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# Assessing Simulations of Forest Hurricane Disturbance and Recovery in Puerto Rico by ELM-FATES Using Field Measurements

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**Abstract** In the past three decades, Puerto Rico (PR) experienced five hurricanes that met or exceeded category three, and they caused severe forest structural damage and elevated tree mortality. To improve our mechanistic understanding of hurricane impacts on tropical forests and assess hurricane-affected forest dynamics in Earth system models, we use in situ forest measurements at the Bisley Experimental Watersheds in Northeast PR to evaluate the Functionally Assembled Terrestrial Ecosystem Simulator coupled with the Energy Exascale Earth System Model Land Model (ELM-FATES). The observations show that before Hurricane Hugo, 77.3% of the aboveground biomass (AGB) is from the shade-tolerant plant function type (PFT). The Hugo-induced mortality rates are over ~50%, and they induce a ~39% AGB reduction, which recovers to a level like the pre-Hugo condition in 2014, following a second, lower intensity hurricane, Georges. We perform numerical experiments that simulate damage from Hugo and Georges on the forests, including defoliation, sapwood and structural biomass damage, and hurricane-induced mortality. ELM-FATES can reasonably represent coexistence between the two PFTs–light-demanding and shade-tolerant–for both the pre-Hugo and post-Hugo conditions. The model represents a reasonable size distribution of mid-and large-sized trees although it underestimates AGB, likely due to the overestimated nonhurricane mortality. ELM-FATES temporarily stimulated leaf biomass and diameter increment after Georges, an effect that should be tested with observations of future hurricane defoliation events. This research indicates that addressing model-data mismatches in tree mortality and understory dynamics are essential to simulation of more extreme hurricane effects under climate change.

**Plain Language Summary** Using both field measurements at the Bisley Experimental Watersheds in the Luquillo Experimental Forest of Northeast Puerto Rico and the Functionally Assembled Terrestrial Ecosystem Simulator coupled with the Energy Exascale Earth System Model Land Model (ELM-FATES), we perform hurricane disturbance simulations, which represent damage of two hurricanes, Hugo (September 1989) and Georges (September 1998), on the Bisley forests. Based on the parametrization that was constrained by field measurements and trait observations, ELM-FATES can reasonably represent coexistence between plant types with different growth and mortality rates at Bisley. The size distribution of trees is also represented well although aboveground biomass is underestimated. The model-data comparison also shows that ELM-FATES can capture the long-term forest canopy dynamics after relatively high- and then low-intensity hurricane disturbances. Overall, ELM-FATES shows promise by capturing the essential demographic processes needed to accurately simulate hurricane disturbance and forest recovery. This research provides a foundation for pantropical simulation of cyclone disturbance and forest recovery in dynamic global vegetation models, although improvements may be required to simulate more extreme hurricane responses.

**Key Points:**

- Hurricane Hugo induced a 39% reduction in aboveground biomass in Bisley forests, which can be represented well by ELM-FATES
- ELM-FATES represents a reasonable size distribution of mid- and large-sized trees but underestimates above-ground biomass
- ELM-FATES captures canopy tree dynamics but fails to capture the observed understory biomass due to the seedling and understory dynamics

**Supporting Information:**

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

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## 1. Introduction

Hurricanes are an important disturbance that reduce aboveground biomass (AGB) (Uriarte et al., 2019; Zhang et al., 2022a, 2022b), and in the long term affect the biodiversity, species interactions, spatiotemporal dynamics of populations and communities, and biogeochemical cycling of coastal tropical forests (Brokaw et al., 2012; Chazdon, 2003; Heartsill-Scalley, 2017; Walker, 2012; Zhang et al., 2022a, 2022b; Zimmerman et al., 2021). Heavy precipitation from hurricanes results in soil saturation, which makes uprooting happen more easily

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(Xi, 2015; Xi et al., 2008), and induces landslides (Arnone et al., 2011, 2015; Lepore et al., 2012, 2013). Moreover, severe hurricanes usually result in elevated tree mortality rates, where strong winds defoliate the canopy, break branches, and uproot and snap stems (Zhang et al., 2022a). The overall impacts of hurricane disturbance on tropical forests are determined by a variety of factors, including hurricane severity (Parker et al., 2018), prehurricane environmental conditions (Hall et al., 2020; Uriarte et al., 2019), forest structure (Zhang et al., 2022c), and traits and size of individual trees (Bannar-Martin & Lewis, 2011; Curran et al., 2008).

Between 1989 and 2017, Puerto Rico experienced five major hurricanes (i.e., category three or above with peak wind speed greater than 178 km $hr^{-1}$). Hurricane Hugo (18 September 1989) is one of the major hurricanes that hit the Luquillo Experimental Forest (LEF) as a category three hurricane (Walker, 1991). Hurricane Hugo defoliated the entire area, and reduced the aboveground biomass by 50% in Bisley (Heartsill-Scalley et al., 2010). Hurricane Georges also hit Puerto Rico (21 September 1998) as a category three hurricane, causing widespread damage across the island. Exposure of the LEF forests to storm winds was far greater during Hurricane Hugo than during Hurricane Georges because of the track of the storms relative to the position of LEF (Uriarte et al., 2019). Irma and Maria are another two major hurricanes that disturbed Bisley in 2017. These hurricanes caused intense forest mortality and severe forest structural damage (Uriarte et al., 2019).

With the establishment of long-term measurements, the LEF, which is located in northeastern Puerto Rico with two intensive study sites, El Verde (18 19’N, 65 49’W; established in 1943) on the west and Bisley Experimental Watersheds (18 20’N, 65 50’W; established in 1987) on the east (Heartsill-Scalley, 2017), has been a key area for the study of hurricane impacts on forests including tree damage, mortality (Zimmerman et al., 1994), and litterfall (Lodge et al., 1991; Scatena et al., 1996). Previous field censuses performed at these two locations have demonstrated similarities and differences between the hurricane effects at two study sites after Hurricane Hugo (Heartsill-Scalley, 2017; Heartsill-Scalley et al., 2010). The overall findings are (a) a rapid increase in stem density of light-demanding species (*Cecropia schreberiana* and *Psychotria berteroana*) at both sites 10 years after the hurricane (Heartsill-Scalley, 2017), (b) a faster shift in species composition at Bisley as a result of stronger hurricane effects on stem density and basal area (Heartsill-Scalley, 2017), and (c) varied recovery rates among different species that experienced different hurricane disturbance intensities (Zimmerman et al., 1994). In this study, we focus on Hugo and Georges, for which census data allow (a) a comprehensive understanding of the long-term hurricane impacts on forest dynamics, and (b) parameterization and evaluation of the forest dynamics simulated by process-based models (Uriarte et al., 2019; Zhang et al., 2022a).

Earth system models (ESMs) are an essential tool to study spatial and temporal variation in land surface processes, and to project terrestrial biosphere change under future climate conditions. Among 37 models from the Climate Model Intercomparison Project Phase 6 (CMIP6; Dirmeyer et al., 2021), nine of the models have dynamic vegetation modules included. For these ESMs with vegetation dynamics implemented, only a few models include processes that can represent hurricane disturbance (e.g., structural damage, crown damage, and windthrow). For example, ORCHIDEE-CAN is the only land surface component that can capture the forest structure changes due to storm disturbance (Chen et al., 2018). Negron-Juárez et al. (2020) used the Functionally Assembled Terrestrial Ecosystem Simulator (FATES), which has been coupled with the Energy Exascale Earth System Model (E3SM) Land Model (ELM-FATES) to simulate windthrow disturbance by imposing an event with 70% tree mortality. A crown damage module, which represents reduction in a tree's crown area and leaf and branch biomass, was developed within ELM-FATES (Needham et al., 2022). This crown damage module allows associated variation in the ratio of aboveground to belowground plant tissue, and generally decreases growth rates. However, processes related to hurricane-induced damage on forests are either not represented or still under development in most dynamic global vegetation models (DGVMs). Therefore, the enhanced representation of forest disturbance and recovery in ESMs is essential to improved quantification of the impacts of disturbance on forest ecosystem function and the carbon cycle at various spatial scales.

Leveraging new ELM-FATES capabilities for representing canopy damage and mortality resulting from hurricanes (Shi et al., 2024), this study performs a detailed model-data comparison at the Bisley Experimental Watersheds in Northeast Puerto Rico, which has long-term (i.e., since 1989) forest observations. This paper aims to enhance the understanding of (a) the short-term (i.e., 3 months before and after) forest plant functional type (PFT) composition, structure, and function changes, (b) the long-term forest recovery following a sequence of hurricanes (i.e., Hugo and Georges) differing in intensities, and (c) strengths and limitations of ELM-FATES in



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**Table 1**
*Observed Hugo-Induced Mortality, ELM-FATES Total Mortality, and the Hurricane Mortality Values Applied to ELM-FATES*

| Mortality | Light-demanding (%) | Shade-tolerant (%) |
|---|---|---|
| Observation | 64.7 | 50.3 |
| ELM-FATES background | 6.2 | 2.8 |
| ELM-FATES hurricane | 58.5 | 47.5 |

reproducing damage and recovery dynamics due to hurricane disturbances. We simulate hurricane-induced forest damage, including defoliation, sapwood and structural organ damage-induced biomass reduction, and hurricane-induced tree mortality. Overall, this research focuses on the dynamic representations of cyclone-induced forest damage and recovery processes within an ESM, and addresses the essential role of physical representations of storm-induced forest disturbance in DGVMs integrated into ESMs.

## 2. Method

### 2.1. Study Site and Field Censuses Data

Puerto Rico experienced agricultural abandonment and forest cover increase since the late 1940s (Marín-Spiotta et al., 2007). The Luquillo Experimental Forest (LEF) is located in northeastern Puerto Rico where land use in the lower elevations changed dramatically between 1936 and 1988 from sugarcane and pasture to forests (Thomlinson et al., 1996). In recent decades, LEF has developed to an ecosystem mostly covered by Tabonuco forest at elevations below 600 m, which is categorized as a subtropical wet forest (Ewel & Whitmore, 1973) characterized by trees with canopies ranging from 25 to 30 m in height, palms, arboreal ferns, and lianas (i.e., woody vines; Heartsill-Scalley, 2017). The climatological monthly temperature ranges from 23.5 to 27°C, and the climatological rainfall is 3,208 mm year$^{-1}$ (Brown et al., 1983; Garcia-Martino et al., 1996) in the watershed. Bisley Experimental Watersheds is on the east side of the LEF.

In 1989, 86 permanent forest plots with a total cumulative sampled area of 0.71 ha were established in Bisley (Heartsill-Scalley et al., 2010; Zhang et al., 2022d). All forest plots in Bisley were censused at a 5-year interval, with height and diameter measurements collected for all stems ≧2.5 cm diameter at 1.3 m above the ground (i.e., DBH). Since the establishment of the plots, three major hurricanes disturbed the forest at this site: Hurricane Hugo in 1989, Hurricane Georges in 1998, and Hurricane Maria in 2017 (Uriarte et al., 2019). Before Hurricane Hugo, basal area at Bisley ranged from 35 to 40 m$^2$ per hectare (Heartsill-Scalley, 2017). Hurricane Hugo caused a 50% reduction of basal area, which nearly recovered in 10 years, and it also induced a reduction of stem density, which reached a maximum value 10 years (i.e., 1999) after the hurricane at Bisley (Heartsill-Scalley, 2017). Due to the availability of repeat forest census data through this interval, we focused our study on forest composition, tree size distribution, and growth rate associated with hurricane disturbance.

### 2.2. Field Data Processing

The key census-based metrics used in this study include hurricane-induced mortality rates, aboveground biomass (AGB), leaf biomass, DBH increment rate, stem density, and litterfall rate. Trees were grouped into size classes from 2.5 to 97.5 cm with a 5-cm DBH span for each size class. All tree species were also classified into two PFTs, light-demanding or shade-tolerant, following the method of Adame et al. (2014).

We calculated mortality rates by both size class and PFT for each census interval following Hurricane Hugo, that is, from 1989 until 2014 with the 5-year interval. To calculate mortality rates, we used the Kohyama et al. (2020) equation

$$M = 1 - (N_2 - N_1)^{(1/n)} \tag{1}$$

where $M$ is mortality, $N_2$ is the number of live stems in census two, $N_1$ is the number of stems in census one, and $n$ is the number of years between census two and one. Here, one of the censuses was performed 3 months after Hugo, and it was used to estimate the hurricane mortality rates induced by Hugo for the light-demanding and shade-tolerant PFTs (Table 1). In this study, the 3 months before and 3 months after Hurricane Hugo time frames are defined as pre- and post-Hugo, respectively.

We calculated AGB values based on census data 3 months before Hugo and 3 months after Hugo by using the Chave et al. (2014) allometric equation



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$$\text{Biomass}_{\text{Aboveground}} = 0.0673 \times \left(\text{Density}_{\text{wood}} \times D^2 \times H\right)^{0.976} \tag{2}$$

where $\text{Biomass}_{\text{Aboveground}}$ is AGB, $\text{Density}_{\text{wood}}$ is wood density, $D$ is DBH, and H is tree height. The values of $D$ and H are from the censuses. We applied the wood density values of the light-demanding and shade-tolerant PFTs used by ELM-FATES (Table S1 in Supporting Information S1) to Equation 2 to estimate the AGB of different PFTs for consistency.

Leaf biomass ($\text{Biomass}_{\text{leaf}}$) is estimated with the Scatena et al. (1993) equation, which has been tested at Bisley and uses diameter (D), tree height (H), and specific wood density ($\text{Density}_{\text{wood}}$):

$$\text{Biomass}_{\text{leaf}} = \exp\left(0.678 \times \ln\left(D^2 \times H \times \text{Density}_{\text{wood}} - 4.154\right)\right. \tag{3}$$

In ELM-FATES, DBH increment is output by the canopy layer, because differences in light availability in canopy and understory cohorts influence allocation to DBH growth. Because we did not have estimates of canopy position for individual trees in the census data, we adopted the method described in Needham et al. (2020), in which DBH increment rates are estimated for slow- and fast-growing trees separately, corresponding roughly to canopy position. Slow-growing trees likely correspond to understory individuals, while fast-growing trees are likely to be individuals in the canopy or in a canopy gap. We thus divided the census data into the 95% of trees with the lowest DBH increment, and the 5% of trees with the highest DBH increment and fit gamma distributions to each group separately.

$$\text{dbh} = \text{Gamma}(a, b) \tag{4}$$

where dbh is the annual DBH increment and a and b are the shape and rate parameters of the gamma distribution, respectively. We compared the expectation of growth for each distribution to the DBH increments in ELM-FATES.

In this study, we also compared the litterfall rates between observations and the model simulations using data from a litterfall database developed by Bomfim et al. (2022). The database includes litterfall information at Bisley covering the time frame before and after Hurricane Hugo. At the Bisley site, litterfall was collected from 0.25 $m^2$ baskets every 2 weeks. Hugo-induced litterfall was collected 9 days after the storm on the regularly scheduled collection date, and sample statistics were calculated from 41 of the 60 baskets that survived the storm (Lodge et al., 1991). Thus, we used this information to evaluate ELM-FATES-simulated litterfall rates 20 days before and 10 days after Hugo.

### 2.3. ELM-FATES and Model Parameterization

In this study, we used ELM-FATES (Fisher et al., 2015; Holm et al., 2020; Koven et al., 2020) to study the prehurricane forest status and posthurricane forest recoveries at the Bisley site. ELM is based on the Community Land Model Version 4.5 (CLM4.5) with new options for representing soil hydrology and biogeochemistry added to enable analysis of structural uncertainty related to carbon-climate feedbacks (Burrows et al., 2020). ELM-FATES is developed with the Ecosystem Demography (ED) concept, which is a cohort-based representation of vegetation dynamics (Moorcroft et al., 2001). Different from the big-leaf structure, ED separates the landscape into explicit patches according to time since the last disturbance. In each patch, plant individuals are grouped into cohorts by PFT and height classes. This grouping method captures the dynamic matrix of disturbance recovery processes in a typical forest ecosystem but is more computationally efficient than tracking individuals. Thus, ELM-FATES tracks the changing abundance of trees of different sizes and PFTs arising from tree growth, mortality, recruitment, and the impact of disturbances. ELM-FATES differs from ED with respect to carbon allocation and allometry and the perfect plasticity approximation (PPA), which describes the crown spatial arrangements throughout the canopy and organizes cohorts into discrete canopy layers (Fisher et al., 2010; Purves et al., 2008).

Using ELM-FATES, Shi et al. (2024) performed comprehensive model parameterization and parameter importance quantification at Bisley. In this study, we used the same light-demanding and shade-tolerant PFTs that were originally defined by Adame et al. (2014) and used by Shi et al. (2024), but updated some key parameters

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that regulate background mortality, the senescence of relatively large-sized trees, and the nitrogen to carbon ratio of leaves. Specifically, the initial parameterizations from Shi et al. (2024) resulted in too many large trees (~7 $ha^{-1}$ > 100 cm; Figure S1 in Supporting Information S1), which are inconsistent with the observations. Therefore, one of the key parameter updates is implementing size-based senescence (Needham et al., 2020) to achieve more realistic stem density distributions (Text S1 in Supporting Information S1). This updated parameterization reasonably represents environmental constraints on the forests of Bisley, and particularly improves the simulation of stem density distribution between DBH groups (Figure 2a).

ELM-FATES has five AGB allometry equation options, and we chose to use the Chave et al. (2014) to be consistent with the method used with field data to estimate AGB. As discussed in Section 2.2, the parameter values in Equation 2 and the wood density values of the two PFTs are exactly matched between field data processing and ELM-FATES. In addition, the Martínez -Cano et al. (2019) diameter to height allometry equation was used in the simulation of this study. Specifically, this diameter to height allometry equation is based on the Generalized Michaelis-Menten (GMM) function (Thomas, 1996), and parameterized with 9,884 individuals at Barro Colorado Island, Panama. The GMM function was also broadly tested in many other regions and shows a reasonably high accuracy in representing the diameter to height relationships (e.g., Fayolle et al., 2016; Howell et al., 2022). Using generalizable allometries rather than locally derived allometries is important for applying ELM-FATES to larger regions and pantropically. The field censuses provide estimates of AGB, while ELM-FATES simulates both the aboveground and total biomass. A parameter determining the fraction of woody biomass that is aboveground is set to 0.78 for both PFTs. The same parameterization is used for both the model spin-up and hurricane damage simulations.

### 2.4. Experimental Design

In this study, we used the meteorological forcing data from the pixel nearest Bisley in the Daymet product (1950–2017) for model spin-up and hurricane-disturbance simulations (Thornton et al., 2021). Daymet was temporally downscaled to a 3-hourly time step, where the temporal downscaling preserved the relative magnitude in each subdaily time step and maintained the total and average Daymet values on each day. The downscaling used both the Global Soil Wetness Project Version 3 (GSWP3; Yoshimura & Kanamitsu, 2013) and the NCEP North American Regional Reanalysis (NARR; Mesinger et al., 2006), and the details were presented in Kao et al. (2022) and Shi et al. (2024). Previous studies suggest that the spin-up time frame of FATES is 300 years in tropical forest, at which point the model reaches relatively stable AGB and stem density distributions (e.g., Koven et al., 2020; Shi et al., 2024). Thus, we used the Daymet data from 1950 to 1959 30 times for the model spin-up. The hurricane-disturbance simulations were initialized with the spun-up results and run for 1950–2017. To represent hurricanes with various intensities and quantify their impacts on the Bisley forests at a long time frame (i.e., over decades), we implemented two hurricane events, Hurricane Hugo and Hurricane Georges, which happened on 18 September 1989 and 21 September 1998, respectively. Hurricane Hugo brought a much larger impact on the Bisley forests than Hurricane Georges did, because the track of Georges was over the southern part of Puerto Rico (Uriarte et al., 2019). Specifically, we assumed that Hurricane Hugo induced defoliation, sapwood and structural damage, and tree mortality, and Hurricane Georges only induced defoliation on the Bisley forests. By simulating both hurricanes in sequence, we quantify how hurricanes with a range of intensities affect the Bisley forest and can compare simulations to observed long-term forest response, which was punctuated by Hurricane Georges.

To implement these different types of hurricane disturbances in ELM-FATES, we first prescribed defoliation via the phenology module, specifying the days with leaf-off based upon the dates of these two hurricanes. The "leaf-on" parameter was set to initiate leaf regrowth 15 days after the hurricanes. Hurricane Hugo-induced sapwood and structural biomass loss was represented by increasing the turnover rates of these two components in the model. The default turnover rate of these two components is 150 years, which was increased to 0.014 years (i.e., 5 days) on the day the forests experienced Hurricane Hugo. This induces an integrated loss of ~20% of the woody biomass. Because Hurricane Hugo brought a severe impact to the Bisley forests, we also implemented hurricane-induced mortality in ELM-FATES (Shi et al., 2024) on the day that Hugo happened. The hurricane mortality rates in ELM-FATES were applied on the date of the hurricane, using the observed Hugo-induced mortality rates minus the climatological total mortality rates estimated by ELM-FATES. This approach excludes other mortality components calculated by the model. The total mortality rate in ELM-FATES arises from a variety of mortality components, including carbon starvation, hydraulic failure, background mortality (i.e., residual mortality that is not explicitly simulated by existing algorithms in ELM-FATES, such as background wind disturbance, insect, or other disease processes), freezing stress, and, optionally, size-dependent senescence and age-dependent senescence, all of which reflect plant responses to environmental factors and to ecosystem structure. The observed Hugo-induced mortality rates, the ELM-FATES climatological mean, and their difference are included in Table 1, and we used the mortality values 58.5% and 47.5% as Hugo-induced mortality rates for the light-demanding and shade-tolerant PFTs, respectively, to perform the hurricane damage simulations. The observed mortality rates from 1994 to 2014 are included in Table S2 of Supporting Information S1. Overall, the three disturbance types were applied into the model in the following order: (a) defoliation, (b) hurricane-induced mortality, and (c) structural damage. Thus, the structural damage was only applied to the surviving trees.

As discussed in Section 2.2, the DBH increment rate is one of the metrics evaluated by this study. We noticed that DBH increment rates in our simulation peaked in 1999, a year after a defoliation event was implemented to represent Hurricane Georges in ELM-FATES. To understand the reasons for the DBH increment peak, we also performed a simulation without implementation of the impacts of Hurricane Georges, that is without the defoliation event in 1998.

## 3. Results

### 3.1. ELM-FATES Spin-Up

In the last spin-up year, the total biomass of the light-demanding and shade-tolerant PFTs is 3.4 and 9.8 kgC $m^{-2}$, respectively, and their contributions to the total biomass are 25.8% and 74.2%, respectively (Figure S3a in Supporting Information S1). The leaf biomass values of the light-demanding and shade-tolerant PFTs are 76.0 and 84.1 g C $m^{-2}$ corresponding to 47.5% and 52.5% of the total leaf biomass, respectively (Figure S3b in Supporting Information S1). The spin-up trajectories suggest that the total biomass is still developing for both PFTs (Figure S3a in Supporting Information S1). Specifically, the total biomass trends are −0.01 and 0.04 kg C $m^{-2}$ $year^{-1}$ in the last 10 spin-up years for the light-demanding and shade-tolerant PFTs, respectively. Bisley forest is not in equilibrium since it is recovering from previous disturbance, and we therefore do not require PFT distributions to have reached equilibrium in our spin-up procedure. We further investigated the ELM-FATES simulated pre-Hugo AGB partitions and found that they are consistent with that suggested by observational data (Section 3.2). Thus, this spun-up status is appropriate to be used for our hurricane-induced forest damage simulations.

### 3.2. The Hurricane Event-Based Model-Data Comparison

#### 3.2.1. Pre- and Post-Hugo Biomass

Overall, AGB values were underestimated by ELM-FATES, and leaf biomass values were overestimated for both the pre-Hugo and post-Hugo conditions. The pre-Hugo total AGB estimated by ELM-FATES was 70.1% of the observed pre-Hugo AGB (Table 2). However, the model reasonably represented the pre-Hugo AGB partition between the light-demanding and shade-tolerant PFTs. The observed pre-Hugo AGB values were 3.57 and 12.19 kgC $m^{-2}$ for the light-demanding and shade-tolerant PFTs, respectively, while the corresponding values from ELM-FATES were 2.49 and 8.56 kgC $m^{-2}$. In contrast, ELM-FATES-simulated pre-Hugo total leaf biomass was 25.1 gC $m^{-2}$ more than that suggested by the field measurements, with ELM-FATES overestimating pre-Hugo leaf biomass of the light-demanding PFT compared to the observations (Tables 2 and 3). This discrepancy between pre-Hugo patterns of AGB and leaf biomass suggests a carbon allocation difference between the observations and the model representation.

The observed Hugo-induced AGB reduction (6.11 kgC $m^{-2}$) and leaf biomass reduction (80.0 gC $m^{-2}$) were realistically represented by ELM-FATES (6.11 and 80.4 gC $m^{-2}$; Tables 2 and 3). While the simulated post-Hugo AGB was only ∼50% of that represented by the observations, the post-Hugo AGB partitions between PFTs were reasonably represented by the model (Table 2). Due to the impacts of Hurricane Hugo, the observed AGB of the light-demanding PFT was reduced by 1.74 kgC $m^{-2}$, while that from ELM-FATES was reduced by 1.54 kgC $m^{-2}$. The AGB of the shade-tolerant PFT was also reduced dramatically, with an observed reduction of 4.37 kgC $m^{-2}$, and ELM-FATES predictions of 4.67 kgC $m^{-2}$. Furthermore, the light-demanding leaf biomass was reduced by 30.0 and 33.1 g C $m^{-2}$ in the observations and ELM-FATES, respectively, with the corresponding leaf biomass reductions for the shade-tolerant PFT 50 and 47.3 g C $m^{-2}$. In general, the simulated post-Hugo total leaf biomass was 24.7 g C $m^{-2}$ more than that in the observations, which is primarily due to the overestimated leaf biomass for the light-demanding PFT (Table 3).



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**Table 2**
*The Pre- and Post-Hugo AGB for the Light-Demanding and Shade-Tolerant PFTs*

| | Pre-Hugo biomass kgC $m^{-2}$ (%) | | | Post-Hugo biomass kgC $m^{-2}$ (%) | | |
|---|---|---|---|---|---|---|
| PFT | Observation | ELM-FATES | Difference | Observation | ELM-FATES | Difference |
| LD | 3.57 (22.7%) | 2.49 (22.5%) | 1.08 | 1.83 (18.5%) | 0.95 (19.2%) | 0.88 |
| ST | 12.19 (77.3%) | 8.56 (77.5%) | 3.63 | 7.82 (81.1%) | 3.89 (80.8%) | 3.93 |
| Total | 15.76 (100%) | 11.05 (100%) | 4.71 | 9.65 (100%) | 4.94 (100%) | 4.71 |

*Note.* LD represents light-demanding, and ST represents shade-tolerant. Columns of "Difference" represent the underestimated biomass by ELM-FATES.

In this study, Hurricane damage was imposed in ELM-FATES to match observations, and this leads to AGB and total biomass decline from 1989 to 1990. The 1989 annual mean AGB values for the light-demanding and shade-tolerant PFTs are 2.04 and 7.21 kgC $m^{-2}$, respectively, while the same two values in 1990 are 1.04 and 4.07 kgC $m^{-2}$, respectively (Figure 1 and Figure S4 in Supporting Information S1). Here, the annual mean AGB in 1989 also considers the pre-Hugo period, when the forests are intact. Overall, these model-data comparisons show that AGB values are underestimated by ELM-FATES and leaf biomass values are overestimated by ELM-FATES for both the pre-Hugo and post-Hugo conditions.

### 3.2.2. Pre- and Post-Hugo Stem Density Changes

To further evaluate ELM-FATES-predicted pre-Hugo forest structure, we examined the stem density across tree size classes (Figure 2a and Table S3 in Supporting Information S1). The size bin with the largest observed stem density is the light-demanding PFT at 5–10 cm (i.e., 7.5 cm for the midsize trees), while that of ELM-FATES is the shade-tolerant PFT at 2.5–5 cm (Table S3 in Supporting Information S1). For mid- and large-size trees (size bins with the mean DBH values ranging from 27.5 to 62.5 cm), the observed stem density is always higher than that simulated by ELM-FATES. In contrast, ELM-FATES simulates a stem density of 10 trees per hectare for mean DBH values ≥ 67.5 cm, while the observed stem density is 6 trees per hectare. Thus, the pre-Hugo stem density is underestimated for midsize trees and overestimated for very large trees by the model.

After Hugo, the stem density of the light-demanding PFT peaks in the 2.5–5 cm size bin in the observations, but in the 5–10 cm bin in ELM-FATES. In contrast, the peak stem density of the shade-tolerant PFT is in the 2.5–5 cm bin in ELM-FATES and the 5–10 cm bin in the observations (Figure 2b and Table S4 in Supporting Information S1). After Hurricane Hugo, observed stem density is generally larger than that of ELM-FATES for midsize trees, except for light-demanding stem PFT density in the 25–30 cm size bin (Table S4 in Supporting Information S1). In the ≥65–70 cm size bins, observations indicate a stem density of 5 trees per hectare, while ELM-FATES predicts 3 trees per hectare. Based on the observations, the 5–10 cm size bin has the largest reduction in stem density (i.e., 508 trees per hectare), while the reduction is greatest in the 2.5–5 cm size bin in ELM-FATES (i.e., 329 trees per hectare). Both the observations and the model show more small-tree (with the mean DBH values 3.8–22.5 cm) than large-tree mortality (Tables S3 and S4 in Supporting Information S1). In other words, both observations and ELM-FATES suggest that large trees are more resistant to hurricane damage.

**Table 3**
*The Pre- and Post-Hugo Leaf Biomass for the Light-Demanding and Shade-Tolerant PFTs*

| | Pre-Hugo leaf biomass gC $m^{-2}$ (%) | | | Post-Hugo leaf biomass gC $m^{-2}$ (%) | | |
|---|---|---|---|---|---|---|
| PFT | Observation | ELM-FATES | Difference | Observation | ELM-FATES | Difference |
| LD | 56.0 (27.2%) | 83.1 (37.6%) | −27.1 | 26.0 (22.4%) | 50.0 (35.5%) | −24.0 |
| ST | 140.0 (72.8%) | 138.0 (62.4%) | 2.0 | 90.0 (77.6%) | 90.7 (64.5%) | −0.7 |
| Total | 196.0 (100%) | 221.1 (100%) | −25.1 | 116.0 (100%) | 140.7 (100%) | −24.7 |

*Note.* LD represents light-demanding, and ST represents shade-tolerant. Columns of "Difference" represents the leaf biomass obtained from observations minus ELM-FATES.

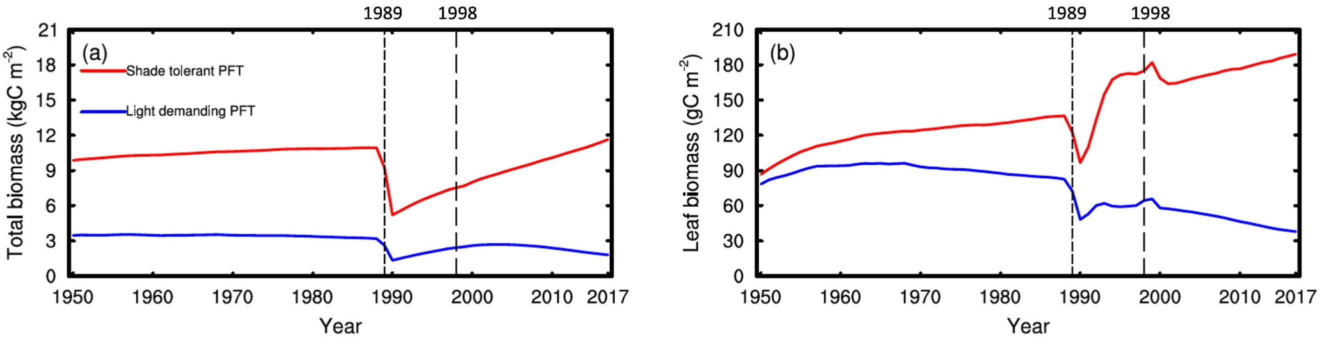


**Figure 1.** The (a) total biomass and (b) leaf biomass trends of the light-demanding and shade-tolerant PFTs during 1950–2017. The changes are at the yearly time scale, and the years representing hurricanes Hugo (1989) and Georges (1998) are labeled with dashed lines. The variations of these two variables at the monthly time scale are included in Figure S4 of Supporting Information S1.

### 3.2.3. Pre- and Post-Hugo Aboveground Litterfall Changes

We also compared the aboveground litterfall rates between the observations and ELM-FATES. The observed pre-Hugo aboveground litterfall rate is 1.14 gC $m^{-2}$ $day^{-1}$, while that from ELM-FATES is 1.80 gC $m^{-2}$ $day^{-1}$, 1.6 times of the observed aboveground litterfall rate. Based on the observation, a dramatic increase in aboveground litterfall (519.84 gC $m^{-2}$ $day^{-1}$) was induced by the disturbance of Hurricane Hugo. Together, defoliation, sapwood and structural biomass damage, and hurricane mortality rates result in an aboveground litterfall rate of 506.22 gC $m^{-2}$ $day^{-1}$, which suggests that ELM-FATES has the hurricane-induced litterfall rates well represented. Overall, the aboveground litterfall rates are reasonably represented by ELM-FATES for both the pre- and post-Hugo conditions.

## 3.3. Forest Recovery Represented by the Observations and ELM-FATES During 1994–2014

### 3.3.1. Post-Hugo AGB

After Hurricane Hugo, both observations and ELM-FATES show AGB increase. In ELM-FATES, it takes 43 months and ∼17 years for leaf carbon and sapwood biomass to recovery to the pre-Hugo levels, respectively (Figure not shown). In 2014, observed AGB was 15.0 kgC $m^{-2}$, which is 95% of observed pre-Hugo AGB (i.e., 15.8 kgC $m^{-2}$), while that from ELM-FATES is 10.1 kgC $m^{-2}$, 91.4% of the pre-Hugo simulated AGB. While ELM-FATES-simulated post-Hugo AGB is still below observations, the model represents a reasonable PFT partition and a AGB recovery trend. Based on the observations, the shade-tolerant AGB was 70%–73.9% of total AGB during 1994–2014, which is lower than the pre-Hugo value (i.e., 77.3%; Table 2), while the ratio from ELM-FATES ranges from 77.1% to 84.3%, which is higher than the ratio before Hugo (77.5%; Table 2). Both

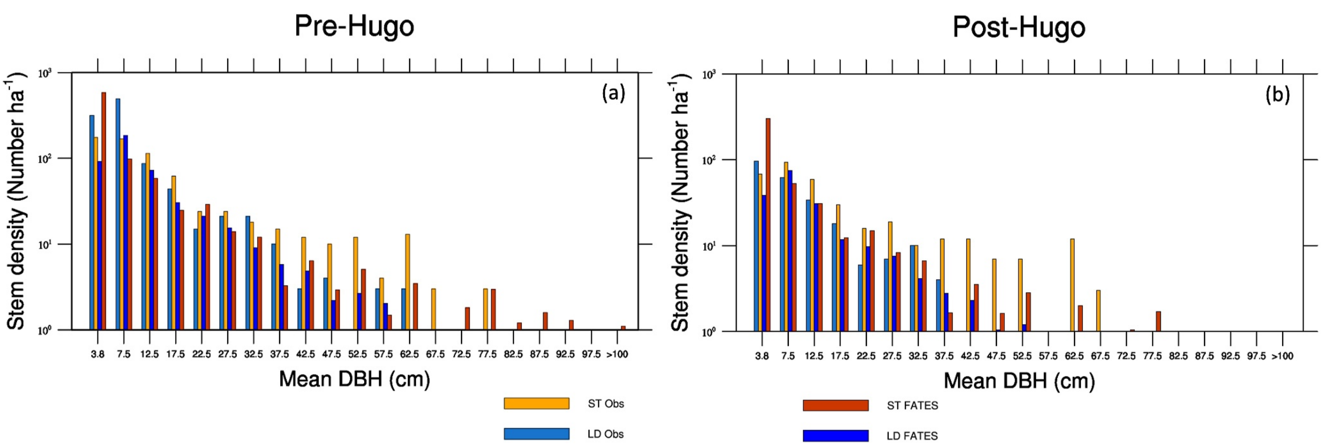


**Figure 2.** (a) Pre-Hugo and (b) post-Hugo stem density distribution between the light-demanding (LD) and shade-tolerant (ST) PFTs for both observations and ELM-FATES. The midsize DBH values are labeled in the *x*-axis.



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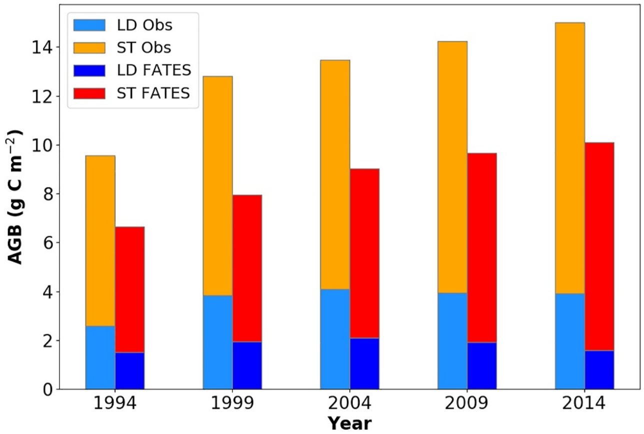


**Figure 3.** Observed and ELM-FATES-simulated post-Hugo AGB for the light-demanding (LD) and shade-tolerant (ST) PFTs in each censused year.

observations and the model represent a peak in the shade-tolerant fraction of AGB 3 months after Hugo (Table 2), and a slow reduction of this ratio afterward. The model-data comparison further shows that the light-demanding AGB values from both the observations and ELM-FATES peaked in 2004, at 4.08 and 2.09 kgC $m^{-2}$, respectively. The post-Hugo biomass increase is primarily attributed to the AGB increase of the shade-tolerant PFT (Figure 3), and during 1994–2014, the shade-tolerant AGB observed values increased from 6.97 to 11.08 kgC $m^{-2}$ and modeled values from 5.12 to 8.52 kgC $m^{-2}$ as suggested by the observations and ELM-FATES, respectively. Thus, the model was able to capture the forest dynamics after a relatively high intensity hurricane disturbance.

### 3.3.2. Post-Hugo and Post-Georges DBH Increment

To study the posthurricane forest recovery, we also compared DBH increment rates between the observations and ELM-FATES for both PFTs. After Hurricane Hugo, the observed DBH increment rates were highest in the first 5 years of recovery (i.e., 1989–1994), with the maximum rates of 1.30 and 1.13 cm DBH $year^{-1}$ across different size groups for the light-demanding and shade-tolerant PFTs, respectively. The DBH increment rates of large trees (i.e., DBH > 60 cm) have a decreasing trend for the light-demanding PFT and an increasing trend for the shade-tolerant PFT after 1994. Starting from 1994, the DBH increment rates for smaller trees (i.e., DBH < 40 cm) tend to increase for the light-demanding PFT and be stable for the shade-tolerant PFT (Figures 4a and 4c). We also estimated the ELM-FATES-simulated DBH increment rates for the same intervals, and found that they are higher than those observed for both PFTs. During 1989–2014, the largest increment rates among all size groups are 2.18 and 1.4 cm DBH $year^{-1}$ for the light-demanding and shade-tolerant PFTs, respectively (Figures 4b and 4d). ELM-FATES-simulated DBH increment rates are relatively low during 1989–1994 and peak during 1994–2004, slightly declining in subsequent intervals. In examining annual model output, we found that ELM-FATES-simulated DBH increment peaked in 1999 for both PFTs (i.e., the dark stripes in Figures 5a and 5b). These peaks are mainly driven by canopy trees across all size classes, while understory trees have declined in DBH increment rates (Figures 5c–5f). Because a defoliation event was implemented in ELM-FATES to represent the impacts of Hurricane Georges in 1998, we infer that these peaks could be associated with the defoliation event in 1998. To test this hypothesis, we performed an ELM-FATES simulation without the defoliation event in 1998 (Section 2.4; Hugo-Only) and confirmed the association of the DBH increment peak following the defoliation event (Figure S5 in Supporting Information S1).

Comparison of the DBH increments with the interannual variability of precipitation and surface air temperature from Daymet (i.e., the meteorological forcing data of ELM-FATES) demonstrates that these DBH increment peaks were not induced by enhanced precipitation or temperature (data not shown). Instead, the short-term increase in DBH increment appears to be associated with changes in the leaf area index (LAI) following defoliation. The simulation with Georges shows that Georges can induce an LAI enhancement after a month of LAI reduction (Figure S6a in Supporting Information S1). After the LAI peaks in November 1998, it starts to decrease. The understory LAI of the Hugo + Georges simulation decreases to a level lower than that of the Hugo-Only simulation in October 1999, and subsequently the canopy LAI shows a higher LAI in the Hugo + Georges than in the Hugo-Only simulation from October 1999 to December 2001 (Figure S6 in Supporting Information S1). These changes indicate initially enhanced light availability and a quick canopy closure, following Hugo or Georges which then limits subsequent leaf development in the understory. The long-term impacts of Hurricane Georges on LAI last for 13 years, from 1999 to 2011, and are attributed to the LAI reduction in the understory (Figure S6 in Supporting Information S1). Similar trends are also seen in the leaf biomass time series of both light-demanding and shade-tolerant PFTs, and they also last for 13 years (Figure S7 in Supporting Information S1). The impact of defoliation on total biomass is minor (Figure not shown).

### 3.3.3. Post-Hugo Mortality Rates

Because growth and mortality rates are the factors determining carbon cycling and carbon pool sizes, we examined mortality rates (Table S2 in Supporting Information S1) to interpret carbon pool size changes. To be comparable with the data, we calculated the mean mortality rate of each PFT every 5 years. The observed



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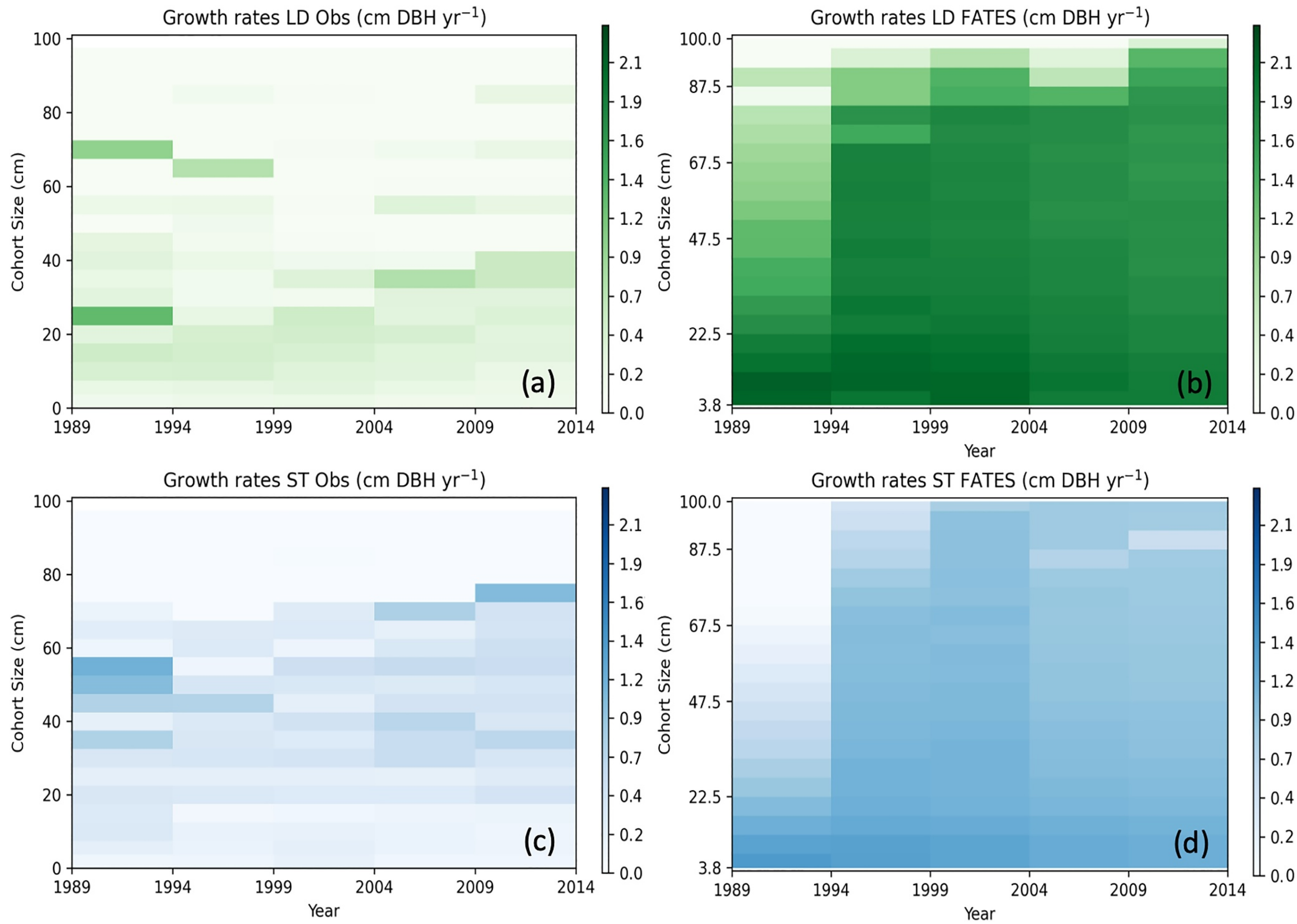


**Figure 4.** Field census-based DBH increment rates for the (a) light-demanding (LD) and (c) shade-tolerant (ST) PFTs and for the same two PFTs, (b) and (d), simulated by ELM-FATES. ELM-FATES-simulated yearly DBH increment rates are averaged over each 5-year time span to be comparable with the field measurements.

mortality rates were lowest during 1989–1994, which could be associated with the reduction in competition due to Hugo-induced damage. The mortality rates during 1994–1999 are also below average, peaking during 1999–2004 due to self-thinning. ELM-FATES also represented reduced mortality rates during 1989–1994, but mortality peaked in 1994–1999 instead of in 1999–2004. Compared to the observations, ELM-FATES simulates higher post-Hugo mortality for the shade-tolerant PFT, and higher mortality rates for the light-demanding PFT from 1994 to 1999 (Table S2 in Supporting Information S1).

### 3.3.4. Post-Hugo Stem Density

To have a comprehensive understanding of post-Hugo changes in forest structure, we also compared the stem densities of each census after Hurricane Hugo. The overestimated pre- and post-Hugo shade-tolerant stem density in the 1.25–10 cm DBH classes (i.e., 1.25–5 cm and 5–10 cm) persisted during the entire post-Hugo period of observations (i.e., 1989–2014), peaking (i.e., 1527 trees per hectare) in 1999 (Figure 6b). This peak coincides with the DBH increment peak in 1999 (Figure 5b). The observed total stem density in 1999 is 486 trees per hectare, which is higher than that in the following years; this trend is consistent with the result that was previously reported by Heartsill-Scalley (2017). The relatively high observed stem density of the shade-tolerant PFT in the 27.5–62.5 cm DBH groups can still be identified during 1989–2009, and these high values diminished in 2014. In 2014, the averaged stem density across the 3.8–22.5-cm DBH groups is 20.2 and 158.4 trees per hectare for observation and ELM-FATES, respectively, and the stem density ratios between the light-demanding and shade-tolerant PFTs of the same DBH groups are 0.96 and 0.16 for observation and ELM-FATES, respectively. This discrepancy is primarily attributed to the small-sized shade-tolerant trees simulated by the model (Figure 6e). In addition, the



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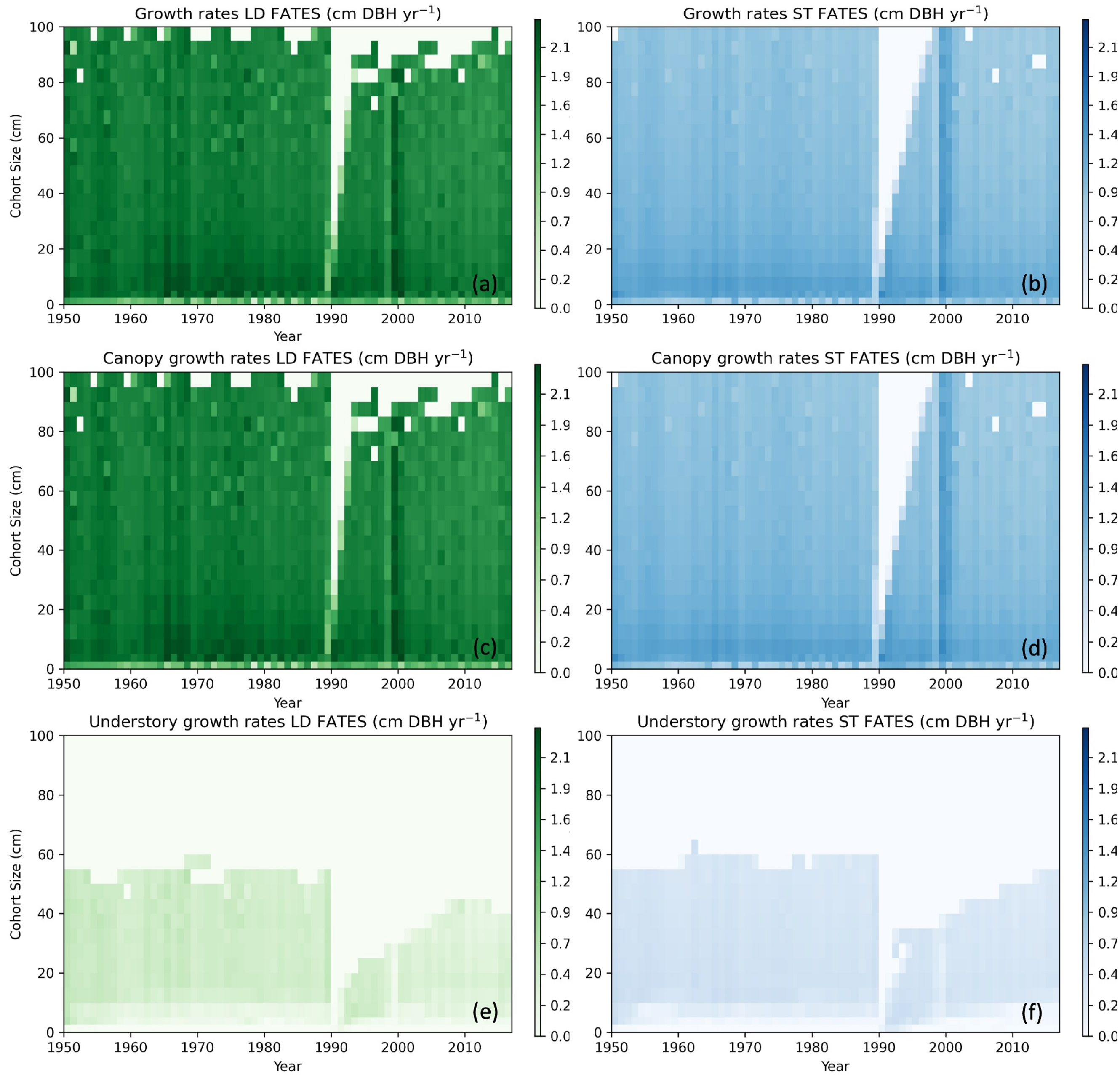


**Figure 5.** ELM-FATES-simulated DBH increment rates for (a) light-demanding (LD) and (b) shade-tolerant (ST) PFTs during 1950–2017. The DBH increment rates for canopy (c) LD and (d) ST PFTs, and for understory (e) LD and (f) ST PFTs are also shown for the same period.

numbers of trees in the DBH groups larger than 62.5 cm are 4 and 7 for observation and ELM-FATES, respectively, indicating that the model still overestimates tree numbers in large-sized DBH groups 25 years after Hurricane Hugo. Here, the ELM-FATES-simulated distribution suggests that during the recovery process, the forest always has many small-sized trees developed and many of them are from the shade-tolerant PFT (Figures 6b–6e). This stem density distribution is inconsistent with the forest recovery suggested by the observational data.

## 4. Discussion

This study provides a comprehensive evaluation of ELM-FATES-simulated hurricane disturbance and forest recovery at the Bisley Experimental Watersheds in Puerto Rico using field observations. Our synthesis of observations used as benchmarks for the modeling reveals the following regarding the pre-Hugo state, and short-and



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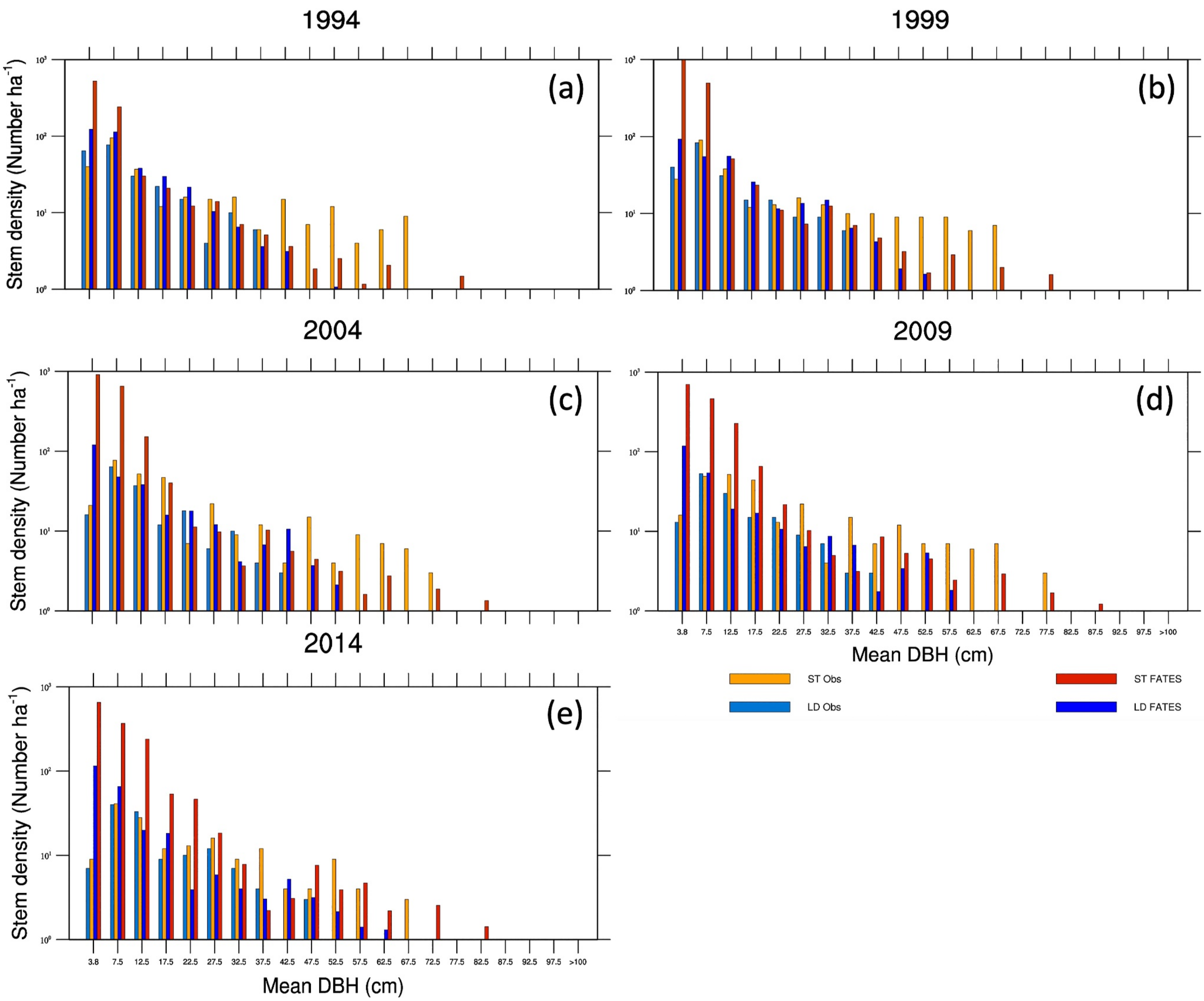


**Figure 6.** Observed and ELM-FATES-simulated stem density for the light-demanding (LD) and shade-tolerant (ST) plant function types in (a) 1994, (b) 1999, (c) 2004, (d) 2009, and (e) 2014. The midsize DBH values are labeled in the *x*-axis.

long-term responses. Before Hurricane Hugo, AGB is 15.8 kgC $m^{-2}$, 77.3% of which is from the shade-tolerant PFT. Hurricane Hugo induced a ~39% (6.1 kgC $m^{-2}$) forest AGB reduction, which recovers to a level comparable to the pre-Hugo condition (i.e., 15.0 kgC $m^{-2}$) in 2014 (Figure 3 and Table 2). However, the stem density values in 2014 remain lower than the pre-Hugo levels for all tree size groups, a persistent forest structure change 25 years after Hugo (Figures 2a and 6e; Zhang et al., 2022b). Hugo-induced mortality rates are higher for the light-demanding than for the shade-tolerant PFT (Table 1), suggesting a higher resistance of shade-tolerant species. Immediately after Hurricane Hugo, the abundance of light-demanding trees is reduced and small trees (i.e., 2.5 cm < DBH < 10 cm) have the largest proportional reduction (Zhang et al., 2022b). We find growth rates to be higher in trees ≤ 40 cm DBH than in the trees > 40 cm DBH for the light-demanding PFT, but vice versa for the shade-tolerant PFT (Figures 4a and 4c), affirming a similar conclusion in Zhang et al. (2022b). This pattern implies that most of the shade-tolerant trees are in larger DBH groups, and the light-demanding trees tend to develop in the hurricane-induced tree gaps (Velázquez & Wiegand, 2020), and reflects the expected competition dynamics between these two PFTs.

In comparison with field data, ELM-FATES underestimates AGB and overestimates leaf biomass both 3 months before and after Hugo. This overestimation is attributed to the relatively large leaf biomass values of the light-



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demanding PFT. The modeled reduction in AGB reasonably reflects the forest damage induced by Hurricane Hugo (Table 2). The PFT-level AGB to total AGB ratios, and these ratios for leaf biomass are accurately represented by ELM-FATES (Tables 2 and 3) during the pre- and post-Hugo periods. Additionally, the model reasonably captures the long-term post-Hugo AGB distribution between PFTs (Figure 3).

ELM-FATES can represent a reasonable tree size distribution for the mid- and large-sized trees even with an underestimate of AGB. In the size bins 1.25–5 cm and 5–10 cm, the post-Hugo stem density is always overestimated by ELM-FATES (Figure 6 and Table S4 in Supporting Information S1). The lower stem density values in the observations reveal the rapid increase of understory trees and subsequent self-thinning due to canopy closure (Bače et al., 2017). However, these dynamics were not captured by ELM-FATES; this discrepancy can be explained by the simple regeneration scheme in ELM-FATES, which allocates carbon to reproduction and creates new seedlings daily and also lacks environmental constraints on seedling establishment and survival (Hanbury-Brown et al., 2022). In size bins with mean DBH values from 27.5 to 62.5 cm, observed stem density is higher than that simulated by ELM-FATES, while for DBH values larger than 67.5 cm, ELM-FATES overestimates stem density. Given that the small trees hold little biomass and are mostly in the dark understory, contributing little to the flux of carbon, the stem density discrepancy between the model and data in the mid- and large-sized groups could contribute to the model-data biomass difference.

We try to further adjust model parameters such as Vcmax at 25°C, to increase AGB and maintain both the biomass partition between PFTs and stem density distribution. However, none of the tests are able to increase the stem density for size bins of 27.5–62.5 cm, and many of the tests fail to simulate PFT coexistence. Thus, while further parameter optimization using a wider array of parameters may improve model performance against observations, Figure 2a shows the best result obtained from all the sensitivity simulations performed in this study.

### 4.1. Using the Allometric Equations to Estimate Pre- and Post-Hurricane Biomass

Allometric equations are typically developed with data collected from harvested trees that have not suffered major damage (Chave et al., 2014; Scatena et al., 1993). The DBH, tree height, and stem density values are measured, and then used to estimate AGB via regression methods. However, with hurricane disturbance, the structure of trees is changed, particularly the relation between DBH and height, which was also encountered by Zhang et al. (2022a). Thus, applying the posthurricane data of tree height to the allometry equations could induce AGB estimate bias. We acknowledge the limitations of applying different allometry equations (e.g., equations in Howell et al., 2022) to the disturbed forests, and did not place our efforts on testing the allometry equations at Bisley. Furthermore, the collected data set at Bisley includes many missing values in the height column, that is, the field data measurements of height were not complete. Thus, we use the Martínez -Cano et al. (2019) diameter-height, which is based on the GMM function and broadly tested in Panama by using a variety of tropical tree species as well as in many other forest ecosystems (e.g., e.g., Fayolle et al., 2016; Howell et al., 2022). We note the inconsistency between the observed and modeled post-Hugo AGB values and acknowledge the limitation and uncertainty of this comparison. Future studies could focus on improving data collection and conducting further tests of the allometry equations at Bisley or throughout the Luquillo watershed.

In this study, the leaf biomass allometry equation from Scatena et al. (1993), which is developed by using data collected at Bisley, is used to estimate observed leaf biomass. ELM-FATES has three allometry options to determine target leaf biomass, which are adjusted through time to prevent leaves with net carbon loss (Koven et al., 2020). Here, we choose to use a power law allometric model, which is well tested at the Barro Colorado Island, Panama, and uses DBH as the key metric for target leaf biomass (Fang et al., 2022; Koven et al., 2020). Because the goal of this study is to test the ability of the existing model to represent disturbance and recovery, we do not implement the Scatena et al. (1993) based equation in ELM-FATES. However, the allometry discrepancy and the underestimated stem density in the 27.5–62.5 cm DBH groups could be the reasons for the lower leaf biomass in ELM-FATES, and imply a strong need of integrating more physical options (e.g., allometry schemes and canopy position descriptions) for different research purposes.

### 4.2. The Uncertainty of the Litterfall Data

Litterfall field sampling usually involves the collection and measurement of the dry weight of leaves, wood <1–2 cm in diameter (i.e., twigs), reproductive materials (e.g., fruits, flowers, and seeds) and miscellaneous plant materials deposited on the forest floor—boles and large branches are always excluded (Lodge et al., 1991).

Compared to the observations, the pre-Hugo litterfall rate is overestimated while the post-Hugo litterfall rate is underestimated by ELM-FATES. In ELM-FATES, the aboveground litterfall includes the litter from leaves and coarse woody debris, where the ratios between debris and organ (i.e., sapwood and structural wood) biomass are parameterized. Furthermore, while litter on broken branches and crowns was classified as suspended litter and excluded from the litterfall in the field, the model does not separate the suspended litter and the forest floor litter. This limits the model-data comparison. Furthermore, we obtain the ELM-FATES litterfall rate by calculating the 10-day mean litterfall rates after Hugo, which is the best estimate of the litterfall rate but could still have time frame inconsistency in terms of the actual time (i.e., days after Hugo) of field litterfall collection.

### 4.3. ELM-FATES Represented Long-Term Posthurricane Forest Dynamics

The canopy at Bisley is significantly more open following hurricane disturbance, and the resulting increase in light to the forest floor leads to rapid ecological succession. After Hurricane Hugo, ELM-FATES suggests higher stem density values than the observations in the 3.8–22.5 cm group (Figure 6). A rapid increase of stem density (Figures 6a–6c) is accompanied by canopy formation and a reduction in light availability, which results in changing conditions in the understory with basal area increase (Shiels et al., 2010). The model-data comparison shows that ELM-FATES overrepresents these dynamics, which explains the higher DBH increment rates and higher stem density of small DBH size groups.

In this study, the growth respiration factor value is 0.2, which is within the observed range of this parameter (i.e., 0.19–0.61) in tropical forests, but lower than the topical forest mean value, 0.39 (Feng et al., 2017). This parameterization could be a reason for the high bias in DBH increment rates. In addition, observed pre-Hugo and historical mortality data are not available, and the post-Hugo nonhurricane mortality evaluation shows that ELM-FATES has higher mortality rates, especially for the shade-tolerant PFT, than observations. ELM-FATES also has higher litterfall rates than the observations. We acknowledge the observational limitations for the periods pre-Hugo and before, but these model-data comparisons in terms of parameter values and model simulation results imply too high turnover rates in the model. The combined effects of these factors contribute to the low AGB bias of the model. An alternative model parameterization, which reduces the model estimated nonhurricane mortality rates (Section 2.4) and growth rates and increases the growth respiration at the same time, may improve the model-represented biomass pool sizes and DBH increment rates. Advanced data collection for allocation (e.g., carbon masses of plant organs) and resprouting is currently limited but also essential to AGB representations in DGVMs.

Both observations and the model show a reduction of stem density after 1999, and this result is consistent with the findings in Heartsill-Scalley (2017) and with the tree abundance variations showed by Zhang et al. (2022b). The posthurricane stem density change in ELM-FATES suggests that hurricane disturbance enables the quick regrowth of small trees, which are mainly the shade-tolerant PFT (Figure 6). Although ELM-FATES-predicted posthurricane DBH increment and stem density do not match the observations, the result shows the sensitivity of forest structure and dynamics to canopy biomass changes (i.e., canopy openings) in ELM-FATES. During the posthurricane period, ELM-FATES-simulated DBH increment rates are within the observed DBH increment ranges in tropical forests (Brienen & Zuidema, 2006; Clark & McLachlan, 2003, 2003, 2003; Lai et al., 2022), but are faster for both the light-demanding and shade-tolerant PFTs compared to the observations at Bisley. Note that the regeneration scheme in ELM-FATES suggests a weak limitation of recruitment and seeding processes (Hanbury-Brown et al., 2022), and these processes are more important to small trees (i.e., DBH < 20 cm) than to large trees (Zhang et al., 2022b). In other words, this model's regeneration scheme induces the faster growth of small trees after Hugo, where the small trees only have limited contributions to AGB (Figure 3). Thus, we acknowledge this limitation of the model, which will not largely affect the conclusion regarding the recovery of AGB and growth rates of mid- and large-sized trees.

To have a comprehensive understanding of posthurricane forest recovery across hurricanes of varying intensity and over a longer time frame, we include Hurricane Georges, represented by a defoliation event, in our simulations. Due to the infrequent observations (i.e., 5-year per census), we are unable to confirm whether the increase in DBH increment and the overshoot of leaf biomass actually occurred after Hurricane Georges. However, the ELM-FATES simulation shows potential forest sensitivity to defoliation, which induces canopy opening without damaging the stem or causing mortality. Thus, more frequent data collection is needed to quantify the sensitivity of canopy regrowth to light availability (Section 3.4.2) and to quantify posthurricane dynamics for hurricanes



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with less severe impacts. Furthermore, we learn from both the observation and model simulation that with intensified hurricane disturbance and increased hurricane frequency, there could be fundamental changes of forest structure and species composition in Puerto Rico (Feng et al., 2017; Zhang et al., 2022c).

### 4.4. Future Improvements of ELM-FATES

As discussed above, future research can focus on testing alternative diameter to height allometry equations over Bisley by using the census data across different tree species. This effort could reduce the tree height simulation uncertainty in ELM-FATES for this specific site. The model also needs a more realistic recruitment and seeding scheme, which relies on enhanced data collection across different tropical tree species. Another future direction will be applying the hurricane motility modeling capacity developed by this study to the crown damage module in ELM-FATES (Needham et al., 2022), through which the damage types, including crown area reduction, leaf and branch biomass reduction, and tree mortality can be more dynamically represented for disturbance with various intensities. When processing the field census data, we followed the previous methods and grouped palms to the shade-tolerant PFT (Feng et al., 2017; Muscarella et al., 2013; Schowalter & Ganio, 1999; Uriarte et al., 2005). This grouping method could cause certain biases as suggested by Zhang et al. (2022b). Thus, based on our current model-data comparison, another future direction is to implement the palm PFT in ELM-FATES, which can enhance the model representation and simulation accuracy in the tropics. We will investigate the measurements of palms that can be used for the ELM-FATES parameterization, and further study ELM-FATES forest dynamics with palm included.

## 5. Conclusion

By using field census data from Bisley, we evaluated the performance of ELM-FATES in representing AGB, leaf biomass, litterfall rate, stem density, mortality rate, and DBH increment rate before and after Hurricane Hugo. The impacts of Hurricane Georges-induced defoliation on DBH increment rates are also evaluated in ELM-FATES. We conclude that ELM-FATES can reasonably represent the pre- and post-hurricane AGB and leaf biomass and their partitioning between PFTs. Although ELM-FATES underestimates AGB in the Bisley forest, the model represents a reasonable tree size distribution for the mid- and large-size trees. The model also tracks the trends of post-Hugo AGB recovery and size-based stem density development, although the stem density in terms of small-sized trees is overestimated by the model. In ELM-FATES, forest structure is sensitive to canopy biomass change, which regulates light availability and can result in varied conditions in the understory. These dynamics could be attributed to the relatively high growth rates in ELM-FATES. In this study, we performed detailed model-data comparison, and the model shows promise by capturing the essential demographic processes needed to accurately simulate forest disturbance and recovery. On the other hand, the results imply shortcomings in the current implementation of ELM-FATES that may be attributable to our limited knowledge of tropical tree carbon allocation, indicating an essential need for advanced field data collection that can guide process-based model enhancement for future studies.

## Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

## Data Availability Statement

The ELM-FATES source code, related surface and domain data files, and the scripts used to develop the figures of this study are available at https://zenodo.org/records/13888147. The Daymet meteorological fields (Kao et al., 2022) are available at https://daymet.ornl.gov/. The field measurements are available through Zhang et al. (2022d).

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