. Croix, US Virgin Islands. *Forest Ecology and Management* 335:270–280.

Bates, D. M., and D. G. Watts. 1980. Relative curvature measures of nonlinearity. *Journal of the Royal Statistical Society: Series B* (Methodological) 42 (1): 1–16.

Bechtold, W.A, and P. L. Patterson. 2005. *The enhanced forest inventory and analysis program--national sampling design and estimation procedures* (No. 80). USDA Forest Service, Southern Research Station.

Birdsey, R. A, and P. L. Weaver. 1982. *The forest resources of Puerto Rico*. Resour. Bull. SO-85. USDA Forest Service Southern Forest Experiment Station. 65.

Brandeis, T. J. 2003. Puerto Rico's forest inventory: Adapting the forest inventory and analysis program to a Caribbean island. *Journal of Forestry* 101 (1): 8–13.

Brandeis, T. J, and S. N. Oswalt. 2007. *The status of US Virgin Islands' forests, 2004*. Resour. Bull. SRS–122. USDA Forest Service Southern Research Station. 61 p.

Brandeis, T. J., and K. C. Randolph. 2010. Modeling Caribbean tree heights and crown widths. *Caribbean Journal of Science* 46 (2–3): 176–185.

Brandeis, T. J, and J. A. Turner. 2013a. *Puerto Rico's forests, 2009*. USDA Forest Service Southern Research Station.

Brandeis, T. J, and J. A. Turner. 2013b. *US Virgin Islands': Forests, 2009*. USDA Forest Service Southern Research Station.

Brandeis, T. J., M. Delaney, B. R. Parresol, and L. Royer. 2006. Development of equations for predicting Puerto Rican subtropical dry forest biomass and volume. *Forest Ecology and Management* 233 (1): 133–142.

Brandeis, T. J., E. H. Helmer, and S. N. Oswalt. 2007. *The status of Puerto Rico's forests, 2003*.Resour. Bull. SRS-119. USDA Forest Service Southern Research Station. 72 p.

Brandeis, T. J., E. H. Helmer, H. Marcano-Vega, and A. E. Lugo. 2009. Climate shapes the novel plant communities that form after deforestation in Puerto Rico and the US Virgin Islands. *Forest Ecology and Management* 258 (7): 1704–1718.

Burkhart, H. E., and M. R. Strub. 1974. A model for simulation of planted loblolly pine stands. In *Growth models for tree and stand simulation* 30:128–135. Royal College of Forestry

Calama, R., and G. Montero. 2004. Interregional nonlinear height diameter model with random coefficients for stone pine in Spain. *Canadian Journal of Forest Research* 34 (1): 150–163.

Curtis, R. O. 1967. Height-diameter and height-diameter-age equations for second-growth Douglas-fir. *Forest Science* 13 (4): 365–375.

El Mamoun, H. O., A. I. El Zein, and M. I. El Mugira. 2013. Modelling height-diameter relationships of selected economically important natural forests species. *Journal of Forest Products & Industries* 2:34–42.

Elzhov, T. V., K. M. Mullen, A-N. Spiess, B. Bolker, M. K. M. Mullen, and M. Suggests. 2016. *Package 'minpack. lm'. Title R Interface Levenberg-Marquardt Nonlinear Least-Sq. Algorithm Found MINPACK Plus Support Bounds.*

Ewel, J. J, and J. L. Whitmore. 1973. *The ecological life zones of Puerto Rico and the US Virgin Islands*. USDA Forest Service, Institute of Tropical Forestry, Research Paper ITF-018 18.

Fang, Z., and R. Bailey. 1998. Height–diameter models for tropical forests on Hainan Island in southern China. *Forest Ecology and Management* 110 (1–3): 315–327.

Flewelling, J. W., and R. D. Jong. 1994. Considerations in simultaneous curve fitting for repeated height–diameter measurements. *Canadian Journal of Forest Research* 24 (7): 1408–1414.

Franco, P., P. Weaver, and S. Eggen-McIntosh. 1999. *Forest resources of Puerto Rico 1990.*

Gelman, A., and J. Hill. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press.

Gompertz, B. 1833. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. In a letter to Francis Baily, Esq. FRS &c. By Benjamin Gompertz, Esq. FR S. *Abstracts of the Papers Printed in the Philosophical Transactions of the Royal Society of London* (2): 252–253. The Royal Society London.

Helmer, E., O. Ramos, Td. M. López, M. Quinones, and W. Diaz. 2002. Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. *Caribbean Journal of Science* 38 (3–4): 165–183.

Holdridge, L. R. 1967. *Life zone ecology*.

Huang, S., S. J. Titus, and D. P. Wiens. 1992. Comparison of nonlinear height–diameter functions for major Alberta tree species. *Canadian Journal of Forest Research* 22 (9): 1297–1304.

Huang, S., D. Price and S. J. Titus. 2000. Development of ecoregion-based height–diameter models for white spruce in boreal forests. *Forest Ecology and Management* 129 (1-3): 125–141.

Jha, S., S.-I. Yang, T. J. Brandeis, O. Kuegler, and H. Marcano-Vega. 2023. Evaluation of regression methods and competition indices in characterizing height-diameter relationships for temperate and pantropical tree species. *Frontiers in Forests and Global Change* 6 : 1282297.

Koenig, N. 1953. *A comprehensive agricultural program for Puerto Rico.* US Government Printing Office.

Kuehne, C., M. Russell, A. Weiskittel, and J. Kershaw Jr. 2020. Comparing strategies for representing individual-tree secondary growth in mixed-species stands in the Acadian Forest region. *Forest Ecology and Management* 459 : 117823.

Lam, T. Y., J. . A. .Jr. Kershaw, Z. S. N. Hajar, K. A. Rahman, A. R. Weiskittel, and M. D. Potts. 2017. Evaluating and modelling genus and species variation in height-to-diameter relationships for Tropical Hill Forests in Peninsular Malaysia. *Forestry: An International Journal of Forest Research* 90 (2): 268–278.

Larsen, D. R., and D. W. Hann. 1987. *Height-diameter equations for seventeen tree species in southwest Oregon.*

Lebedev, A., and V. Kuzmichev. 2020. *Verification of two-and three-parameter simple height-diameter models for birch in the European part of Russia*.

Lugo, A. E., and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190 (2–3): 145–161.

Lugo, A. E., J. E. Smith, K. M. Potter, H. M. Vega, C. M. Kurtz. 2022. *The contribution of nonnative tree species to the structure and composition of forests in the conterminous United States in comparison with tropical islands in the Pacific and Caribbean*.

Lundqvist, B. 1957. On the height growth in cultivated stands of pine and spruce in Northern Sweden. *Medd Fran Statens Skogforsk* 47 (2): 1–64.

Marcano-Vega, H. (2023). *Puerto Rico Forests 2019*. Resource Update FS-461. USDA Forest Service Southern Research Station.

Marcano-Vega, H. 2020. *US Virgin Islands' forests, 2014*. Resour. Bull. SRS–227, pp. 1–54. USDA Forest Service Southern Research Station.

Mehtätalo, L., S. de-Miguel, and T. G. Gregoire. 2015. Modeling height-diameter curves for prediction. *Canadian Journal of Forest Research* 45 (7): 826–837.

Menten, L., and M. I. Michaelis. 1913. Die Kinetik der Invertinwirkung. *Biochemische Zeitschrift* 49:333–369.

Meyer, H. A. 1940. A mathematical expression for height curves. *Journal of Forestry* 38 (5): 415–420.

Michailoff, I. 1943. Zahlenmäßiges verfahren für die Ausführung der bestandeshöhenkurven. *Forstwissenschaftliches Centralblatt und Tharandter Forstliches Jahrbuch* 6:273–279.

Näslund, M. 1936. *Skogsförsöksanstaltens gallringsförsök i tallskog*.

Ogana, F. 2018. Comparison of a modified log-logistic distribution with established models for tree height prediction. *Journal of Research in Forestry, Wildlife and Environment* 10 (2): 49–55.

Paulo, J. A., J. Tomé, and M. Tomé. 2011. Nonlinear fixed and random generalized height–diameter models for Portuguese cork oak stands. *Annals of Forest Science* 68 (2): 295–309.

Pearl, R., and L. J. Reed. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proceedings of the national academy of sciences* 6 (6): 275–288.

Peschel, W. 1938. Mathematical methods for growth studies of trees and forest stands and the results of their application. *Tharandter Forstliches Jahrburch* 89:169–247.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, S. Heisterkamp, B. Van Willigen, and R. Maintainer. 2017. Package 'nlme.' *Linear and Nonlinear Mixed Effects Models, Version* 3 (1): 274.

Ratcliffe, S., M. Liebergesell, P. Ruiz-Benito, J. Madrigal González, J. M. Muñoz Castañeda, G. Kändler, A. Lehtonen, J. Dahlgren, J. Kattge, and J. Peñuelas. 2016. Modes of functional biodiversity control on tree productivity across the European continent. *Global Ecology and Biogeography* 25 (3): 251–262.

Ratkowsky, D. A. 1990. *Handbook of nonlinear regression models*.

Richards, F. J. 1959. A flexible growth function for empirical use. *Journal of Experimental Botany* 10 (2): 290–301.

Rudel, T. K., M. Perez-Lugo, and H. Zichal. 2000. When fields revert to forest: Development and spontaneous reforestation in post-war Puerto Rico. *Professional Geographer* 52 (3): 386–397.

Schumacher, F. X. 1939. *A new growth curve and its application to timber-yield studies*.

Sharma, M., and S. Yin Zhang. 2004. Height–diameter models using stand characteristics for *Pinus banksiana* and *Picea mariana*. *Scandinavian Journal of Forest Research* 19 (5): 442–451.

Sibbesen, E. 1981. Some new equations to describe phosphate sorption by soils. *Journal of Soil Science* 32 (1): 67–74.

Staudhammer, C., and V. LeMay. 2000. Height prediction equations using diameter and stand density measures. *The Forestry Chronicle* 76 (2): 303–309.

Stoffels, A., and J. van Soest. 1953. The main problems in sample plots. *Nederlands Boschbouw Tijdschrift* 25:190–199.

Strand, L. 1958. *The accuracy of some methods for estimating volume and increment on sample plots*.

Temesgen, H., D. Affleck, K. Poudel, A. Gray, and J. Sessions. 2015. A review of the challenges and opportunities in estimating above ground forest biomass using tree-level models. *Scandinavian Journal of Forest Research* 30 (4): 326–335.

Temesgen, H., V. Monleon, and D. Hann. 2008. Analysis and comparison of nonlinear tree height prediction strategies for Douglas-fir forests. *Canadian Journal of Forest Research* 38 (3): 553–565.

USDA Forest Service. 2017. *Forest Inventory and Analysis national core field guide: Volume I. Field data collection procedures for phase 2 plots, version 7.1*. USDA Forest Service.

Wadsworth, F. H. 1950. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. *Caribbean Forester* 11 (1): 38–56.

Weibull, W. 1951. A statistical distribution function of wide applicability. *Journal of Applied Mechanics.*

Wykoff, W., N. Crookston, and A. Stage. 1982. *User's guide to the stand prognosis model.* USDA Forest Service Gen Tech Rep INT-133.

Yang, S.-I., T. J. Brandeis, E. H. Helmer, and H. Marcano-Vega. 2025. Predicting species-specific diameter growth rate for Caribbean trees using mixed-effects extreme gradient boosting. *Forest Ecology and Management* 580 : 122520.

Yang, S.-I., T. J. Brandeis, E. H. Helmer, M. P. Oatham, T. Heartsill-Scalley, and H. Marcano-Vega. 2022. Characterizing height-diameter relationships for Caribbean trees using mixed-effects random forest algorithm. *Forest Ecology and Management* 524 : 120507.

Zhang, L. 1997. Cross-validation of non-linear growth functions for modelling tree height–diameter relationships. *Annals of Botany* 79 (3): 251–257.

Authors and Affiliations

Samjhana Wagle[1] · Sheng-I Yang[1] · Thomas J. Brandeis[2] · Humfredo Marcano-Vega[3] · Bronson Bullock[1]

✉ Samjhana Wagle
swagle@uga.edu

Sheng-I Yang
syang23@uga.edu

Thomas J. Brandeis
thomas.j.brandeis@usda.gov

Humfredo Marcano-Vega
humfredo.marcano@usda.gov

Bronson Bullock
BronsonBullock@uga.edu

[1] Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green Street Athens, Athens, GA 30602, USA

[2] USDA Forest Service, Southern Research Station, 4700 Old Kingston Pike Knoxville, Knoxville, TN 37919, USA

[3] USDA Forest Service, Southern Research Station, Jardín Botánico Sur 1201 Calle Ceiba San Juan, San Juan, PR 00926, USA