



RESEARCH ARTICLE

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Key Points:

- An ecosystem demography model is used to examine how vegetation and hydrologic parameters jointly affect tropical forest dynamics
- Soil hydrologic properties, particularly a parameter related to the soil retention curve, play a key role in controlling forest diversity
- Belowground components such as the fraction of deeper tree roots are important for regulating dry-season forest dynamics

Supporting Information:

Supporting Information may be found in the online version of this article.

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Modeling the Joint Effects of Vegetation Characteristics and Soil Properties on Ecosystem Dynamics in a Panama Tropical Forest

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Abstract In tropical forests, both vegetation characteristics and soil properties are important not only for controlling energy, water, and gas exchanges directly but also determining the competition among species, successional dynamics, forest structure and composition. However, the joint effects of the two factors have received limited attention in Earth system model development. Here we use a vegetation demographic model, the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) implemented in the Energy Exascale Earth System Model (E3SM) Land Model (ELM), ELM-FATES, to explore how plant traits and soil properties affect tropical forest growth and composition concurrently. A large ensemble of simulations with perturbed vegetation and soil hydrological parameters is conducted at the Barro Colorado Island, Panama. The simulations are compared against observed carbon, energy, and water fluxes. We find that soil hydrological parameters, particularly the scaling exponent of the soil retention curve (B_{sw}), play crucial roles in controlling forest diversity, with higher B_{sw} values (>7) favoring late successional species in competition, and lower B_{sw} values ($1 \sim 7$) promoting the coexistence of early and late successional plants. Considering the additional impact of soil properties resolves a systematic bias of FATES in simulating sensible/latent heat partitioning with repercussion on water budget and plant coexistence. A greater fraction of deeper tree roots can help maintain the dry-season soil moisture and plant gas exchange. As soil properties are as important as vegetation parameters in predicting tropical forest dynamics, more efforts are needed to improve parameterizations of soil functions and belowground processes and their interactions with aboveground vegetation dynamics.

Plain Language Summary Through their impacts on the energy, water, and gas exchanges, vegetation characteristics and soil properties may influence ecosystem dynamics in tropical forests. This study examines how these two factors affect tropical forest dynamics simultaneously, including forest growth and composition. We use a state-of-the-art ecosystem demography model and evaluate the modeling results with field data collected at a primary tropical forest site, the Barro Colorado Island, Panama. The results show that soil hydrological parameters are as important as plant traits for regulating tropical forest successional dynamics and composition. The response of forest diversity to vegetation characteristics and soil properties has important implications for how climate and land use/land cover changes influence tropical forests and their role in carbon-water-climate feedback.

1. Introduction

Tropical forests only occupy less than 7% of the Earth's terrestrial surface but they play a critical role in regulating global energy, water, and carbon dynamics (Baccini et al., 2017; Ogden et al., 2013; Y. Pan, Birdsey et al., 2011; Wohl et al., 2012). Intact tropical forests are a major carbon sink contributing to almost half of the terrestrial carbon uptake (Blanc et al., 2009; Houghton, 2005; Watson et al., 2018). The structure and function of tropical forests are affected by both vegetation characteristics and soil properties. Vegetation characteristics determine forest photosynthesis capacities (Wu et al., 2017), carbon allocations (Ghimire et al., 2016), turnover times

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(Negrón-Juárez et al., 2015), and species competition strategies (Fisher et al., 2015). Soil hydrological properties affect various water fluxes, including infiltration, runoff generation, groundwater recharge, and plant water uptake in tropical forests (Bennett et al., 2021; Bruijnzeel, 1989, 2004; Powers et al., 2020; Sousa et al., 2020; Wohl et al., 2012). This will ultimately affect the productivity (Levine et al., 2019; Robinson et al., 2008), structures (Detto et al., 2013; Melton et al., 2015), compositions (Masaki et al., 2015; Russo et al., 2005), and functioning (Ito & Inatomi, 2012; Yan et al., 2020) of tropical forests (He et al., 2016; Kupers et al., 2019; Lohse et al., 2009). In addition, observational studies show that tropical forests undergo a range of successional regrowth pathways after disturbance (Mesquita et al., 2001). The successional balance between early and late successional species within a tropical forest ecosystem is also observed to be sensitive to soil properties (Baltzer et al., 2007; Marthews et al., 2008; Mendingelso et al., 2013; Silvertown et al., 2015).

To date, very few studies have considered the impact of soil properties and consequently the joint influence of vegetation characteristics and soil properties on tropical forest dynamics (e.g., Longo et al., 2019; Longo & Keller, 2019). More specifically for modeling, the sensitivity of tropical forest dynamics to both vegetation and soil hydrological parameters has received limited attention in the context of land surface models (LSMs), either due to inadequate representation of canopy heterogeneity in LSMs with a big leaf approach (which use area-averaged leaf layer information of different vegetation types to represent plant communities within a land grid cell) or insufficient consideration of hydrological responses (Wohl et al., 2012). Meanwhile, achieving coexistence in vegetation demography models is still an ongoing research challenge (Koven et al., 2019) (Detto et al., 2021) and the impact of soil hydrology on plant coexistence is particularly poorly understood.

Vegetation traits and soil properties not only affect tropical forest structure and successional balance, but also regulate many critical hydrological and biogeochemical processes in tropical forests through the interplay between aboveground vegetation processes (e.g., photosynthesis, canopy transpiration) and belowground components (e.g., tree roots, decomposition) (Porazinska et al., 2003). These mechanisms are, however, also not well represented in LSMs with a big leaf representation. Therefore, there is a critical need to elucidate the joint impacts of vegetation traits and soil properties in LSMs toward a more realistic representation of ecosystem processes and tropical forest dynamics, especially under a changing environment.

Here we use the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) (Fisher et al., 2015; Koven et al., 2019) implemented in the Energy Exascale Earth System Model (E3SM) land model (ELM) (Leung et al., 2020), ELM-FATES, to investigate the joint effects of vegetation characteristics and soil properties on tropical forest dynamics. In contrast to the “big leaf” model used in the majority of traditional LSMs, FATES explicitly simulates ecological demographic processes in forests, such as discretization in vegetation heights, light competition of different plant functional types (PFTs) within the same vertical profile, and heterogeneity in light availability along disturbance and recovery trajectories (Fisher et al., 2018; Longo et al., 2019). The structured demography in FATES facilitates simulation of successional variation and coexistence of vegetations. This allows a more realistic representation of forest age and composition (Fisher et al., 2010, 2018; Longo et al., 2019). In comparison to observations at a tropical forest site, Koven et al. (2019) reports two systematic biases across a large perturbed parameter ensemble of FATES simulations. First, the default calibration of FATES overestimates the difference between the wet season and dry season gross primary production (GPP), as compared to observations. Second, FATES-simulated latent and sensible heat (SH) fluxes are lower and higher than observations, respectively. Similar biases have been reported in other areas when using FATES, including the Amazon basin (Huang et al., 2020).

We hypothesize that these biases are due to errors in representing soil hydrological processes, belowground competitions, and ultimately the mechanisms that maintain coexistence between different PFTs. For example, soil hydrologic properties and root depth distribution may help maintain a high dry-season soil moisture and lead to better simulated dry-season GPP for mature tropical forest. Furthermore, the right combinations of soil hydrological parameters and plant traits may help achieve long-term coexistence among different PFTs. To test this hypothesis, we conduct a large ensemble of ELM-FATES simulations that specify two PFTs, corresponding to early successional and late successional plants, to examine the sensitivity of tropical forest dynamics to parameters in the hydrological and vegetation physiology elements of the model concurrently, through a case study over the Barro Colorado Island (BCI), Panama. We compare ELM-FATES simulations against a wide range of observations, including carbon, energy, and water cycle fluxes and states. A logical starting point is to assume two contrasting PFTs (e.g., early and late successional PFTs). Although the tropical forest in BCI contains

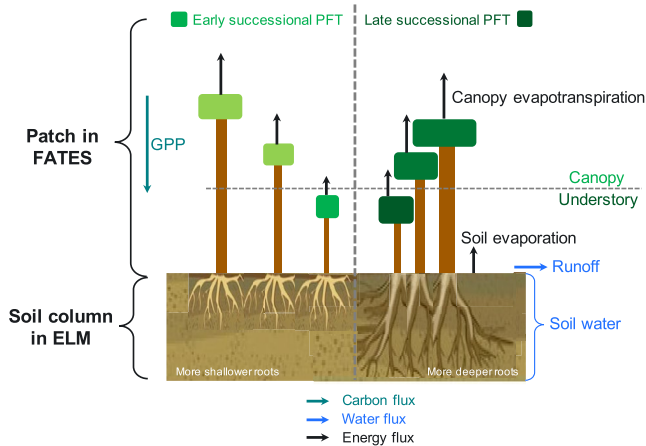


Figure 1. Schematic illustration of forest structure and composition and soil hydrology in Earth Land Model-Functionally Assembled Terrestrial Ecosystem Simulator (ELM-FATES). Light/dark green shows early/late successional plant functional types (PFT). Understory cohorts are shaded darker than canopy cohorts. Cohorts within a patch in FATES can compete for light based on their canopy heights and positions. Patches share and compete a common underground pool of water and nutrients within an ELM soil column. The early/late successional PFTs have greater fractions of shallow/deep roots.

hundreds of species, these two PFTs will provide enough complexity to explore the interactions between hydrology and forest dynamics along a successional axis and, at the same time, address questions about coexistence. The two PFTs differ in their photosynthetic traits, aboveground and belowground allocations, tissue turnovers, and survival rates. Plant hydraulics are not considered because it is unclear how early and late successional PFTs differ in this aspect and it would require more data for parameterization, adding more uncertainties. The sensitivity analysis conducted in this study for plant traits and soil parameters is an important first step to shed light on understanding the joint impacts of vegetation characteristics and soil properties on tropical forest dynamics.

2. Data and Methods

2.1. Model Description

The FATES is a size- and age-structured and cohort-based ecosystem demography model (Fisher et al., 2015; Hurtt et al., 1998; Koven et al., 2019; Moorcroft et al., 2001). A cohort, in this context, is a group of individuals of a particular vegetation type within a given size range, which is modeled as one representative individual. Cohorts with a similar size are grouped into spatially implicit ‘patches’ that are themselves grouped by similar disturbance history at the landscape scale. Individual plants are scaled to a forest canopy based on the perfect plasticity approximation (Purves et al., 2008). FATES

must be run with a ‘host’ land surface model, which provides water boundary conditions. In this study, FATES is embedded in the E3SM ELM, called ELM-FATES. In ELM-FATES, ELM simulates the terrestrial water cycle and energy fluxes, while FATES simulates vegetation processes, including photosynthesis, growth, allocation, competition, and ecosystem assembly (Figure 1). Cohorts within a patch compete for light based on their canopy heights and positions. Patches share a common pool of soil water within an ELM ‘column’ (Figure 1). For a full overview of ELM-FATES, readers are referred to Leung et al. (2020), Fisher et al. (2015), Koven et al. (2019), and the FATES technical note (<https://fates-docs.readthedocs.io/>).

2.2. Study Site and Data

In this study, we use observational data from the BCI, Panama (9.151°N, 79.855°W) for model validation. The BCI site is covered by a primary forest. The mean annual precipitation is 2,700 mm yr⁻¹, with distinct dry (mid-December to mid-April) and wet (late-April to early-December) seasons. Hourly meteorological data (i.e., precipitation, temperature, wind speed, relative humidity, radiation) from 2003 to 2016 (Faybishenko et al., 2018; Knox et al., 2019) are recycled to spin up the ELM-FATES simulations. Observational data used to validate the model include the aboveground biomass (AGB) (Chave et al., 2003), tree size distribution (Condit et al., 2017), GPP, SH, latent heat (LH), upper layer (top 15 cm) soil water content (SWC15), (Pau et al., 2018) and runoff (Cheng et al., 2018).

2.3. FATES and Soil Hydrological Parameters

We select a comprehensive set of soil hydrological parameters, including saturated hydraulic conductivity (K_s), saturated soil water content (θ_s), the scaling exponent of the Clapp and Hornberger soil retention curve (B_{sw}) (Clapp & Hornberger, 1978), saturated soil matric potential (Ψ_s), maximum fractional saturated area (f_{max}), mean topographic slope (*slope*), decay factor that represents the distribution of surface runoff with depth (f_{over}), and decay factor that represents the distribution of subsurface runoff with depth (f_{drain}) (Hou et al., 2012). For the plant physiology parameters in FATES, we investigate the sensitivity of the model to a selection of the most sensitive parameters that were identified in prior sensitivity studies (Huang et al., 2020; Koven et al., 2019; Massoud et al., 2019). The selected FATES parameters are maximum carboxylation rate of RuBisCO at the reference temperature (25°C; $V_{c,max}$), specific leaf area at the top of canopy (sla_{top}), background mortality rate (*mort*), root and leaf turnover times (τ_{root} and τ_{leaf}), and wood density (ρ_{wood}). ELM-FATES assumes an exponential decay

Table 1
Summary of Soil Hydrologic Parameters and Plant Traits Benchmarked in This Study for ELM-FATES

	Symbol	Parameter name	Relevant process	Unit	Bound	Reference
Soil hydrologic parameters	K_s	Saturated hydraulic conductivity	Soil water	mm/s	0.00001, 0.02	(Hou et al., 2012; Huang et al., 2013)
	θ_s	Saturated water content (porosity)	Soil water	m ³ /m ³	0.35, 0.6	
	B_{sw}	Clapp and Hornberger exponent	Soil water	-	1.0, 30.0	
	ψ_{sar}	Saturated soil matric potential	Soil water	mm	50.0, 350.0	
	f_{max}	Maximum fractional saturated area	Surface runoff	-	0.01, 0.9	
	<i>Slope</i>	Mean topographic slope	Surface runoff	-	0.01, 0.9	
	f_{over}	Decay factor that represents the distribution of surface runoff with depth	Surface runoff	1/m	0.1, 5.0	
	f_{drain}	Decay factor that represents the distribution of subsurface runoff with depth	Subsurface runoff	1/m	0.5, 5.0	
Plant traits	$V_{c,max,early}$	Maximum carboxylation rate of Rub. at 25C, canopy top for early PFT	Photosynthesis	umol CO ₂ /m ² /s	10, 106	(Domingues et al., 2005)
	$V_{c,max,late}$	Maximum carboxylation rate of Rub. at 25C, canopy top for late PFT			7.7, 95	
	$sla_{top,early}$	Specific Leaf Area (SLA) at top of canopy, projected area basis for early PFT	Leaf growth and turnover	m ² /g C	0.007, 0.039	(Wright et al., 2004)
	$sla_{top,late}$	Specific Leaf Area (SLA) at top of canopy, projected area basis for late PFT			0.005, 0.037	
	$mort_{early}$	Background mortality rate for early PFT	Mortality	1/yr	0.01, 0.1	(Longo et al., 2019)
	$mort_{late}$	Background mortality rate for late PFT			0.004, 0.06	
	$\tau_{root,early}$	Root turnover time for early PFT	Root growth and turnover	yr	0.1, 1.5	(Huang et al., 2020)
	$\tau_{root,late}$	Root turnover time for late PFT			0.2, 4.0	
	$\tau_{leaf,early}$	Leaf turnover time for early PFT	Leaf growth and turnover	yr	0.1, 1.5	
	$\tau_{leaf,late}$	Leaf turnover time for late PFT			0.2, 4.0	
	$\rho_{wood,early}$	Mean density of woody tissue in plant for early PFT	Stem growth	g/cm ³	0.2, 1.0	(Longo et al., 2019)
	$\rho_{wood,late}$	Mean density of woody tissue in plant for late PFT			0.3, 2.0	
	$roota_{early}$	Root distribution parameter 1 for early PFT	ET, soil water, root growth	1/m	0.1, 8.0	(Zeng, 2001)
	$roota_{late}$	Root distribution parameter 1 for late PFT			0.07, 7.5	
	$rootb_{early}$	Root distribution parameter 2 for early PFT	ET, soil water, root growth	1/m	0.1, 8.0	
$rootb_{late}$	Root distribution parameter 2 for late PFT			0.07, 7.5		

using a two-parameter (*roota* and *rootb*) function (Equation S1 in Supporting Information S1) to represent the rooting depth distribution (Zeng, 2001) and we investigate sensitivity to these two parameters as well. Detailed explanations of the soil hydrological parameters and plant traits are provided in Table 1. For simplicity, leaf and root turnover times are set to be the same for the early PFT. This also holds true for the late PFT.

2.4. Model Experiment Design

To test the responses of tropical ecosystems to a wide range of field conditions, we run ensemble simulations in which both soil hydrological parameters and plant traits can cover a full spectrum of parameter values within reasonable physical bounds. Latin Hypercube Sampling (LHS) (McKay et al., 2000) is used to assemble 1,000 parameter sets using the ranges defined in Table 1. The LHS approach samples the parameter space more evenly and efficiently than simple random sampling. It splits the distribution of each parameter into a certain number of regions with equal probability. These unique parameter sets are used to drive the ELM-FATES model at the BCI site.

It should be noted that the default setup of soil thickness in ELM is a spatially uniform value (i.e., 3.4 m) with 10 discretized layers (Figure S1 in Supporting Information S1). To reduce the ensemble size, we aggregate these 10 layers into five in this study (Figure S1 in Supporting Information S1), given the similarity of soil hydraulic properties in adjacent layers. The most straightforward and brute force method to determine the parameters for each layer is to randomly sample soil hydraulic properties in the five layers independently, but this could induce some unrealistic hydrologic behaviors. For instance, various field studies find that as soil depth increases, K_s and θ_s generally decrease (Hassler et al., 2011; Litt et al., 2020; Zwartendijk et al., 2017) and B_{sw} generally increases. To account for the layer dependence of the parameter values, the LHS samples related to K_s , B_{sw} , and θ_s are constrained to follow simple linear functions that vary with soil layers.

The ecosystem-level dynamics of tropical forests comprise a mosaic of plants of different PFTs. In particular, we expect that a vegetation model can represent canopy heterogeneity by accommodating at least two functional types, the light-demanding, fast-growing and early successional plants, and the shade-tolerant, slow-growing and late-successional plants (Huang et al., 2020; Koven et al., 2019; Needham et al., 2020). The representation of two contrasting PFTs with multiple distinct axes of trait variation is a logical starting point to explore the complex interactions between climate and plant strategies in a competitive environment. Therefore, in ELM-FATES, we parameterize two PFTs (i.e., early and late successional PFTs) to represent the primary axis of variability in tropical forests. Here, we assume that the early successional PFT has a lower wood density, shorter leaf and root lifetimes, a higher background mortality, and a greater fraction of shallow roots (Bretfeld et al., 2018). The late successional PFT has denser woody tissues, longer leaf and root turnover times, a lower background mortality, and a greater fraction of deep roots (Figure 1, Table S1 in Supporting Information S1) (Huang et al., 2020; Koven et al., 2019; Zhu et al., 2018). The early successional PFT can grow rapidly under high light conditions, while the late successional PFT can survive under a deeply shaded and closed canopy (Huang et al., 2020; Koven et al., 2019; Zhu et al., 2018). We use a set of early and late successional pairs to explore the effect of soil hydrologic and physiologic parameters on their dominance and coexistence. Importantly, the model, in the current stage, cannot represent seasonal phenological changes in LAI and other leaf traits. Although BCI does not have a dramatic seasonal variation in plant phenology (e.g., LAI varies in about $0.5 \text{ m}^2/\text{m}^2$) (Detto et al., 2018; Wirth et al., 2001), we recognize this is a limitation that needs to be addressed in future model developments.

3. Results

3.1. Large Ensembles of ELM-FATES Simulations

We assess the skill of each of the 1,000 ensemble ELM-FATES simulations against observed carbon (GPP), energy (LH, SH), water (SWC15, runoff), and forest (tree size distribution, AGB) dynamics at the BCI site (Figures 2 and S4a in Supporting Information S1). Overall, the ensemble output encompasses the observed mean annual dynamics of biogeochemical and hydrological fluxes, with the ensemble median close to observations. Compared to the single-PFT simulation results in Koven et al. (2019), our two-PFT simulations have much narrower ranges of tree size distributions (Figure 2a). Another difference compared to Koven et al. (2019) is that allometric parameters were not varied in this study. Moreover, our simulations well capture the water cycle dynamics (e.g., ET, runoff, and soil moisture, Figures 2d–2f). These improvements are likely due to the joint consideration of physiological and soil hydrological parameters and the parameterization for early and late PFTs, while Koven et al. (2019) only benchmarked physiology parameters for one PFT. Note that some ensemble members have very low simulated plant productivity, and some are even not able to establish (Figure 2b), suggesting sensitivity of the rates of forest establishment, growth, and mortality to physiological and soil hydrological parameters as well as their combinations. We examine the sensitivity of forest establishment to the ELM-FATES parameters in Section 3.3. In addition, compared to the systematic underestimation of LH and overestimation of SH in FATES compared to observations (Koven et al., 2019), the current ensemble simulations can better capture the total energy partitioning (Figures 2c and 2d).

3.2. Sensitivity of Carbon, Energy, and Water Fluxes

Sensitivity of simulated water, carbon, and energy fluxes to hydrologic parameters and plant traits at the annual level is shown in Figure 3 via regression model sensitivity analysis following Xu and Gertner (2008), F. Pan, Zhu, et al. (2011), and Cheng et al. (2019). Consistent with previous studies that examined the sensitivity of carbon

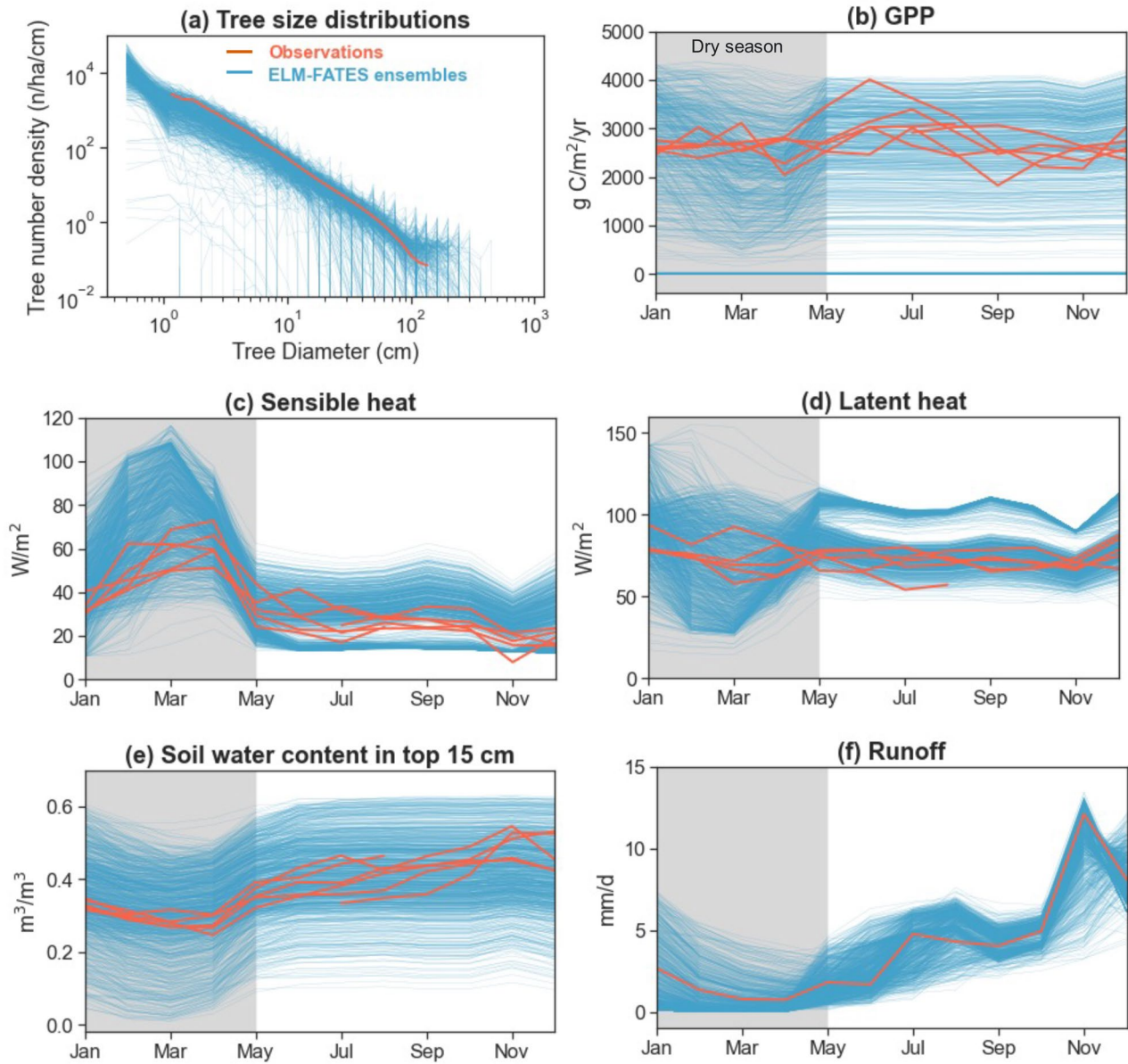


Figure 2. Mean monthly (a) tree size distribution, (b) gross primary productivity, (c) sensible heat, (d) latent heat, (e) upper-layer (top 15 cm) soil water content, and (f) runoff between the Functionally Assembled Terrestrial Ecosystem Simulator implemented in the Energy Exascale Earth System Model Land Model (ELM-FATES) ensemble simulations (blue lines) and observations from Barro Colorado Island, Panama (orange lines). Gray area represents the dry season.

cycle variables (Koven et al., 2019), the current ensemble simulations show that GPP, LAI, biomass, mortality and growth rates for canopy and understory plants are more sensitive to the physiological parameters, such as $V_{c,max}$, sla_{top} , τ_{root} , and τ_{leaf} , than they are to soil hydrological parameters (Figure 3a). In particular, model simulations tend to be slightly more sensitive to the parameters of late successional PFT (e.g., $V_{c,max}$, τ_{root} , and τ_{leaf}). Water budget components, such as upper-layer (top 15 cm) and total soil moisture, are more sensitive to soil hydraulic parameters than they are to plant traits (Figure 3a). In particular, soil moisture is most sensitive to B_{sw} and θ_s . There is no significant difference in sensitivity across the five soil layers. In contrast to the sensitivity of runoff to f_{over} noted in previous modeling studies using prescribed satellite-derived plant phenology (Hou et al., 2012; Huang et al., 2013), we find that runoff is sensitive to physiological parameters (e.g., sla_{top} , τ_{root} , and τ_{leaf}) when the model prognostically simulates vegetation dynamics (Figure 3a). The behavior of energy cycle fluxes is more

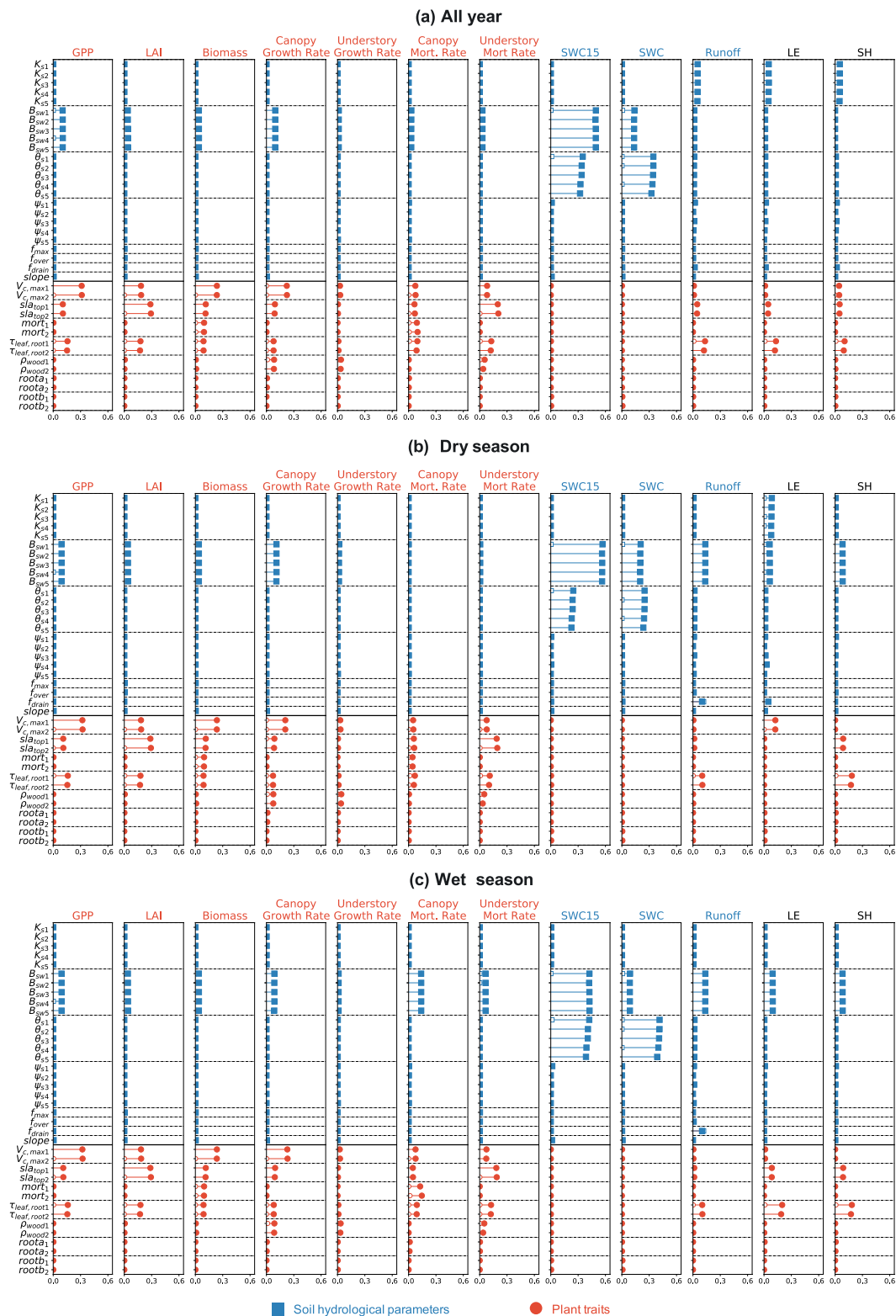


Figure 3. Sensitivity indices (total sensitivity in filled markers, uncorrelated sensitivity in open markers) of soil hydrological parameters (blue rectangle) and plant traits (red circle) for carbon (red title), water (blue title), and energy (black title) cycle fluxes and states over (a) all year, (b) dry season, and (c) wet season. The numbers 1 to 5 in soil hydrological parameters are corresponding to the first to fifth soil depth layers. The numbers 1 and 2 in plant traits represent for early and late successional plant functional types, respectively. The dashed lines separate each parameter and the solid lines separate soil hydrologic parameters and plant traits. Filled markers and associated lines show total sensitivity of each parameter, and open markers show independent sensitivity contributed by the uncorrelated variance of each parameter.

complicated as they are sensitive to both soil hydrological (e.g., K_s and B_{sw}) and physiological parameters (e.g., $V_{c,max}$, sla_{top} , τ_{root} , and τ_{leaf}), as energy partitioning is controlled by both soil processes (e.g., soil evaporation) and vegetation growth (e.g., canopy evaporation and transpiration). For physiological parameters, LH and SH are sensitive to $V_{c,max}$ and sla_{top} as LAI is a key variable in determining these two energy fluxes. In addition to photosynthesis and leaf growth parameters, the heat fluxes are also sensitive to leaf turnover time (τ_{leaf}). This is because leaf biomass and LAI are controlled by the turnover processes besides processes of phenology and allocation. Consequently, τ_{leaf} controls energy fluxes through its impact in determining LAI (Figure 3). This is further evidenced by the fact that large variances of τ_{leaf} in explaining simulated energy fluxes are contributed by correlated variances rather than its isolated contribution.

Sensitivity of energy and water variables to hydrologic parameters and plant traits has a stronger seasonal dependence than that of carbon cycle variables. During the dry season (mid-December to mid-April), there are no significant changes in sensitivity of carbon cycle variables (Figure 3b) compared to the simulated annual level (Figure 3a). However, for energy fluxes, the impact of physiological parameters decreases, and the impact of soil hydrological parameters increases. In addition, the sensitivity of water states and energy fluxes to B_{sw} increases. Over the wet season (late-April to early-December), rather than B_{sw} , θ_s explains the largest variance in soil moisture (Figure 3c). This occurs because θ_s determines the maximum soil moisture when water is not a limiting factor during the wet season. The physiological parameters (e.g., sla_{top} , τ_{root} , and τ_{leaf}) become more important for energy fluxes, as LH/evapotranspiration is dominated by canopy transpiration during the wet period.

3.3. Sensitivity of Forest Establishment

The sensitivity of forest establishment to plant traits and soil hydrological parameters is examined in Figure 4. Forest can establish in 597 scenarios among the 1,000 ensembles. The potential reason for the large number of simulations that forest failed to establish is our sampling over a wide range of parameters; some parameter combinations may have led to elevated tree mortality in the model runs. Overall, the soil hydrological properties do not have much influence on forest establishment, as can be seen from the random scattering of dead and alive forests within the hydrologic parameter distributions (Figure 4a). Plant physiology parameters are key in controlling forest establishment, which is evident by the clear separation of dead and alive plants in the distributions for plant traits, especially for $V_{c,max}$, sla_{top} , and $\tau_{leaf,root}$ (Figure 4b). This is within our expectation, as the physiology parameters determine photosynthesis rates and leaf areas, which are key for forest growth (Koven et al., 2019). We focus on the ensembles in which forest can successfully establish in the following analysis.

3.4. Sensitivity of Dominance and Coexistence of Early and Late Successional PFT

By parameterizing two PFTs in this study, early and late successional plants, ELM-FATES is capable of simulating successional outcomes. Simulation results range from competitive exclusion by late successional species to competitive exclusion by early successional species (Figure 5). While there is not a clear relationship between individual plant traits and the dominance of the two PFTs (Figure 5b), hydrologic parameters have a clearer relationship with their dominance (Figure 5a). Specifically, B_{sw} is a key parameter in maintaining functional diversity in humid tropical forests. Late successional PFT becomes dominant when B_{sw} is higher (>7); therefore, only small values of B_{sw} ($1 \sim 7$) can support coexistence for early and late successional PFTs (Figures 5a and 6). B_{sw} is strongly dependent on soil texture and increases from coarse to fine soils. A higher value of B_{sw} means a stronger water retention capacity. Therefore, the impact of B_{sw} in controlling coexistence is highly related to its impact in controlling soil moisture. We discuss the underlying mechanism in Section 4.1.

3.5. Impact of Tree Root Profile on Dry-Season Soil Moisture and GPP Dynamics

It is worth noting that some ensemble members can maintain a high GPP throughout the dry season (Figure 2b), consistent with observations. We select these ensemble members (Text S2 in Supporting Information S1) to investigate the potential underlying mechanisms (Figure 7). In addition to better simulating dry-season GPP, these ensemble members are also the ones that can better simulate water and energy cycle fluxes and

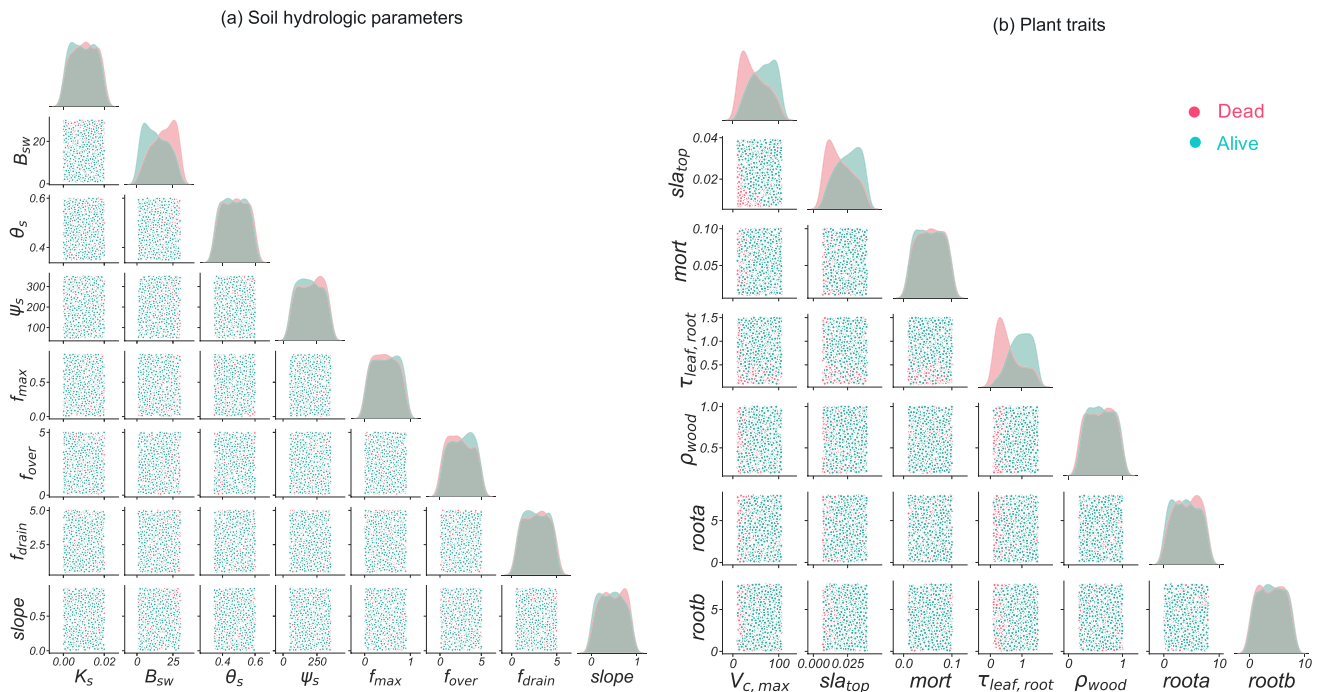


Figure 4. Matrix of (a) soil hydrologic parameters and (b) plant traits used in this study, separated by dead (red dots) and alive (blue dots) forests. The diagonal plots are kernel density estimates for parameters in the horizontal axis, separated by dead (red color) and alive (blue color) forests. Forest establishment is sensitive to plant traits, evidenced by the clear separation between dead and alive forests in the distributions for $V_{c,max}$, sla_{top} , and $\tau_{leaf,root}$. This figure only includes the top layer hydrologic parameters and early successional plant functional types (PFT) for illustration purposes, but results are similar for other soil layers and the late successional PFT (see Figure S2 in Supporting Information S1).

states as well as AGB and tree size distributions, compared to other ensemble members (Figures S4b and S5 in Supporting Information S1). For example, the average root mean square errors (RMSEs) of the selected ensembles/other ensembles are 13.9/32.1 kg C/m², 310/1,718 g C/m²/yr, 19.9/36.8 W/m², 22.2/47.4 W/m², 8.8%/9.4%, and 1.0/1.4 mm/d for AGB, GPP, SH, LH, SWC15, and runoff, respectively. In particular, all the selected ensemble members tend to have a high simulated dry-season shallow layer soil moisture (Figure 7e), corresponding to the high simulated dry-season GPP (Bretfeld et al., 2018; Bruijnzeel & Veneklaas, 1998; De Gouvenain et al., 2007; Maréchaux et al., 2018). There could be two possible pathways to explain the maintenance of dry-season soil moisture and GPP, either through changes in soil hydraulic properties or root system characteristics. Our results support the latter mechanism because we found that the ELM-FATES simulations that can maintain the dry-season soil moisture and GPP consistently have greater fractions of deeper roots (Figures 8a and 8b). For example, the mean root fraction below 34 cm of the selected ensembles/other ensembles are 0.06/0.03 and 0.07/0.04 for the early and late PFTs, respectively (Figures 8c and 8d). Meanwhile, the soil matric potential that limits root water uptake and the soil water stress index (β_{sw} , Text S4 in Supporting Information S1) that represents root-weighted water availability, are highly different between the shallower and deeper soil layers (Figure S6 in Supporting Information S1). The shallower soil layers consistently have a higher soil matric potential and a lower β_{sw} in the dry season than that in the wet season, indicating larger difficulties for plants to uptake soil water in the surface layers during the dry season. Because the deeper rooting systems allow trees to preferentially extract water from deep soil depths that have a lower soil matric potential and a higher root-weighted water availability rather than from surface soil layers, a high dry-season water content is maintained in the shallow layers. In addition, the distribution of β_{sw} along the vertical soil depth (Figure S7 in Supporting Information S1), which integrates the impacts of both soil properties and rooting parameters (Text S4 in Supporting Information S1), consistently follow the patterns of root distribution profiles for both early and late PFTs (Figures 8a and 8b). This further demonstrates the dominant impact of root distribution profiles on soil moisture.

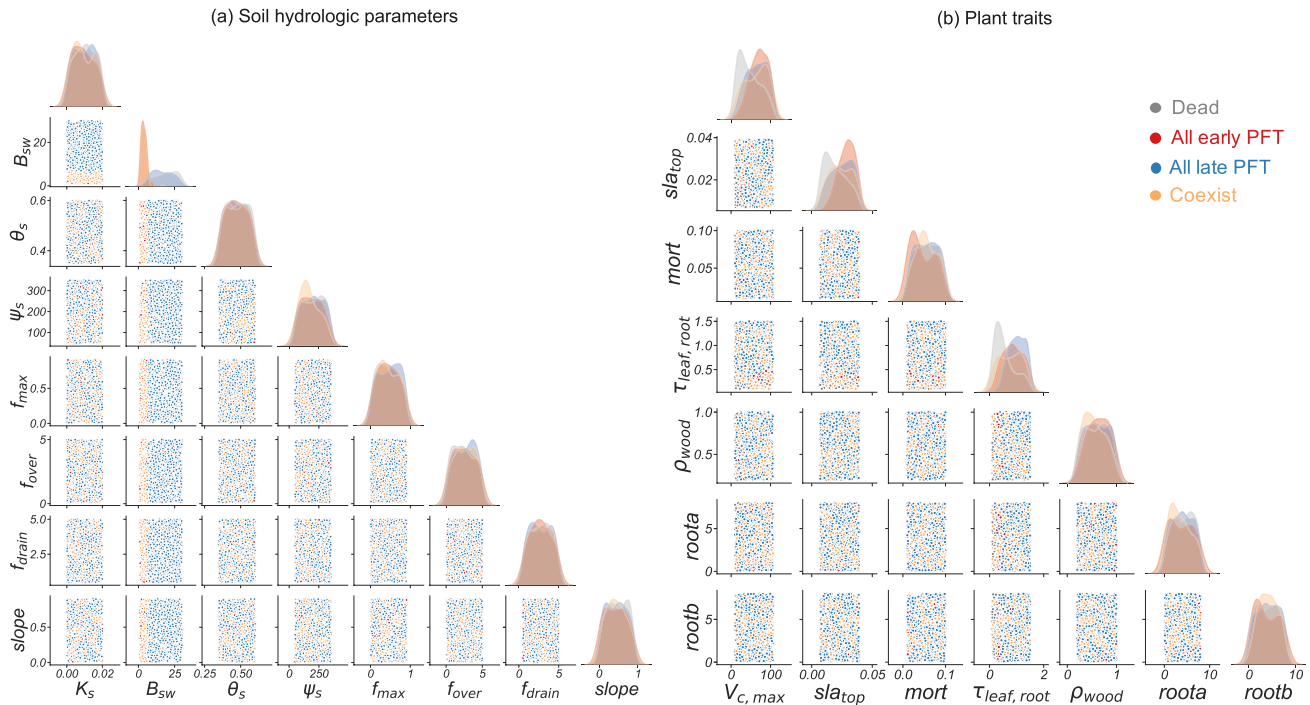


Figure 5. Same as Figure 4, but separated by coexistence (orange dots) and dominance of early (red dots) and late (blue dots) successional plant functional types (PFTs). The B_{sw} parameter is key in controlling coexistence, evidenced by the clear separation between coexist (orange dots) and non-coexist simulations in its distribution. Increases in B_{sw} promotes the late successional PFT. This figure only includes the top layer soil hydraulic parameters and early successional PFT for illustration purposes, but results are similar for other soil layers and the late successional PFT (see Figure S3 in Supporting Information S1).

In addition to better capturing carbon, water, and energy cycle dynamics, the parameter values for these selected ensemble members also agree with field data collected in tropical forests. Specifically, for soil hydrological parameters, the median values of K_s and θ_s for these selected simulations are 33 mm/hr and $0.56 \text{ m}^3/\text{m}^3$, respectively, which are consistent with field observations collected in Panama sites (K_s and θ_s are 26 mm/hr and $0.57 \text{ m}^3/\text{m}^3$, respectively) (Hassler et al., 2011; Litt et al., 2020). The median value of B_{sw} for the selected ensemble members is 14.8, similar to the mean (standard deviation) value of typical B_{sw} for the clay soil in BCI (Powell et al., 2018), which is 11.4 (3.7) (Clapp & Hornberger, 1978). We further compare the simulated soil water retention curve of the selected ensembles with the soil water potential and soil water content data measured in BCI, Panama (Kupers et al., 2019; Text S2, Figures S4c-d in Supporting Information S1). Importantly, the retention curves of these selected ensembles that work best in simulating tropical forest dynamics are consistent with those typical soil water retention data in the BCI site (Figure S4d in Supporting Information S1).

The median values of $V_{c,max}$ for early and late PFTs are 46.7 and $36.8 \mu\text{mol CO}_2/\text{m}^2/\text{s}$, respectively. The median ρ_{wood} values for early and late PFTs are 0.6 and $1.1 \text{ g}/\text{cm}^3$, respectively. These physiological parameter values for the selected ensemble members also agree with field measurements for mature tropical forests (observed $V_{c,max}$ ranges from 18 to $59 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ in a wet evergreen tropical forest site, and ρ_{wood} is 0.5 and $0.9 \text{ g}/\text{cm}^3$ for early and late PFTs, respectively) (Gu et al., 2016; Longo et al., 2019; Rogers, 2014; Wu et al., 2017).

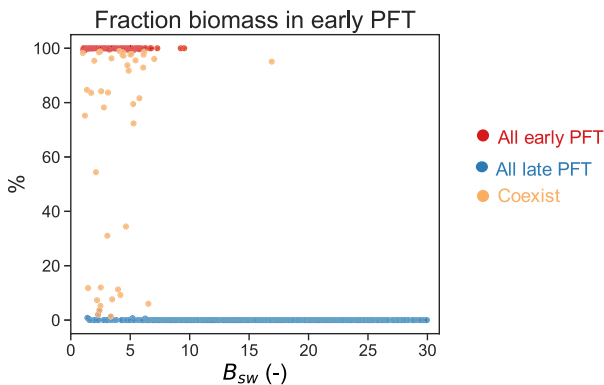


Figure 6. Relationship between the B_{sw} parameter and the fraction of biomass in early successional plant functional types (PFT), separated by all early PFT (red dots), all late PFT (blue dots), and coexistence (orange dots). Late successional PFT becomes dominant when B_{sw} increases. Only small values of B_{sw} can support coexistence.

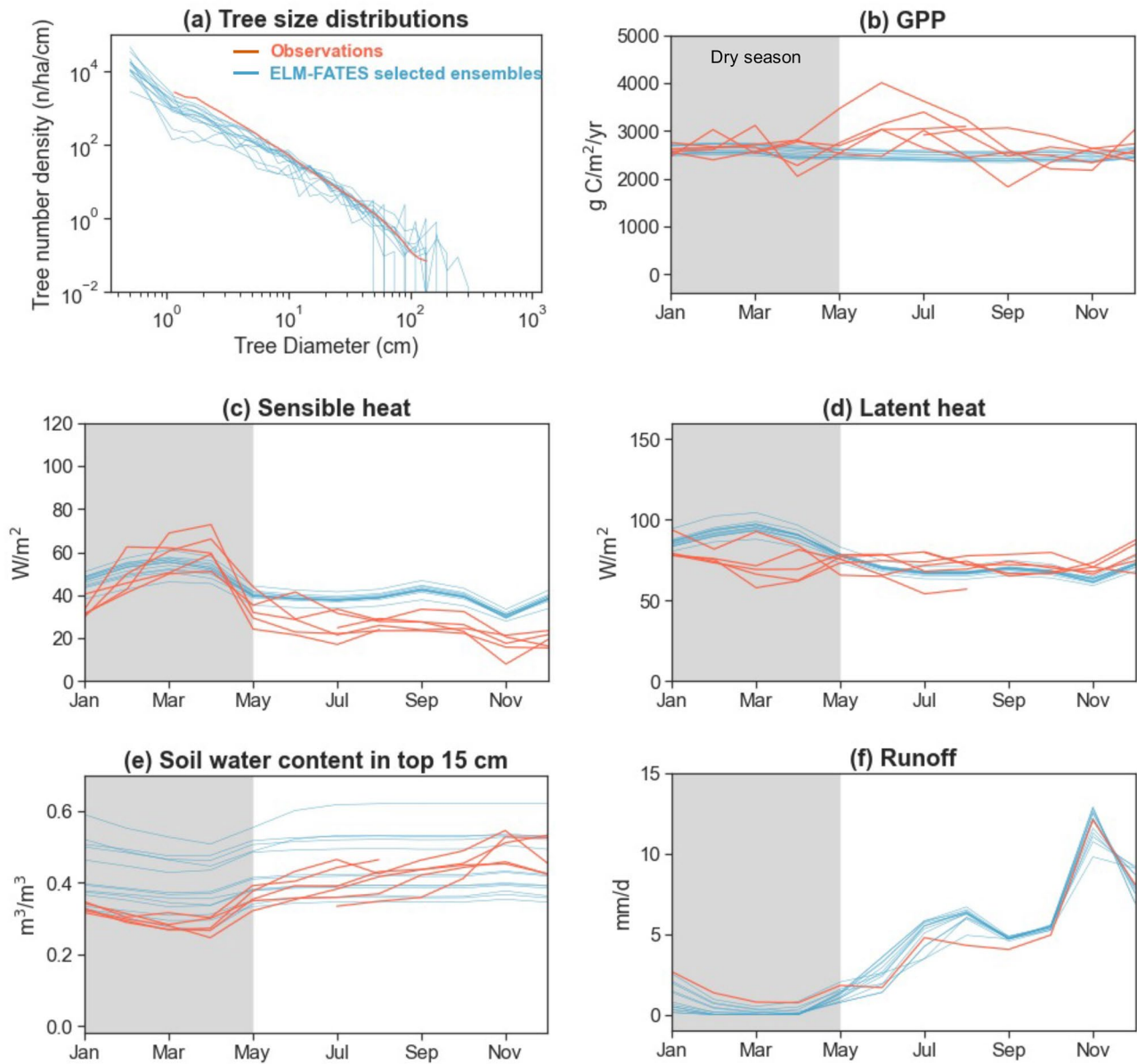


Figure 7. Same as Figure 2, but for selected Earth Land Model-Functionally Assembled Terrestrial Ecosystem Simulator simulations that can maintain a high dry-season gross primary productivity. The parameter values for these selected ensembles are shown in Figures 8 and S6 in Supporting Information S1.

4. Summary and Discussions

4.1. Joint Effects of Vegetation Characteristics and Soil Features on Tropical Forest Dynamics

Numerous studies have demonstrated the critical role of plant physiology characteristics in determining the response of tropical forest dynamics to global changes, such as tree mortality rates (Needham et al., 2020), stomatal conductance (Wu et al., 2020), and allocation to leaves and reproduction (Detto et al., 2018; Rademacher et al., 2019). However, studies to examine the role of hydrological properties are still limited (Baker et al., 2009; Christoffersen et al., 2014; Manoli et al., 2018). This study uses an advanced ecosystem demography model, ELM-FATES, at BCI, Panama to investigate the joint role of vegetation characteristics and soil properties in altering tropical forest dynamics. Our results are consistent with previous studies (Huang et al., 2020; Koven et al., 2019) in several perspectives. First, carbon cycle fluxes (e.g., GPP, LAI, biomass, and tree growth and mortality rates) are more sensitive to the vegetation parameters (e.g., $V_{c,max}$, sla_{top} , τ_{leaf} , and τ_{root} , Figure 3) than to the soil hydrological parameters. Second, energy fluxes (e.g., SH and LH fluxes) are more sensitive to the

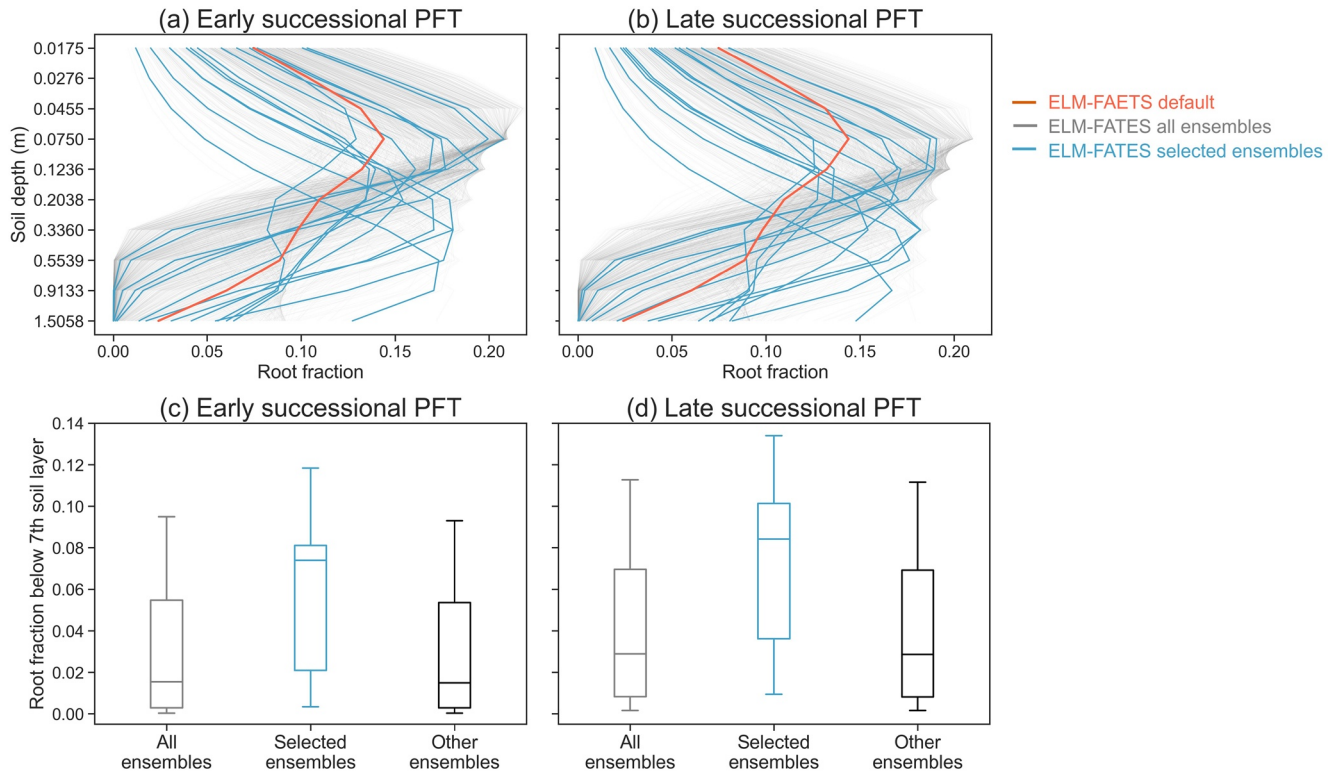


Figure 8. (a–b) Root depth distributions and (c–d) boxplot of mean deep layer root fraction for early (first column) and late (second column) successional plant functional types. Orange line shows the default root profile in Earth Land Model-Functionally Assembled Terrestrial Ecosystem Simulator (ELM-FATES). Gray lines are sampled root fraction distributions for all the ELM-FATES ensembles. Blue lines are selected ELM-FATES ensembles that can maintain a high dry-season soil moisture and gross primary productivity.

physiological parameters during the wet season (Figure 3c) when canopy transpiration dominates the LH flux. Third, physiological parameters (e.g., $V_{c,max}$, sla_{top} , τ_{leaf} , and τ_{root}) are key in controlling forest establishment in the model (Figure 4b).

Our results also demonstrate, however, that jointly perturbing plant traits and soil hydrological parameters can correct the systematic bias in previous FATES simulations (Koven et al., 2019), especially for simulations of energy partitioning (Figures 2c and 2d). This is because the model can simulate a better plant productivity (Figure 2b) and water budget including ET (Figure 2d), soil moisture (Figure 2e), and runoff (Figure 2f). These results have important implications as accurate predictions of energy partitioning are necessary to represent the biophysical effect of land surface processes at regional scale, which can feedback to climate through land-atmosphere interactions (Bonan, 2008; Cheng et al., 2021).

Consistently, soil hydraulic parameters (e.g., B_{sw} , θ_s) drive hydrological responses (e.g., soil moisture, Figure 3). Energy fluxes are more sensitive to soil hydraulic parameters (e.g., B_{sw} , K_s) than they are to plant traits during the dry season (Figure 3b) when soil evaporation is an important component of evapotranspiration. In addition, B_{sw} plays the most important role in modulating soil moisture variation, which is more profound during the dry season. It should be noted that ESMs usually assign soil hydraulic properties using a pedotransfer function derived from some easily measured soil texture attributes (e.g., percentages of sand and clay). Rather than using the estimated pedotransfer functions, this study directly specified all the soil hydraulic parameters. However, uncertainties in pedotransfer functions should not be overlooked, as these functions are not uniform across ESMs, varying from simple linear regression to complicated non-linear forms (e.g., Tóth et al., 2015). These formulas can yield different soil hydraulic properties even with the same observed soil texture.

Moreover, B_{sw} , which is a function of soil type, is a key parameter in controlling functional diversity for early and late successional PFTs (Figure 5a). Higher B_{sw} values (>7) favor late successional species in competition, therefore only a small range of B_{sw} values ($1 \sim 7$) can achieve coexistence for early and late successional PFTs

(Figure 6). This successional balance (i.e., either early or late PFT dominant or coexist) associated with changes in B_{sw} is a result of responses of soil moisture to changes in B_{sw} . Higher B_{sw} values are associated with higher percentage of clay fraction, thereby soil water content would decrease slower with increased positive suction head. As a result, the water retention capability is higher as B_{sw} increases. This is evident from the statistically significant difference in soil water content between scenarios with low and high B_{sw} values (Figure S8 in Supporting Information S1). The higher soil water content associated with higher B_{sw} values promote late PFTs. In summary, the changes in soil moisture resulting from changes in B_{sw} differentiate which species is more competitive and determine which species can establish and if there is coexistence for early and late successional PFTs. Evidence of the impacts of soil hydrology on composition and diversity of tree species has been reported in tropical forests (e.g., Chaturvedi, 2018; Hulshof & Spasojevic, 2020; Jiang et al., 2016; Kursar et al., 2005; Martins et al., 2015; Sarvade et al., 2016; Sollins, 1998; Wan et al., 2019). For example, Martins et al. (2015) found that soil types influence tropical forest structure and composition in southern Brazil. Jiang et al. (2016) examined plant composition/diversity and their abiotic determinants across six tropical forest types in Hainan, China. They found that forest composition/diversity is closely associated with soil properties. These results suggest that simultaneous considerations of plant traits and soil hydrological parameters are necessary to capture and predict the overall ecosystem dynamics and species composition in tropical forests.

Furthermore, not only soil properties affect the plant composition/diversity, but tropical forests also tend to modify these properties of soil (Zhang et al., 2018, 2019; Zinke, 1962), which generates important plant-soil feedbacks (Kulmatiski et al., 2008). More field and experimental efforts are needed to gain a better understanding of the hydrology-vegetation feedback mechanisms to explain and maintain species diversity in tropical forests (Sollins, 1998). Such investigation will improve understanding and prediction of the vulnerability and resilience of tropical forest diversity under global changes such as climate change and re/deforestation (Pugh, Arneeth et al., 2019; Pugh, Lindeskog et al., 2019), which is critical for water and forest management (Ghimire et al., 2014; Jirka et al., 2007).

4.2. Uncertainties and Limitations

We note several uncertainties in our study. First, while we derived the ranges for the soil hydrological and physiological parameters from literature to cover a possibly full spectrum of parameter values within reasonable physical bounds (Table 1), it may still be insufficient to fully cover the field conditions, especially across different tropical regions, and no trait covariances (Osnas et al., 2013) were used. For instance, although simulations in this study can better capture the differences in GPP between the wet and dry seasons (Figures 2b and 7b), deficiency in capturing wet-season GPP still exists (Figures 2b and 7b). The capacity and covariance of the selected parameter sets can be expanded to improve the trade-off of the model performance between the wet and dry seasons for GPP to better understand the mechanisms of the dry/wet season differences in tropical rain forest (Fisher et al., 2015).

Second, though modeling two contrasting PFTs provides enough complexity to explore the complicated interactions between hydrology and plant strategies, in reality, tropical forests have richer tree species diversity than the early and late successional PFTs considered in this study. Similar experimental design might apply to larger numbers of PFTs, by which the results can help assess how the number of PFTs can influence the model simulation results.

Third, several previous studies have demonstrated the importance of seasonal and age variations in plant traits in regulating tropical forest seasonality (Kim et al., 2012; Manoli et al., 2018; Restrepo-Coupe et al., 2017; Wu et al., 2016). Although the seasonal and age variations of leaf traits is not implemented in the current model, it is intriguing that the model is still able to simulate the seasonal cycles of water and energy fluxes. This suggests that the seasonal and age variations of leaf traits is not the only factor necessary to explain the tropical forest seasonality. Despite this, we recognize this is a limitation that deserves more efforts in future model developments. On BCI, there are multiple strategies of leaf phenology, such as evergreen, dry deciduous, brevi-deciduous, leaf exchangers, with new flushes occurring at the transition of wet-to-dry and dry-to-wet seasons, even species with multiple flushes a year. For this reason, the effect of phenology might not be so intuitive as it might seem. For example, a more open canopy in the dry season will give access to lower layers to light, which can burst photosynthesis in the understory and partially compensate for the reduced photosynthesis in the canopy. Actually, many species in the understory rely on the dry season for access to light and are prepared to maximize productivity during this time of the year (Tang & Dubayah, 2017). Thus, representing these phenological strategies in models

will be a great challenge that the modeling community needs to face to better predict fluxes in seasonal tropical forests. Representing these seasonality and forest age dependency for plant traits is underway in ELM-FATES but beyond the scope of this study.

Moreover, this study examines the impact of vegetation characteristics and soil properties on tropical forest dynamics through a case study in Panama. Despite the general applicability of the model framework this study developed, we note that the mechanism for supporting plant composition and diversity discussed here may depend on the site conditions in BCI, Panama. For instance, there is small seasonality of GPP in BCI, Panama, while there is modest seasonality of GPP for most of tropical forests in Amazon (Restrepo-Coupe et al., 2017). Further study can be conducted to understand whether the mechanisms to maintain dry-season GPP and plant diversity are robust across different tropical areas.

4.3. Future Directions

4.3.1. Belowground Processes

We find that belowground components play an important role in simulating the dry-season soil moisture and GPP in the humid tropical forests. A greater fraction of deeper roots can better capture dry-season soil moisture and GPP because it allows trees to extract water from deep soil layers. This is consistent with several studies (e.g., Baker et al., 2009; Christoffersen et al., 2014; Restrepo-Coupe et al., 2017). These results highlight the importance of below-ground components in regulating the hydrological and vegetation dynamics in tropical forests and the linkage between aboveground and belowground processes (Porazinska et al., 2003; Schröter et al., 2004). However, the representation of roots is still simplified in current ecosystem demographic models, which usually assume a fixed exponential decay distribution (Zeng, 2001) and therefore limits its capability to capture the response and feedback of roots to the environment (e.g., soil moisture heterogeneity). In addition, root profiles in most ecosystem demographic models do not vary with plant size and height, ignoring the fact that different plants (e.g., canopy and understory species) have very different root distribution, depth, and fraction in different soil layers. Therefore, a time-varying (e.g., related to age and size) rooting system (e.g., DREWNIAK, 2019) should be implemented to improve the representation of belowground processes and investigate the effect of dynamic roots on water uptake and plant productivity.

Though this study illustrates the role of root depth distribution in controlling soil moisture and GPP during the dry season, plant hydraulic redistribution can relocate water from deep to shallow soil layers (Caldwell et al., 1998; Dawson, 1996; Oliveira et al., 2005). This hydraulic lift could be another potential mechanism for sustaining the high GPP and shallow layer soil moisture during the dry season (Caldwell et al., 1998; Oliveira et al., 2005). Including the diversity of plant hydraulic traits may increase in the ability of the model to differentiate the strategies of extracting water from the soil. Without including a plant hydraulics scheme and consideration of sensitivities of plant hydraulics-associated parameters may skew the sensitivity to soil hydrology-related parameters explored in this study. A more comprehensive analysis of plant hydrologic traits using a plant hydrodynamic module should provide additional insights to further explore the mechanisms that sustain the dry-season soil water content, plant gas exchange, and maintain diversity.

4.3.2. Soil Functions

A growing body of literature has documented the overlooked importance of small-scale soil structure features in affecting large-scale hydrologic and climatic processes (e.g., Wei et al., 2014). For instance, tree root growth and decay, earthworm burrowing, and soil shrinking/swelling create preferential flow paths and can change the partitioning of precipitation into runoff, root zone moisture, and groundwater recharge in tropical catchments (Beven & Germann, 2013; Cheng et al., 2017, 2018, 2019; Litt et al., 2020). These hydrological processes can interact with the carbon cycle to further alter the surface fluxes and plant growth (Bundt et al., 2001; Don et al., 2011; Hagedorn & Bundt, 2002). However, inadequate representation of soil structural characteristics in the context of ESMS constrains our ability to accurately assess and attribute these impacts. Additional sensitivity analysis could be conducted by incorporating soil structure parameters/functions into ESMS (Clark et al., 2015; Fisher & Koven, 2020). Moreover, more field studies, such as water partitioning using stable isotopes (Silvertown et al., 2015), measuring soil water retention curve (Hodnett & Tomasella, 2002) and root architecture (Guo et al., 2020), are needed to determine the soil texture parameters and below-ground allocations and processes (Robinson et al., 2008).

Conflict of Interest

The authors declare no conflict of interest.

Data Availability Statement

The ELM-FATES outputs are publicly available at <https://doi.org/10.5281/zenodo.5242991>. The meteorological data were provided by the Physical Monitoring Program of the Smithsonian Tropical Research Institute.

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