RESEARCH ARTICLE

Improving predictions of tropical tree survival and growth by incorporating measurements of whole leaf allocation

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Abstract

1. Individual-level demographic outcomes should be predictable upon the basis of traits. However, linking traits to tree performance has proven challenging likely due to a failure to consider physiological traits (i.e. hard-traits) and the failure to integrate organ-level and whole plant-level trait information.

2. Here, we modelled the survival rate and relative growth rate of trees while considering crown allocation, hard-traits and local-scale biotic interactions, and compared these models to more traditional trait-based models of tree performance.

3. We found that an integrative trait, total tree-level photosynthetic mass (estimated by multiplying specific leaf area and crown area) results in superior models of tree survival and growth. These models had a lower AIC than those including the effect of initial tree size or any other combination of the traits considered. Survival rates were positively related to higher values of crown area and photosynthetic mass, while relative growth rates were negatively related to the photosynthetic mass. Relative growth rates were negatively related to a neighbourhood crowding index. Furthermore, none of the hard-traits used in this study provided an improvement in tree performance models.

4. *Synthesis*. Overall, our results highlight that models of tree performance can be greatly improved by including crown area information to generate a better understanding of plant responses to their environment. Additionally, the role of the hard-traits in improving models of tree performance is likely dependent upon the level of stress (e.g. drought stress), micro-environmental conditions or short-term climatic variations that a particular forest experiences.

KEYWORDS

community ecology, demographic rate, forest ecology, functional trait, trait integration

1 | INTRODUCTION

Variation in individual performance (i.e. survival and growth) determines the structure and dynamics of natural populations and communities. Differential performance is largely determined by the interaction between the individual phenotype and the abiotic and biotic environment (Arnold, 1983; McGill et al., 2006). Ecologists have linked commonly measured morphological and physiological traits, known as functional traits, to demographic rates, to facilitate predictive models of populations and communities into the future.

There is a core suite of functional traits widely measured in plant ecology. These include specific leaf area (SLA), maximum height, wood density and seed mass. These traits are often

referred to as 'soft-traits' due to their relative ease of measurement across many individuals and species and because they are, typically, indirectly related to a physiological rate or life history trade-off of interest (Hodgson et al., 1999; Westoby, 1998). These soft-traits are those most commonly used in tree demographic models (Poorter et al., 2008; Wright et al., 2010). Maximum height (Bazzaz et al., 2000; Poorter et al., 2005; Westoby, 1998; Westoby et al., 2002), wood density (Chave et al., 2009; Enquist et al., 1999) and seed mass (Rees, 1996; Westoby, 1998) typically explain the greatest amount of variance in tree performance in tropical forests when compared to leaf traits like SLA (Poorter et al., 2008; Wright et al., 2010). However, forest ecologists have had variable success in linking these core commonly measured suite of functional traits to tree growth and mortality rates (Iida & Swenson, 2020; Paine et al., 2015; Poorter et al., 2008; Worthy & Swenson, 2019; Wright et al., 2010; Yang et al., 2018).

There are multiple ways in which trait-based models of tree survival and growth may be improved (Yang et al., 2018). These include, (a) measuring traits on individuals instead of using species mean values, (b) considering less easily measured traits, (c) integrating leaf-level trait data into the context of whole biomass allocation and (d) accounting for biotic interactions. The first of these possibilities has been shown to be important in studies that have measured individual-level trait data on thousands of individuals from tens to hundreds of co-occurring subtropical and tropical tree species (e.g. Liu et al., 2016; Umaña et al., 2017). However, this approach may prove impractical in many cases. Therefore, here, we focus on the remaining three issues: considering less easily measured traits (i.e. hard-traits) more closely aligned with plant physiological rates, the integration of leaf-level trait data into the context of whole biomass allocation and accounting for local-scale biotic interactions.

One way forward for trait-based predictions of tree demographic performance is to measure additional traits, linked to physiological processes, beyond the core suite of commonly measured soft functional traits. Soft-traits may be strongly correlated with traits that are more difficult to measure (e.g. photosynthetic rates), making them the most pragmatic approach for predicting tree population and community structure and dynamics (e.g. Díaz et al., 2004). However, soft-traits may be weakly correlated or not correlated at all with important physiological rates and trade-offs. Thus, tree survival and growth may be best predicted by less commonly measured traits. Such traits often referred to as 'hard-traits', are often difficult to measure, but are more closely linked to physiological processes of interest (Hodgson et al., 1999; Lavorel & Garnier, 2002; Swenson et al., 2017; Yang et al., 2018). For example, traits directly related to water use efficiency, such as leaf carbon stable isotope composition (Dawson et al., 2002; Farquhar et al., 1982) and leaf vein length per unit area (Sack & Frole, 2006; Brodribb et al., 2007; Sack & Scoffoni, 2013, but see Gleason et al., 2016), should be strongly associated with individual tree performance under hydraulic stress or drought events by significantly affecting photosynthetic capacity and leaf hydraulic conductance (Angert et al., 2007; Correia et al., 2008; Gebrekirstos et al., 2011; Iida et al., 2016; Sack

et al., 2013). Thus, it is crucial to determine the importance of these traits in tropical forests, in which drought events are expected to increase (Chadwick et al., 2016). These hard-trait data can be used in tree performance models and then competed against models that include only soft-trait data.

A second potential way forward is placing organ-level trait data into a whole plant allocation context. Previous work has demonstrated that tree architectural traits such as crown width (Iida, Poorter, et al., 2014) or estimates of the amount of leaf area deployed for light interception (e.g. Falster et al., 2011) are valuable for understanding the functional strategies of plants and/or their performance. The most evident and important starting place for accomplishing this goal is an integration of the most commonly measured leaf traits, SLA (i.e. the inverse of leaf mass per area [LMA]), and whole crown biomass leaf area allocation (i.e. an estimation of leaf area ratio). SLA reflects a fundamental trade-off relating resource capture, leaf investment and leaf life span at the scale of a leaf (Reich et al., 1997). However, individuals and species vary widely in their relative allocation to whole crowns and this variation makes it unlikely that SLA alone will serve as a robust predictor of tree demographic rates (Yang et al., 2018). Individual-level and interspecific variation in crown biomass allocation or whole plant leaf mass divided by whole plant mass have been identified as critical predictors of plant growth or relative growth rate respectively (Enquist et al., 2007; Garnier, 1991). Despite this, a placement of leaf traits into a crown context is not frequently done in the current trait-based tree growth modelling literature, which likely greatly reduces our ability to predict plant performance (Yang et al., 2018, 2020). Thus, variables representing allocation to leaves should also be considered in models of tree survival and growth and these models should be compared to models lacking this information.

Lastly, the role of local-scale biotic interactions (e.g. competition) needs to be considered to understand the survival and growth responses resulting from the interactions between focal trees and their neighbours. Plant performance is expected to be affected by local population densities via positive or negative interactions (Chesson, 2000; Pacala & Silander, 1985; Uriarte et al., 2010). Neighbourhood models that consider the density, size and distance of neighbouring trees have been increasingly used in trait-based studies to determine the role of neighbourhood competition in tree community structure and dynamics (e.g. Canham et al., 2004; Uriarte et al., 2004, 2010; Zambrano et al., 2019).

Here, we compare models of tropical tree survival and growth that incorporate traits linked to tree water use (i.e. leaf carbon isotope composition (leaf δC^{13}), leaf hydraulic capacity and photosynthetic rates (i.e. leaf vein length per unit area), a measure of crown area multiplied by LMA to estimate tree-level allocation to photosynthetic mass (M_p) and neighbourhood crowding. In this work, we ask the following questions.

(1) How correlated are soft-traits with hard-traits? We predict a strong positive correlation between leaf traits associated with hydraulic and photosynthetic capacity (e.g. Brodribb et al., 2007) (i.e. vein length per unit area and LMA), and between leaf traits related

to water use efficiency such as leaf carbon isotopic composition with phosphorus concentration (Brück et al., 2000), and wood density (Santiago et al., 2004). Answering this question is critical because if these two types of traits are significantly correlated, it would indicate that hard-traits may not be as valuable to measure and will likely not dramatically improve tree survival and growth models. (2) Does the use of an estimate of total tree-level photosynthetic mass (M_p) improve model fits of tree survival and growth as compared to models that do not include this information? We predict that the inclusion of M_p will improve model fit as it relates to crown resource allocation of the whole tree-level that ultimately affects survival and growth rates. (3) Do models of tree survival and growth that include traits related to water use and photosynthetic capacity (i.e. hard-traits) outperform models that include commonly measured soft-traits? We expect that including hard-traits will improve tree performance models as these traits are closely linked to physiological responses such as photosynthetic capacity and leaf hydraulic conductance. (4) Does including the effects of neighbourhood crowding improve the models of tree survival and growth? We predict strong neighbourhood crowding effects on tree survival and growth, due to either competition for similar resources or shared enemies reducing individual performance.

2 | MATERIALS AND METHODS

2.1 | Luquillo forest dynamics plot

This study was conducted in the Luquillo Forest Dynamics Plot, a 16-ha long-term forest plot located in northeast Puerto Rico (18°20′N, 65°49′W; LTFP). The plot, divided into 400 20 m × 20 m quadrats, has been censused every five years since 1990, where all free-standing woody stems ≥1 cm in diameter at breast height (*dbh*) were identified and measured (Zimmerman, 2010). The plot is located in a subtropical wet forest type with *Dacryodes excelsa* (Burseraceae) and the palm *Prestoea acuminata* (Arecaceae) as the most dominant species. The mean annual rainfall is 3,500 mm/year and mean monthly temperatures range between 21 and 25°C. The plot experienced severe hurricane damage in 1989, 1998 and 2017 due to hurricanes Hugo, Georges and Maria. The censuses used in this study included only those most distant from hurricane disturbance (2005 and 2011) and previous work has shown that the forest largely recovered from Hugo and Georges prior to the 2005 census (Swenson et al., 2012).

2.2 | Functional trait measurement

We used soft-trait data for 111 woody plant species that were previously collected (Swenson et al., 2012; Swenson & Umana, 2015; Umaña et al., 2015). These traits were collected from 5 to 10 adult trees per species and included: leaf phosphorus (P; percentage P of dry mass), leaf carbon (C; percentage C of dry mass) and leaf nitrogen

(N; percentage N of dry mass) concentration; wood specific gravity (referred to as wood density WD); leaf area (LA; cm^2); specific leaf area (SLA; cm^2/g); maximum tree height (H_{max}; m); and seed dry mass (SM; g). In addition to these traits, we also measured two hard-traits related to plant hydraulics. The first was vein length per unit area (VLA; mm/mm^2) measured following the protocol described in Iida et al. (2016). Briefly, two leaves from the outer crown per species were cut into 1 cm × 1 cm squares, cleared with NaOH, stained with safranin, mounted on slides and imaged at 20× magnification. Next, the length of non-primary veins in the image was quantified by tracing the veins in ImageJ. A VLA value for 60 of the species was generated by averaging values from 3 to 5 individuals per species. Detailed physiological studies have shown that VLA is strongly positively correlated with photosynthetic capacity (Brodribb et al., 2007). We also quantified leaf carbon stable isotope ratios (leaf δC^{13}; ‰) using leaves collected between January and March 2008 (i.e. midway between censuses and during the driest part of the year). The isotope analyses were conducted using mass spectrometry at the Cornell University Stable Isotope Laboratory using leaves from 1 to 3 adult trees per species. Carbon stable isotope levels are indicative of water use efficiency (Dawson et al., 2002; Farquhar et al., 1982) and, therefore, may indicate plant performance during periods of limited water.

2.3 | Trait correlations

Trait values were first log-transformed to approximate normality if their distributions from the raw data were not approximately normal. Correlations between the hard-traits and soft-traits (Table 1) were examined using Pearson's correlation coefficient. In addition, we applied

TABLE 1 Soft- and hard-traits considered as potential predictors of tree survival and growth rates

Soft-traits		
Commonly measured but weakly correlated or not correlated at all with important physiological rates	Leaf phosphorus concentration	P (%P)
	Leaf carbon concentration	C (%C)
	Leaf nitrogen concentration	N (%N)
	Wood density	WD
	Leaf area	LA (cm^2)
	Specific leaf area	SLA (cm^2/g)
	Maximum tree height	H (m)
	Seed dry mass	SM (g)
Hard-traits		
Difficult to measure but closely linked to physiological processes of interest	Stable leaf carbon isotope composition	δC^{13} (‰)
	Vein length per unit area	VLA (mm/mm^2)

a principal component analysis (PCA) to all traits from the same 60 species from which all trait data were available to determine trait relationships and the contribution of each trait to the principal components.

2.4 | Total tree-level photosynthetic mass

Total tree-level photosynthetic mass (M_p) was calculated for each individual from 17 of the 30 most common species in the plot. These 17 species account for ~56% of the individuals (excluding palm species) and 13% of the species in the plot in the 2005 census. We established species-specific crown allometries from field measurements (Table S1). Specifically, we measured the stem diameter and the crown radius in two cardinal directions for 5–25 individuals (with dbh ranging from =0.5 cm to 56.3 cm) per species to produce species-specific allometries (Equation 1; Table S1; Figure S1; $r^2 = 0.66$–0.97). The species-specific M_p was obtained implementing Equations 1–3 that describe the crown area allometry in terms of individual tree crown radius as follows (Hunt, 1978; Niklas & Enquist, 2001; Poorter, 1989; Yang et al., 2018):

$$\log(\text{radius}) = \text{slope} \times \log(\text{dbh}) + \text{intercept}, \tag{1}$$

$$CA = \pi \times \text{radius}^2, \tag{2}$$

$$M_p = LMA \times CA, \tag{3}$$

where intercept and slope are species-specific estimates from the $\log_{10}$–$\log_{10}$ allometric regressions, and leaf mass per area (LMA) = 1/SLA, which is related to leaf life span and photosynthetic rates (Reich et al., 1997). We estimated the M_p across all individuals (i) of each species based upon their dbh_i values and crown area (CA_i). It is important to note that this approach simplifies the estimate of M_p by making the unrealistic, but a most simple, assumption that all individuals and species have an identical leaf area index.

2.5 | Neighbourhood crowding index

We examined the effects of neighbours by calculating a total Neighbour Crowding Index (NCI). The negative influence of a neighbour was calculated as follows:

$$NCI_i = \sum_j \frac{\text{dbh}_j^2}{d_{ij}^2}. \tag{4}$$

The index varies as a function of the squared dbh of the neighbour (j) and an inverse function of the squared distance (d) of the focal tree (i) to the neighbour (j) (Canham et al., 2004; Uriarte et al., 2004). The effect was calculated within a 20-m radius around the focal tree (i) and summed over all neighbours. Previous studies have shown that the effects of the neighbours can be detected within a radius smaller than 20 m (Hubbell et al., 2001; Uriarte et al., 2004, 2010), and that, in this

forest, the effects of NCI are consistent across different radii (5–30 m) (Zambrano et al., 2020). We used all 128 species in the 2005 census as neighbours (j) and estimated NCI for all individuals (i) of the 17 species for the demographic models.

2.6 | Modelling tree demographic rates: Including total photosynthetic mass

We used census data for the same 17 non-palm species for which we had species-specific allometries including all individuals with dbh values ≥1. We included 17,007 individuals for the survival models and 10,538 individuals for the growth models (see Table S4 for individuals per species). We measured tree survival by determining the presence of the individual in the next census. In addition, we calculated tree relative growth rate (RGR, cm/year) as follows:

$$RGR = \left(\ln \text{dbh}_{t+\Delta t} - \ln \text{dbh}_t\right) / \Delta t, \tag{5}$$

where dbh_t is measured at successive time steps t (Δt, measured in years). A value of 1 was added to the observed data before log-transforming. Additionally, negative values obtained ($n = 1,056$), possibly due to stem shrinkage, measurement error, or breakage, were discarded before the log-transformation. Tree survival was fitted using a binomial function while tree growth was modelled using a Gaussian function. For both survival and growth, we used generalized linear mixed effect models (*lmer* and *glmer* functions from the LME4 package in R, Bates et al., 2015) as follows:

$$Y_{isk} = \alpha_S + \beta_S \text{Variable} + \tau_S + \tau_k, \tag{6}$$

where Y_{iSk} represents survival (1: alive or 0: dead) or log-transformed RGR values for each individual tree i of species S, *Variable* represents any of the following (see Model selection and assessment): dbh_{0_i} (the initial dbh in 2005), M_{p_i} (the tree-level total photosynthetic mass), CA_i (crown area) of each individual i or LMA_S (leaf mass per area) of species S. τ_S and τ_k are random effects of differences in species S and quadrat k respectively. α_S is species-specific intercept and β_S are species-specific coefficients representing the effect of the parameters. Parameters were z-score standardized (subtracting the mean and dividing by the standard deviation) prior to analyses.

2.7 | Model selection and assessment

First, we examined whether including M_p or any of its components, LMA_S and CA_i, instead of dbh_i increased the quality of the tree survival and growth models by fitting one model for each variable with a similar structure (intercept and the random effects) (Equation 6; Table 2). We used three different methods to select the best model: (a) the Akaike's information criterion (AIC), (b) Akaike weights (w_i) and (c) Cross-Validation/loss function (C-V loss). For AIC, we used a

TABLE 2 Survival (S) and growth (RGR) models. The table shows the models compared to determine whether including total photosynthetic mass estimates (M_p) outperformed models that included the components of M_p by themselves. Also included were an intercept (β_o), crown area (CA), initial diameter at breast height (dbh) and leaf mass per area (LMA). Variables that are significant in a model are bolded. Moreover, Akaike's value (AIC), ΔAIC ($AIC_i - AIC_{min}$), Akaike weights (w_i) and Cross-Validation loss (C-V loss) are shown for each model. Lower Cross-Validation loss (C-V loss) values are underlined showing the model with best goodness-of-fit and higher probability of being the best model

Model	AIC	ΔAIC	w_i	C-V loss
$S \sim \beta_o + M_p$	16,049.8	0	0.495	0.453323
$S \sim \beta_o + CA$	16,058.6	0	0.498	0.453323
$S \sim \beta_o + dbh$	16,049.8	8.8	0.006	0.453670
$S \sim \beta_o + LMA$	17,063.6	1,013.77	<0.001	0.485296
$RGR \sim \beta_o + M_p$	28,388.4	0	0.615	0.281690
$RGR \sim \beta_o + CA$	28,389.4	1	0.381	0.281712
$RGR \sim \beta_o + dbh$	28,398.5	10.1	0.004	0.281812
$RGR \sim \beta_o + LMA$	28,548.7	160.3	<0.001	0.282589

delta-AIC threshold of 2 units (AIC differences relative to the smallest AIC value: $AIC_i - AIC_{min}$). For Akaike weights, we compared the likelihood (weight of evidence) of each model to the best model by computing their Akaike's weights (Burnham & Anderson, 2002). Lastly, for the C-V loss method we calculated the test error (loss) associated to each model (i.e. goodness-of-fit) by performing a 10-fold cross-validation. This approach provides a direct estimate of the test error and makes fewer assumptions about the true underlying model (James et al., 2013). We chose the 'best model' or 'best models' as the one/ones with low AIC, high Akaike weight and low C-V loss scores. To calculate the C-V loss, the data were randomly divided into 10-folds of approximately equal size. Nine of the folds were used to train the models and the one remaining fold to test the models (James et al., 2013). This process was repeated ten times in which a different group was treated as the test set. For the ten folds, we calculated the averaged loss for each model (the error associated with fitting each of the models on the data). We implemented two loss functions to assess the goodness-of-fit of a model (i.e. model quality) by estimating its prediction error on new (i.e. test) data (Hastie et al., 2009). For tree survival models only, we used a log-loss function (cross-entropy cost function from the package MLMETRICS in R, Yan, 2016) that accounts for uncertainty in the predictions. For tree growth, we calculated the Huber loss that uses a quadratic loss function for small residuals or a linear loss function when residuals exceed the minimum value of the 90th quantile (package QRMIX in R, Resa et al., 2017). Thus, this function avoids the effects of large outliers that make the quadratic loss less robust (Hastie et al., 2009). When comparing models using the loss function values, the smallest value indicates the model with higher performance when predicting unseen data. In other words, this value indicates which model can be expected to perform better on other sets of data (James et al., 2013).

2.8 | Modelling tree demographic rates: Including soft- and hard-traits

Following the selection of the best predictor (M_p, LMA, CA or dbh) of survival and growth using Equation 6 (Table 2), we fit all different model combinations that included the selected predictors, both soft- and hard-traits and the neighbour crowding index. The models were fit controlling for multicollinearity among traits (excluding trait combinations with Pearson's correlation coefficient $|r| \geq 0.60$) using the function *pdredge* from the package MuMIn in R (Bartoń, 2018), setting:

$$Y_i = \alpha_S + \beta_{1S}\,\text{Variable} + \beta_{2S}\,\text{soft}_S + \beta_{3S}\,\text{hard}_S + \beta_{4S}\,\text{NCI}_i + \tau_S + \tau_k, \quad (7)$$

where Variable represents the selected parameter (M_p, CA, dbh or LMA), soft$_S$ and hard$_S$ represent all the soft- and hard-traits used at the species level S and NCI$_i$ represents a neighbourhood crowding index at the individual level i. The τ_S and τ_k parameters are random effects for species S and quadrat k respectively. The α_S is a species-specific intercept, $\beta_{1S}-\beta_{4S}$ are species-specific coefficients representing the effect of the parameters. The data were z-score standardized (subtracting the mean and dividing by the standard deviation). We performed model selection following the same methodology described above in the Model selection and assessment section.

2.9 | Model averaging

When multiple models were indiscernible ($AIC_i - AIC_{min} \leq 2$) due to similar Akaike weights and C-V losses, we carried out multi-model inference to increase precision and reduce bias (Burnham & Anderson, 2002). This methodology first selects a model set from which model averaging is performed including model selection uncertainty from the set of models. We compared the standardized coefficients to determine the relative importance of the variables in the averaged model. Predicted versus observed values were plotted to test the fit of the model. All the analyses were carried out with the R software version 3.5.1 (R Development Core Team, 2018).

3 | RESULTS

3.1 | Correlations between soft- and hard-traits

We found positive correlations between leaf δC^{13} and leaf phosphorus concentration ($r = 0.27$, $p = 0.004$, $n = 105$; Figure 1a), between leaf δC^{13} and wood density ($r = -0.20$, $p = 0.03$, $n = 105$; Figure 1b) and between VLA and leaf carbon concentration ($r = 0.45$, $p < 0.001$, $n = 60$; Figure 1c). No significant correlations were found between the other traits studied (Table S2). In the PCA, the first three principal components (PCs) accounted for 60.2% of the total variance. PC1 accounted for 27.8% of the total variance and was possibly related to resource capture. At the negative end of this axis, we found
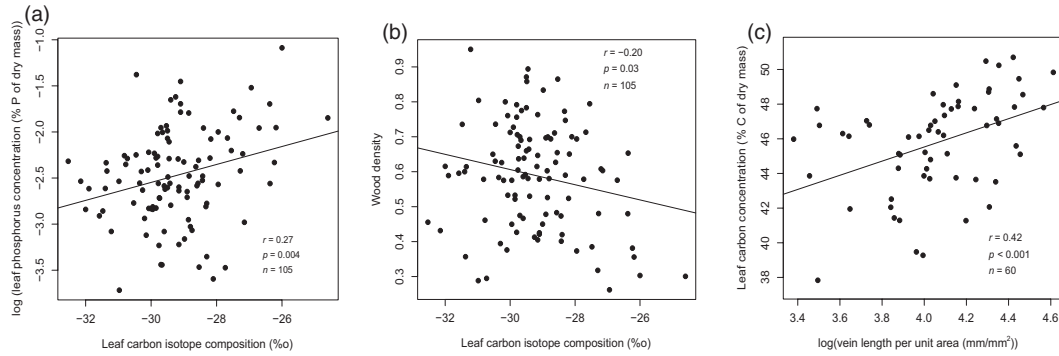
FIGURE 1 (a) Correlation between leaf carbon isotope composition and leaf phosphorus concentration. (b) Correlation between leaf carbon isotope composition and wood density. (c) Correlation between vein length per unit area (VLA) and leaf carbon concentration. The Pearson correlation coefficient (r), sample size (n), and p-value are shown for each graph

Model	AIC	ΔAIC	w_i	C-V loss
$S \sim \beta_o + M_p + C + H_{max} + P$	16,047.6	0	0.095	0.453325
$S \sim \beta_o + M_p + C + H_{max} + P + N + SM + VLA$	16,047.7	0.1	0.089	0.453337
$S \sim \beta_o + M_p + C + H_{max} + P + NCI$	16,048.1	0.4	0.076	0.453288
$S \sim \beta_o + M_p + C + H_{max} + N + P + SM + NCI + VLA$	16,048.2	0.5	0.073	0.453301
$S \sim \beta_o + M_p + P$	16,048.4	0.8	0.065	0.453317
$S \sim \beta_o + M_p + C + P$	16,048.5	0.9	0.061	0.453324
$S \sim \beta_o + M_p + C + H_{max} + P + c13$	16,048.7	1.0	0.056	0.453331
$S \sim \beta_o + M_p + P + NCI$	16,048.8	1.2	0.053	0.453281
$S \sim \beta_o + M_p + C + H_{max} + N + P + SM + VLA + c13$	16,048.9	1.3	0.051	0.453344
$S \sim \beta_o + M_p + C + P + NCI$	16,048.9	1.3	0.049	0.453287
$S \sim \beta_o + M_p + H_{max} + P$	16,049.0	1.3	0.048	0.453314
$S \sim \beta_o + M_p + C + P + wsg$	16,049.1	1.4	0.046	0.453325
$S \sim \beta_o + M_p + C + H_{max} + P + NCI + c13$	16,049.1	1.5	0.045	0.453294
$S \sim \beta_o + M_p + C + H_{max} + P + wsg$	16,049.2	1.6	0.042	0.453327
$S \sim \beta_o + M_p + H_{max} + P + NCI$	16,049.4	1.8	0.039	0.453277
$S \sim \beta_o + M_p + P + LA$	16,049.4	1.8	0.039	0.453311
$S \sim \beta_o + M_p + C + P + NCI + wsg$	16,049.5	1.9	0.037	0.453289
$S \sim \beta_o + M_p + C + c13$	16,049.6	2	0.035	0.453336
$S \sim \beta_o + CA + C + H_{max} + P$	16,045.0	0	0.268	0.453334
$S \sim \beta_o + CA + C + H_{max} + P + NCI$	16,045.4	0.4	0.217	0.453298
$S \sim \beta_o + CA + C + H_{max} + P + N + SM + VLA$	16,046.0	1.0	0.163	0.453347
$S \sim \beta_o + CA + C + H_{max} + N + P + SM + NCI + VLA$	16,046.4	1	0.134	0.453311
$S \sim \beta_o + CA + C + H_{max} + P + c13$	16,046.7	1.7	0.115	0.453336
$S \sim \beta_o + CA + C + H_{max} + P + wsg$	16,046.9	1.9	0.104	0.453335

TABLE 3 Survival (S) models that include total photosynthetic mass (M_p) or crown area (CA). The table shows the set of models for survival with ΔAIC ≤ 2 that include the intercept (β_o), and soft- and hard-traits (refer to Table 1 for abbreviations). Moreover, Akaike's value (AIC), ΔAIC (AIC$_i$ – AIC$_{min}$), Akaike weights (w_i) and Cross-Validation loss (C-V loss) are shown for each model

species with high leaf phosphorus and nitrogen concentrations, and low wood density, while the positive end had species with low values of leaf phosphorus and nitrogen concentrations, and high wood density. The PC2 accounted for 18.4% of the total variance and was possibly related to maximum height, with large-statured, low specific leaf area and large seeded species found at positive values of this axis, while at negative values of this axis we found small-statured
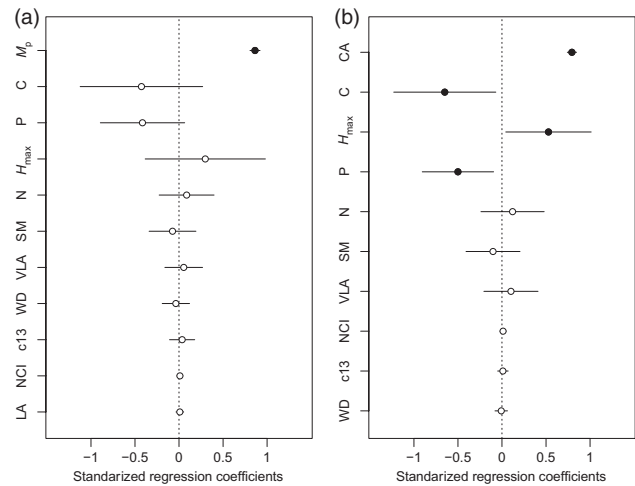
species with high specific leaf area and small seeds. The PC3 accounted for 13.9% of the total variance and was possibly related to water use, with species showing low values of vein length area, and leaf carbon concentration, and high values of leaf δC^{13} at high values of this axis, while at negative values of this axis species display high values of leaf vein length area and leaf carbon concentration, and low values of leaf δC^{13} (Table S3; Figure S2).

3.2 | Demographic models

For tree survival the models that included M_p or CA, instead of LMA or dbh, showed a slight improvement in the model quality (Table 2). Therefore, we fit all the different combinations of tree survival models, controlling for multicollinearity among traits, (models with M_p: 588; models with CA: 588) that included M_p, neighbourhood crowding, and soft- and hard-traits (Table S5), and models that included CA, neighbourhood crowding and soft- and hard-traits (Table S6). We selected the models that had a ΔAIC ≤ 2 (Table 3), but since multiple models had indiscernible AIC values, and the Akaike weights provided no strong evidence for a single superior model, we performed model averaging (see results in Table 4). The averaged model that included total photosynthetic mass (M_p) as a predictor showed that survival increases with total photosynthetic mass, but the other traits were not significantly related to survival (Figure 2a; Table 4). The averaged model that included crown area (CA) as a predictor
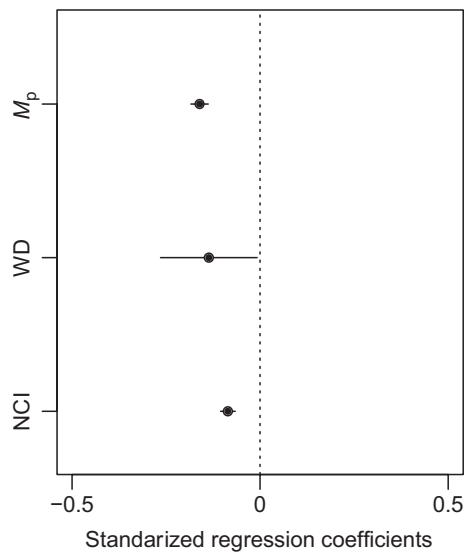

FIGURE 2 Standardized regression coefficients for the averaged survival models. Two averaged models were applied: (a) a model including photosynthetic mass (M_p) and traits; and (b) a model including photosynthetic crown area (CA) and traits. Refer to Table 1 for abbreviations. Variables are displayed in order of importance. Lines represent 95% confidence intervals, while circles represent the model estimated value. Open circles are non-significant effect, and filled black circles represent a significant parameter at alpha = 0.05. Refer to Table 4 for details

TABLE 4 Average survival (S) models that include total photosynthetic mass (M_p) or crown area (CA), and soft- and hard-traits (refer to Table 1 for abbreviations). Variables are displayed in order of importance. Also included are the unconditional (model selection uncertainty not conditional in any particular model from the set) sampling standard error ($\widehat{SE}$), unconditional confidence intervals (Lower CI and Upper CI) and absolute Wald values that are shown for each variable

Variable	Estimate	$\widehat{SE}$	Lower CI	Upper CI	|Wald Z|
$S \sim \beta_o + M_p + C + H_{max} + P + N + SM + VLA + NCI + c13 + WD + LA$					
M_p	0.863	0.029	0.806	0.919	29.8
C	−0.427	0.355	−1.122	0.269	1.20
H	0.298	0.348	−0.384	0.980	0.86
P	−0.415	0.244	−0.894	0.064	1.70
N	0.086	0.159	−0.225	0.398	0.54
SM	−0.073	0.136	−0.339	0.192	0.54
VLA	0.053	0.109	−0.160	0.267	0.49
NCI	0.010	0.017	−0.023	0.043	0.61
c13	0.035	0.073	−0.108	0.178	0.48
WD	−0.036	0.079	−0.191	0.119	0.45
LA	0.010	0.022	−0.034	0.053	0.43
$S \sim \beta_o + CA + C + H_{max} + P + N + SM + VLA + NCI + c13 + WD$					
CA	0.794	0.027	0.742	0.846	29.8
C	−0.649	0.296	−1.229	−0.070	2.20
H	0.528	0.247	0.043	1.013	2.13
P	−0.500	0.206	−0.904	−0.096	2.42
N	0.120	0.183	−0.239	0.479	0.66
SM	−0.102	0.156	−0.408	0.204	0.65
VLA	0.102	0.157	−0.205	0.409	0.65
NCI	0.012	0.018	−0.023	0.047	0.69
c13	0.010	0.030	−0.049	0.070	0.34
WD	−0.009	0.036	−0.080	0.063	0.24

TABLE 5 Growth (RGR) models. The table shows the set of models with indiscernible ΔAIC ≤ 2 that include intercept (β_o) and traits (refer to Table 1 for abbreviations). Moreover, Akaike value (AIC), ΔAIC ($AIC_i − AIC_{min}$), Akaike weights (w_i) and Cross-Validation loss (C-V loss) are shown for each model

Model	AIC	ΔAIC	w_i	C-V loss
RGR $\sim \beta_o + M_p +$ WD + NCI	28,321.7	0	0.67	0.281006
RGR $\sim \beta_o + M_p + NCI$	28,323.1	1.4	0.33	0.281043

showed, in order of importance, CA, carbon concentration, maximum height and leaf phosphorus concentration as significant predictors of tree survival, with survival increasing with CA and maximum height, and decreasing with leaf carbon and phosphorus concentrations (Figure 2b; Table 4). Leaf nitrogen concentration, seed mass, vein length per unit area, neighbourhood crowding, leaf δC^{13}, leaf area and wood density showed low support and no statistical significance. In addition, the observed versus predicted plots (Figure S3) showed no difference between the survival averaged models with M_p and CA suggesting that both models perform equally well.

For tree growth, the model that included M_p instead of its components (LMA, CA or dbh) showed an improvement in the model quality as evidenced by a reduction in both AIC and the C-V loss (Table 2). The inclusion of soft- and hard-traits and the neighbourhood crowding information in growth models resulted in two models with indiscernible AICs that included M_p, wood density and neighbourhood crowding as strong predictors of tree growth (Table 5). The averaged growth model showed that tree growth decreases with high values of M_p, wood density and neighbourhood crowding

FIGURE 3 Model standardized regression coefficient for the averaged growth model. Variables are displayed in order of importance. Refer to Table 1 for abbreviations. Lines represent 95% confidence intervals, while the circles represent the model estimated value. Filled black circles represent a significant effect. Standardization was performed by log-transforming and scaling (z-scoring, subtracting the mean and dividing by the standard deviation) the variables. Refer to Table 6 for details

TABLE 6 Average growth (RGR) models that include total photosynthetic mass (M_p) and soft- and hard-traits (refer to Table 1 for abbreviations). Variables are displayed in order of importance. Also included are the unconditional (model selection uncertainty not conditional in any particular model from the set) sampling standard error ($\widehat{SE}$), unconditional confidence intervals (Lower CI and Upper CI) and absolute Wald values are shown for each variable

Variable	Estimate	$\widehat{SE}$	Lower CI	Upper CI	|Wald Z|
RGR ~ $\beta_o + M_p$ + WD + NCI					
M_p	−0.161	0.012	−0.184	−0.138	13.71
WD	−0.136	0.065	−0.265	−0.008	2.08
NCI	−0.086	0.010	−0.105	−0.066	8.72

(Figure 3; Figure S4; Table 6). Similar to survival models, none of the tree growth models with indiscernible AIC or |r| < 0.6 for tree relative growth rate included leaf δC^{13} or vein length area as independent variables at a significance level of 0.05.

4 | DISCUSSION

Modelling individual-level performance including trait information is a key goal in ecology (e.g. Iida, Kohyama, et al., 2014; Iida et al., 2016; Paine et al., 2015; Poorter et al., 2008). It has been suggested that tree survival and growth models may be improved by integrating leaf-level traits with whole plant allocation to leaf area, through the

measurement of less commonly measured traits more directly linked to physiological rates and the inclusion of local-scale biotic interactions (Yang et al., 2018). Here, we have shown that growth models that integrate leaf-level traits (i.e. 1/SLA) with whole tree crown allocation were superior to models that did not include crown information. Similarly, survival models that integrate leaf-level traits with whole tree crown allocation or total crown area were superior to models that did not include them. Surprisingly, less commonly measured traits (hard-traits), such as leaf δC^{13} and leaf vein length per area, were not better predictors of tree survival and growth compared to traits widely measured in plant ecology. In addition, neighbourhood crowding showed a strong effect on tree growth, but not tree survival. In the following section, we discuss our key results in more detail.

4.1 | How are soft-traits with hard-traits correlated?

Plant ecologists often utilize easily measured functional traits in their research to estimate key trade-offs relating to organismal form and function. These traits are referred to as soft-traits, which are contrasted with hard-traits that are potentially more directly tied to physiological rates and performance, but less easily measured. Thus, trait-based analyses of plant performance may be strengthened by the measurement of hard-traits, but this may largely hinge on the degree of correlation between soft- and hard-traits. Our results showed little to no correlation between the hard-traits measured (leaf δC^{13}, vein length per area (VLA)) and commonly measured soft-traits (wood density, maximum tree height, seed mass, leaf nitrogen concentration, leaf phosphorus concentration, leaf carbon concentration, leaf area and specific leaf area (SLA)) (Table S2). The only exceptions were correlations found between leaf δC^{13} with leaf phosphorus concentration, and with wood density, and VLA with leaf carbon concentration (Figure 1; Table S2). A positive relationship between leaf δC^{13} and leaf phosphorus concentration has been previously described in other tropical forests (e.g. Baraloto et al., 2010). High values of soil phosphorus, which directly determine leaf phosphorus concentration (Wright et al., 2004), have been shown to increase plant water use efficiency (e.g. glasshouse experiment by Brück et al., 2000; Tibetan plateau by Song et al., 2010; and Canadian prairies by Kröbel et al., 2012), which corresponds with less negative values of leaf δC^{13}. Contrary to our expectations, the weak negative relationship between leaf δC^{13} and wood density could be explained by a decoupling of stem and leaf hydraulic traits in this forest (but see Santiago et al., 2004 for scaling of these traits). A positive correlation between VLA and leaf carbon concentration, highlighting the role of VLA with respect to within-leaf support investment and not only its relation with hydraulics, has been reported previously (Niinemets et al., 2007). Leaf veins are composed of xylem and phloem cells (Sack & Scoffoni, 2013), which contain mainly lignin, cellulose and other structural carbohydrates. Thus, an increase in the number of veins per unit area should be associated with an increase in the amount of lignin in the leaf, which coincides with the concentrations of total carbon (Poorter & Villar, 1997).

The negligible correlations between hard-traits with soft-traits in our study suggest that the soft-traits measured here are insufficient proxies of VLA and leaf δC^{13}. Nevertheless, it is possible that the strength of the correlations shown here, and the importance of these hard-traits for modelling plant performance would be different if we included ontogenetic differences (Grime et al., 1997; Poorter et al., 2008; Wright et al., 2010), considered another set of species (Sack et al., 2013) or focused on a period time after intense drought events given the association of these hard-traits with tree performance under hydraulic stress.

4.2 | Total tree-level photosynthetic mass and crown area as better predictors of tree performance

Studies that have only considered leaf-level traits such as SLA (e.g. Paine et al., 2015; Wright et al., 2010) on large organisms (e.g. trees) likely have a reduced capacity to predict demographic rates due to individual- and species-level variation in overall crown allocation and architecture. Instead, total photosynthetic mass (M_p), as others have proposed (e.g. Enquist et al., 2007; Garnier, 1991; Hunt, 1978; Poorter, 1989; Yang et al., 2018) should be a stronger predictor of plant survival and growth than SLA. By estimating M_p via measurements of crown area integrated with LMA (i.e 1/SLA), we generated stronger models of tree demographic rates than those including initial dbh (Table 2).

The fact that survival models including crown area and models including total photosynthetic mass performed similarly suggests that omitting LMA and measuring crown area alone would be sufficient to improve the predictions of tree survival in this forest (Table 3; Figure S3). This result highlights the importance of individual-level measurements (i.e. crown area, leaf area index) for improving predictions of tree performance (Iida & Swenson, 2020; Poorter et al., 2008; Wright et al., 2010; Yang et al., 2018, 2020). It is also important to note the negative effect of M_p on growth. This result could be driven by big trees, expected to have big canopies, growing slower or by variations in individual crown depths not included in this study.

We note that our estimates of M_p are still crude in that they do not consider overall crown volume and measurements of the leaf area index, but they do provide a marked improvement of the traditional paradigm of relating leaf-level traits to demographic rates without context relating to crown allocation. It is, potentially, also important to note that the impact of M_p (reduced AIC, included in all the best models, and high variable importance/significance) in our models was large relative to that gained by adding or removing soft- and hard-traits (see below, Tables 2, 3 and 5). Thus, future work should start from a foundation of crown measurements in models of tree demographic rates.

4.3 | Hard-traits did not improve model predictions of tree survival and growth

Contrary to our expectations, soft-traits were better predictors of tree performance than hard-traits related to water use. These soft-traits have been found to be related to tree survival and growth in other tropical forests (e.g. Chave et al., 2009; Enquist et al., 1999; Poorter et al., 2008; Wright et al., 2010). In a study of five neotropical forests, Poorter et al. (2008) found that wood density was the best predictor of relative growth rates while survival rates increased with maximum height. Using the forest plot used in this study, Uriarte et al. (2010) found that models in which the effects of neighbourhood interactions were scaled to trait values such as wood density provided stronger predictions of tree performance. Similarly, Zambrano et al. (2020) found that maximum height and leaf phosphorus concentration influenced the strength (positively and negatively respectively) of neighbourhood interactions on survival rates.

Several explanations can be attributed to the limited model improvement when adding hard-traits. One potential, but unlikely, reason is that water-related traits are not an important predictor of performance. These traits are expected to be strongly associated with individual performance under hydraulic stress or drought events, but they might not be critical for tree performance during periods lacking intense dry events (such as the period evaluated in this study: 2005–2011). Rather, these water-related traits may be more important in the context of future drought events or in other forests experiencing strong droughts (Chadwick et al., 2016; Santiago et al., 2018). A second possibility is that these traits must be considered in light of more contextual information regarding regional-to-local-scale abiotic gradients (Yang et al., 2018; Zambrano et al., 2017). A third possibility that we consider to be the most probable is that these hydraulic traits can be sensitive to micro-environmental conditions or short-term climatic variations and they may need to be measured at those scales (Baraloto et al., 2010; Correia et al., 2008; Paine et al., 2015; Seibt et al., 2008). Thus, links between leaf δC^{13} values and growth may be detected at a finer temporal scale than we could assay in this study. Lastly, it could be possible that the link between these hard-traits (VLA and leaf δC^{13}) and tree performance is directly influenced by changes in plant allocation resulting from differences in ontogeny and tree size (Falster et al., 2011, 2018; Gibert et al., 2016; Iida, Kohyama, et al., 2014; Iida et al., 2016). For example, plant traits such as LMA are known to change as the plant grows (Wright et al., 2010) due to changes in specific-size plant requirements to allocate biomass or increments on construction costs (Gibert et al., 2016; Iida & Swenson, 2020). Therefore, tree survival and growth models need be further refined to consider changes associated with plant ontogenetic stage or size (Falster et al., 2018) in order to detect significant patterns.

Finally, including information regarding neighbour crowding only improved the quality of our tree growth models (Table 5). Increased neighbourhood crowding reduced tree growth, which was consistent with previous work in this forest (Uriarte et al., 2004, 2010; Zambrano et al., 2019, 2020). Although the previously described negative impact of crowding on tree survival (e.g. Hubbell et al., 2001; Weiner, 1990), neighbourhood crowding was not a strong predictor of survival in this study. Specifically, survival models including neighbourhood crowding had indiscernible AIC values compared to

other models (Table 3), but in the averaged survival models, the effect of neighbourhood crowding was relatively small suggesting that removing it from the models does not impact the predictions. This may be due to species responding differentially to neighbourhoods by having variable effective radii (Uriarte et al., 2004; Zambrano et al., 2020), or because the neighbourhood crowding index did not include species-specific functional trait values (Uriarte et al., 2010).

5 | CONCLUSIONS

Studies linking traits to tree performance usually fail to include physiological traits and whole plant allocation information. In this study we considered the importance of hard-traits, crown allocation, an integration of organ-level traits and crown allocation and biotic interactions to determine whether models of tropical tree performance could be improved in comparison to models that only use easily measured soft-traits. Given that the leaf δC^{13} and VLA traits failed to improve the models and did not strongly correlate with the leaf and stem traits, we suggest that soft-traits used in this study might not be useful as proxies of leaf δC^{13} and VLA in this forest, and that these hard-traits might not be useful without contextual information regarding water availability (i.e. drought events) and/or finer scale sampling.

Lastly, the inclusion of a whole crown allocation data or crown area improved our predictions of tree performance. This result underscores the importance of integrating organ-level trait data with whole plant allocation data when modelling the performance of tropical trees and how they interact with the abiotic and biotic environment. Thus, future studies should strive to incorporate individual-level crown data and continue to seek out additional less commonly measured traits and biotic interactions that will improve tree survival and growth models.

AUTHORS' CONTRIBUTIONS

V.E.R. and N.G.S. generated the research idea; N.G.S., Y.I. and M.N.U. organized and conducted trait data collection; V.E.R. and J.Z. analysed the data; and V.E.R. and N.G.S. wrote the paper with comments from all other authors.

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SUPPORTING INFORMATION

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