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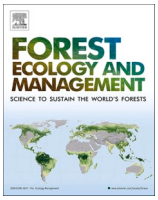

Allometric relationships for the linear dimensions and biomass of Puerto Rican mangroves

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ABSTRACT

Accurate biomass estimation is essential for carbon stock assessment and coastal ecosystem management. Despite decades of research and interest in Puerto Rican mangroves, we lack species specific allometric models with only 10 *Rhizophora mangle* individuals having been collected previously. To address this gap, we developed allometric equations for four mangrove species (*Avicennia germinans, Laguncularia racemosa, Rhizophora mangle, and Conocarpus erectus*) by harvesting and analyzing 152 individuals. Biomass estimation models were developed using standardized major axis (SMA) regression, incorporating DBH, tree height, crown diameter, and wet mass. Analysis of bivariate relationships between the linear dimensions and mass reveal common allometric slopes between species in 5 out of the 6 relationships. Local equations had a lower RMSE than global models, with DBH-based equations achieving the highest predictive accuracy ($R^2 = 0.94$), while crown diameter showed the weakest correlation ($R^2 = 0.74$). At the species level, DBH was the best predictor of both wet and dry mass in all cases examined. These results enhance biomass estimation accuracy for Puerto Rican mangroves, providing a critical tool for carbon stock assessments, conservation planning, and regional ecosystem management strategies.

- Future allometric harvesting efforts should focus on filling gaps in existing data by sampling new areas and by increasing sample sizes to capture more variability.
- When collecting allometric data, researchers should collect trees across the entire range of available sizes.
- Collecting allometric data from a broad range of forest types and environments will help to understand the extent of morphological and allometric variability.

1. Introduction

Within intertidal zones around the globe, woody plants are mostly excluded by salt, shifting soils, high intensity storms, and episodic tidal flooding. Nevertheless, 73 species from 20 different families have adapted to thrive in these harsh coastal environments (Spalding et al., 2010). Known collectively as mangroves, this group of species has an outsized impact on the marine and terrestrial ecosystems they adjoin. Mangroves serve as habitat and recruitment zones for a suite of marine and terrestrial species (Laegdsgaard and Johnson, 2001; Mumby et al., 2004; Branoff and Campos-Cerqueira, 2021). Their anoxic soils tend to accumulate detritus, making soil carbon levels among the highest in the tropics (Donato et al., 2011). Mangroves have also been highlighted for their ability to buffer against damage, to both the natural and built environments, from storm surges (Alongi, 2008; Zhang et al., 2012). These trees and their habitats also provide wood products, food, and fuel to human communities throughout many parts of their global range (Spalding et al., 2010).

Increased recognition of the importance of mangroves has led to their protection in many countries, and has motivated efforts to better

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understand their spatial distribution and function at both local and global scales. Standing biomass is often a focus of these efforts, due to its link to forest health and functional capacity. Especially in mangroves, and particularly areas prone to high-intensity cyclonic storms that create episodic large-scale disturbance events, standing biomass is correlated with productivity (Pugh et al., 2019). Estimating the biomass of mangrove forests typically relies on allometric relationships for the dominant species they contain, and a number of regional studies have collected and published such relationships (Fromard et al., 1998; Ross et al., 2001; Sherman et al., 2003; Osland et al., 2014). Due to variability in site-specific conditions (e.g., soil salinity, hydrology, climate, tidal influence) and their influence on mangrove growth, it is widely thought that locally developed allometric equations will be superior to global ones because they better account for these local factors when predicting biomass and other ecosystem attributes (Sherman et al., 2003; Soares and Schaeffer-Novelli, 2005; Yepes et al., 2016; Santos et al., 2017; Zanvo et al., 2023).

Mangroves in Puerto Rico (PR) have been the subject of study for decades (Dachnowski-Stokes and Roberts, 1934; Holdridge, 1940; Lugo and Snedaker, 1974). Similar to other Caribbean Islands and the US Gulf Coast, the mangrove community in PR is species poor with three "true" mangroves, *Avicennia germinans* L., *Laguncularia racemosa* (L.) C.F. Gaertn. and *Rhizophora mangle* L., plus *Conocarpus erectus L.*, a common associated species. While global and regional allometric models exist (Imbert and Rollet, 1989; Ross et al., 2001; Sherman et al., 2003; Smith and Whelan, 2006; Price et al., 2024), their applicability to Puerto Rican mangroves is uncertain due to local variability in environmental conditions, tree morphology, and growth patterns. The lack of comprehensive species-specific biomass models limits accurate carbon stock assessments and forest management strategies in the region. We are aware of only one study that has collected allometric biomass data for PR mangroves (Golley et al., 1962), which presents data for 10 *R. mangle* individuals. Other studies present similar data and models for regional mangroves in Florida (Smith and Whelan, 2006) and French Guiana (Fromard et al., 1998), representing 8,10, and 14 and 57, 37, and 4 individuals each for *A. germinans*, *L. racemosa*, and *R. mangle*, respectively. Recent work has shown that sample sizes in allometric studies should trend higher, with estimates ranging from 17 to 95 individuals per species (Chave et al., 2004; Roxburgh et al., 2015). However, due to habitat loss, over-harvesting, and the resulting protection in much of their range, including PR, sanctioned opportunities for destructive sampling are rare.

During a recent data collecting trip to Piñones State Forest in Loíza, PR, we learned of plans to clear an area of mangroves within the adjacent San Juan airport property. US Federal Aviation regulations stipulate that airports maintain a Runway Safety Area (RSA-250 ft) plus a Runway Object Free Area (ROFA-150 ft) totaling 400 ft on either side of the runway. Over time, the mangroves growing adjacent to the runway at Luis Muñoz Marín Airport have encroached upon this ROFA and thus were slated to be cleared to comply with regulations. After a preliminary reconnaissance trip by one of us (H.M.-V.), we learned that all four of PR's mangrove species were growing abundantly within the mitigation area. This presented a unique opportunity to harvest mangroves cut down for ROFA maintenance, to develop allometric equations to underpin biomass estimation for the greater area.

Here, we report novel allometric relationships for the four aforementioned species (which we refer to hereafter as San Juan data) and compare our new allometric data to a recently compiled global dataset for three of the four species (Price et al., 2024). This allows us to test the following three hypotheses:

H1.) Equations describing allometric growth will not differ statistically between San Juan species.

H2.) Local (San Juan) allometric equations will have higher correlation coefficients and lower root mean squared error than global equations at both intra and interspecific levels.

H3.) As found in other studies, *DBH* will outperform height or crown diameter in predicting above ground biomass for the San Juan data.

2. Methods

2.1. Field data collection

We applied for a "scientific purposes" permit with the Department of Natural and Environmental Resources (DNER) of PR, which authorized our team to measure and cut mangrove individuals of all four species within the area to be cleared as part of the runway safety and regulatory compliance. In collaboration with the mitigation contractor, we obtained additional clearances to access the area adjacent to the runway, in accordance with their Security Credentials Department requirements. All trees were harvested within a 20-m wide swath parallel to the runway and within the 120 m ROFA boundary. All trees were collected within a two-week field campaign from 20 October 2024–1 November 2024.

For each tree we measured basal stem diameter (*BSD*) at a point just above the butt swell, diameter at 30 cm (*D30*) above the *BSD* measurement point, and diameter at 137 cm (*DBH*) above the *BSD* measurement point. The height of each tree was measured with a hypsometer (tall trees; > 6 m) or tape measure (short trees). The crown spread was measured at its widest point, and then again on an axis perpendicular to the first measurement to estimate crown diameter, with the mean of these two measures reported here. All trees were cut at ground level and the fresh mass (hereafter *wet mass*) of each tree was measured with either a digital scale (small trees, grams) or spring scale (large trees, kilograms) suspended from a tall aluminum step-ladder. For large individuals, the trees were cut into numerous sections to facilitate weighing. For *R. mangle*, prop roots, any of the many supportive arches from the mainstem to the surrounding soils, were separated from the remaining above ground material and weighed separately.

Under ideal circumstances one would separate leaf, bole, stem and root components, collecting wet (fresh) weights for each and then dry the entire sample to obtain dry weights (Brandeis et al., 2006; Perez-Harguindeguy et al., 2013; Kauffman JB et al., 2016). Due to logistical and time constraints imposed by the mitigation contractor, we were limited to 10 seven-hour working days in the field to collect our data. As such we prioritized collecting as many trees as we could and weighing their entire above ground mass, rather than taking the time to separate and weigh individual bole/branch/leaf components.

2.2. Wood discs

Without a local option to dry the significant biomass volume created by harvesting 152 entire trees, we used a subsampling approach where we collected wood discs from stems and branches of varying size for each species which were subsequently dried to constant mass at **40°C**, and weighed. Constant mass was determined by repeated weighing. We determined the dry mass fraction of each sample as dry mass/wet mass. We then multiplied the dry mass fraction by the plant *wet mass* to yield above ground *dry mass* estimates. This method is quite similar to that used by several other researchers reporting allometric relationships for mangroves or other tropical tree species (Sherman et al., 2003; Soares and Schaeffer-Novelli, 2005; Smith and Whelan, 2006; Santos et al., 2017; Zanvo et al., 2023).

2.3. Global allometric dataset

We compared the allometric relationships we obtained for three of our species, *A. germinans*, *L. racemosa*, and *R. mangle*, to those in a recently published meta-analysis of data from these species' global range (Price et al., 2024). The lone allometric study we found for *C. erectus* examined biomass allocation under different experimental spacings, with all trees harvested at 3 years (Hegazy et al., 2008), thus it

was unsuitable for comparison with our data.

2.4. Allometric analyses

We utilized common regression models of the form $\log_{10}(Y_{variable}) = \alpha + \beta * \log_{10}(X_{variable})$ (Schumacher, 1933), where β and α are reported here as the slope and intercept. Bivariate relationships between all field measured variables (*height, BSD, D30, DBH, prop root mass, wet mass, dry mass, crown diameter)* were estimated using standardized major axis regression (SMA), a commonly used method for testing slopes when both variables have measurement error (Warton et al., 2006). We utilized the software package Standardized Major Axis Tests and Routines (SMATR) to estimate regression exponents (Falster et al., 2006; Warton et al., 2006). Data were log transformed (base 10) prior to regression fitting to better meet the assumption of homogeneity of variance. When used in allometric regression, logarithmic

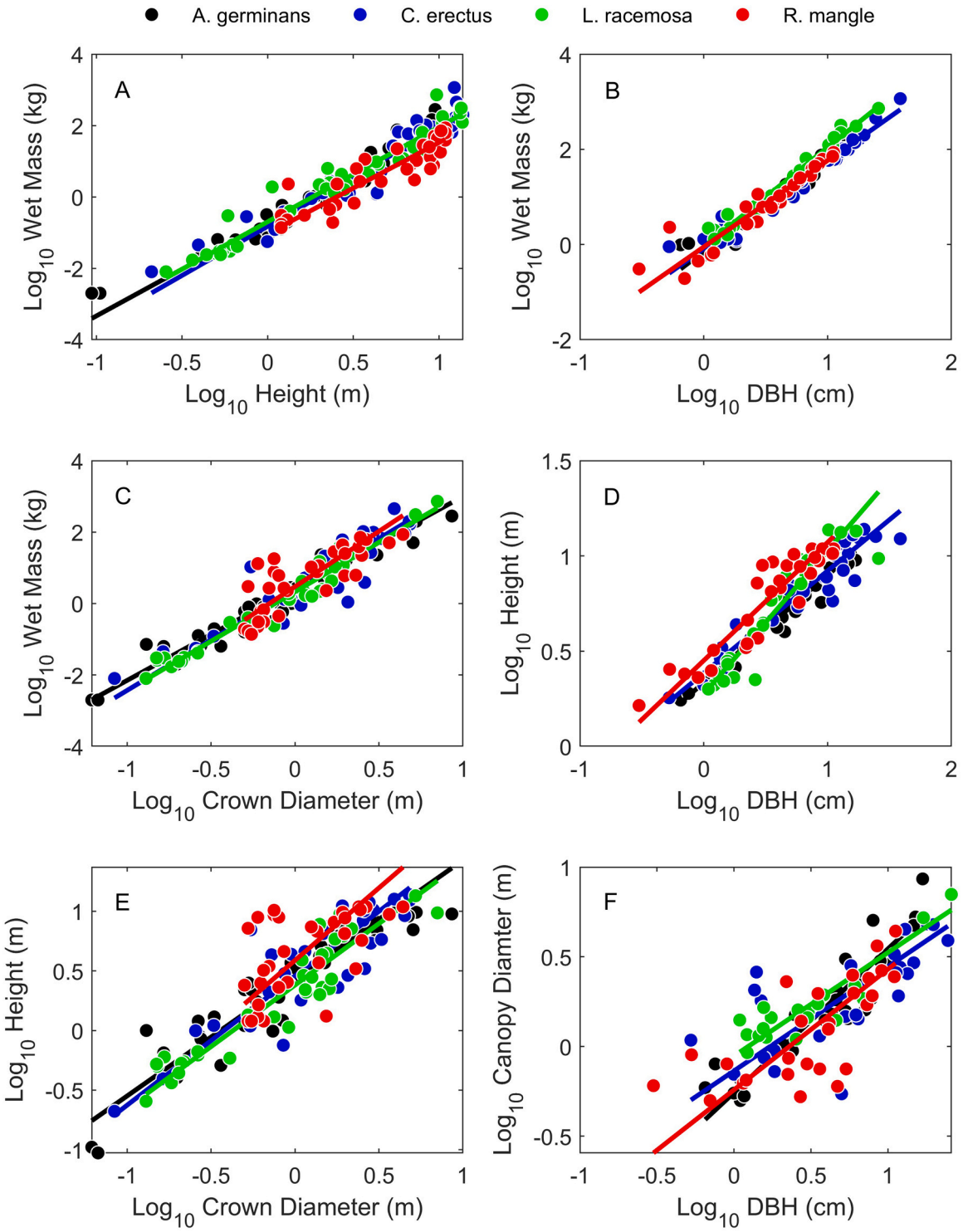

Fig. 1. Allometric relationships for the four mangrove species. Regression statistics for these six relationships are given in Table 1. Note the low variance in the Wet Mass to DBH regression (mean R^2=0.94). Here Wet Mass is taken directly from field measurements, while Dry Mass is estimated using an average dry matter constant of 60%.

transformation using base 10 or base *e* (Euler number) produces identical slopes (but different intercepts). We chose base 10 simply because it can be easier to do some calculations (back transformation) in one's head (i.e. 10^2 vs *e*^2) when reading figures.

For the San Juan data, regression functions were fit both interspecifically and intraspecifically. For the intraspecific regressions we tested whether each relationship (i.e. *mass-DBH* or *crown diameter-height*) had a common slope across species (Warton et al., 2006). If two (or more) relationships had a common slope, they were subsequently tested to determine if there was a shift in elevation of the lines between groups (change in Y-intercept, see Fig. 1, Warton et al., 2006). All regression functions were tested at the $p < 0.05$ significance level.

2.5. Root mean squared error

To determine which variable (*height*, *DBH*, or *crown diameter*) best predicts total above ground biomass (*wet mass* or *dry mass*), and to compare results between regression models at different grouping levels (global interspecifically, global intraspecifically, San Juan interspecifically, San Juan intraspecifically) we calculated the root mean squared error (RMSE) using standard formula, which represents the square root of the mean difference between the values predicted by the regression model and the actual measured values. To facilitate comparison of the performance of regression models at different grouping levels we also calculated the normalized root mean squared error (NRMSE) as:

$$NRMSE = (RMSE_{best}\text{-}RMSE_{model})/\text{mean mass}$$

where $RMSE_{best}$ is the error value of the best performing regression model and $RMSE_{model}$ is the error value of the model compared to the best performing model. We normalized our variables by both the mean and maximum mass values in the San Juan dataset.

3. Results

We collected sample discs from 20 *A. germinans*, 27 *C. erectus*, 10 *L. racemosa* and 14 *R. mangle* individuals to estimate dry mass fraction. The species-specific dry mass fraction distributions strongly overlapped and there were no significant differences between groups (one-way ANOVA, $p = 0.417$). The mean dry mass fraction across all species was 0.6046, so we used 60 % of the *wet mass* for all trees as the estimate of their *dry mass*.

We were able to collect 40 *A. germinans*, 32 *C. erectus,* 39 *L. racemosa*, and 41 *R. mangle* individual trees. Allometric relationships for all four species are shown in Fig. 1, with corresponding regression equations in Table 1. Raw data for the San Juan data and global dataset can be found in Table S4. We used *wet mass* for the data in Fig. 1 and Table 1 as it is field measured and thus more accurate than *dry mass* which is estimated based on the 60 % dry mass fraction determined from the wood discs. However, for comparisons with the global data, we used *dry mass* since that is what is reported by other groups (Price et al., 2024).

Among the species-specific regressions for the San Juan data, five out of the six bivariate relationships in Table 1 had a common slope providing some support for H1. However, of those, four out of the five had between-species shifts in the elevation (Y-intercept) of the lines fitted to the data. For example, looking at Fig. 1, Panel E, the data for *R. mangle* is shifted upwards in the Y-axis, relative to the other species. This is shown in Table 1 where, while there is a common slope across species, *R. mangle* is different from the other species in elevation (see Table legend).

Looking at the variables used to predict mass (Table 1, rows 2–13), the relationships with the highest R^2 (column 5) on average were those using *DBH* with a mean value of 0.94 (supporting H3), followed by height (mean=0.898) and crown diameter (mean=0.743). Those relationships involving crown diameter generally had lower R^2 values, indicating that, among the variables one could choose for allometric biomass analyses, it is among the poorest.

Based on R^2 the best predictor of both wet mass and dry mass for each species was DBH in all cases (Table 1) providing support for H3. The R^2's for each relationship (wet and dry mass respectively) were: *A. germinans* 0.951, 0.954, *C. erectus* 0.884, 0.884, *L. racemosa* 0.95, 0.947 and *R. mangle* 0.974, 0.974.

Using the regression equations from the four different levels (global interspecifically, global intraspecifically, San Juan interspecifically, San Juan intraspecifically) and the three commonly used predictor variables (DBH, height, crown diameter) to estimate mass, we found that the lowest RMSE value for the San Juan intraspecific equations were those using DBH and height, and for the global intraspecific equation it was for crown diameter (Table 2). Looking at the NRMSE values based on the mean or maximum values in the San Juan data, the error added using global equations instead of local equations would be less than 2 % in all cases and less than 1 % in most (Table 3).

The comparison of San Juan regressions to the entire global data set within each species showed that 10 of 18 slopes were not different from one another (Table S1, Figs. 2–4). Of those 10 relationships, 5 had no shift in elevation while the other 5 had a significant shift. *Avicennia germinans* (Fig. 2) had the most similarities between the San Juan and global data sets (4/6), whereas *L. racemosa* (Fig. 3) had the least (1/6 with an elevation shift). When comparing the San Juan data to the global dataset across species, we found that only 1/6 relationships had the same slope between groups (Table S2).

At the species level, San Juan regression data comparisons to each individual site in the global dataset revealed that out of 83 pairwise relationships, 53.01 % (44/83) were not different from one another (Table S3). Of those that were different, 18 were *R. mangle*, 13 were *L. racemosa*, and 13 were *A. germinans*. Looking at the number of slopes that were not different between sites (Table S3), we found the highest fraction of similarities between San Juan and Puerto Rico datasets (3/3), followed by Everglades (7/9), Bertioga (7/12), Biscayne (10/18), Guaratiba (6/12), Benin (3/6), Louisiana (0/3) and French Guiana (0/2).

4. Discussion

Estimating the biomass of mangrove forests is an area of considerable interest and a number of different methods have been employed to this end, from field-based tree measurements to remotely sensed tree heights or crown dimensions (Komiyama et al., 2008; Heumann, 2011; Feliciano et al., 2017). The most common approach is to harvest trees of varying size for each species to generate allometric functions that will then allow subsequent investigators to take field measurements such as tree height or *DBH*, and use the allometric equations to estimate their mass (Komiyama et al., 2008). Most published work operates under the assumption that local, species-specific allometric data is ideal due to variability in growth conditions from place to place (Golley et al., 1962; Imbert and Rollet, 1989; Fromard et al., 1998; Ross et al., 2001; Soares and Schaeffer-Novelli, 2005; Osland et al., 2014). However, a recent meta-analysis has shown that not all local equations outperform global ones, and the results are highly dependent on sample size and collection methodology (Price et al., 2024).

Our results align with Price et al. (2024) in demonstrating that global allometric models remain broadly applicable. However, our study suggests that local equations can offer small but measurable improvements in biomass prediction, particularly for Puerto Rican mangroves. For example, we find that local equations outperform global ones in two of three relationships (Table 2). The lowest RMSE value for two of the three linear dimensions (*DBH* and *height*) used to predict mass was the San Juan intraspecific equation. The lowest for crown diameter was the global intraspecific equation. This supports the idea that local equations can offer more accurate predictions providing some support for H2, but the improvement was marginal within our data. For example, using the global equation to predict mass from *DBH* in our data would have added

Table 1
Intraspecific allometric relationships for the three linear dimensions and wet mass. The first two columns are the Log_{10} of the Y-variable and X-variable, followed by the species, sample size (n), R^2 value, slope with lower and upper 95 % confidence interval, intercept with lower and upper 95 % confidence interval, the figure where the data are shown, the p-value indicating whether a common slope was found, and if so, four columns of p-values indicating whether there was a shift in elevation (i.e., change in Y-intercept) between the species. AG stands for *A. germinans*, CE - *C. erectus*, LR - *L. racemosa*, and RM - *R. mangle*. For example, looking at the first four rows (not counting the header), we can see that a common slope was found among the four species for the Wet Mass to Height relationship, and that there was a significant elevation shift in the data for *C. erectus*, which differs from the other three species ($p < 0.05$). Not all plants were tall enough to have DBH measures which is why the sample sizes differ between relationship groupings.

Log_{10} Y variable	Log_{10} X variable	Species	n	R2	Slope	LowCI	UppCI	Interc	LowCI	UppCI	Figure	P-val	AG	CE	LR	RM
Wet Mass (kg)	Height (m)	*A. germinans*	39	0.941	2.620	2.416	2.841	−0.715	−0.846	−0.585	2 A	0.815	1	0.000	0.747	0.667
Wet Mass (kg)	Height (m)	*C. erectus*	32	0.805	2.550	2.164	3.004	−1.028	−1.338	−0.718	2 A		0.000	1	0.000	0.000
Wet Mass (kg)	Height (m)	*L. racemosa*	39	0.900	2.758	2.483	3.064	−0.823	−1.049	−0.596	2 A		0.747	0.000	1	0.480
Wet Mass (kg)	Height (m)	*R. mangle*	41	0.945	2.658	2.464	2.867	−0.698	−0.831	−0.564	2 A		0.667	0.000	0.480	1
Wet Mass (kg)	DBH (cm)	*A. germinans*	26	0.951	1.987	1.810	2.181	−0.143	−0.272	−0.014	2B	0.062	1	0.919	0.284	0.001
Wet Mass (kg)	DBH (cm)	*C. erectus*	27	0.884	1.817	1.579	2.089	−0.051	−0.214	0.113	2B		0.919	1	0.350	0.013
Wet Mass (kg)	DBH (cm)	*L. racemosa*	32	0.950	1.843	1.696	2.002	−0.089	−0.230	0.052	2B		0.284	0.350	1	0.000
Wet Mass (kg)	DBH (cm)	*R. mangle*	27	0.974	2.090	1.957	2.233	−0.048	−0.149	0.052	2B		0.001	0.013	0.000	1
Wet Mass (kg)	Crown Diameter (m)	*A. germinans*	38	0.523	2.521	2.000	3.177	0.056	−0.271	0.383	2 C	0.59	No elevation shift			
Wet Mass (kg)	Crown Diameter (m)	*C. erectus*	32	0.660	3.096	2.495	3.841	0.474	0.279	0.670	2 C		between groups			
Wet Mass (kg)	Crown Diameter (m)	*L. racemosa*	31	0.829	2.832	2.423	3.311	0.402	0.206	0.599	2 C					
Wet Mass (kg)	Crown Diameter (m)	*R. mangle*	33	0.959	2.767	2.569	2.979	0.331	0.235	0.427	2 C					
Height (m)	DBH (cm)	*A. germinans*	27	0.950	0.565	0.515	0.620	0.335	0.299	0.372	2D	0.003	No common slope			
Height (m)	DBH (cm)	*C. erectus*	27	0.855	0.620	0.530	0.725	0.451	0.389	0.514	2D					
Height (m)	DBH (cm)	*L. racemosa*	32	0.896	0.536	0.476	0.605	0.385	0.326	0.445	2D					
Height (m)	DBH (cm)	*R. mangle*	27	0.879	0.752	0.652	0.868	0.275	0.196	0.354	2D					
Height (m)	Crown Diameter (m)	*A. germinans*	39	0.488	0.973	0.768	1.232	0.302	0.173	0.431	2E	0.664	1	0.012	0.714	0.158
Height (m)	Crown Diameter (m)	*C. erectus*	32	0.330	1.214	0.899	1.640	0.589	0.474	0.704	2E		0.012	1	0.048	0.000
Height (m)	Crown Diameter (m)	*L. racemosa*	31	0.747	1.084	0.896	1.310	0.458	0.365	0.551	2E		0.714	0.048	1	0.135
Height (m)	Crown Diameter (m)	*R. mangle*	33	0.884	1.032	0.911	1.168	0.381	0.321	0.442	2E		0.158	0.000	0.135	1
Crown Diameter (m)	DBH (cm)	*A. germinans*	26	0.857	0.802	0.685	0.940	−0.257	−0.347	−0.167	2 F	0.073	1	0.244	0.736	0.023
Crown Diameter (m)	DBH (cm)	*C. erectus*	27	0.511	0.673	0.506	0.894	−0.241	−0.369	−0.114	2 F		0.244	1	0.566	0.004
Crown Diameter (m)	DBH (cm)	*L. racemosa*	24	0.485	0.581	0.425	0.794	−0.136	−0.294	0.023	2 F		0.736	0.566	1	0.072
Crown Diameter (m)	DBH (cm)	*R. mangle*	19	0.812	0.577	0.463	0.719	−0.053	−0.130	0.024	2 F		0.023	0.004	0.072	1

Table 2
RMSE results for the three predictor variables across four different groupings. The variable used to predict mass is given in the first column, the equation and which grouping it corresponds two in the second column, followed by the RMSE value (kg) on the Log_{10} and linear scale. For each predictor, the relationship with the lowest RMSE value is in bold. For DBH and Height, the San Juan interspecific relationship was the best predictor of above ground dry mass. For Crown Diameter it was the Global intraspecific relationship. Predicted values for each individual plant are included in Table S3.

Predictor	Equation	RMSE Log Scale (kg)	RMSE Linear Scale (kg)	NRMSE:Mean	NRMSE:Max
DBH	Global Inter	0.2548	1.7980	0.8290	0.0334
DBH	Global Intra	0.2526	1.7890	0.7971	0.0321
DBH	San Juan Inter	0.2161	1.6446	0.2831	0.0114
DBH	**San Juan Intra**	**0.1945**	**1.5651**	-	-
Height	Global Inter	0.4377	2.7398	1.6342	0.0658
Height	Global Intra	0.4346	2.7201	1.5642	0.0629
Height	San Juan Inter	0.3866	2.4354	0.5511	0.0222
Height	**San Juan Intra**	**0.3580**	**2.2806**	-	-
Crown Diameter	Global Inter	0.4254	2.6632	0.4466	0.0180
Crown Diameter	**Global Intra**	**0.4044**	**2.5377**	-	-
Crown Diameter	San Juan Inter	0.4132	2.5894	0.1840	0.0074
Crown Diameter	San Juan Intra	0.4115	2.5795	0.1487	0.0060

Table 3
Summary statistics for the San Juan data. For each species (columns 2–5) we report the sample size, mean and range for the following measured variables: BSD, D30, DBH, Height, Crown Diameter, Wet Mass and Dry Mass.

	A. germinans	*C. erectus*	*L. racemosa*	*R. mangle*
Sample Size	40	32	39	41
Mean BSD (cm)	5.125	5.463	11.135	5.202
Range BSD (cm)	17.395	13.700	58.360	28.295
Mean D30 (cm)	4.778	4.793	10.356	5.009
Range D30 (cm)	17.000	13.400	52.740	27.570
Mean DBH (cm)	5.488	4.433	9.749	6.165
Range DBH (cm)	16.150	10.900	38.175	24.710
Mean Height (m)	3.775	5.810	6.306	4.680
Range Height (m)	9.706	9.700	13.590	13.445
Crown Diameter (m)	1.546	1.401	1.826	1.265
Range Crown Diameter (m)	8.539	3.900	4.746	6.921
Mean Wet Mass (kg)	26.265	16.583	83.045	55.566
RangeWet Mass (kg)	282.298	85.862	1163.792	726.992
Mean Mass Dry (kg)	15.759	9.950	49.827	33.340
Range Mass Dry (kg)	169.379	51.517	698.275	436.195

~233 g of error to the average tree compared to that obtained from a local interspecific equation. For tree height, the global model would have added ~459 g of error. The average estimated dry mass of trees in our dataset is 28.1 kg and the maximum, 698.3 kg, indicating that the use of the global interspecific equation for diameter would have added about 0.82 % error on average: for height it would be 1.63 % (Table 2). Of course, the magnitude of the error is greater for smaller trees than for larger ones, but since most investigators will be interested in the mass contribution of larger trees, perhaps this level of error would be acceptable.

We did not find differences in species mean dry mass fractions using the wood discs we collected. This supports the use of a single correction factor when converting our field measured wet mass to estimates of dry mass. This approach has been widely utilized in the field due to the difficulty in processing entire trees to obtain dry mass fraction measures (Sherman et al., 2003; Soares and Schaeffer-Novelli, 2005; Brandeis et al., 2006; Smith and Whelan, 2006; Santos et al., 2017; Zanvo et al., 2023).

Similar to the findings from the global analysis in Price et al. (2024), the plant dimension with the tightest correlation with above ground mass is *DBH*, in support of H3. The mean R^2 for the intraspecific mass to *DBH* relationships is highest (0.94) and the RMSE for intraspecific *DBH* is the lowest (1.565 kg).

Notably, the three relationships that were measured for *R. mangle* in Golley et al. (1962) did not differ from our new allometric relationships (Table S2), despite the lower sample number in their study (n = 10). Golley et al. (1962) collected *R. mangle* trees on Magueyes Island just off the southern coast of PR, and, despite being over 120 km away from our study location and subject to different weather patterns (lower rainfall, higher temperatures), the allometries from these two locations did not differ.

Our work contributes to both local and global mangrove datasets, for which there are now 742 individuals in the combined San Juan and global datasets (Table S4). For the three true mangrove species, sample sizes are over 200 individuals per species. However, not all individuals have all measurements (Table S1). For very small individuals, DBH or even D30 may not exist. Moreover, some researchers did not measure all the variables, or only measured trees above a certain size. Nonetheless, the data collection is sufficiently large to speculate as to whether it captures enough of the existing across-site variation to be representative of the species allometries at a global scale. There may be forests yet to be analyzed that have divergent growth patterns that require site and species specific allometric data. In those forests, preliminary surveys of linear dimensions (Height, DBH, Crown Diameter) may indicate whether their growth is divergent enough to warrant destructive harvesting.

Roughly forty percent of mangroves worldwide are under some type of protected status, making them among the most protected forest types in the world, despite representing only 0.4 % of forests globally (Schmitt et al., 2009; Pandisamy et al., 2020). This disproportionate level of protection reflects a reaction to high deforestation rates at the turn of the 21st century combined with a surge of scientific interest in mangrove ecosystem services (Qin et al., 2025). Although this protection has proven at least partially beneficial in slowing mangrove losses, its partnership with scientific study presents a unique challenge to management, especially in weighing the contrasting impacts of destructive sampling.

Mangroves in Puerto Rico have suffered fragmentation and losses in areal extent that are consistent with global patterns (Martinuzzi et al., 2009). However, since their legal protection in 1972, their area has expanded. A growing body of work has highlighted their importance in maintaining the health of Puerto Rican marine and terrestrial flora and fauna including, fish (Aguilar-Perera and Appeldoorn, 2007), bird (Acevedo and Aide, 2008; Branoff and Campos-Cerqueira, 2021) and human communities (Branoff, 2018; Garcia-Quijano et al., 2023). This is reflected in mangrove studies worldwide, which increasingly highlight the myriad ecosystem services provided by these forests (Dahdouh-Guebas et al., 2022).

Recently however, carbon has dominated the field of mangrove research, placing allometric relationships at the top of the management tool box. Mangroves are typically carbon sinks due to the sequestration of detritus in their anoxic soils (Donato et al., 2011; Alongi, 2012) and the quantity and rate of that sequestration is strongly related to standing biomass (Saenger and Snedaker, 1993; Augusto and Boča, 2022) for which allometric equations are essential and have become ubiquitous in

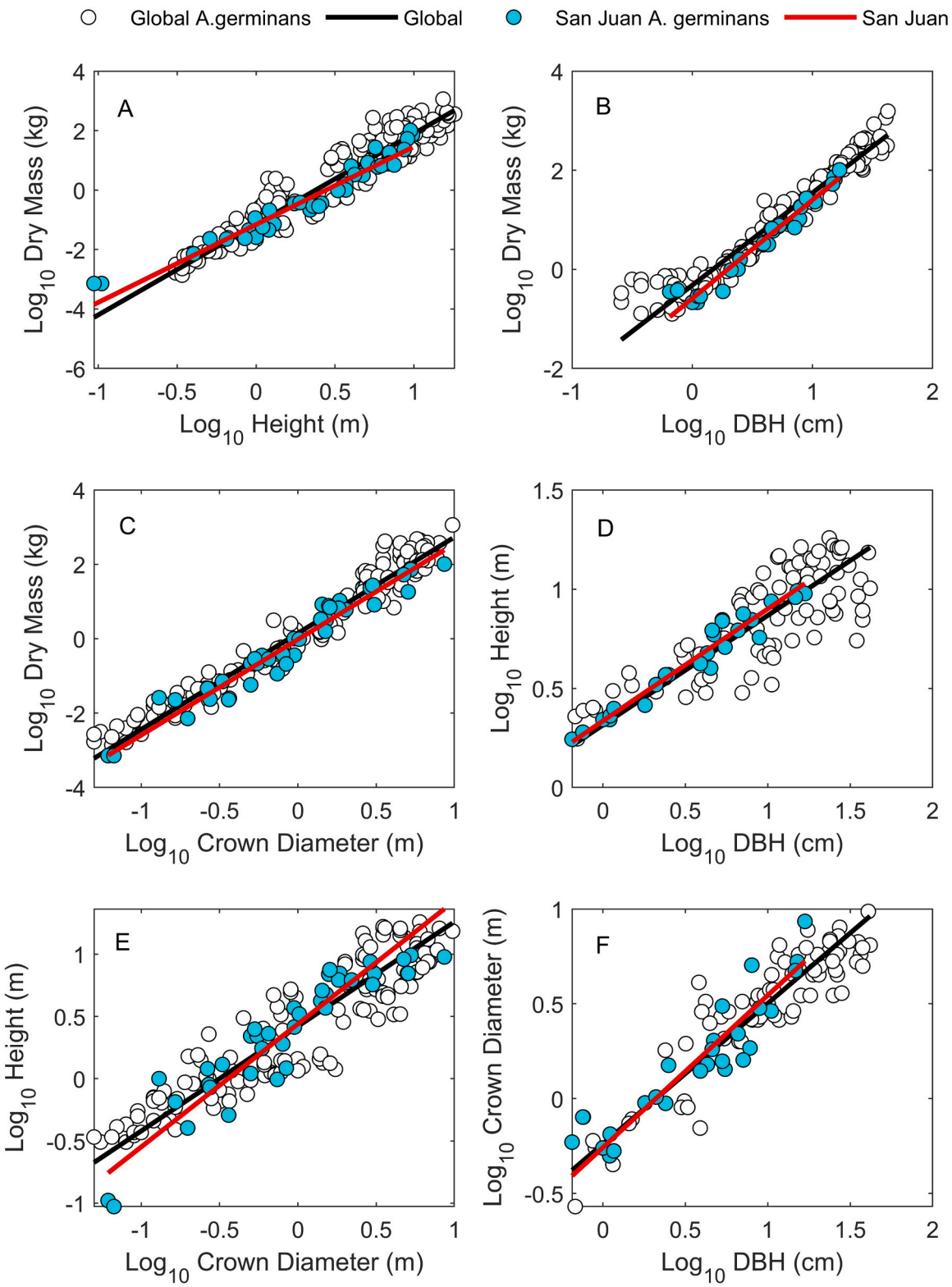

Fig. 2. Comparing San Juan data to the Global data compilation for *A. germinans*. Regressions statistics comparing the San Juan dataset to the Global dataset are in Table S1. Regressions statistics comparing the San Juan dataset to each individual site in the Global dataset are in Table S2.

the crowded field of global mangrove mapping (Rovai et al., 2016, 2021; Tang et al., 2018; Hu et al., 2020). New allometric equations for Puerto Rico will improve the accuracy of efforts to estimate standing biomass and ecosystem flux of carbon and other key nutrients (Branoff, 2018; Wigand et al., 2021). Additionally, a more nuanced understanding of the importance of location-specific equations will help guide regional and global scale blue-carbon and climate modelling efforts.

Puerto Rico, the Caribbean, and other mangrove regions are also subject to frequent disturbance in the form of tropical cyclones. Damage assessments following such events often use remotely sensed plant dimensions such as height combined with allometric relationships to estimate mangrove tree damage/mortality and the potential change in

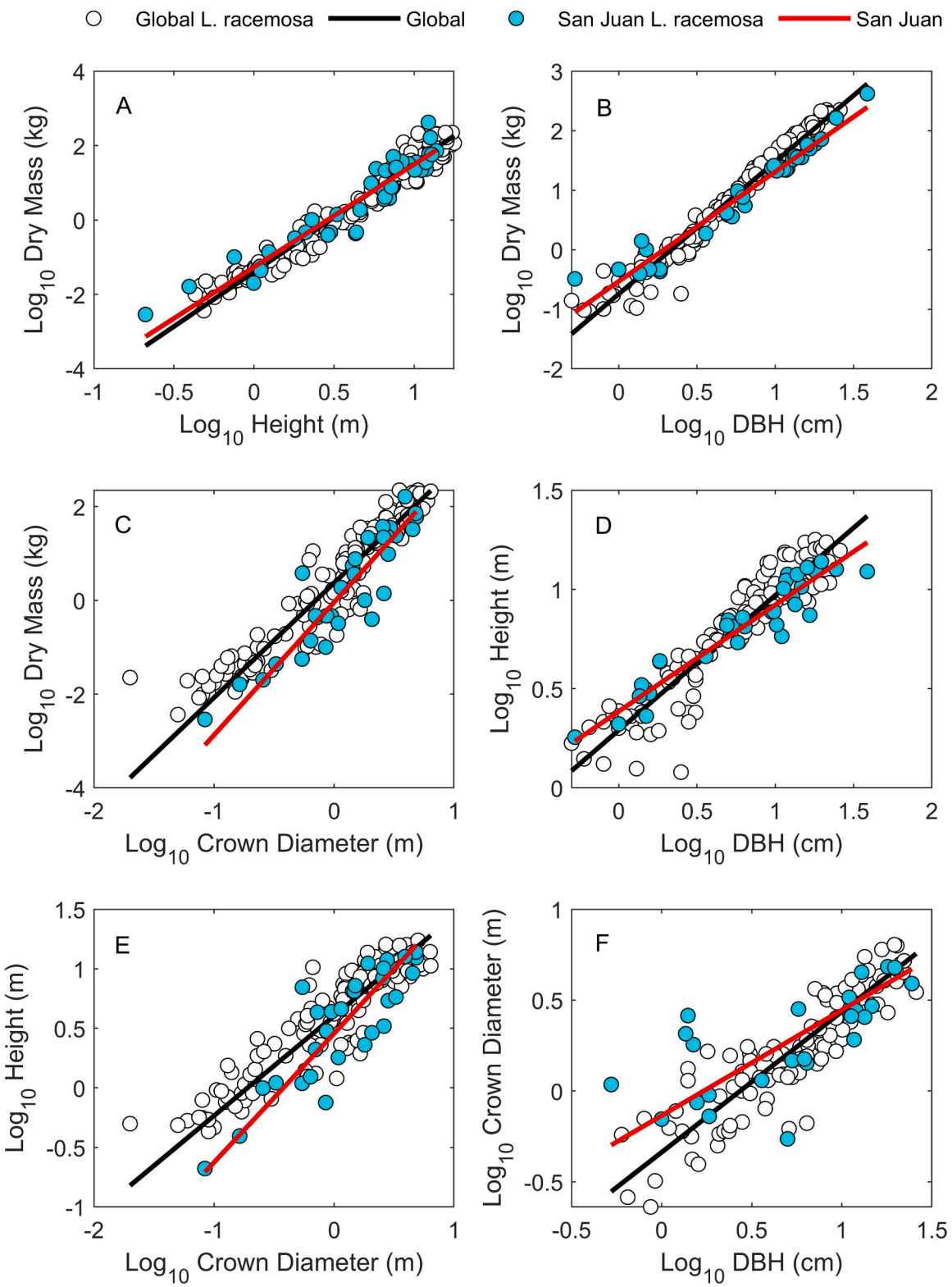

Fig. 3. Comparing San Juan data to the Global data compilation for *L. racemosa*. Regressions statistics comparing the San Juan dataset to the Global dataset are in Table S1. Regressions statistics comparing the San Juan dataset to each individual site in the Global dataset are in Table S2.

biomass storage/ flux (Howe et al., 2025). Improved allometric relationships will aid these efforts in providing more accurate assessments and thus more efficient recovery and post-disturbance management practices, in addition to more widely applicable substitutes for destructive sampling at a time when management is strongly focused on conservation.

5. Recommendations

Allometric relationships underpin the estimation of mangrove forest biomass and dynamics from local to global scales. A key issue is the extent to which local allometric relationships improve biomass estimation over global ones. Our ability to draw conclusions on this issue is

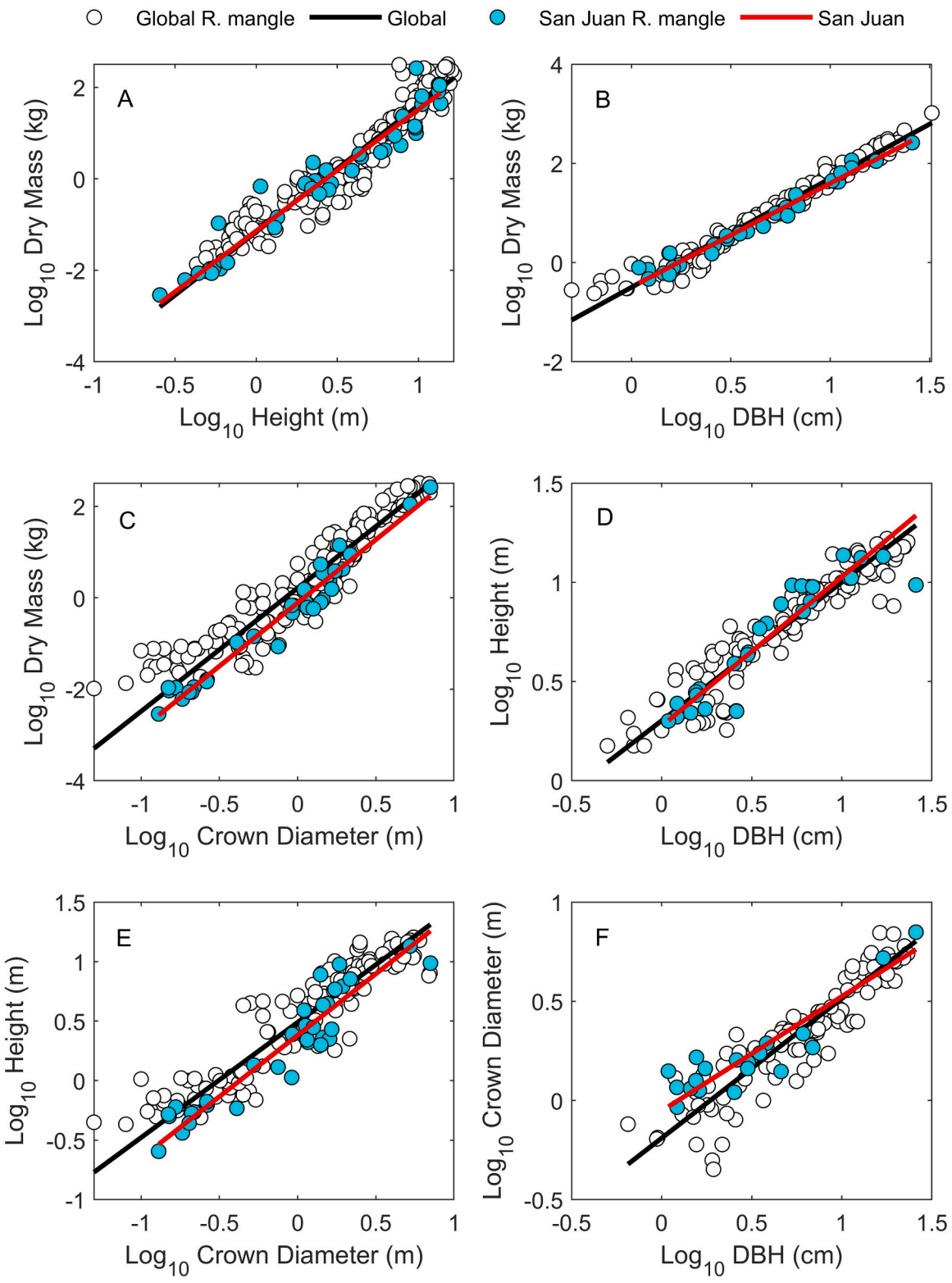

Fig. 4. Comparing San Juan data to the Global data compilation for *R. mangle*. Regressions statistics comparing the San Juan dataset to the Global dataset are in Table S1. Regressions statistics comparing the San Juan dataset to each individual site in the Global dataset are in Table S2.

limited by the amount and quality of data from mangrove forests both regionally and globally. Future efforts to collect local allometric datasets should prioritize increased sample sizes, and collecting data across the range of tree sizes available. Further, sampling across a broader range of forest types with increased variability in climatic and edaphic drivers, will aid researchers in understanding the breadth of allometric variability and the extent to which that variability influences biomass estimates derived from measured tree dimensions. These caveats aside, based on our findings here and in Price et al. (2024) we suspect that global allometric equations will be sufficient for many, if not most research questions. When local equations exist, they may offer modest increases in prediction accuracy, although decisions will need to be

made on a case by case basis considering the proximity to where local equation data were collected, and how local climatic and edaphic factors influence mangrove growth and allometry.

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CRediT authorship contribution statement

Schroeder Todd A: Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Price Charles A:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Humfredo Marcano-Vega:** Writing – review & editing, Resources, Project administration, Methodology, Conceptualization. **Papes Monica:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Chaudry Morgan H:** Writing – review & editing, Investigation. **Nicole Pillot-Torres:** Writing – review & editing, Resources, Investigation, Data curation. **Van Bloem Skip J:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Benjamin Branoff:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Monica Papes reports financial support was provided by The University of Tennessee Knoxville. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Material

Table S1. Comparison of the intraspecific San Juan data to the intraspecific Global dataset. The first column is the species, followed by the *Y* and *X* variables, the grouping, sample size (*n*), R^2 value, slope with lower and upper 95 % confidence interval, intercept with lower and upper 95 % confidence interval, the figure where the data are shown, the *p*-value indicating whether a common slope was found, and if so, whether or not there was a significant shift in elevation (i.e., change in Y-intercept) between groups. For example, looking at the rows 3 and 4 (not counting the header), we see that there was a common slope found between the San Juan and Global data for the relationship between mass and DBH ($p > 0.05$) and that there was not a shift in elevation between groups. If a common slope was not found, we did not check whether there was a shift in elevation between groups. Shading is included simply to aid readers in identifying which two relationships were being compared. The last six rows are for *C. erectus,* for which we do not have global data to compare to.

Table S2. Interspecific regression results for San Juan and Global data sets. The first and second column contain the *Y* and *X* variables, followed by the sample size (*n*), R^2 value, slope with lower and upper 95 % confidence interval, intercept with lower and upper 95 % confidence interval, and the p-value for the common slope test. Only one of the relationships had a common slope (Height vs DBH).

Table S3. Comparison between the San Juan data and each species-site relationship from the Global dataset. The first column is the species being examined, followed by the *Y* and *X* variables, sample size (*n*), R^2 value, slope with lower and upper 95 % confidence interval, intercept with lower and upper 95 % confidence interval, the site that the data came from and lastly, a p-value indicating whether there were differences between the San Juan data and each site. For example, looking at the first row (not including the headers) we see that a common slope was found between the Everglades and San Juan data for the relationship between mass and height ($p > 0.05$). Summary statistics from this Table are included in the Results. Comparisons across all the sites (other than San Juan) are reported in Price et al. (2024).

Table S4. Raw data for the San Juan and Global datasets including predicted values. The first column indicates the name of the first author of the paper that the data came from (see Price et al. 2024 for detailed description). The second column indicates the species followed by the site location, followed by a code for the dataset and species. Columns 6–12 include the raw measurements for mean BSD, mean D30, mean DBH, tree height, above ground wet mass, above ground dry mass and the mean crown diameter. Columns 14–25 include the predicted values from DBH, Height and Crown Diameter at interspecific global, intraspecific global, interspecific San Juan, and intraspecific San Juan levels. The interspecific and intraspecific global equations we used come from Table 1 in Price et al. (2024). The intraspecific and interspecific San Juan equations come from Tables S1 and S2, respectively.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122908.

Data availability

Data are freely available in Table S4

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