

Improving predictions of tropical forest response to climate change through integration of field studies and ecosystem modeling

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Abstract

Tropical forests play a critical role in carbon and water cycles at a global scale. Rapid climate change is anticipated in tropical regions over the coming decades and, under a warmer and drier climate, tropical forests are likely to be net sources of carbon rather than sinks. However, our understanding of tropical forest response and feedback to climate change is very limited. Efforts to model climate change impacts on carbon fluxes in tropical forests have not reached a consensus. Here, we use the Ecosystem Demography model (ED2) to predict carbon fluxes of a Puerto Rican tropical forest under realistic climate change scenarios. We parameterized ED2 with species-specific tree physiological data using the Predictive Ecosystem Analyzer workflow and projected the fate of this ecosystem under five future climate scenarios. The model successfully captured interannual variability in the dynamics of this tropical forest. Model predictions closely followed observed values across a wide range of metrics including aboveground biomass, tree diameter growth, tree size class distributions, and leaf area index. Under a future warming and drying climate scenario, the model predicted reductions in carbon storage and tree growth, together with large shifts in forest community composition and structure. Such rapid changes in climate led the forest to transition from a sink to a source of carbon. Growth respiration and root allocation parameters were responsible for the highest fraction of predictive uncertainty in modeled biomass, highlighting the need to target these processes in future data collection. Our study is the first effort to rely on Bayesian model calibration and synthesis to elucidate the key physiological parameters that drive uncertainty in tropical forests responses to climatic change. We propose a new path forward for model-data synthesis that can substantially reduce uncertainty in our ability to model tropical forest responses to future climate.

KEYWORDS

carbon flux, climate change, ecosystem demography model, GPP, NPP, sensitivity analysis, tropical forest, variance decomposition

1 | INTRODUCTION

Tropical forests play a critical role in the global carbon cycle (Bonal, Burban, Stahl, Wagner, & Hérault, 2016) by accounting for 33% of

terrestrial net primary production, 25% of stored terrestrial carbon, and annually sequestering roughly 3 billion tons of carbon (Beer et al., 2010; Bonan, 2008). However, with tropical estimates having the largest uncertainties (Joetzjer, Douville, Delire, & Ciais, 2013;

Pan et al., 2011), the locations and drivers of the terrestrial carbon sink are still relatively poorly constrained. Indeed, our limited understanding of how tropical plant and soil carbon cycling will respond to climate change is one of the greatest sources of uncertainty in modeling future global carbon cycling and climate (Bonan & Levis, 2010; Booth et al., 2012; Piao et al., 2013; Ziehn, Kattge, Knorr, & Scholze, 2011). The rapid change in climate expected to occur in tropical regions over the coming decades (Anderson, 2011; Mora et al., 2013) demands that we develop a better understanding of the effects of climate change on tropical forests, and the potential feedback effect of changing tropical forest structure and function.

The most optimistic predictions from climate models indicate that global mean temperatures will increase by 2°C within the next couple of decades (Anderson, 2011; Diffenbaugh & Scherer, 2011). Precipitation patterns are also expected to shift in future climate scenarios (Dai, 2013; Feng, Porporato, & Rodriguez-Iturbe, 2013; Mora et al., 2013; Neelin, Münnich, Su, Meyerson, & Holloway, 2006), with many parts of the tropics getting drier. Although models diverge on predictions of drought more so than on temperature extremes (Good, Martin, & Rayner, 2013), most predict stronger droughts in the Amazon (Joetzer et al., 2013), Central America, and the Caribbean (Neelin et al., 2006), West Africa, and peninsular S.E. Asia (Zelazowski, Malhi, Huntingford, Sitch, & Fisher, 2010). Drought and heat-induced tree mortality events could lead to large carbon losses from tropical forests, reduced regional net primary productivity, and decreases in evaporative cooling, creating a positive feedback that exacerbates global warming (Bonal et al., 2016; Bonan, 2008; Zhao & Running, 2010). In short, if we ignore potential changes in solar radiation that can accompany drought, under a warmer and drier climate, tropical forests are likely to become net sources of carbon, rather than sinks (Corlett, 2016). However, our understanding of tropical forests response to drought and warming and their implications on the carbon and hydrological cycles are very limited (Cavaleri, Reed, Smith, & Wood, 2015; Luo et al., 2011).

Tropical tree responses to drought and heat are complex (Meir, Mencuccini, & Dewar, 2015a; Wood, Cavaleri, & Reed, 2012). Over the past decade, considerable effort has gone toward improving our understanding of the effects of drought on tropical forests and studies have demonstrated that by suppressing tree growth and increasing tree mortality, droughts reduce carbon storage in tropical forest (Chazdon, Redondo Brenes, & Vilchez Alvarado, 2005; da Costa et al., 2010; Phillips et al., 2009; Uriarte, Lasky, Boukili, & Chazdon, 2016). However, constant NPP has also been observed during drought due to shifts in carbon allocation (Doughty et al., 2015). High tree mortality rates have been observed during extreme drought events (Allen et al., 2010; da Costa et al., 2010; Phillips et al., 2010). Early-successional species appear to be particularly vulnerable to drought (Markesteyn, Poorter, Bongers, Paz, & Sack, 2011; Phillips et al., 2010; Uriarte et al., 2016) because of their high photosynthetic and respiration rates and low wood density. Studies also have shown that larger trees suffer higher mortality rates than small trees (Bennett et al., 2015; Phillips et al., 2010; Uriarte et al., 2016), which could result in large carbon losses since these

individuals account for the majority of forest biomass. The physiological mechanism underlying demographic responses to drought, however, is the subject of intense debate (Meir et al., 2015a).

Our understanding of temperature effects on tropical forests is even more limited than those of drought and represents a key uncertainty that hinders our ability to predict feedbacks between atmosphere and biosphere in a warming world (Slot & Winter, 2016). Recent reviews highlight the potential for increased temperatures to reduce carbon storage in forest ecosystems (Corlett, 2011; Wood et al., 2012; Wright, Muller-Landau, & Schipper, 2009), but empirical observations are scant. Long-term studies in tropical forests that span a broad range of temperatures have shown that high temperatures reduce tree growth rates (Clark, Piper, Keeling, & Clark, 2003; Feeley, Joseph Wright, Nur Supardi, Kassim, & Davies, 2007; Vlam, Baker, Bunyavejchewin, & Zuidema, 2014). These declines have been attributed to temperature-induced increases in respiration rates. Additional evidence of tropical tree species' responses to altered temperature also comes from diurnal temperature gradients (Slot, Wright, & Kitajima, 2013), growth chamber experiments (Cheesman & Winter, 2013; Cunningham & Read, 2003a, 2003b), cut leaves in warmed chambers (Doughty & Goulden, 2008), or branch warming experiments (Slot et al., 2014). While some of these studies found that tropical tree species exhibit sharp declines in leaf-level photosynthesis between 33 and 40°C (Doughty, 2011; Doughty & Goulden, 2008) possibly as a result of temperature-induced increases in vapor pressure deficit (Wu et al., 2017), others have demonstrated enhanced growth at temperatures as high as 35°C (Cheesman & Winter, 2013) or even above 35°C as long as stomata remains open (Slot & Winter, 2017). Previous studies also highlight striking variation in species responses to high temperature. For example, canopy whole leaf respiration for early-successional species responded more to elevated temperature than mid- or late-successional species (Slot et al., 2013) and relative growth rates of seedlings of pioneer species increased under warming, while growth rates for old-growth species were severely depressed (Cheesman & Winter, 2013). These results were from leaf- or branch-level studies, and it remains unclear whether leaf- and canopy-level observations are quantitatively compatible (Doughty & Goulden, 2008), highlighting the challenges of synthesizing data across leaf to canopy scales (Reed, Wood, & Cavaleri, 2012).

Studies focusing on plant physiological responses have shown that carbon dioxide (CO₂) fertilization could reduce plant stomata conductance and hence increase water-use efficiency (WUE) (Holtum & Winter, 2010; Morgan, Lecain, Mosier, & Milchunas, 2001; Robredo et al., 2007). Therefore, rising atmospheric CO₂ concentration has potential to mitigate future drought-related stress on plant carbon assimilation and growth. A recent pantropical tree ring study has shown that although increases in CO₂ over the past 150 years led to 30%–35% increases in WUE, there was no concurrent acceleration of tree growth (Van Der Sleen et al., 2015). However, we do not know how elevated CO₂ will change net ecosystem carbon uptake. Because the capacity of tropical ecosystems to act as a carbon sink depends on the relative effects of elevated CO₂, drought

and warming, and their potential interaction on both plant and soil processes (Roy et al., 2016), an integrated assessment of all carbon fluxes under future climate scenario is important if we are to estimate overall carbon balance.

Reliable predictions of interactions between tropical forests and climate depend on well-developed and parameterized models. Efforts to model the impacts of climate change on carbon fluxes in tropical forests have not yet reached a consensus on the magnitude or even the direction of these effects (Bonal et al., 2016; Malhi et al., 2008; Rowland et al., 2015a; Vieilledent et al., 2016). This is in part because most models that simulate the effects of climate on tropical forests are simplistic, calling into question the reliability of their predictions (McMahon et al., 2011; Rowland et al., 2015a). Small changes in the sensitivity of tropical forests to shifts in temperature and rainfall dramatically affect model output (Zhou, Fu, Zhou, Li, & Luo, 2013), highlighting the need to improve the representation of tropical forests in models in order to make robust predictions. The high diversity of tree species with a potential for very different responses to climate change within a single community (Cheesman & Winter, 2013; Phillips et al., 2009; Uriarte et al., 2016) is one of the factors that complicates model development (Maréchaux et al., 2015). Nevertheless, accurate representation of tropical forest responses to climate change must move past notions of a single tropical plant functional type, and will require identification of the physiological traits that best predict tree responses to climate changes.

Both models and empirical data predict more intense droughts over the Caribbean with a warming trend under future climate change scenarios (Gamble & Curtis, 2008; Khalyani et al., 2016; Neelin et al., 2006). Therefore, in this study, we use *ECOSYSTEM DEMOGRAPHY* model (version 2.1, hereafter ED2) to predict carbon fluxes of a tropical forest in Puerto Rico under realistic climate change scenarios. ED2 is a cohort-based terrestrial ecosystem model that predicts both ecosystem structure and corresponding ecosystem fluxes from climate inputs (Medvigy, Wofsy, Munger, Hollinger, & Moorcroft, 2009; Moorcroft, Hurtt, & Pacala, 2001). By coupling tree physiology with stand dynamics via a size- and age-structure approach, ED2 can capture the response of individual trees to climate variability and change. For this reason, ED2 offers a promising template for a second generation of land surface models, which can be incorporated in large-scale climate simulations.

With the goal of identifying the contribution of different parameters to model uncertainty, we couple ED2 with the scientific workflow Predictive Ecosystem Analyzer (PEcAn 1.1) (LeBauer, Wang, Richter, Davidson, & Dietze, 2013). PEcAn is an eco-informatic workflow for model analysis (LeBauer et al., 2013) that addresses the challenge of synthesizing available data in a way that accounts for the different scales and sources of model uncertainty (i.e., uncertainty in carbon stocks and fluxes). By streamlining the tracking, processing and synthesis of data and model output, PEcAn addresses information management issues that typically hinder model development, utility and widespread adoption, lending greater accessibility, transparency, and credibility to the models (LeBauer et al., 2013). The specific objectives of the present study are to (i) parameterize

ED2 with species-level physiological tree trait data for predicting the carbon cycle in a wet tropical forest of the Caribbean; (ii) compare model performance to observations from field studies; (iii) reduce model uncertainty in predictions of tropical forest responses to future climate variability and change; and (iv) identify model parameters that account for the majority of uncertainty in model outputs.

2 | MATERIALS AND METHODS

2.1 | Model description

The *ECOSYSTEM DEMOGRAPHY* model (ED2) is a cohort-based, terrestrial biosphere model that couples age- and stage-structured plant community dynamics with physiological and biogeochemical modules. ED2 incorporates an efficient and sophisticated scaling of ecosystem dynamics from individual trees to landscapes (Medvigy & Moorcroft, 2012; Medvigy et al., 2009; Moorcroft et al., 2001). ED2 predicts plant growth using established submodels of plant physiology, allocation, biogeochemistry, and hydrology. It calculates photosynthetic rates using the enzyme kinetic model developed for C_3 plants (Ball, Woodrow, & Berry, 1987; Farquhar & Sharkey, 1982). In addition to photosynthesis, ED2 also accounts for carbon allocation to growth, respiration, and the turnover rate of carbon pools.

The ED2 predicts transient carbon, water, and energy fluxes accounting for the fast, short-term physiological responses of plants to changes in environmental conditions as well as responses to realistic, long-term successional changes in ecosystem structure and composition (Moorcroft et al., 2001). ED2 provides information of many details of ecosystem dynamics including community succession and predictions of gross primary production (GPP), net primary productivity (NPP), and aboveground carbon stocks. This feature of ED enables us to predict aboveground biomass (AGB) of forests in tropical region as well as the carbon fluxes and their contribution to global carbon cycling.

The ED2 has been previously tested to simulate regional carbon fluxes (Desai, Moorcroft, Bolstad, & Davis, 2007; Medvigy & Moorcroft, 2012) and net ecosystem productivity of tropical forests in the Amazon basin (Kim et al., 2012; Moorcroft et al., 2001) and Central America (Hurtt et al., 2004; Xu, Medvigy, Powers, Becknell, & Guan, 2016), and temperate (Albani, Medvigy, Hurtt, & Moorcroft, 2006) and boreal forests (Trugman et al., 2016) in North America. These simulations indicate that ED can accurately capture the community dynamics and the different carbon pools in different types of forests under both current and future climate conditions (Levine et al., 2016; Powell et al., 2013).

2.2 | Model parameterization and calibration

Data were synthesized using a Bayesian meta-analysis, and the meta-analysis posterior estimates of empirical data (i.e., sample means, sample size, and sample error statistics for plant traits and physiological measurements) were used as parameters in ED2 (Medvigy et al., 2009; Moorcroft et al., 2001). PEcAn (LeBauer et al.,

2013) then carries out a set of ED2 model runs (model ensemble) with parameter values drawn from the meta-analysis posterior distributions of the data. Output from the ED2 model ensemble represents the posterior predictive distributions of ecosystem responses that incorporate parameter uncertainty. The model ensemble produces a posterior distribution of ecosystem model outputs that can be summarized with standard statistics (e.g., mean, standard error, and credible intervals).

2.2.1 | Initial conditions and parameters

At the start of the simulations, initial stand density and stem diameter at breast height (dbh) were set using values from census data (See Section 2.3.2 below) collected in the Luquillo Forest Dynamics Plot (LFDP) which is part of the Center for Tropical Forest Science-Forest Global Earth Observatory (CTFS-ForestGEO) network (Anderson-Teixeira et al., 2015). Eleven parameters were initially considered for parameterization based on our previous

experience (Dietze et al., 2014; LeBauer et al., 2013) with ED2 (Table 1). Available trait data were synthesized from the literature and field observations at the site using a hierarchical Bayesian meta-analytical model described by LeBauer et al. (2013). Briefly, this approach generates posterior distributions by integrating prior information and observations of parameter estimates. Each parameter was assigned an informed prior functional form and parameter specification that varies by parameter and Plant Functional Type (hereafter PFT) for meta-analysis. These priors were specified by fitting distributions to raw data collected from literature searches, unpublished datasets, or from expert knowledge or default ED2 parameterization of tropical trees. When species-level data were not available, the posterior distributions were set equivalent to the priors. Detailed descriptions of meta-analysis procedures are provided in LeBauer et al. (2013). Calibration runs with default parameters of ED2 were also conducted (Fig. S1) for comparison to see improvement of model performance with locally calibrated physiological parameters.

TABLE 1 Prior distributions and data used in meta-analysis and model parameterization

Parameter	Description	Unit	Prior		Data <i>n</i>	Posterior			Reference for priors	
			Distribution	a		b	Mean	LCL		UCL
Dark respiration factor	Coefficient for leaf respiration	Ratio	Inorm	-3.90	0.40	10	0.02	0.01	0.03	Slot et al. (2013), Atkin et al. (2015)
Leaf width	Mean leaf width	mm	Gamma	12.80	0.18	4	139.01	94.72	179.50	Rozendaal, Hurtado, and Poorter (2006)
Quantum efficiency	Slope of the relation between light and carbon assimilation rate (<i>A</i>)	mol CO ₂ mol ⁻¹ photon	Weibull	6.32	0.06	12	0.05	0.03	0.06	Skillman (2008)
SLA	Specific leaf area	m ² kg ⁻¹	Weibull	2.10	12.10	52	13.34	10.08	16.57	Wright et al. (2004)
Stomatal slope	Slope of the relation between stomatal conductance and <i>A</i>	Ratio	Weibull	7.11	6.29	10	5.40	4.87	5.95	LeBauer et al. (2013)
<i>V</i> _{max} at 25°C	Maximum carboxylation rate	umol CO ₂ m ⁻² s ⁻¹	Weibull	2.72	40.60	12	25.23	15.54	35.03	Wullschlegler (1993)
Wood density	Mass of wood contained in a unit volume	10 ³ kg m ⁻³	Inorm	-0.34	0.11	66	0.74	0.71	0.77	Reyes, Brown, and Chapman (1992)
Fineroot allocation	Ratio of fine root to leaf biomass	Ratio	Inorm	0.14	0.37	0	1.24	0.56	2.37	Silver et al. (2005)
Growth respiration factor	Proportion of daily carbon gain lost to growth respiration	Proportion	Beta	7.24	11.40	0	0.39	0.19	0.61	Waring, Landsberg, and Williams (1998), Litton, Raich, and Ryan (2007)
Photosynthesis minimum temperature	Photosynthesis begins to rapidly decline below this temperature	°C	Norm	5.00	2.00	0	5.00	0.10	9.90	Allen and Ort (2001)
Root turnover rate	Rate of fine root loss	year ⁻¹	Weibull	1.85	0.42	0	0.36	0.06	0.85	Gill and Jackson (2000)

Columns a and b denote parameters of the prior distributions. Data column shows sample size of data collected from species at study site. Mean is the mean of the posterior distribution. LCL and UCL are the lower and upper 95% confidence limits of posterior mean.

The meta-analysis model was fitted in the computer program JAGS run through the R package 'rjags' (version 4-6; Plummer 2016) using standard Markov chain Monte Carlo (MCMC) methods with four parallel chains of length 10^5 . The first half of each chain was discarded as "burn-in". Trace plots and Gelman–Rubin's statistic were used to assess model convergence (Gelman & Rubin, 1992). The resulting posterior distributions of tree trait values were then sampled to generate an ensemble of 500 model runs. This ensemble was used to estimate the predicted mean model outputs (e.g., AGB) and credible intervals.

2.2.2 | Ensemble runs

To evaluate the effects of future climate scenarios on forest dynamics and carbon fluxes, an ensemble of 500 runs were conducted from 2002 to 2050. Ensemble runs between 2002 and 2016 were used for validation (see Section 3.2 below). From 2017 to 2050, we applied a gradual linear change in precipitation (50% reduction) and temperature (2°C warming) (see Section 2.3.1 below) and then projected the fate of the forest under combined drought and warming, drought-only, and warming-only scenarios, respectively. Parameter uncertainty was propagated into model projections with an estimation of a forecast confidence interval.

2.2.3 | Sensitivity analysis

In order to determine the magnitude of change in model output that accompanies a change in each model parameter, we estimated sensitivities using a global univariate sensitivity analysis. The sensitivity analysis was conducted in PEcAn by running ED2 across the eleven parameters of interest. Specifically, ED2 was evaluated for each parameter at the posterior median and at six posterior quantiles equivalent to $\pm (1, 2, 3) \sigma$ in the standard normal while holding all the other parameters constant at their median. The relationship between model output (e.g., AGB and NPP) and each model parameter (p_i) was then approximated by a natural cubic spline ($g_i(p_i)$) through these seven evaluation points. The sensitivity to each parameter is the derivative of the spline at the posterior median \bar{p}_i . In order to compare sensitivity among parameters, despite differences in units and ranges of parameters, sensitivity was normalized by the ratio of median model output to median parameter value as follows:

$$\text{Sensitivity} = \frac{dg_i(p_i)}{dp_i} \bigg/ \frac{\bar{f}_i}{\bar{p}_i} \quad (1)$$

where (dg_i/dp_i) is the derivative of the spline at the parameter median, \bar{f}_i is the median of model output and \bar{p}_i is the median of a parameter.

2.2.4 | Variance decomposition

The variance in model output contributed by each input parameter was quantified using variance decomposition analysis. We used results from the meta-analysis and sensitivity analysis to estimate the contribution of each parameter to uncertainty in modeled forest AGB

and NPP from the model ensemble. The approximation for decomposition of the total variance in model output is formulated as:

$$\text{Var}(f(p)) = \sum_{i=1}^n \text{Var}(g_i(p_i)) + \omega \quad (2)$$

where $\text{Var}(f(p))$ is the total variance of the model ensemble; $g_i(p_i)$ is the spline approximation of the model response (f) to each parameter (p_i) in the sensitivity analysis that transforms posterior variance of p_i obtained from the meta-analysis from the parameter to the model domain; $\text{Var}(g_i(p_i))$ is the univariate contribution of each parameter to variance of model output; and the final term ω is the closure between the right-hand side and the left-hand side of the equation, representing unaccounted parameter interactions (Feng & Dietze, 2013; Wright et al., 2004) in the variance decomposition. The proportional contribution of each parameter (p_i) to the total variance was calculated by dividing its partial variance by the total variance. A full description of this variance decomposition analysis is available in LeBauer et al. (2013).

2.3 | Model validation and prediction

2.3.1 | Climate data

We evaluated the efficacy of ED2 in capturing forest responses to climate between 2002 and 2016 using hourly temperature, humidity, radiation, precipitation, wind, and atmospheric pressure data collected at Bisley and El Verde weather stations within El Yunque National Forest (<http://criticalzone.org/luquillo/data/datasets/#meteorology>). Weather data of Bisley station were used as primary meteorological driver and weather data of El Verde station was used for periods with gaps in weather data from the Bisley station. For long-term trends we assumed that by 2050, mean annual precipitation will gradually decline to 50% of 2002–2016 average rainfall and mean annual temperature will gradually increase by 2°C. These projections were inferred based on model projections that predict increasing drought and temperatures for the Caribbean (Khalyani et al., 2016; Neelin et al., 2006). Climate models derived from field and satellite data predicted a decrease in rainfall of 5%–50% over the next few decades for the Caribbean (Khalyani et al., 2016; Neelin et al., 2006). We used the most extreme scenario in our model although lower declines in precipitation are plausible. An increase in atmospheric carbon dioxide (CO_2) concentration was also included in long-term climate change projections. We assumed atmospheric CO_2 concentration will gradually increase to 540 ppm by 2050 based on the RCP 8.5 scenario (Riahi et al., 2011). In order to understand responses of tropical forest to climatic variability, we applied three climatic scenarios in model projections including drought-only, warming-only, and combined drought and warming. We then added the elevated CO_2 scenario to the drought-only and combined drought and warming scenarios. The meteorological drivers were generated at an hourly time step and were structured for driving the ED2 model. To generate stochastic climate data for prediction of forest responses between 2017 and 2050, we used a method based on the decomposition of variability into trend, annual to decadal, and

subannual components (Greene, Hellmuth, & Lumsden, 2012). In the simulation process, a first-order vector autoregressive (VAR) model was fitted to the detrended climate data series. The deterministic response from observational data on which the simulation model is to be trained was removed by a detrending procedure. The VAR model was then used in the simulation step to project forward in time with estimation of how the mean process level evolves in the future in order to include trends in the simulated future climate data [see Greene et al., (2012) for details].

2.3.2 | Tree data

To validate ED2, modeled PFT-level aboveground biomass (AGB) was compared to AGB calculated from data collected in the Luquillo forest dynamics plot (LFDP) between 2000 and 2016. The LFDP is a 16-ha forest plot (SW corner 18°20'N, 65°49'W) located near El Verde Field Station in the Luquillo Mountains of Puerto Rico. The plot was established in 1990 and censused at approximately 5 year intervals starting in 1990, 1995, 2000, 2006, 2011 and 2016 using standard protocols (Condit, 1998). Briefly, all stems with diameter at breast height of 1.3 m from the ground (dbh) ≥ 1 cm) were mapped, measured and identified to species. In each census, new stems were added, stems were remeasured, and their status (alive/dead) was updated.

Large plots are required to cover local environmental variation, include sufficient numbers of individuals of both the common and rare species, and to determine plant spatial relationships. Population monitoring over many years is required to elucidate forest response to environmental changes and disturbance. The highly dynamic nature of the tree population in the LFDP makes this plot ideal for model validation. For model validation, we used the 2000, 2006, 2011, and 2016 censuses. We were restricted to these censuses by the availability of high-resolution climate data. For each census, we calculated aboveground biomass from dbh using an allometric equation from Scatena, Silver, Siccama, Johnson, and Sanchez (1993) that was formulated based on site-specific tree data from Luquillo forests in Puerto Rico:

$$AGB = e^{2.475} [\ln(\text{dbh} - 2.399)] \quad (3)$$

All 154 species present in the LFDP census (2000–2002) were assigned to three tropical PFTs (early-, mid-, or late-successional tropical PFT) (Table 2) for model initialization and parameterization based upon wood density data. When wood density data were lacking, we assigned species to PFTs based on literature (Grau et al., 2003; Ross, Carrington, Flynn, & Ruiz, 2001; Uriarte, Canham, Thompson, & Zimmerman, 2004; Uriarte et al., 2009; Zimmerman, Comita, Thompson, Uriarte, & Brokaw, 2010) and expert opinion. We validated ED2 predictions using three metrics: AGB, forest size structure and relative dbh growth. We calculated AGB for each PFT and census period, for size structure, we calculated plant density for several size classes: 0–10, 10–20, 20–40, 40–60, 60–80, 80–100, and >100 cm (Fig. S2). We then calculated the ratio of large (≥ 10 cm dbh) to small trees to examine how the size distribution of the forest changes with time. The average dbh growth calculated from whole plot censuses was not used for validation because calculating dbh growth using the difference between average dbh of two censuses would not capture the actual growth rate of live stems. This is because mortality of large trees and new recruits between censuses offset the increase in dbh due to growth of live stems resulting in much slower changes in the average dbh of the whole community. Therefore, the third metric we used was annual growth rate of 921 selected trees in LFDP collected between 2013 and 2015 using dendrometers. Although these trees included fewer species (total of 58) than those in the whole plot, they included the dominant species and each PFT accounted for a similar proportion of trees as those in the LFDP 2011 census with 11 species (127 trees) in the early-successional, 24 species (288 trees) in the mid-successional, and 23 species (506 trees) in the late-successional PFT. However, the trees measured with dendrometers had a higher average dbh than trees in the whole LFDP census, which is dominated by small trees by tree count (<10 cm dbh). For this reason, relative rather than absolute dbh growth rate was used for model validation.

Abundance	Early successional	Mid successional	Late successional
1	<i>Palicourea riparia</i>	<i>Casearia arborea</i>	<i>Prestoea montana</i>
2	<i>Psychotria brachiata</i>	<i>Casearia sylvestris</i>	<i>Sloanea berteriana</i>
3	<i>Cecropia schreberiana</i>	<i>Inga laurina</i>	<i>Manilkara bidentata</i>
4	<i>Psychotria berteriana</i>	<i>Cordia borinquensis</i>	<i>Dacryodes excelsa</i>
5	<i>Schefflera morototoni</i>	<i>Ocotea leucoxydon</i>	<i>Hirtella rugosa</i>
6	<i>Piper glabrescens</i>	<i>Alchornea latifolia</i>	<i>Guarea guidonia</i>
7	<i>Miconia prasina</i>	<i>Tabebuia heterophylla</i>	<i>Trichilia pallida</i>
8	<i>Gonzalagunia spicata</i>	<i>Myrcia deflexa</i>	<i>Tetragastris balsamifera</i>
9	<i>Urera baccifera</i>	<i>Byrsonima spicata</i>	<i>Eugenia stahlia</i>
10	<i>Chionanthus domingensis</i>	<i>Myrcia splendens</i>	<i>Guarea glabra</i>

TABLE 2 All tree species (with total of 154) in the forest were assigned to three tropical plant functional types (PFTs) including early-, mid-, and late-successional PFTs

The most abundant 10 species for each PFT are listed here. All of the species-level data to parameterize ED2 were collected from this pool of species. The species are ranked by their abundance in the studied forest over all censuses from 2002 to 2016. Within each PFT, these species accounted for more than 80% of all trees.

3 | RESULTS

3.1 | Model parameterization and calibration

3.1.1 | Meta-analysis

Meta-analysis was conducted for 11 parameters selected based on previous experience of model sensitivity to parameters (Dietze et al., 2014; LeBauer et al., 2013). Species-level data were collated for the abundant species in each PFT (Table 2) and were available for seven parameters: leaf dark respiration rate, leaf width, quantum efficiency, specific leaf area (SLA), stomatal slope, V_{cmax} , and wood density (Table 1). Data to constrain seven parameters were available for all three PFTs with the greatest amount of data available for the late-successional PFT. Parameters with no empirical data including growth respiration, fine root allocation, root turnover rate, and photosynthesis minimum temperature, were constrained by prior distributions. The majority of the trees and those with largest diameters belonged to the late-successional PFT, making this group the most significant contributor to aboveground biomass (AGB). For the late-successional PFT priors, trait data, and meta-analysis posteriors are presented in

Figure 1 and for early- and mid-successional PFTs are shown in Supporting Information (Figs S3, S4). Bayesian meta-analysis generally reduced parameter uncertainty relative to the prior distributions (Figures 1, S3, S4), especially for traits with a large amount of empirical data, such as specific leaf area (SLA) and wood density.

3.1.2 | Sensitivity analysis

Sensitivity analysis demonstrated that parameters varied widely in their effects on AGB (Figure 2) and NPP (Fig. S5). Since the sensitivity analyses for all three PFTs showed similar patterns for AGB (Figure 2) and NPP (Fig. S5), we only elaborate results of sensitivity analysis for AGB. The sensitivity analysis of mid- and late-successional tropical PFTs showed that model parameters exhibited a similar pattern in their effects on AGB (Figure 2c,d). For these two PFTs, parameters associated with photosynthesis (including leaf dark respiration, SLA, V_{cmax} and quantum efficiency) and carbon allocation (growth respiration and root allocation) were relatively sensitive, with parameters associated with carbon allocation having the highest sensitivity. However, for the early-successional PFT, photosynthetic parameters, especially V_{cmax} and quantum efficiency, had the highest

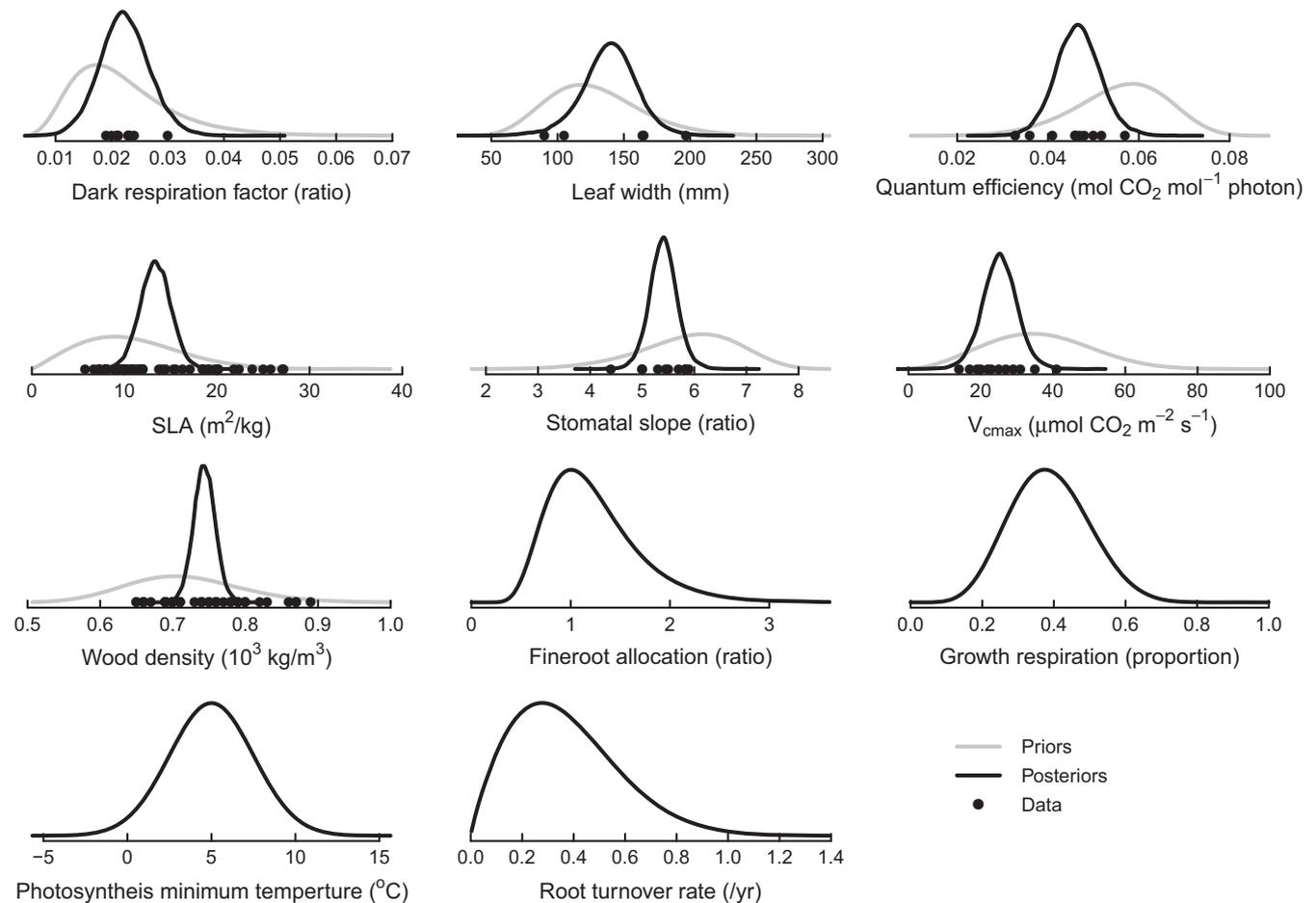


FIGURE 1 Probability distributions of eleven ED2 parameters for late-successional PFT. Parameter values are shown on the x-axis and probability on y-axis. Data used to constrain priors are depicted with black dots and are available for 7 of the 11 parameters. Priors for the remaining four of eleven parameters were not informed by data, and thus the posterior distributions remain the same as prior distributions

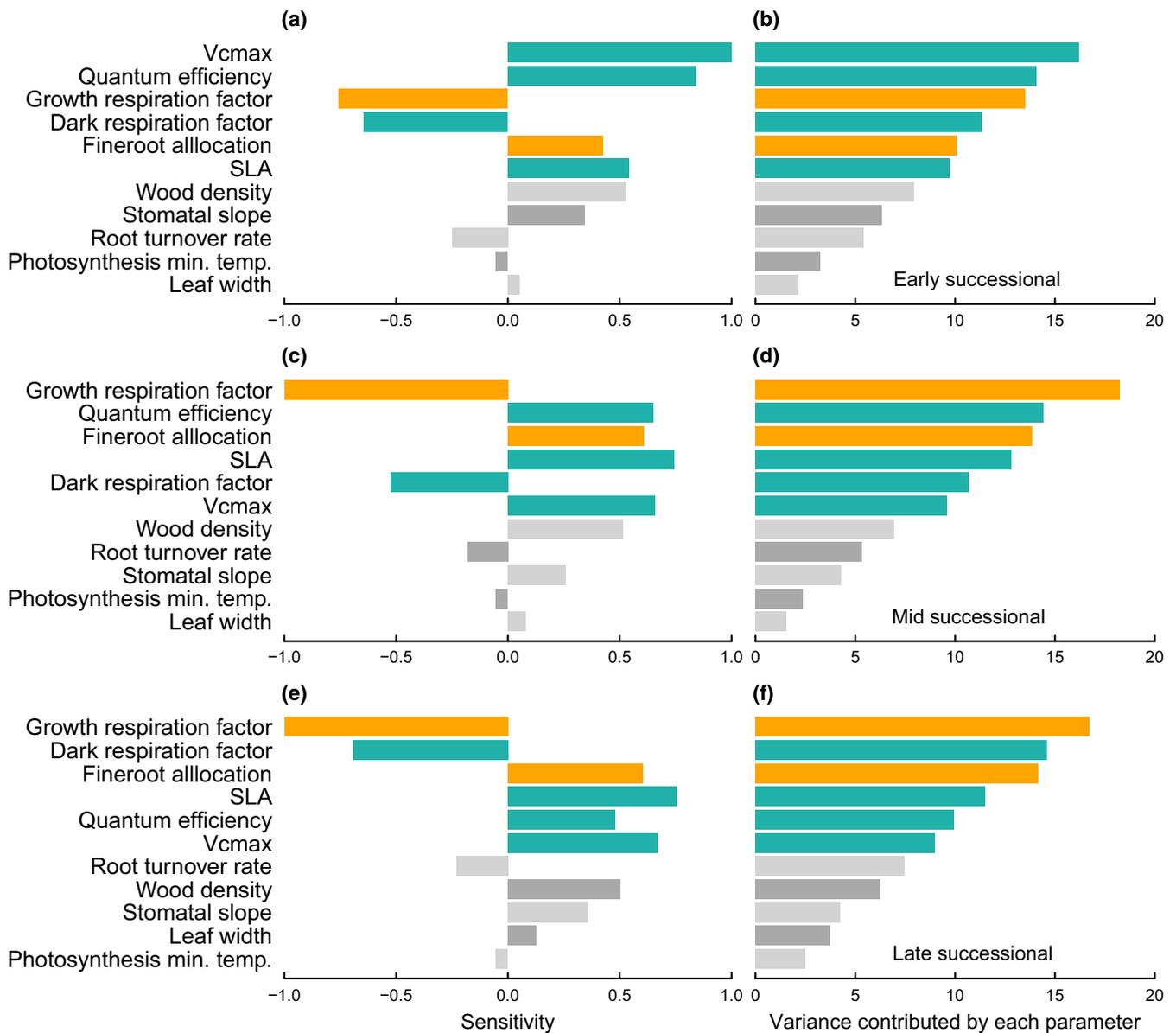


FIGURE 2 Sensitivity analysis (left column) and variance decomposition (right column) for the three PFTs. Parameters are ranked by the amount of uncertainty contributed to model output (AGB). Green denotes parameters associated with photosynthesis, orange represents parameters associated with biomass allocation, and gray represents contributions of other parameters to the uncertainties in the model output. Sensitivities are unitless measurements of the magnitude of change in model output that is effected by a change in a model parameter and are scaled to 0–1. Negative sensitivity values indicate that AGB decreases with increase in parameters' values. Variance decomposition quantifies the proportional contribution of each parameter to the total variance in model output (AGB). The sum of all the bars in panels b, d, and f equals 100

sensitivity. For all three PFTs, AGB was largely insensitive to root turnover, minimum photosynthesis temperature, and leaf width.

3.1.3 | Variance decomposition

The variance decomposition analysis indicated that some parameters contributed substantially more than others to uncertainty in modeled AGB (Figure 2). For late-successional PFT, parameters controlling photosynthetic processes (such as dark respiration and SLA), allocation (growth respiration and fine-root allocation), and belowground processes (root turnover rate) contributed most to model uncertainty

(Figure 2). Parameters causing high model uncertainty, including growth respiration and fine root allocation, tended to have both high uncertainties in parameter values due to the scarcity of data available for these parameters and high sensitivities. Model uncertainty contributed by parameters such as V_{cmax} and SLA was reduced by greater availability of data, but their contribution to model variability was still relatively high due to high sensitivity. The contribution of root turnover rate to model uncertainty was mainly driven by high meta-analysis posterior uncertainty, despite the low sensitivity of AGB to this parameter (Figure 2e). On the other hand, stomatal slope and wood density had a high sensitivity (Figure 2e) but

contributed little to the model uncertainty (Figure 2f) because these parameters were well constrained by data (Figure 1). Leaf width and photosynthesis minimum temperature had very low sensitivity, and thus contributed little to model variance despite having high parameter uncertainty.

3.2 | Model validation

The mean of model ensemble runs was comparable to field observations. At the beginning of simulation period (2002), ED2 slightly underestimated biomass of early- and mid-successional PFT, but overestimated biomass of the late-successional PFT. Mean AGB of early-, mid-, and late-successional PFT in the first year were 19.83, 85.49, and 123.61 Mg/ha, respectively, while modeled AGB was 15.92, 76.37, 134.61 Mg/ha. However, this model-data mismatch became smaller over time (Figure 3a). AGB calculated from census data for all three tropical PFTs fell within the uncertainty range of

ensemble output for the simulation period (2002–2016) (Figure 3a). Total aboveground forest carbon storage at the study site between 2002 and 2016 did not change significantly, with total observed AGB ranging from 227.93 to 241.83 Mg/ha and predicted means ranging from 225.58 to 240.94 Mg/ha. The late-successional PFT contributed 50%–60% of the total biomass. Total observed AGB of late-successional trees showed an increase from 123.61 to 144.68 Mg/ha (or 17.05%) during the study period (2002–2016) while modeled AGB of this group showed a weaker increase from 134.61 to 145.82 Mg/ha (8.33%). Observed early-successional PFT biomass also increased from 19.83 to 27.49 Mg/ha (38.63%), while modeled AGB was lower than observed values but showed a similar increasing trend from 15.93 to 21.77 Mg/ha (36.70%). Biomass of the mid-successional PFT decreased by 17.55% from 84.49 to 69.66 Mg/ha from 2002 to 2016. However, the declining pattern of modeled AGB of mid-successional PFT (from 76.37 in 2002 to 71.86 Mg/ha in 2011) was not as marked as for observed AGB and remained relatively stable after 2011.

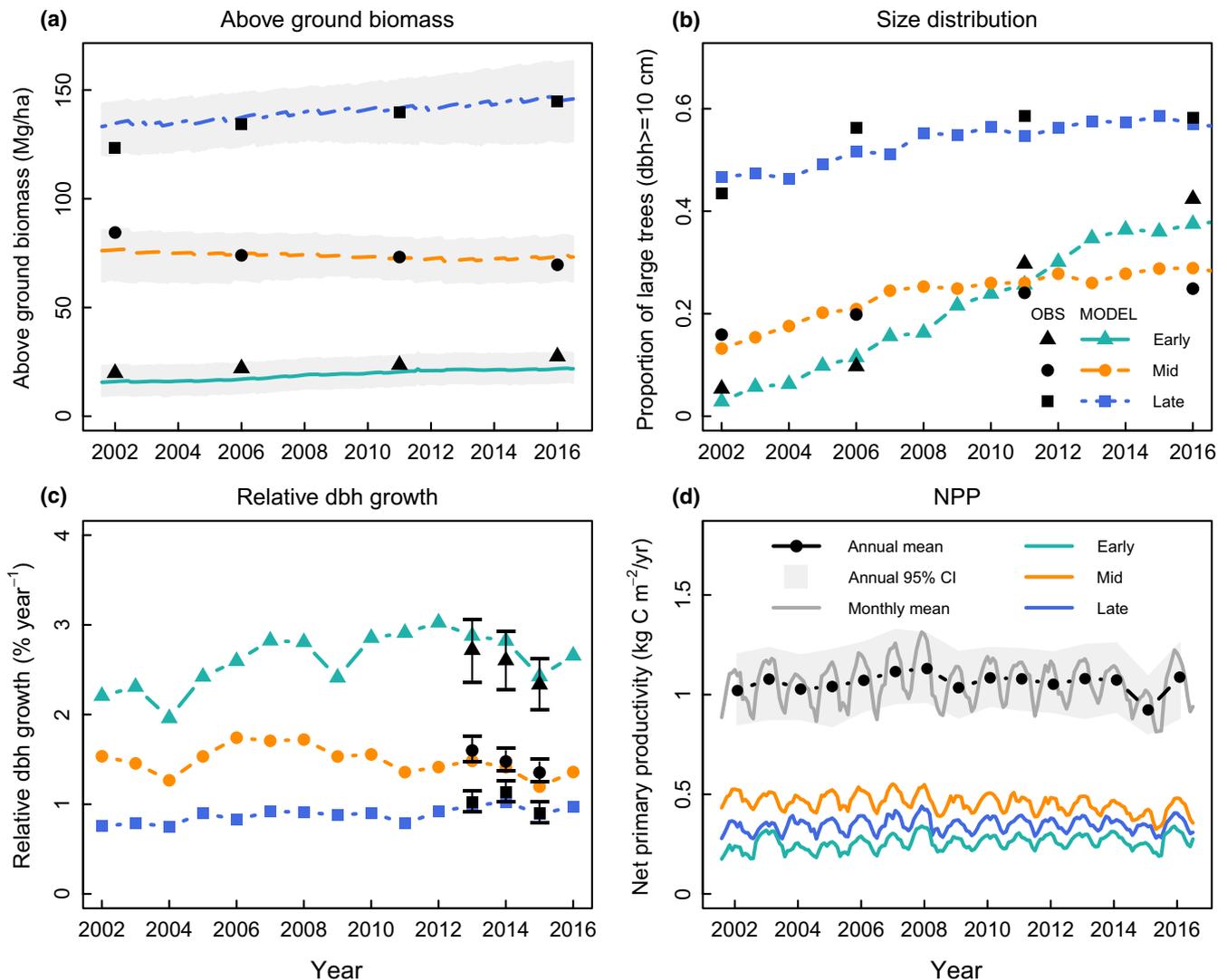


FIGURE 3 Model predictions (2002–2016) were validated with observations for (a) Aboveground biomass, (b) Proportion of large trees (≥ 10 cm dbh) at each LFDP census, (c) Relative dbh growth with observed annual growth from trees fitted with dendrometer bands, and (d) Net primary productivity

The size structure of the modeled forest was also validated using census data. There was an increase in the ratio of large diameter (dbh ≥ 10 cm) to small (dbh < 10 cm) trees for all three PFTs with the highest increase in the early-successional PFT group (Figure 3b). This was due to the high mortality of small trees in this group. After Hurricane Georges in 1998, the majority of new recruits recorded in the 2000–2002 census belonged to the early-successional PFT while very few individuals of the late-successional PFT recruited. However, most posthurricane recruits died within a few years resulting in the shift in the size structure of the forest recorded in the following censuses. This increased recruitment in early-successional PFT trees with the subsequent high posthurricane mortality led to an increase in the proportion of large trees in the early-successional PFT over the study period. Our model was initialized using the census data and predicts a similar pattern to that observed in the census data.

Predictions of relative diameter growth were validated using annual dendrometer data collected between 2013 and 2015. Diameter (dbh) growth of the early-successional PFT was the highest among the three PFTs while the late-successional PFT that represented the majority of trees in the plot had the lowest growth rate (Figure 3c). A severe drought in 2015 (precipitation was $\sim 50\%$ of average normal years) reduced observed dbh growth relative to typical years. ED2 model predictions showed the same pattern in growth as the observed, with the mean modeled value falling within the error range of observed values (Figure 3c).

Changes of predicted leaf area index (LAI) of early- and mid-successional PFTs exhibited similar patterns as biomass, with an increase for the early-successional PFT (0.81–1.12 m^2/m^2) and a slight decrease (2.23–1.99 m^2/m^2) for the mid-successional PFT over time. However, LAI of the late-successional PFT stayed relatively constant with an average of 3.46 m^2/m^2 despite a slight increase in biomass for this group over the validation period (2002–2016). Total modeled mean LAI of this tropical forest was 6.45 m^2/m^2 (95% CI was 4.62–8.27 m^2/m^2). These values were consistent with the numbers reported by other studies (Jordan, 1969; Zimmerman et al., 1995). Mid-successional trees had the highest NPP among all three PFTs (Figure 3d). NPP of the early-successional PFT rose along with increases in biomass and the NPP of the late-successional PFT remained relatively stable. These results correspond with our understanding of tropical tree physiology. Early-successional pioneer species had high photosynthetic rates (Fig. S3) while late-successional species had much lower photosynthetic rates (Figure 1). Mid-successional PFT had higher photosynthetic rates compared to late-successional PFT (Figures 1, S4) and higher biomass and LAI compared to early-successional PFT (Figure 3a). Therefore, the high NPP of the mid-successional PFT reflects the combination of its photosynthesis and biomass.

3.3 | Long-term projections under combined drought and warming

The combined drought and warming scenario modeled in ED2 was a gradual linear change in precipitation and temperature over the

projection period (2017–2050). Under this scenario, ED2 predicted a decline in biomass for mid-successional PFT (73.34 Mg/ha in 2016 to 56.53 Mg ha^{-1} in 2050, a decline of 22.92% from initial conditions), and a more severe decline in biomass for the late-successional PFT which went from 145.82 Mg/ha in 2016 to 98.02 Mg/ha in 2050 (-32.78%) (Figure 4a). However, the biomass of the early-successional PFT consistently increased from 2016 to 2034 from 21.77 to 27.10 Mg/ha and declined only after 2034 down to 18.89 Mg/ha by 2050. By 2050, total forest biomass had decreased by $\sim 30\%$ from 240.94 to 173.45 Mg/ha (Figure 4a).

The shift in predicted tree size structure paralleled the AGB trends (Figure 4a,b). For all three PFTs, the proportion of large trees decreased by 2050 with the highest decline in the late-successional PFT (Figure 4b). Between 2002 and 2016, average dbh growth for all PFTs increased with the highest increase in early-successional PFT (Figure 4c). This increase in mean absolute dbh growth was associated with an increase in the proportion of large trees from 2002 to 2016, and thus was not shown in relative dbh growth (Figure 3c). Between 2017 and 2050 the projected average dbh growth of trees in all three PFTs declined (Figure 4c). This was driven by the reduced proportion of large trees and lower NPP under drought and warming (Figure 4b,c). By 2050, NPP had decreased to 50.02% of the 2016 value ($1.09 \text{ kg C m}^{-2} \text{ year}^{-1}$) while growth rates decreased to 40.13% of 2016 value for early-, 42.21% for mid-, and 37.97% for late-successional PFT (Figure 4c). The greater declines in dbh growth rates compared to NPP could be the result of reductions in average tree dbh due to reduced proportion of large trees (Figure 4b). The altered forest structure was caused by reduced number of large trees due to mortality and fewer trees entering the large size category with suppressed growth. As a result of these predicted changes in forest structure and growth, the model predicted that net ecosystem productivity (NEP) was going to flip from positive to negative in 2036 (Figure 4d). Relative to 2016 conditions, precipitation at this time point in 2036 was predicted to have reduced by $\sim 30\%$ and temperature has increased by $\sim 1.2^\circ\text{C}$, which is the threshold climate scenario that turns this tropical forest from a carbon sink to a source.

3.4 | Carbon fluxes under different climate change scenarios

Under combined drought and warming scenario, GPP and NPP reduced by 45.72% and 49.98%, respectively, from 2016 to 2050; NEP flipped from positive to negative (Figure 5a). Decreases in GPP, NPP, and NEP under the drought-only and warming-only scenarios were not as strong as those under the combined warming-drying scenario and showed different patterns (Figure 5a). These differences were the result of variation among scenarios in the responses of autotrophic and heterotrophic respiration. While total ecosystem respiration decreased strongly under drought-only and the combined drought and warming scenario due to reduction in primary productivity, the effects of warming-only scenario on ecosystem respiration were far weaker (Figure 5b).

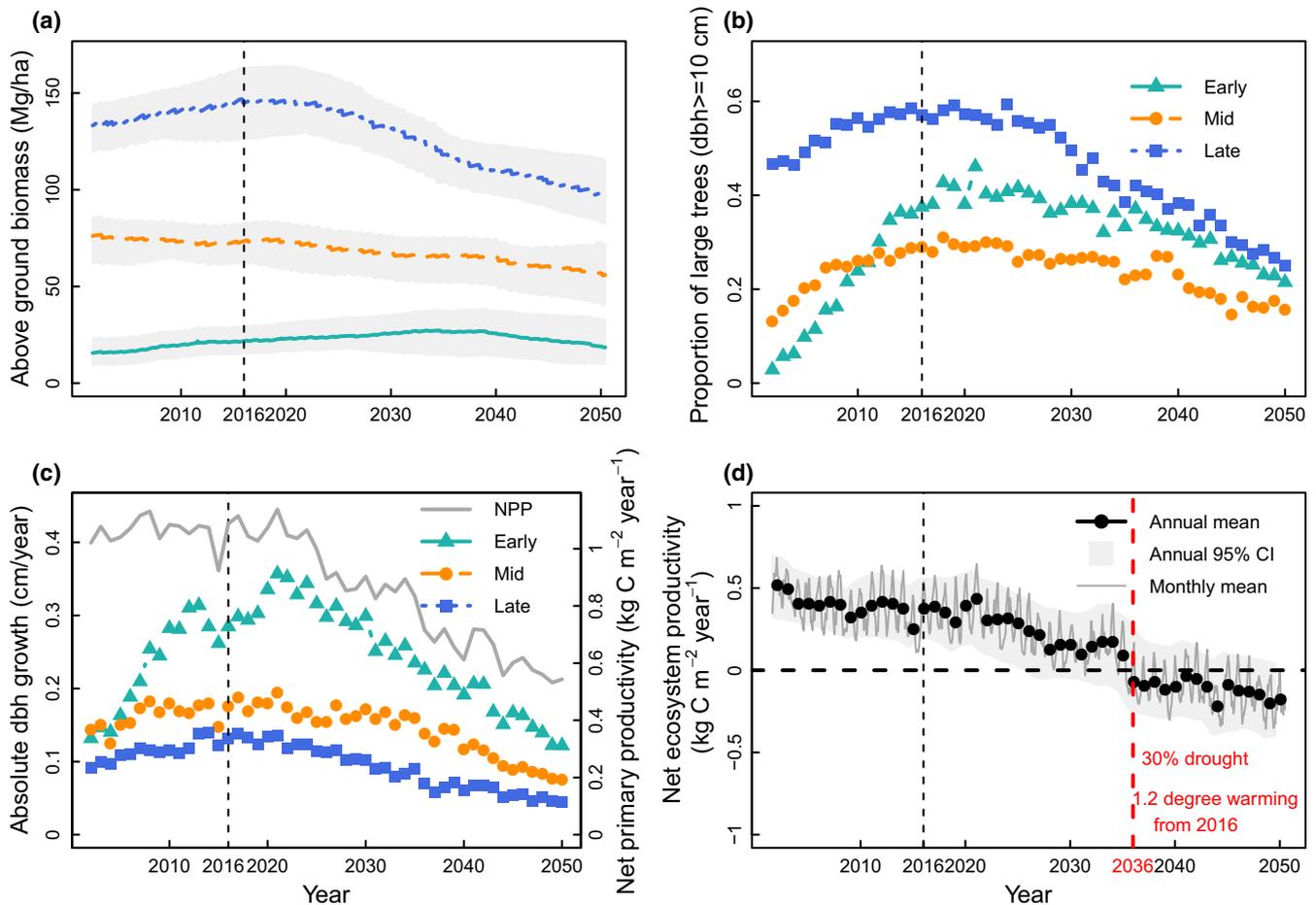


FIGURE 4 Model projections (2017–2050) under combined warming-drying scenario for (a) Aboveground biomass, (b) Proportion of large trees, (c) Absolute dbh growth, and NPP (d) Net ecosystem productivity. Directional shifts in temperature and precipitation were included in the model from 2017 to 2050 (right side of black vertical dashed line in 2016)

Between 2016 and 2050, GPP decreased under all climatic scenarios with a concomitant decrease in plant respiration, which is coupled with productivity (Figure 5). The greatest decline in GPP was observed in the combined warming-drying scenario and the least in the warming-only scenario. Since both foliar and root respiration increased at high temperature, plant respiration initially exhibited a slight increase under the warming-only scenario. Therefore, the reduction in plant respiration by 2050 was not as great as the reduction in GPP under the warming-only scenario (Figure 5a,b). The effects of the three scenarios on NPP were similar to the effects on GPP (Figure 5a). However, the differences in NPP among the three scenarios were much less than the differences for GPP because the differences in predicted GPP were offset by plant respiration.

Heterotrophic respiration exhibited a slight decline under the drought-only scenario due to limited soil moisture (Figure 5b). However, the total amount of dead plant matter available increased due to dieback of trees under drought. As a result, the decline of heterotrophic respiration was small despite much lower decomposition rate under lower soil moisture level. Under the warming-only scenario, heterotrophic respiration increased initially then stayed stable after 2040. Under the combined drought and warming, heterotrophic

respiration stayed relatively constant. Although higher temperature caused greater decomposition rate under the combined scenario, this effect was offset by limited moisture. Due to the different effects of the three climatic scenarios on heterotrophic respiration, NEP trajectories under the three scenarios differed from those of NPP and GPP, with the combined warming-drying scenario having the strongest effect on NEP and the drought-only scenario showing the least.

Elevated CO₂ alleviated the effects of drought and warming stress. Under combined drought and warming scenario, GPP and NPP increased accumulatively from 2017 to 2050 by 10.36% and 14.84%, respectively, with elevated CO₂. As a result of the mitigating effect of CO₂ enrichment, the turning point from carbon sink to source was postponed to 2043 from 2036 (Figure 6a). Therefore, even under elevated CO₂, the forest still turns into a carbon source under a drier and warmer climate.

The mitigating effect of CO₂ elevation was stronger in the drought-only scenario compared to combined drought and warming scenario. Under drought-only scenario, GPP and NPP increased accumulatively by 14.58% and 18.22% for 2017–2050 period with elevated CO₂. However, for both scenarios, the effects of CO₂ were

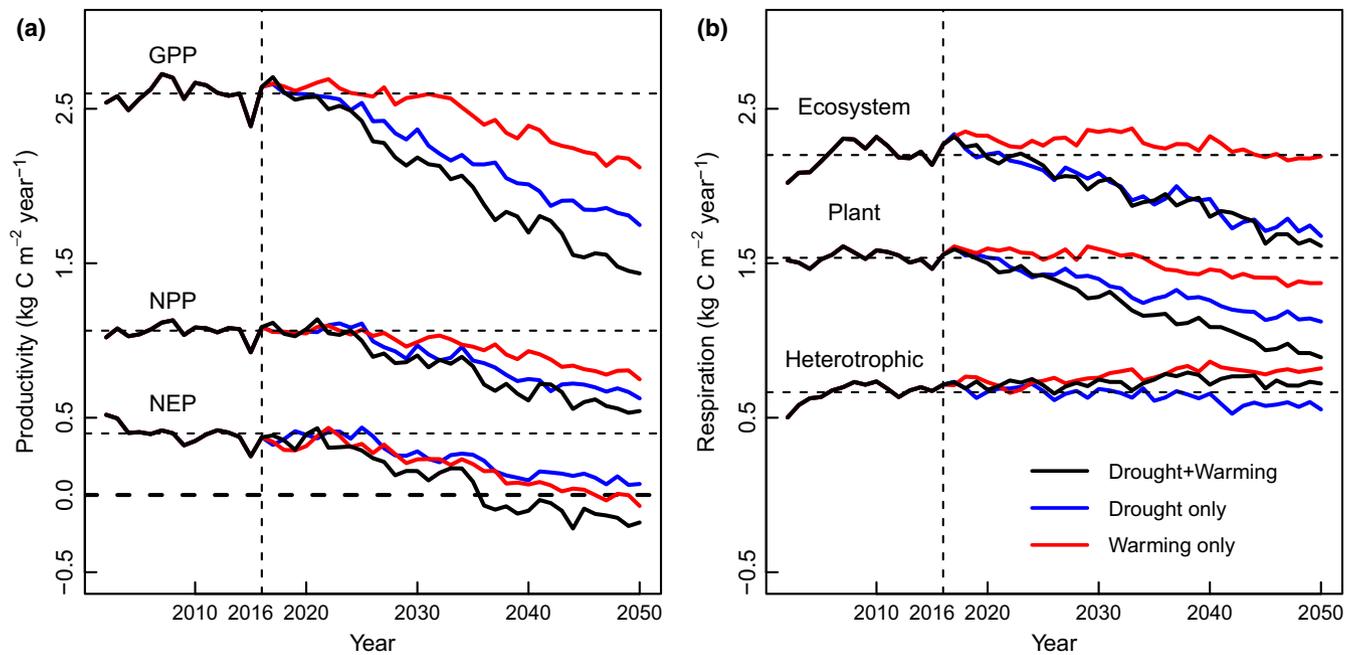


FIGURE 5 Model predicted productivity and respiration fluxes. (a) GPP, NPP, and NEP under three climate change scenarios: Drought + Warming, Drought-only, and Warming-only. (b) Ecosystem, plant, and heterotrophic respiration under the three climatic scenarios

strongest during the middle period under moderate stress and reached highest in 2037 with a 25.81% increase in GPP for combined drought and warming scenario and peaked for drought-only scenario in 2042 (GPP increased by 26.19%) (Figure 6a). CO_2 fertilization effects weakened with increasing water stress toward the end of simulation period. Ecosystem respiration also showed an increase under elevated CO_2 (Figure 6b).

4 | DISCUSSION

Our study is the first effort to employ Bayesian model calibration and synthesis to elucidate the key physiological parameters that drive uncertainty in tropical forests responses to climatic change. The Bayesian calibration synthesized available data and knowledge about the parameter values with measures of uncertainty. This approach provides probability distributions as output, instead of point estimates, which enables propagation of parameter uncertainty to subsequent analyses and forecast for both validation (2002–2016) and prediction (2017–2050). Most importantly, the variance decomposition identified the parameters that make the largest contribution to model uncertainty, information that can be leveraged to target future data collection efforts in tropical forest ecosystems.

Our results demonstrated that the ED2 model calibrated within the PEcAn framework successfully captured interannual variability in stand and carbon dynamics of a tropical forest in Puerto Rico. Modeled values closely followed observed values across a wide range of metrics including aboveground biomass, diameter growth, tree size class distributions, and leaf area index. Under a future warming and drying climate scenario, the model predicted reductions in carbon

storage and tree growth rates together with large shifts in forest structure and community composition. These rapid changes in climate led the forest to transition from a carbon sink to a source by 2036 (Figure 4). Although the effects of drought-only and warming-only scenarios were not as strong as the combined stressor scenario, the results suggest either warming or drying alone could greatly reduce the magnitude of the carbon sink in this tropical forest. Elevated CO_2 mitigated but did not completely offset the effects of drought and warming stress.

4.1 | Community composition

Studies have demonstrated that larger trees suffer higher mortality rates under drought (Bennett et al., 2015; Phillips et al., 2010; Uriarte et al., 2016). Consistent with these findings, our model predicted large declines in AGB under a drier and warmer climate with the highest decline for late-successional trees with an average mortality rate of $4.92\% \text{ year}^{-1}$ for large trees and $3.27\% \text{ year}^{-1}$ for small trees from 2040 to 2050. Larger trees have shown higher mortality toward the end of simulation period under extreme drought and warming conditions within all three PFTs. Since late-successional PFT had the highest proportion of large trees and made the greatest contribution to forest biomass, mortality of large trees under drought caused greatest declines in AGB of late-successional PFT accompanied by a shift of size structure toward smaller statured trees. The variation in the effects of drought on different tree sizes could lead to variations in drought responses among different PFTs since size composition differs among PFTs. Species within each PFT are also likely to be differentially affected by drought due to variation in their size distribution, structure, and physiology. Although shifts in

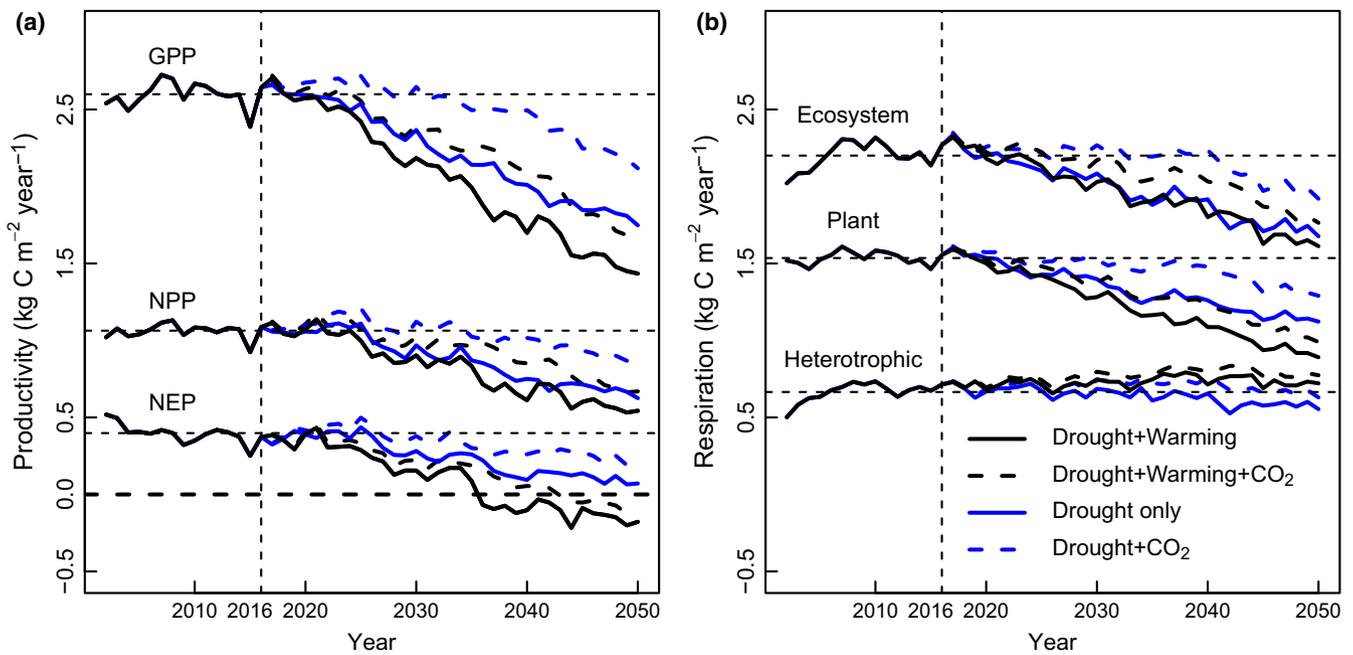


FIGURE 6 Model predicted productivity and respiration fluxes after CO₂ elevation was included. (a) GPP, NPP, and NEP under four climate change scenarios: Drought + Warming, Drought + Warming + CO₂ elevation, Drought-only, and Drought + CO₂ elevation. (b) Ecosystem, plant, and heterotrophic respiration under the four climatic scenarios. The climate conditions that lead to the tipping point with drought, warming, and elevated CO₂ are a ~40% reduction in precipitation, an increase in ~1.6°C in temperature and CO₂ levels of ~500 ppm

precipitation are expected to differ across the tropics under a changing climate, species composition will be shaped by water availability and can change rapidly in response in regions subject to increasing drought (Bennett et al., 2015; Fauset et al., 2012; Feeley, Davies, Perez, Hubbell, & Foster, 2011; Uriarte et al., 2016).

Tropical tree species are also likely to be particularly sensitive to global warming because they are adapted to limited geographic and seasonal variation in temperature (Wright et al., 2009). However, species that have passed through warmth similar to 2,100 levels (Dick, Lewis, Maslin, & Bermingham, 2013) may survive better in the absence of other major environmental challenges. The large variation in the response of species to warming will exacerbate the negative effect of drought with higher growth rates observed in pioneer species under warming, at least up to some temperature threshold (Cheesman & Winter, 2013). These pioneer early-successional species are also likely to colonize gaps created by the mortality of large trees. This suggests that, together, long-term drought and warming could lead to dramatic shifts in community composition and demography of tropical forests (van Mantgem et al., 2009).

Tropical forests may be particularly vulnerable to a changing climate when subject to natural disturbances. Although ENSO events are associated with lower frequency of hurricanes in the North Atlantic (Gamble & Curtis, 2008), it is unclear how the frequency and intensity of tropical storms will change under future climates (Knutson et al., 2010). Nevertheless, it will be interesting to explore the inclusion of hurricane regimes in model predictions. Our forest site has experienced hurricanes on a recurring basis during past decades (Uriarte et al., 2009). Tree census data recorded before and

after hurricanes could be used to include hurricane regimes in the modeling process.

4.2 | Carbon flux and storage

Modeled net ecosystem productivity (NEP) in this study shifted from positive to negative in ca. 20 years under a gradual warming and drying scenario (Figures 4d and 5a), indicating the transition of this forest from a carbon sink to a net source. Drought-only and warming-only scenarios also reduced the carbon sink effects of the tropical forest but not in such a marked and rapid manner. These changes in NEP resulted from changes in gross primary productivity (GPP) and ecosystem (autotrophic plus heterotrophic) respiration (ER).

Our model predicts a 33% decline of GPP under the drought-only scenario. Tropical rainforest ecosystems are characterized by high annual rainfall. Nevertheless, rainfall regularly fluctuates within and across years and seasonal soil droughts do occur. Studies elsewhere have shown that photosynthesis can decline due to limited moisture availability under dry conditions (Doughty et al., 2015; Rowland et al., 2015a, 2015b). However, an increase in GPP could also be expected during dry periods if the drought is moderate. Such an increase in GPP is caused by production of new leaves (Restrepo-Coupe et al., 2013; Wu et al., 2016) and increased radiation due to reduced cloud cover compared to wet periods (Dong et al., 2012; Guan et al., 2015; Jones, Kimball, & Nemani, 2014). This potential increase may be counterbalanced to some extent by the negative effect of drought on photosynthesis for shallow-rooted trees when the dry season is moderate, or for most trees if the drought is

severe. Although photosynthesis declines if moisture availability is limiting, leaf dark respiration is generally maintained, potentially acclimating upwards in the longer term (Meir, Metcalfe, Costa, & Fisher, 2008; Rowland et al., 2015b).

Our predictions show that the effects drought stress increased over decades of constant and prolonged drying leading to continuously declining forest productivity and growth. Severe and prolonged drought events cause broad-scale mortality events during which the capacity of forests to absorb CO₂ was strongly reduced due to leaf area loss. Large amounts of carbon can also be released into the atmosphere as dead trees decompose (Clark et al., 2003; Potter, Klooster, Hiatt, Genovese, & Castilla-Rubio, 2011). Although the decomposition of this dead matter is slow and may take one to several decades, biomass loss due to high mortality could change a large, long-term carbon sink into net source as predicted by our model. Past studies of Amazon forests response to the intense 2005 drought (Phillips et al., 2009, 2010) showed that forests lost biomass, reversing a carbon sink, with the greatest effects observed where the dry season was unusually intense. Tropical forests appear vulnerable to increasing moisture stress, with the potential for large carbon losses into the atmosphere to exert a feedback on climate change (Phillips et al., 2009). This scenario can be viewed as a possible analog of future events, particularly in the Amazon, Central America, and the Caribbean, West Africa, and peninsular S.E. Asia, regions where drought is expected to be more frequent. However, accurate characterization of plant hydraulic traits is essential to simulate forest growth and mortality for long-term projections. Two recent studies have demonstrated that variation in plant hydraulic traits explain the seasonal vegetation dynamics in dry tropical forests (Xu et al., 2016) and drought tolerance of wet forest species (Powell et al., 2017). Parameterization of plant hydraulic traits in this Puerto Rican forest should be considered for future data collection and modeling efforts.

Increases in temperature also have the potential to affect carbon cycling in tropical forests. Climate warming is expected to decrease primary production by increasing respiration rates in these ecosystems (Doughty & Goulden, 2008), which may negatively affect the carbon balance of tropical forests (Beer et al., 2010; Wood et al., 2012). Increases in temperature have also been linked with declines in wood production (Clark et al., 2003). On the other hand, previous studies (Cheesman & Winter, 2013; Dong et al., 2012) have also shown that increases in nighttime temperatures can increase tree growth. However, this potential positive effect from nighttime temperature increases were not incorporated in ED2. Under the warming-only scenario when water is not limiting, our model projects a decline of primary productivity but only after 2034. High temperatures during the growing season could cause a reduction of CO₂ uptake and canopy conductance. Empirical studies elsewhere found a 35%–40% reduction in gross CO₂ exchange with a 3°C rise in air temperature above 28.5°C (Doughty & Goulden, 2008). In our study, warming accelerated the effect of drought and caused a 45% reduction of GPP and a shift of NEP from positive to negative. These combined effects of warming and drying on NEP, which were not

evident when considering each stressor separately, can lead to a fundamental shift in the functioning and persistence of tropical rainforests.

In addition to reduced GPP under a warmer climate, carbon storage of tropical forests will decrease owing to higher soil and plant respiration rates associated with warming temperatures. The temperature sensitivity of ecosystem respiration processes is a key determinant of the interaction between climate and the carbon cycle (Beer et al., 2010). In our study, heterotrophic soil respiration was positively affected by warming and negatively affected by drought, with combined drought and warming stressors showing no significant response (Figure 5b). These patterns are well aligned with field experiment data of temperature and moisture effects on this large CO₂ flux (Meir et al., 2015b; Wood et al., 2012). Foliar respiration varied with temperature and our projections matched expectations based on the range of carbon sink vs. source behavior (Cavaleri, Oberbauer, & Ryan, 2008). Our variance decomposition analyses suggested that leaf dark respiration contributes a high amount of uncertainty in the model output. Dark respiration and its temperature sensitivity varied among plant functional types, with higher temperature sensitivities observed in early-successional tree species compared to other functional types (Slot et al., 2013). However, Slot et al. (2014) also suggested that leaf respiration of tropical forest plants can acclimate to nighttime warming, thereby potentially reducing the magnitude of the positive feedback between climate change and the carbon cycle. Therefore, understanding leaf dark respiration and its temperature and moisture sensitivity are essential for efforts to model carbon fluxes in tropical forests under current and future temperature and precipitation regimes. However, we lack sufficient data to make generalizations about dark respiration processes and patterns in species-rich tropical forests, particularly in response to climate variability and change (Atkin et al., 2015; Cheesman & Winter, 2013; Rowland et al., 2015b). This data gap combined with the complexity and diversity of tropical forests make it difficult to determine the effects of warming with any certainty (Wood et al., 2012). Given the major role tropical forests play in regulating global carbon fluxes and stocks, resolving this uncertainty is a research priority. Improving our ability to quantify the role of ecosystem respiration in regional scale carbon emissions will require long-term experiments across a range of spatial scales and development of robust moisture and temperature response functions. (Drake, Hanson, Lowrey, & Sharp, 2017; Koutavas, 2013; Roy et al., 2016).

By restricting stomatal conductance and improving water-use efficiency, one study showed that CO₂ fertilization can enhance resistance to drought, overcompensating for growth declines anticipated under drier climate (Koutavas, 2013). Elevated CO₂ can also have negative impacts on NEP during extreme drought and heat waves but at the same time, can compensate for these negative impacts by speeding up recovery of ecosystem uptake after short-term drought and heat events (Roy et al., 2016). Our predictions show that under prolonged drought and warming, the effect of elevated CO₂ did not completely offset the effects of drought and warming. In addition, the mitigating effect of elevated

CO₂ was strongest during moderate stress suggesting that the alleviating effects of elevated CO₂ depend on the intensity and length of stress. Under chronic stress when stomata are fully closed, the effect of elevated CO₂ can be negligible (Franks et al., 2013).

Ecosystem respiration was predicted to increase in our model under elevated CO₂ due to increases in autotrophic and heterotrophic respiration. Studies have reported that increase in soil respiration could offset the increase in GPP since rising atmospheric CO₂ is expected to stimulate plant growth and soil carbon input but may also alter microbial decomposition (van Groenigen, Qi, Osenberg, Luo, & Hungate, 2014). Although our model also predicts an increase in ecosystem respiration, it is small compared to the increase in GPP under elevated CO₂. Soils contain the largest pool of terrestrial organic carbon and are a major source of atmospheric CO₂ (Scharlemann, Tanner, Hiederer, & Kapos, 2014). Thus, they may play a key role in modulating climate change. Long-term studies are needed to understand the combined effect of these responses on long-term carbon storage.

4.3 | Tree diameter growth

Our results showed that under a drier and warmer climate, tree growth strongly declined corresponding with the reduction in predicted GPP and NPP. Uncertainty analysis showed that the allocation parameters made the largest contribution to uncertainty in modeled NPP. More data are needed to improve the allocation scheme of models to capture the seasonal and interannual variation of tree growth rates in tropical forests (Bonal et al., 2016; da Costa et al., 2010; Metcalfe et al., 2010; Phillips et al., 2009). Several studies have showed that tropical forests display strong seasonal variation in tree wood growth rates, which are largely explained by shifts in carbon allocation, and not by shifts in total productivity (Doughty et al., 2014, 2015; Malhi et al., 2015). It has been proposed that changing tree growth rates are more likely to reflect these shifts in carbon allocation. Only a whole NPP allocation perspective will allow us to correctly interpret the relationship between changes in growth and productivity.

4.4 | Parameter uncertainty decomposition

Our approach provides a robust estimate of model uncertainty, and identifies key data requirements to reduce predictive uncertainty in tropical forest ecosystems. Results from the variance decomposition can inform future targeted data collection required to efficiently constrain forecast uncertainty. Growth respiration was responsible for the highest fraction of predictive uncertainty in modeled AGB. Previous work in temperate biomes has also observed the highest uncertainty to be contributed by allocation parameters (Dietze et al., 2014; LeBauer et al., 2013; Wang, LeBauer, & Dietze, 2013). Uncertainty decomposition informs new measurements by targeting processes and parameters with the biggest knowledge gap and the most limiting effect on predictive capacity.

Previous modeling efforts have shown that correlations among key functional traits can be important (Christoffersen et al., 2016; Xu et al., 2016). We incorporated a closure term (ω in Equation 2) in the uncertainty decomposition analysis to account for parameter interactions that are excluded from the univariate variance decomposition. This coordination parameter accounted for ~15% of the predictive uncertainty, suggesting that although parameter interactions are important, univariate parameter uncertainty drives overall model variance. Although the assumption of parameter independence in the Bayesian meta-analysis and sensitivity analysis allows for a tidy decomposition of the total variance, we could obtain stronger parameter constraints by including parameter covariance. The absence of parameter interactions could be improved by a multivariate meta-analysis and sensitivity analysis accounting for parameter correlations which is planned for future development of PEcAn (LeBauer et al., 2013).

There is a growing need to improve the predictive power of ecological models. The availability of colossal amounts of data at many scales opens up the possibility of model-data synthesis, and this synthesis is of growing importance. Models can be thought of as scaffolds that enable data at different scales to interact with each other through our understanding of the underlying processes (Dietze, LeBauer, & Kooper, 2013). The biggest challenge for data synthesis and prediction is that data are recorded on different scales, such as leaf-level gas exchange, eddy-flux measurements and remote sensing, and thus do not inform each other directly. However, such datasets provide partial information about the underlying biological mechanisms. These disparate datasets, such as the ones used here, can be synthesized via models that encapsulate our current understanding of a system by representing processes at a hierarchy of spatial, temporal, phylogenetic, and organizational scales. A failure to properly take advantage of the breadth of expertise and data from the ecological community has been a fundamental impediment to improving the predictive capacity of models (Dietze et al., 2013). Our study sets an example of model-data synthesis in the tropical ecosystem by using plant trait data to parameterize ED2 and demography data for validation.

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SUPPORTING INFORMATION

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