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Future Hurricanes will Increase Palm Abundance and Decrease Aboveground Biomass in a Tropical Forest

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Key Points:

- Future hurricanes will alter forest composition and decrease aboveground biomass accumulation
- Predicted temperature and CO_2 changes will have smaller effects on forest composition than future hurricane disturbances
- Predicted temperature and CO_2 changes cannot compensate for the biomass loss due to intense and frequent hurricane disturbances

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Abstract

Hurricanes are expected to intensify throughout the 21st century, yet the impact of frequent major hurricanes on tropical ecosystems remains unknown. To investigate tropical forest damage and recovery under different hurricane regimes, we generate a suite of scenarios based on CMIP6 climate projections and increased hurricane recurrence and intensity for the Luquillo Experimental Forest, Puerto Rico. We then use the Ecosystem Demography Model to predict changes in carbon stocks, forest structure and composition. Our results indicate that frequent hurricane disturbances in the future would decrease the overall aboveground biomass, decrease the dominance of late-successional species, but increase the dominance of palm species. Warmer climates with increased CO_2 would have little effect on the functional-type composition but increase the aboveground biomass. However, the predicted climate and CO_2 fertilization effects would not compensate for the biomass loss due to more frequent severe-hurricane disturbances.

Plain language summary

Tropical forests are subject to hurricane disturbances. The recovery of forests from hurricane disturbances is affected by both the hurricane events and the climate conditions (such as the CO_2 concentration and temperature). Climate change will lead to warmer climate conditions and higher frequency and intensity of hurricane events over tropical areas. To study the effect of climate conditions and hurricane events on tropical forests under the changing climate, we simulated the responses of a tropical forest to different climate and hurricane scenarios using a vegetation dynamics model. Our simulation results show that frequent and intense hurricane events in the future will lead to carbon loss, which will not be compensated by carbon gain resulting from a warmer and higher-CO_2 climate.

1 Introduction

Tropical forests have long been considered carbon sinks that absorb carbon dioxide from the atmosphere and reduce the carbon concentration in the atmosphere (Lugo and Brown 1992; Lugo and Wisniewski 1992; Phillips et al. 1998; Lewis et al. 2009). However, recent studies reveal that tropical forests could also be carbon sources that release more carbon than they absorb due to anthropogenic and natural disturbances (Dialynas et al. 2016a, 2016b, 2017; Baccini et al. 2017).

Disturbances affect vegetation, and the recovery may result in a different forest structure and composition (Vandermeer et al. 2000). Such changes in structure and composition may alter the role of forests in the global carbon balance. Furthermore, those changes in structure and composition consequently affect how future disturbances impact these forests (Zhang et al. 2022c). This is particularly important given the prospect of changes in intensity and frequency of disturbances, particularly hurricanes, resulting from climate change (Wang and Eltahir 2000; Knutson et al. 2008, 2010; Bender et al. 2010; Knutson et al. 2020; McDowell et al. 2020).

Climate change alters the intensity, duration, and frequency of hurricane disturbances (Emanuel 1987, 2005; Webster et al. 2005; Knutson et al. 2008, 2010; Bender et al. 2010; Knutson et al. 2020), as well as the environmental conditions that affect the forest carbon cycle (Lewis et al. 2009; Medlyn et al. 2000; Zhang et al. 2015; Feng et al. 2018). Both immediate disturbance impacts (mortality) and the subsequent effects on growth of remaining trees will affect the recovery speed and the long-term state of population, size structure, species composition, and biomass accumulation of forests.

Many studies have investigated the impact of climate change on forest structure and composition (e.g., Deb et al. 2018; Longo et al. 2018; Claeys et al. 2019) and carbon and biomass productivities (e.g., Medlyn et al. 2000; Zhang et al. 2015; Feng et al. 2018). The impact of hurricane disturbances on forest recovery has also been studied for specific hurricane events (e.g., Imbert and Portecop 2008; Heartsill Scalley 2017; Parker et al. 2018), but none of them investigated the implications of increased frequency and/or intensity of hurricanes predicted for future climate change scenarios.

Here we focus on the impact of climate change and corresponding hurricane disturbances on forest structure, composition, and biomass accumulation. As different species respond differently to hurricane disturbances, species that are resistant to hurricanes likely become abundant after the disturbances (Lugo et al. 1998; Zhang et al. 2022d). Therefore, we hypothesize that frequent hurricanes in the future would alter forest species composition and increase the abundance of species that are resistant and resilient to hurricane winds, such as palms. Furthermore, both warmer air temperature and higher CO_2 concentration are expected to increase tropical forest ecosystem photosynthesis (Tan et al. 2017) and biomass accumulation (Holm et al. 2019). Therefore, we

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hypothesize that warmer climates with elevated CO_2 concentrations accelerate the speed of biomass recovery. To test our hypotheses, we use the Ecosystem Demography model modified to consider hurricane disturbances, ED2-HuDi (Zhang et al. 2022b), to simulate the composition and biomass changes of a tropical forest after frequent hurricane disturbances in the future under different climate scenarios.

2 Materials and Methods

2.1 Study site

The tropical forest at Bisley Experimental Watersheds (BEW) in the Luquillo Experimental Forest, Puerto Rico has been subject to three hurricane events in recent decades: hurricane Hugo in September 1989, hurricane Georges in September 1998, and hurricanes Irma and Maria in September 2017. The effect of each hurricane varied markedly. Hurricane Hugo caused extensive damage to the forest and altered forest composition and structure immediately after the hurricane and during the succession after the disturbance (Zhang et al. 2022d). Hurricane Georges had minimal impact on the forest (Ayala Silva and Twumasi 2004). Hurricane Maria, with the aid of hurricane Irma's heavy precipitation a few days earlier, caused significant damage to forest vegetation, although not as drastic as the effects of hurricane Hugo (Zhang et al. 2022c). Between 1989 and 2017, eight censuses have been conducted in more than 85 plots in the forest. The censuses recorded the species and diameter at breast height (1.3m) (DBH) for each stem with DBH ≥ 2.5 cm (Zhang et al. 2020; 2022a). The latest census was conducted three months after hurricane Maria with auxiliary information on hurricane damage to each stem, and thus provided the pre-Maria stem community as well. Following Zhang et al. (2022b), the species were grouped into four plant functional types (PFTs): early, mid, and late successional tropical trees and palms (hereafter Early, Mid, Late, and Palm PFTs). The Early, Mid, and Late PFTs are species that dominate the corresponding succession stages after a disturbance (Kammesheidt, 2000; Moorcroft et al. 2001; Medvigy et al. 2009; Longo et al. 2019a). The Palm PFT is newly identified as it cannot be grouped into any of the existing PFTs (Zhang et al. 2022b).

2.2 Model setup

The ecosystem demography model (ED2) (Moorcroft et al. 2001; Medvigy et al. 2009; Longo et al. 2019a and 2019) describes the growth, reproduction, and mortality of each cohort, a group of trees with the same diameter size and PFT, in a plant community by simulating the transient fluxes of carbon, water, and energy. Therefore, the model describes the short-term physiological responses and long-term compositional and structural responses to changes in the environmental conditions. The ED2-HuDi model implements hurricane disturbances and the Palm PFT in the ED2 model and represents the compositional and structural responses to hurricane disturbances (Zhang et al. 2022b). The ED2-HuDi model has been calibrated for the recovery from hurricane Hugo with the census data at the study site. When compared to the nine observations, the calibrated model captures well the recovery of forest in terms of aboveground biomass (r=0.79, p=0.0199; MAE=30.8 Mg/ha), size structure (r=0.96, p=0.0002; MAE=2.8% for the proportion of stems with DBH < 10 cm), and PFT composition (r=0.96, 0.40, 0.99, and 0.67, p=0.0002, 0.3328, <0.0001, and 0.0707; MAE=3.5%, 6.9%, and 1.9%, and 6.9% for the proportion of Early, Mid, Late, and Palm PFTs, respectively) (Figure S1). Although the model overestimates Palm proportion and underestimates Mid proportion, nearly all estimates are within one standard deviation of the observations among the plots in the forest (Figure S1). Hence, we use this calibrated model to simulate the recovery of the BEW forest after hurricane Maria. Specifically, the initial forest condition is the pre-Maria observations, and the values of important parameters are from the optimal parameter set obtained in Zhang et al. (2022b). The uncertainty of model parameters has been discussed in detail in Zhang et al. (2022b). Here we will focus on the impact of different climate and hurricane scenarios.

The climate scenarios include one current-climate scenario and several Shared Socioeconomic Pathways (SSPs) scenarios from the Coupled Model Intercomparison Project Phase 6 (CMIP6). For the current-climate scenario (SSP0 hereafter), future climate corresponds to observations between 1989 and 2017 (González, 2017) and the observations of each year are recycled randomly. We include bias-corrected climate projections for ten SSP245, nine SSP370, and ten SSP585 scenarios from ten CMIP6 models (Text S1). A higher SSP scenario is associated with higher temperature, higher CO_2 concentration, and higher specific humidity, whereas the precipitation and solar radiation among SSP scenarios are not significantly different (Text S1).

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The hurricane scenarios include one realization of no-hurricane scenario (FnIn), ten realizations of current-hurricane scenario (F0I0) where the frequency and intensity of future hurricanes remain unchanged from current conditions, and ten realizations of 10%, 20%, or 40% increase of intensity with 0% or 20% increase of frequency for future hurricanes (F0I10, F20I10, etc.). For example, F20I10 indicates increasing frequency by 20% and intensity by 10%. The frequency increase is reflected in the increase of the arrival rate compared to the current one which follows a Poisson distribution with arrival rate of 0.49 $year^{-1}$. The intensity increase is reflected in the increase in mean wind speed compared to the current scenario, which follows a log-normal distribution with mean wind speed 2.66 m/s and standard deviation 0.63 m/s (Text S2). The climate and hurricane scenarios are listed in Table S1.

3 Results and Discussion

3.1 Recovery from Hurricane Maria under no-Hurricane Current-Climate Scenario

To establish a baseline for the simulated forest dynamics, we first investigate the recovery of the forest after hurricane Maria between 2018 and 2100 under the no-hurricane current-climate scenario (FnIn-SSP0). Because of the wind resistant structure and composition at the time of hurricane Maria—dominated by Palm PFT and medium- and large-size stems, the forest did not experience severe damages from hurricane Maria. According to the model, the recovery of stem density would be relatively slow (Figure 1 a); the forest would not reach a pre-Maria state until year 2045. In contrast, AGB and BA could exceed the pre-disturbance level before year 2030 (Figure 1 b and c) due to the biomass accumulation of a group of large Late trees (Figure S2).

The predicted change in PFT composition and size structure are generally consistent with the succession theory that Early PFT increases right after a hurricane disturbance, then Mid PFT, and then Late PFT. However, the Mid PFT is predicted to decrease throughout the 80 years of simulation (Figure S3 b), possibly due to the low-competition parameterization of Mid compared to other PFTs (i.e., intermediate growth rate and intermediate mortality rate) (Zhang et al. 2022b). The coexistence of Early and Late PFTs supports the idea from previous studies that the trade-offs between growth and mortality facilitate the coexistence of early (high growth rate and high mortality rate) and late (low growth rate and low mortality rate) successional PFTs (Koven et al.

2020). Palm PFT has high growth rate in open canopies and low mortality, which facilitate its establishment after a disturbance (Zhang et al. 2022d). Palm PFT is predicted to establish and gradually increase in abundance right after the disturbance, reach the maximum 20 years after the disturbance, and be replaced by Late PFT after 20 years (Figure S3 b). The predicted increase in Palm abundance is consistent with previous census observations that identified an increase in seed production (Gregory and Sabat 1996) and stem abundance (Zhang et al. 2022d) after hurricane disturbances. By 2100, Late PFT would reach 69% of the total stem abundance, higher than that before the disturbance (46%). The size structure is predicted small-stem dominated right after the disturbance due to higher mortality of intermediate and large stems than small stems. Within 20 years after the hurricane, the structure changes to intermediate- and large-stem dominated (Figure S3 a) due to establishment of Palm PFT (Figure S3 b). After 20 years, it changes to small-stem dominated (Figure S3 a) due to recruitment of Late PFT (Figure S3 b).

The above results indicate that the no-hurricane current-climate environment will put the forest in a state that is dominated by small stems and Late PFT. This is consistent with the observations in the pre-Hugo census (1989) at the study site. At that time the forest had not experienced a hurricane disturbance for ~60 years (prior to that time the only hurricanes were San Felipe in 1928 and San Ciprián in 1932) and the dominant size and species in this long undisturbed forest were Late PFT and small stems (Zhang et al. 2022b). This further validates our model in capturing the long-term succession of the structure and composition of the forest after a hurricane disturbance.

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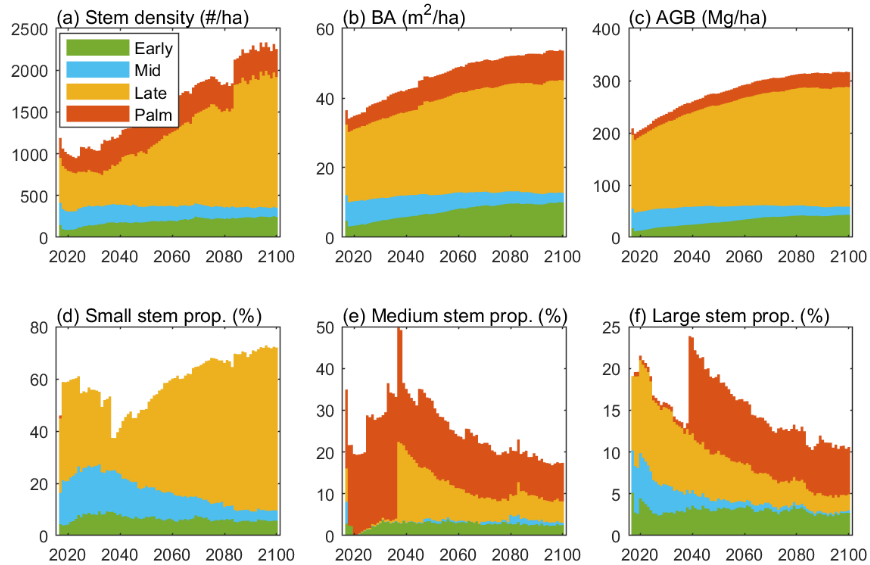

Figure 1. Time series of the projected variables between 2018 to 2100 under the no-hurricane current-climate scenario (FnInSSP0). (a) The stem density (DBH ≥ 2.5 cm), (b) basal area (BA), (c) aboveground biomass (AGB), and the proportion of (d) small (2.5 ≤ DBH < 10 cm), (e) medium (10 ≤ DBH < 20 cm), and (f) large stems (DBH ≥ 20 cm) for each PFT.

3.2 Impact of Hurricane Severity on the Recovery

With hurricane disturbances in the future, the forest would take different recovery trajectories and succession dynamics and reach divergent steady states in terms of stem density, biomass accumulation (Figure S4), PFT composition and size structure (Figure S5). Recurring hurricane disturbances (all scenarios with hurricanes) will slightly decrease the stem density (-5%), BA (-8%), AGB (-7%), and LAI (-5%) in the first 40 years but significantly (-21%, -20%, -19%, -12%, respectively) after 40 years. The differences between the two periods are due to the differences in structure and composition that affect hurricane-induced mortality. In the first 40 years, the forest is predicted to be dominated by the medium and large stems and have a high proportion of Palm PFT (Figure S5), which are resistant to hurricane disturbance, and thus the forest would be protected when a hurricane occurs. After 40 years, the size structure and PFT composition is predicted to change as the succession continues, and the forest becomes dominated by small stems and the Palm abundance decreases (Figure S5). Such forest state would experience high mortality when a hurricane strikes, and thus the stem density, BA, AGB, and LAI are predicted to decrease significantly (Figure S4).

During succession after severe hurricane (hurricanes exceeding a wind threshold, see Figure 2 for definition) disturbances, Palm is predicted to increase in stem proportion by 10% and Late to decrease by -12% (Figure S5). The proportion of medium and large stems will increase (9%; Figure S5) as Palm recruits and small trees grow big with the open canopy. The high proportion of wind-resistant large-DBH stems and Palm PFT will in turn protect the forest from further hurricane disturbances. Late will be the most dominant PFT in the forest in all hurricane scenarios at the end of 2100, but the PFT composition of the forest will change (Figure 2). With the presence of hurricanes, Early PFT would increase its proportion (0.21 for the average of hurricane-presence scenarios) compared to the no-hurricane condition (0.11), consistent with observations of early successional species having high recruitment after hurricane disturbances due to canopy opening (Brokaw 1998). However, the overall relationship between Early PFT proportion and severe hurricane frequency is not significant (Figure 2 a). Late PFT proportion has a weak negative relationship with severe hurricane frequency (p=0.07) (Figure 2 c), but this is largely due to the contrast between the no-hurricane scenario and the hurricane-presence scenarios. When considering scenarios with hurricanes, the negative relationship becomes insignificant (p=0.72). Palm PFT proportion has a significant positive relationship with severe hurricane frequency (Figure 2 d), which supports the idea that Palm will increase its abundance and dominance in forests that are subject to frequent hurricane disturbances (Gregory and Sabat 1996, Zhang et al. 2022d). With the probability of severe hurricane increasing 0.01 per year, the proportion of Palm is predicted to increase 2.48% (p=0.0016). Note that the calibrated model tends to overestimate Palm proportion (Figure S1), and thus the increase in Palm proportion with increasing severe-hurricane probability could be partially due to such overestimation.

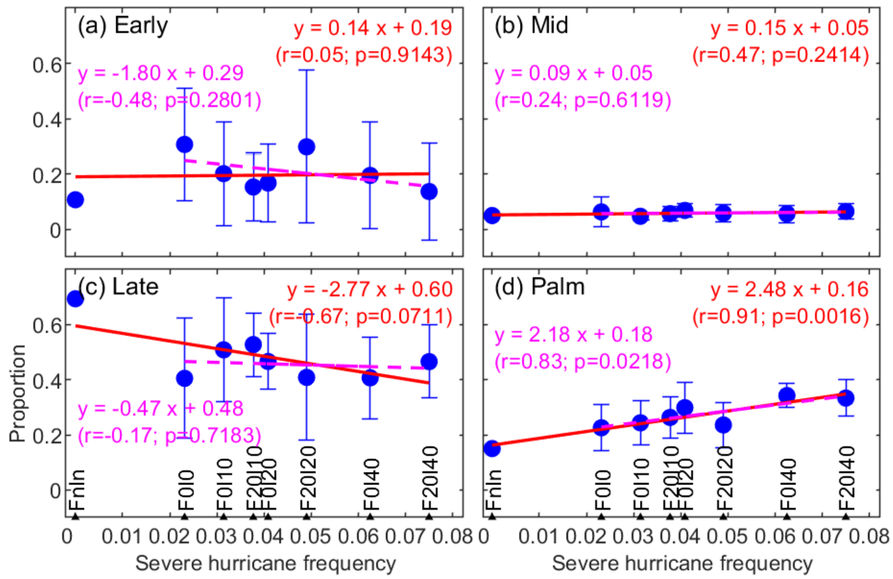

Figure 2. The relationship between severe hurricane frequency and the proportion of (a) Early, (b) Mid, (c) Late, and (d) Palm PFT during 2091–2100 under the current-climate scenario (SSP0). The severe hurricane frequency is calculated as the probability of hurricanes exceeding the wind speed threshold for disturbance occurrence in the ED2 model (41m/s). The proportion of each PFT is the average proportion of the stem abundance during 2091–2100. The error bars show the mean and standard deviation from the replications of the scenarios (see Table S1). The lines and texts are the linear regression for all scenarios (red) and for hurricane-presence scenarios (magenta).

3.3 Impact of Climate on the Recovery

Compared to the current-climate scenario (SSP0), SSP scenarios (SSP245, SSP370, and SSP585) (a higher SSP scenario is associated with a warmer and CO_2-richer condition; Text S1) would increase AGB (11%, 13%, and 15%, respectively) and BA (10%, 12%, and 13%) under the no-hurricane scenario (FnIn) after 2060 (Figure 3). The increase in AGB and BA is because trees grow larger in DBH in higher SSP scenarios (Figure S6 a, b, and c). Larger trees mean larger crowns and thus stronger competition for understory trees. Therefore, AGB loss due to tree mortality is higher in higher SSP scenarios, which is especially significant for the Early PFT

(Figure S6 e). However, the growth effect exceeds the mortality effect, especially for the Late PFT, and thus higher SSP scenarios without further hurricane disturbances would enhance the overall biomass accumulation in the forest (Figure 3 b). A higher SSP scenario increases biomass but the differences in biomass are small among the three scenarios, suggesting that further enhancement above the SSP245 scenario was marginal.

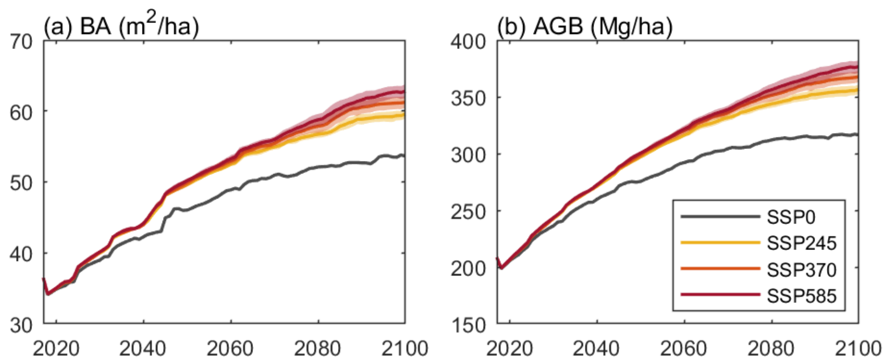

Figure 3. Time series of the simulated (a) BA and (b) AGB between 2018–2100 for each climate scenario under no-hurricane condition (FnIn). The three colored lines represent the mean from the CMIP6 models for the three climate scenarios (SSP245, SSP370, and SSP585), respectively. The shadings represent the 95% confidence interval of the mean. The black line represents the current-climate (SSP0) scenario.

3.4 Joint Impact of Hurricane Severity and Climate on the Recovery

Hurricane disturbances alone decrease biomass accumulation, while higher-SSP-scenario climates alone increase biomass accumulation. The joint effect of hurricane disturbances and higher-SSP-scenario climates is less straightforward. Figure 4 shows the recovery time (time to the pre-disturbance AGB level) and recovery state (the AGB state between 2091 and 2100) of AGB. Without hurricane disturbances (FnIn), the forest will take 5 years to recover to the pre-disturbance level under the current-climate scenario (SSP0), and higher-SSP-scenario climates (SSP285+SSP370+SSP585) will decrease the recovery time to 4.07±0.17 years. With the presence

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of hurricane disturbances (all hurricane-presence scenarios), the recovery time will increase to 6.82±1.22 years.

By 2100, the AGB without hurricane disturbance will reach 316 Mg/ha under the current-climate scenario (SSP0), and the AGB will increase by 12%, 16%, and 18% under SSP245, SSP370, and SSP585 scenarios, respectively. However, biomass loss due to hurricane disturbances will reach -30% by 2100, and the higher-SSP-scenario climates cannot compensate for the biomass loss due to hurricane disturbances (Figure 4 b). With the 40% increase in hurricane intensity (F0I40), the forest will be at a very low AGB state (208 Mg/ha), and warmer climates further decrease the biomass accumulation (193, 205, and 205 Mg/ha under SSP245, SSP370, and SSP585, respectively). This is because higher-SSP-scenario climates enhance the recruitment of small Late trees in the short term (Figure S7 a and g), which decreases the proportion of large stems (Figure S7 d) and the proportion of wind-resistant palm PFT (Figure S7 h) and thus puts the forest into a state that is vulnerable to hurricane disturbances. These results reveal that higher-SSP scenarios would not always enhance AGB accumulation, especially under severe hurricane conditions.

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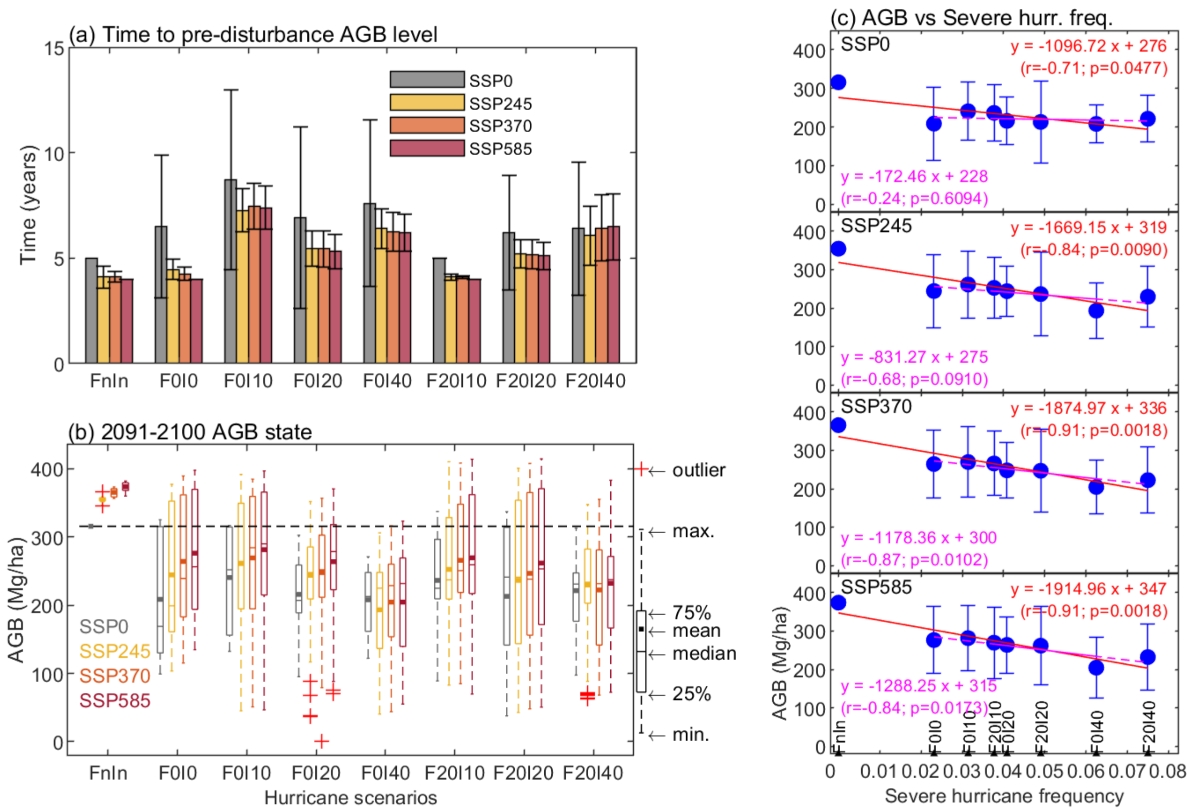

Figure 4. (a) Recovery time and (b) recovery state of the forest for each hurricane and climate scenarios, and (c) the relationship between recovery state and severe hurricane frequency for each climate scenario. The recovery time in (a) is the time to pre-disturbance AGB level and the recovery state in (b) and (c) is the average AGB between 2091 and 2100. The bars and error bars in (a) show the mean value and the 95% confidence interval, respectively, from the replications of the scenario. The boxplots in (b) show the outliers, minimum and maximum, 25% and 75%, and the median and mean from the replications of the scenario. The error bars in (c) show the mean and standard deviation from the replications of the scenarios. The lines and texts in (c) show the linear regression for all scenarios (red) and for hurricane-presence scenarios (magenta).

The biomass accumulation at the end of the 21st century would decrease with increasing severe hurricane frequency under SSP370 and SSP585 scenarios, but this relationship does not exist under SSP0 and is only marginal (*p*=0.0910) under SSP245 (Figure 4 c). Every 0.01 increase in the probability of severe hurricane occurrence each year will lead to 8.31 Mg/ha (*p*=0.0910), 11.78 Mg/ha (*p*=0.0102), and 12.88 Mg/ha (*p*=0.0173) AGB loss under the SSP245, SSP370, and SSP585 scenarios, respectively. This result further suggests that a climate with higher temperature and CO_2 concentration would exacerbate the AGB loss from hurricane disturbances in the future.

4 Conclusions

Disturbances and extreme climates shift forest structure and composition (Levine et al. 2016; Longo et al. 2018; Esquivel-Muelbert et al. 2019). Hurricane disturbances, among others (e.g., fires, windstorms, insects), damage trees and cause gaps in the forest canopy, allowing secondary succession (Zhang et al. 2022c). Hurricanes are becoming more frequent and intense under the changing climate; the recovery from the impact of a single hurricane has been studied (Heartsill Scalley 2017; Parker et al. 2018), but the impact of frequent hurricanes remains unknown, especially in the context of a changing climate. This study shows that hurricane disturbances and climate conditions could play a significant role in determining the recovery pathway of a tropical forest, including AGB and the PFT composition. With a high frequency of hurricanes, the forest will not have enough time to reach a steady state before it is again disturbed by a hurricane. Stronger hurricane disturbances favor the dominance of the Palm PFT in terms of stem proportion, as Palm has low hurricane-induced mortality and high recruitment rate when the canopy is open. More frequent and more intense hurricanes will lead to a lower level of AGB by 2100. Higher-SSP-scenario (warmer and higher CO_2 concentration) climates will increase the AGB accumulation when hurricane disturbance is absent but exacerbate the AGB loss from intense and frequent hurricane disturbances. Although this study focused on hurricane impacts on one particular tropical forest, the results presented here provide insights on the PFT recovery of tropical forests to frequent and intense disturbances. For example, our results indicate that frequent and intense disturbances alter the PFT composition and biomass accumulation, and such changes are strongly dominated by PFT resistance and resilience to disturbances. Since PFTs categorization and the disturbance impacts on PFTs could be site specific, cautions must be paid when extrapolating the results regarding dominant PFT and AGB changes to other regions. As the hurricane-disturbance module in this study is based on limited observation data, future works should revisit the module if more data on hurricane impacts are available.

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Open Research

Data Availability Statement The ED2-HuDi model is archived on Zenodo at https://doi.org/10.5281/zenodo.5565063. The tree census data are available at https://doi.org/10.2737/RDS-2020-0012 and at https://doi.org/10.2737/RDS-2022-0025. The observations of meteorological data are available from https://www.hydroshare.org/resource/a6baaaf051cd4319a8aa3e17dbd42c08/. The CMIP6 climate projections are available from https://esgf-node.llnl.gov/search/cmip6/.

Author contributions. R.L.B. and J.Z. conceptualized the work and developed the methodology, T.H.S. contributed the census data, J.Z. conducted the simulation and performed the analyses, J.Z. and M.L. interpreted results, J.Z. wrote the first draft of the manuscript. All authors reviewed and edited the manuscript.

Competing interests. Authors declare no competing interests.

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