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Modeling the Effects of Increased Hurricane Frequency on the Tropical Forest Carbon Cycle

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Abstract

Models project that climate change is increasing the frequency of severe storm events such as hurricanes. Hurricanes are an important driver of ecosystem structure and function in tropical coastal and island regions and thus impact tropical forest carbon (C) cycling. We used the DayCent model to explore the effects of increased hurricane frequency on humid tropical forest C stocks and fluxes at decadal and centennial timescales. The model was parameterized with empirical data from the Luquillo Experimental Forest (LEF), Puerto Rico. The DayCent model replicated the well-documented cyclical pattern of forest biomass fluctuations in hurricane-impacted forests such as the LEF. At the historical hurricane frequency (60 years), the dynamic steady state mean forest biomass was 80.9 ± 0.8 Mg C/ha during the 500-year study period. Increasing hurricane frequency to 30 and 10 years did not significantly affect net primary productivity but resulted in a significant decrease in mean forest biomass to 61.1 ± 0.6 and 33.2 ± 0.2 Mg C/ha, respectively ($p < 0.001$). Hurricane events at all intervals had a positive effect on soil C stocks, although the magnitude and rate of change of soil C varied with hurricane frequency. However, the gain in soil C stocks was insufficient to offset the larger losses from aboveground biomass C over the time period. Heterotrophic respiration increased with hurricane frequency by 1.6 to 4.8%. Overall, we found that an increasing frequency of tropical hurricanes led to a decrease in net ecosystem production by − 0.2 ± 0.08 Mg C/ha/y to − 0.4 ± 0.04 Mg C/ha/y for 30–10-year hurricane intervals, respectively, significantly increasing the C source strength of this forest. These results demonstrate how changes in hurricane frequency can have major implications for the tropical forest C cycle and limit the potential for this ecosystem to serve as a net C sink.

Key words: Climate change; Hurricanes; Tropical forest; Biomass; Soil carbon; Luquillo Experimental Forest.

Highlights

- Increasing hurricane frequency significantly decreased forest biomass over the long-term and increased rates of heterotrophic respiration.
- Soil carbon stocks increased, but the increase was

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insufficient to offset biomass losses.
- Net ecosystem production declined as hurricanes became more frequent significantly increasing the C source strength of this forest.

Introduction

Humid tropical forests play an integral role in the global carbon (C) cycle, representing a hotspot of terrestrial C storage in vegetation and soils (Jobbágy and Jackson 2000; Pan and others 2013). The favorable climate conditions that characterize these ecosystems (that is, year-round warm temperatures, abundant rainfall) promote high rates of ecosystem C fluxes such as heterotrophic respiration and net primary productivity (NPP) (Bond-Lamberty and Thomson 2010; Cleveland and others 2015). These large C stocks and fluxes have been shown to be sensitive to temporal fluctuations in climate and disturbance events, highlighting their vulnerability to climate change (Scatena and others 1996; Waide and others 1998; Vargas 2012; Feng and others 2018; Muller-Landau and others 2021). Humid tropical forest soils disproportionately contribute to the global C cycle relative to their spatial extent storing over 20% of the global soil C stock in just 14% of the land area (Jobbágy and Jackson 2000; Scharlemann and others 2014); thus, it is critical to understand the long-term effects of changing climate and disturbance regimes on tropical forest biogeochemistry (McDowell and others 2020; Zimmerman and others 2021).

Natural disturbance regimes play an important role in ecosystem development (Lugo and Waide 1993; Hogan and others 2018; Lin and others 2020). Across large areas of the humid tropics, the occurrence of periodic extreme events such as hurricanes has been recognized as one of the principal factors shaping forest structure and function (Tanner and others 1991; Lugo 2008; Simard and others 2019). For example, the frequency and intensity of hurricanes can result in fluctuations in live biomass and determine vegetation succession patterns, which help to explain the geographic variation in tropical forest C stocks and fluxes across the hurricane belt (Shiels and others 2015; Holm and others 2017; Lin and others 2020).

Multiple lines of evidence indicate that climate change is affecting hurricane disturbance regimes. Changes in hurricane disturbance differ across regions (Wu and others 2022), but the frequency of hurricanes occurring outside of the historical hurricane season has increased significantly in both the Atlantic and Pacific basins from 1900 to 2019 (Hernández Ayala and Méndez-Tejeda 2020), and an increase in landward migration of hurricanes has also been detected recently (1982–2018) (Wang and Toumi 2021). There has been a significant increase in the frequency of major hurricanes (Emanuel 2005, 2013), stimulated by the rapid intensification of sea surface temperatures (Bender and others 2010; Bhatia and others 2019). Increasing hurricane frequency related to changing climate may already be impacting forests; the Luquillo Experimental Forest (LEF), Puerto Rico, was hit by three major hurricanes within a period of less than 30 years from 1989 to 2017; the historical return interval was one storm every 60 years on average (Zimmerman and others 2021). Within this context of changing climate and disturbance regimes, it is important to determine the long-term fate of tropical forest C stocks and fluxes.

Hurricanes cause large-scale defoliation and massive reductions in live biomass, as well as the deposition of large masses of organic matter debris (necromass) on the forest floor (Lodge and others 1991; Scholl and others 2021). The loss of canopy cover across the landscape also causes a transient change in microclimate, with warmer temperatures and increased light availability in the understory (Brokaw and Walker 1991; Fernandez and Fetcher 1991; Nicholas and Grear 1991). Warm temperatures and abundant fresh litter can stimulate high rates of litter decomposition and associated soil CO_2 fluxes from heterotrophic respiration (Ostertag and others 2003; Vargas 2012). Despite the severity and magnitude of these short-term effects, most tropical forest vegetation has been shown to be resilient to the historical hurricane regime with regard to ecosystem structure, usually recovering to canopy conditions similar to pre-disturbance environments during the periods between storms (Everham and Brokaw 1996; Weaver 2002; Chazdon 2003; Zimmerman and others 2021). This resilience to hurricanes can be attributed to evolutionary adaptations of the biota to frequent wind disturbances (that is, fast growth of early-successional species, high abundance of decomposers, high resistance to wind damage; Basnet and others 1993; Zimmerman and others 2021). However, there is still considerable uncertainty regarding the long-term (decades to centuries) implications of an increase in the hurricane regime (that is, long-term hurricane return interval) for the humid tropical forest C pools and fluxes (Lugo 2000). Questions remain about the effects of increasing frequency of severe storms on C uptake by vegetation relative to C losses by soil heterotrophs and the ultimate impacts on ecosystem C balance over time.

Ecosystem models are useful tools for studying the long-term effects of projected changes in climate and disturbance regime on tropical forest biogeochemistry (Wieder and others 2015; Wieder and others 2018). The Century model and its daily timestep version, the DayCent model, have successfully been applied to study the role of hurricanes on tropical forest structure and function, and biogeochemical cycling (Sanford and others 1991; Parton and others 1994; Parton and others 1998; Wang and Hall 2004). Here, the DayCent model was parameterized with empirical data from the wet tropical forest at the LEF to study the effects of increasing hurricane frequency on ecosystem C stocks and fluxes at decadal and centennial timescales. We tested the hypothesis that increasing hurricane frequency would result in correspondingly greater losses in aboveground biomass C due to shorter recovery times between storms. We also tested the hypothesis that increasing hurricane frequency would decrease the tropical forest C sink due to disproportionate increases in heterotrophic respiration relative to rates of C storage in biomass and soils. The DayCent model was used to determine the direction and magnitude of the long-term effects of increasing hurricane frequency from the historical 60-year frequency to 30 or 10 years on major tropical forest C stocks in live biomass and soil C fractions, as well as major C fluxes including heterotrophic respiration and NPP.

Methods

We used the DayCent biogeochemical model (Parton and others 1998) to explore the effects of increased frequency of intense hurricanes on the LEF. DayCent is the widely used daily time step version of the Century biogeochemical model (Parton and others 1994). It is a process-based mechanistic model that simulates fluxes of C and N among the atmosphere, vegetation, and soil (Parton and others 1998; Del Grosso and others 2001). The model simulates plant production and allocation, soil organic matter and litter decomposition, nitrogen (N) transformations including mineral, organic, and N gas emissions from nitrification and denitrification, and CH_4 oxidation in non-saturated soils. Nitrogen gas emissions are based on diffusivity parameters of soil (water-filled pore space, texture, bulk density, field capacity, temperature) as well as pH and mineral N concentrations. DayCent also includes an output for heterotrophic and total (autotrophic and heterotrophic) soil CO_2 respiration. The movement of C and N through different operationally defined soil pools is controlled by the pool size, C/N ratio, lignin, and moisture and temperature where decomposition is modeled using first-order kinetics (Parton and others 2001). Three discrete soil C pools include the active pool with turnover times < 1 years, the slow pool with decadal-scale C turnover, and the passive pool where C turns over on millennial time scales.

In DayCent, live trees have five components: leaves, fine branches, large wood (boles), fine roots, and coarse (woody) roots. The model does not predict tree height or diameter. Leaves, fine branches, and large wood that die during the hurricane disturbances we simulated are deposited on the ground as litter and coarse woody debris. Dead leaves are partitioned into surface metabolic and structural litter and these litter pools are then decomposed at different rates into active and slow surface pools. The dead wood on the surface decomposes directly into surface active and slow pools. Surface slow pools are mixed gradually into soil slow pools through bioturbation. Fine roots that die are partitioned into soil metabolic and structural litter and then decomposed, and dead coarse roots are decomposed directly into active and slow soil pools. The passive pool is formed primarily by the sorption of active organic matter and to a lesser extent slow organic matter onto clay particles. Each pool (metabolic litter, structural litter, wood, active, slow, and passive) has a predefined maximum rate of decomposition that is modified by soil moisture, soil temperature, pH, and lignin content (for structural litter and wood).

As live biomass recovers disturbance, new material is added to the five live tree components. The tree prioritizes reestablishing its leaf canopy, and that process is regulated by the amount of live aboveground wood biomass that remains to support the live leaf biomass. When trees are completely killed reestablishment takes longer. Biomass accumulation is a balance between growth and turnover. In the absence of disturbance, the turnover of the different plant components depends on background turnover rates, temperatures, and soil moisture conditions. DayCent is not a spatial model, so it does not simulate variations in disturbance rates and other processes that would be influenced by topography and wind direction.

The DayCent model was parameterized using long-term climate, soils, and vegetation data (Table S1) from the Luquillo Experimental Forest (LEF) in northeast Puerto Rico (Sanford and others 1991; Wang and Hall 2004). The parameterization used data from the subtropical wet forest type (locally known as Tabonuco forest), which represents the dominant vegetation type and Holdridge life zone in the lowlands of the LEF (< 600 m) and is also a common forest type throughout the Caribbean (Beard 1949; Ewel and Whitmore 1973; Lugo and others 1981). The historic hurricane return interval in the LEF is approximately 60 years (Scatena and Larsen 1991). Notably, this has increased over the past 30 years (for example, one major hurricane per decade; Fassig 1930; Wadsworth 1951; Zimmerman and others 2021). The effects of the hurricane regime on the structure and function of these forests cannot be overstated; extensive research has described ecological and biogeochemical dynamics driven by hurricanes impacts to the LEF, most recently as part of the US-LTER program (for example, Lodge and McDowell 1991; Steudler and others 1991; Scatena and others 1996; Silver and others 1996; Lugo 2000; Beard and others 2005; Shiels and others 2015).

Long-term temperature and precipitation data collected at the Bisley Experimental Watersheds (hereafter Bisley) and El Verde Research Area (hereafter El Verde) within the LEF were used as input data for the model (Scatena 1989). Both sites are classified as lowland wet subtropical forests, with a mean annual precipitation of approximately 3,500 mm and a mean annual temperature of approximately 24°C (Heartsill-Scalley and others 2007; Harris and others 2012). We did not consider climate warming or other climate changes apart from increases in hurricane frequency. Soils are classified as clay-rich Oxisols derived from volcaniclastic sandstone and dominated by kaolinite and iron/aluminum hydroxides (Huffaker 2002; Table S1). Data on soil bulk density, texture, and pH came from soil profiles in Tabonuco forest collected across the LEF (Ping and others 2013).

Climate models are unclear about the effects of warming on hurricane intensity in this region. Therefore, we simulated a random distribution of hurricanes in categories 2 and 4, while maintaining their relative proportions consistent across hurricane frequency treatments. We chose these two categories to capture some of the background heterogeneity that results from differences in hurricane intensity. Moreover, categories 2 and 4 bracket the most common intensities experienced in this forest based on the historical record (Boose and others 2004).

We assigned damage classes relative to observed values from Hurricane Hugo, a category 3 hurricane (Table 1). The percent of biomass from leaves, branches, and large wood transferred to the forest floor as hurricane debris was calculated from measurements conducted in the Bisley Experimental Watersheds before-and-after Hurricane Hugo (Scatena and others 1993). Fine-root biomass loss was estimated based on data collected pre- and post-Hurricane Hugo at Bisley and El Verde (Parrotta and Lodge 1991; Silver and Vogt 1993). We note that the magnitude of damage is dependent upon wind duration and intensity as well as rainfall, landscape position, species traits, and preexisting environmental conditions such as soil saturation, rooting depth, past, unrelated disturbances (Zimmerman and others 1994; Everham and Brokaw 1996; Hall and others 2020). Thus, these damage classes should be considered as generalized benchmarks for comparison only.

The model spin-up consisted of a disturbance-free period of 4,000 years to reach a stable state, followed by a 1000-year period with a randomized sequence of category 2 and 4 hurricanes occurring at the historical 60-year frequency. This sequence of spin-ups was designed to begin the experimental treatments on a hurricane-impacted forest (as is the case for the LEF) and allowed for a pre-treatment comparison of the historical 60-year frequency model output with available empirical data as a validation test of the model. This comparison revealed that the model captured the cyclical patterns of biomass fluctuations observed. Modeled biomass values at the 60-year historical hurricane frequency were within the range of those found in Tabonuco forests at the LEF (Scatena and Lugo 1995; Table S2; Lugo and Heartsill Scalley 2014). Modeled values of NPP were also comparable with long-term field-based estimates from the LEF, although these values did not include belowground productivity (Weaver and Murphy 1990; Table S2). The model output tended to underestimate maximum leaf area index (LAI) attained by the forest, which may be related to the limits of the model in representing the upper range of LAI values (Jordan 1969; Weaver and Murphy 1990; Table S2).

The experimental treatment period consisted of the final 500 years of the model runs (from 2020 to 2520), when hurricane frequency was increased from 60-years to 30 or 10 years. Eight separate model runs for each of the three hurricane frequencies were used to calculate means and standard errors of the time series for each treatment over the 500-year interval. The date of hurricane occurrence was randomly distributed within each interval with a few constraining factors. First, intervals between hurricane events were allowed to fluctuate ± 2 standard deviations from the means of 60, 30, and 10 years in each treatment to represent the natural variability of the recurrence of these events. Second, while the hurricane intensity for each event was determined randomly

Table 1. Hurricane-induced Percentage Loss of Each Biomass Fraction

Biomass fraction	Category 2 (%)	Category 3 (Hugo)	Category 4
Live leaves	50	91	100
Live branches	40	54	80
Live wood	20	48	60
Fine roots	50	> 50	90
Coarse roots	30	n/a	60

Empirical data from Hurricane Hugo (Parrotta and Lodge 1991; Scatena and others 1993; Silver and Vogt 1993) were used to estimate the effects of Category 2 and 4 hurricanes on different biomass fractions.

(Cat. 2 vs. 4), at least one category 2 hurricane occurred between category 4 hurricane events at both the 30- and 10-year frequencies to avoid the compounded impacts of back-to-back category 4 events. Our goal here was not to focus on the rare probability of back-to-back extreme hurricanes but determine a more likely scenario of hurricanes of different magnitudes increasing in frequency.

Model output included forest biomass C, total soil C, active soil C (defined in the model as live microbes and microbial byproducts), slow soil C (modeled as organic material chemically resistant to decomposition), passive soil C (modeled as organic matter that is physically protected by soil clay particles), background litterfall C, and hurricane-induced litterfall C. Model output also included heterotrophic respiration, autotrophic respiration, and NPP; the above values were used to calculate gross primary productivity (GPP; the summation of autotrophic respiration and net primary productivity) and net ecosystem productivity (NEP; the difference between NPP and heterotrophic respiration). Model LAI output was considered due to its importance for forest productivity.

All statistical analyses were conducted in R (R Core Team 2021). The R package '*segmented*' was used to identify breakpoints during the simulated treatment period where trends changed in magnitude or direction. Linear models were used to test for significant trends throughout the entire treatment period, as well as over specific time periods identified by the breakpoint analyses. The significance of mean differences between treatments was determined using one-way analyses of variance or Kruskal–Wallis rank sum test, after testing for homogeneity of variance (Levene's test). Statistical significance was determined as $p < 0.05$ unless otherwise noted. Values reported in the text are means ± standard errors (SE) unless otherwise noted.

Results

Forest Structure

The model replicated the documented cyclical pattern of forest biomass fluctuations in hurricane-impacted forests such as the LEF (Figure 1). After modeling the historical hurricane frequency of 60 years sustained during a 500-year period, the dynamic steady state mean forest biomass was 80.9 ± 0.8 Mg C/ha compared to the reported value of 71–141 Mg C/ha assuming that aboveground biomass was 75% of the total (Scatena and others 1993; Figure 1; Table 2; Scatena and others 1996). Increasing hurricane frequency to 30- and 10-years for the 500-year time period caused a significant decrease in mean forest biomass to 61.1 ± 0.6 and 33.2 ± 0.2 Mg C/ha, respectively (Figure 1; Table 2; $p < 0.001$). Increased hurricane frequency was also associated with a decrease in the magnitude of hurricane-induced fluctuations in biomass (Figure 1).

Breakpoint analysis allowed us to calculate the time required for forest biomass to stabilize in response to a change in hurricane frequency. The steepest decline in forest biomass occurred with the 10-year hurricane return interval, and biomass stabilized after approximately 40 years. The magnitude of this decline (biomass loss of 47.7 ± 0.4 Mg C/ha) amounted to a loss of 59% of background levels at the historical hurricane frequency (Table 2). A similar pattern was observed for the initial transition period at the 30-year hurricane return interval with a decline in forest biomass of 24% compared to the 60-year hurricane frequency amounting to biomass loss of 19.8 ± 0.3 Mg C/ha (Table 2). This initial reduction in forest biomass at the 30-year frequency took nearly twice as long to stabilize compared to the 10-year frequency (70 vs. 40 years). Following this initial transition period, forest biomass continued to fluctuate in response to individual hurricane events at all frequencies, albeit biomass fluctuations of the

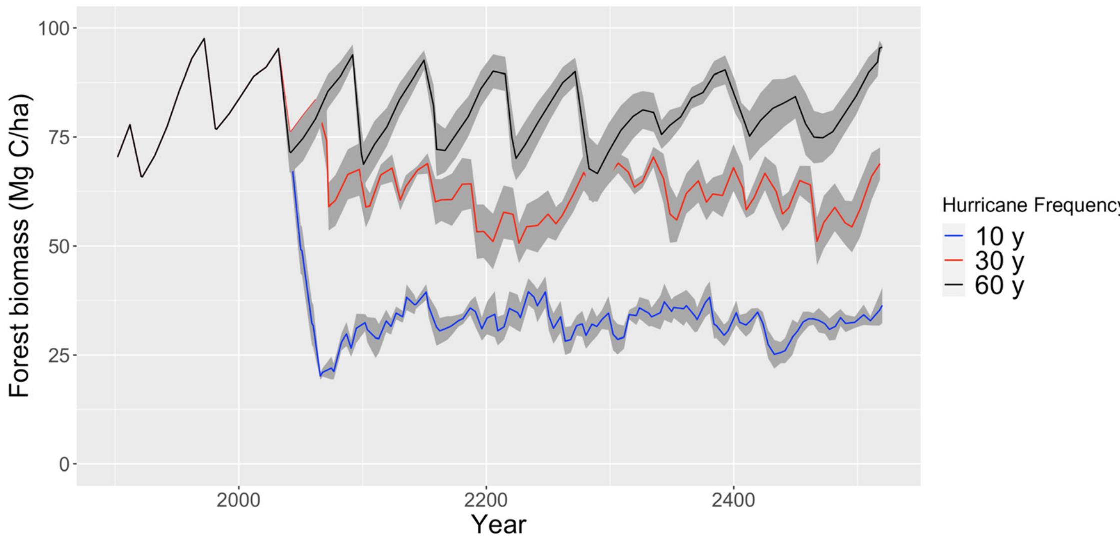

Figure 1. Time series of forest biomass C (mean ± 1 SE; $n = 8$) by hurricane frequency: Black = 60-year average return interval; Red = 30-year average return interval; Blue = 10-year average return interval. Shading represents confidence intervals around the mean.

Table 2. Forest C Stocks and Annual Aboveground C Inputs (Mean ± Standard Error; $n = 8$) for the Luquillo Experimental Forest by Hurricane Frequency

Hurricane frequency (years)	Carbon stocks (Mg C/ha)			Annual carbon inputs (Mg C/ha/yr)	
	Vegetation	Soil	Vegetation/Soil	Litterfall	Hurricane debris
60	80.9 ± 0.8[a]	76.9 ± 0.06[a]	1.1 ± 0.010[a]	5.0 ± 0.02[a]	0.25 ± 0.001[a]
30	61.1 ± 0.6[b]	77.8 ± 0.03[b]	0.8 ± 0.008[b]	5.1 ± 0.02[b]	0.45 ± 0.002[b]
10	33.2 ± 0.2[c]	79.0 ± 0.06[c]	0.4 ± 0.003[c]	5.3 ± 0.01[c]	0.89 ± 0.003[c]

Letters denote significant differences among treatments at $p < 0.05$. Soil and vegetation C stocks represent the mean and standard errors over the last 400 years of the model runs.

greatest magnitude occurred at the 60-year hurricane frequency.

Across all treatments, LAI responded negatively to individual hurricane events, but revealed a strong capacity for resilience in agreement with field observations (Figure 2). Increasing hurricane frequency caused a significant decrease in LAI, which, after a transition period of approximately a century, stabilized for the duration of the simulation (400 years) around mean values of 3.5 ± 0.01 m^2/m^2, 3.4 ± 0.01 m^2/m^2, and 3.1 ± 0.004 m^2/m^2 at the 60-, 30-, and 10-year frequencies, respectively ($p < 0.001$).

Soil Carbon Pools

Hurricane-induced debris pulses were followed by a peak in soil C after each hurricane event at the 60-year interval (Figure 3). There was a significant increase in total soil C of approximately 0.9 to 2.1 Mg C/ha with increasing hurricane frequency over the 500-year period (Table 2; Figure 3). Hurricane events had a positive effect on soil C stocks in all treatments, and the fastest rate of change in total soil C, as well as the highest mean values after 500 years were found at the 10-year hurricane frequency (Figure 3). Breakpoint analysis indicated that the initial transition period lasted approximately 90 years for the 10-year frequency, while it took approximately 175 years for the rate of change to stabilize at the 30-year frequency. Following the transition period, soil C stocks continued to increase significantly over time at the 10-year frequency. Notably, after nearly 300 years with a positive trend in the 60-year treatment, a shift occurred toward a negative trend that was not apparent at higher hurricane frequencies.

The average active soil C pool was 1.90 ± 0.01 Mg C/ha at the 60-year hurricane

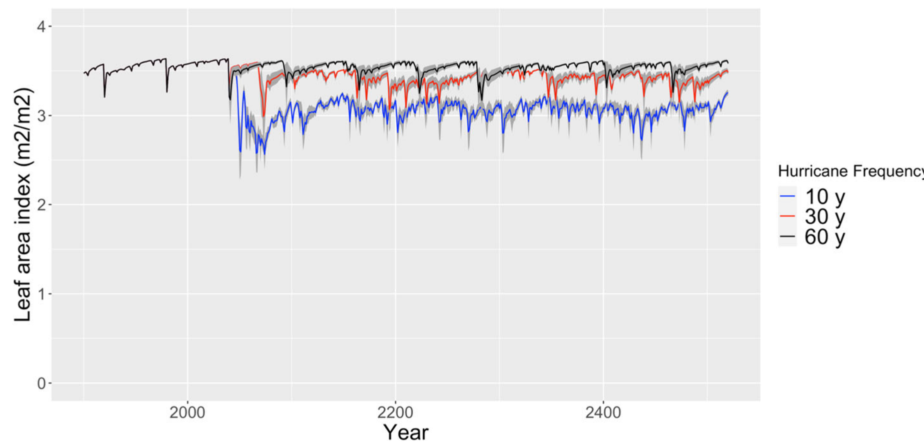

Figure 2. Time series of leaf area index (mean ± 1SEM; $n = 8$) by hurricane frequency: Black = 60-year average return interval; Red = 30-year average return interval; Blue = 10-year average return interval. Shading represents confidence intervals around the mean.

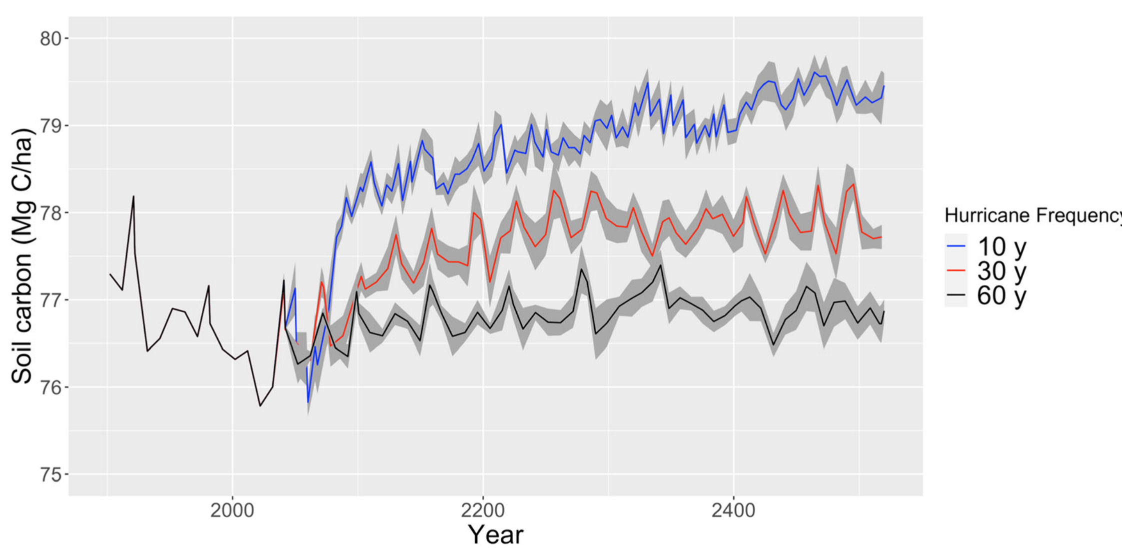

Figure 3. Time series of total soil C (mean ± 1SEM; $n = 8$) by hurricane frequency treatment (note inset with shortened y-axis that allows for improved visualization of patterns during treatment period). Black = 60-year average return interval; Red = 30-year average return interval; Blue = 10-year average return interval. Shading represents confidence intervals around the mean.

Table 3. Soil C Pools (Mean ± 1 SE; $n = 8$) Across Hurricane Frequency Treatments Averaged Over the Final 400 Years of Simulation

Hurricane frequency (years)	Soil carbon pools (Mg C/ha)		
	Active	Slow	Passive
60	1.90 ± 0.01^{a}	12.97 ± 0.02^{a}	59.90 ± 0.07^{a}
30	1.93 ± 0.01^{b}	13.14 ± 0.01^{b}	60.51 ± 0.03^{b}
10	2.01 ± 0.01^{c}	13.45 ± 0.02^{c}	61.07 ± 0.07^{c}

Letters denote significant differences among treatments at $p < 0.05$.

frequency and 2.01 ± 0.01 Mg C/ha at the 10-year hurricane frequency over the last 400 years of the simulation after the initial jump in soil C stocks (Table 3). Increasing hurricane frequency had a positive effect on the active soil C pool, with a significant increase of 0.11 ± 0.05 Mg C/ha (0.22 ± 0.11 kg C y^{-1}) at the 10-year hurricane frequency by the end of the modeled period (Table 3; Figure 4a; $p < 0.05$). The second largest modeled soil C pool was slow soil C, which averaged 12.97 ± 0.02 Mg C/ha under the historical 60-year hurricane frequency and showed large fluctuations in response to each hurricane (Table 3; Figure 4b). The effects of increasing hurricane frequency on the slow soil C pool were similar in sign to active soil C but of a larger magnitude with an average increase during the treatment period of 0.48 ± 0.07 Mg C/ha at the 10-year relative to the 60-year hurricane frequency (Table 3). The largest soil C pool was passive soil C, with an average of 59.90 ± 0.07 Mg C/ha under the historical hurricane frequency (Table 3; Figure 4c). The passive soil C pool showed the largest increase in response to increasing hurricane frequency, with a significant increase over the last 400 years of 1.17 ± 0.13 Mg C/ha at the 10-year relative to the 60-year hurricane frequency (Table 3; Figure 4c; $p < 0.001$). Across all hurricane frequencies, passive soil C increased significantly over time, but this temporal trend became stronger as hurricane frequency increased (Figure 4c; $p < 0.001$).

Changes in the Distribution of Forest Carbon Stocks

The ratio of vegetation C to soil C stocks decreased from 1.1 ± 0.01 at the historical hurricane frequency to 0.4 ± 0.003 at the 10-year hurricane frequency (Table 2; $p < 0.001$) based on the mean values during the last 400 years of the simulation (that is, after the initial breakpoint). There was a significant increase in background litterfall with more frequent hurricanes over the 400-years period (0.3 ± 0.06 Mg C/ha; Table 4; $p < 0.05$). Moreover, there was a significant positive treatment effect of hurricane frequency on hurricane-induced debris inputs ($p < 0.001$; Table 2; Figure 5). These inputs to the soil surface increased soil C stocks, but the gain in soil C was insufficient to offset the larger losses of aboveground biomass over the same period.

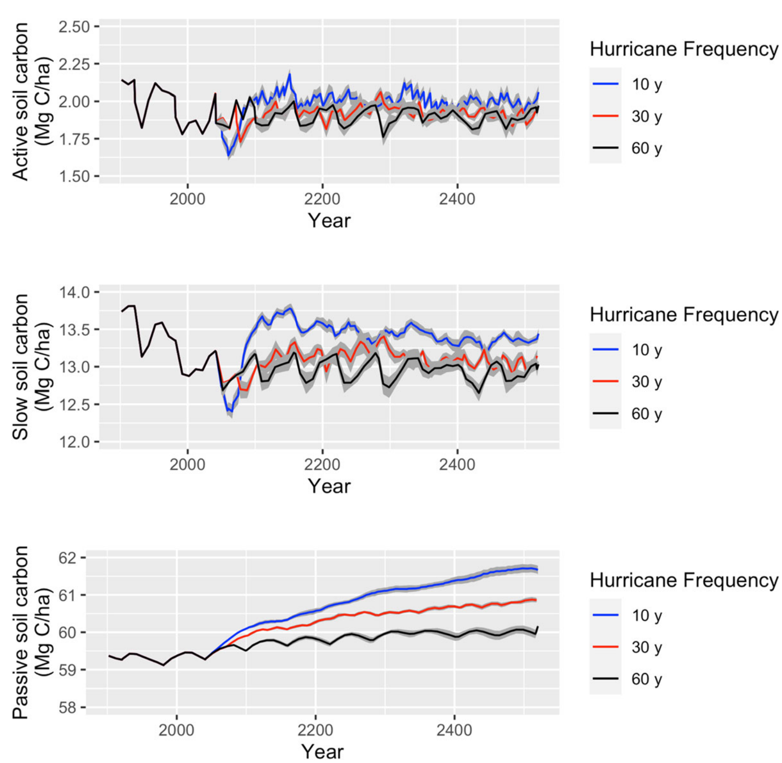

Figure 4. Time series of soil C fractions (mean ± 1 SE; $n = 8$) across hurricane frequency treatments: **a** active soil C **b** slow soil C **c** passive soil C (note differences in ranges and increasing magnitudes of y-axes from **a**–**c**. Shading represents confidence interval around the mean.

Table 4. Annual Ecosystem C Fluxes (Mean ± S.E.; $n = 8$) for the Luquillo Experimental Forest Across Hurricane Frequency Treatments Indicate Ecosystem is a C Source

Hurricane frequency (years)	Annual ecosystem carbon fluxes (Mg C/ha/y)				
	NPP	Het	Auto	GPP	NEP
60	6.3 ± 0.03^{a}	6.4 ± 0.02^{a}	4.6 ± 0.03^{a}	10.90 ± 0.04^{a}	-0.14 ± 0.02^{a}
30	6.2 ± 0.03^{a}	6.5 ± 0.01^{a}	3.8 ± 0.02^{b}	10.09 ± 0.04^{b}	-0.31 ± 0.03^{b}
10	6.3 ± 0.03^{a}	6.7 ± 0.01^{b}	2.7 ± 0.01^{c}	9.07 ± 0.04^{c}	-0.37 ± 0.03^{c}

Letters denote significant differences among treatments at $p < 0.05$.
NPP, net primary productivity; Het, heterotrophic respiration; Auto, autotrophic respiration; GPP, gross primary productivity; NEP, net ecosystem productivity.

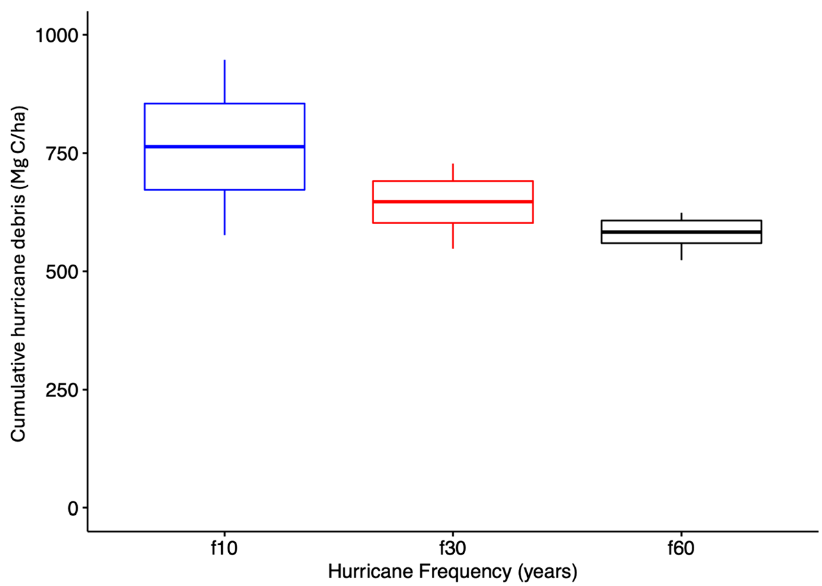

Figure 5. Boxplot of the cumulative hurricane debris inputs over 500-year treatment period showing the significant increase in magnitude at the highest hurricane frequencies ($p < 0.001$).

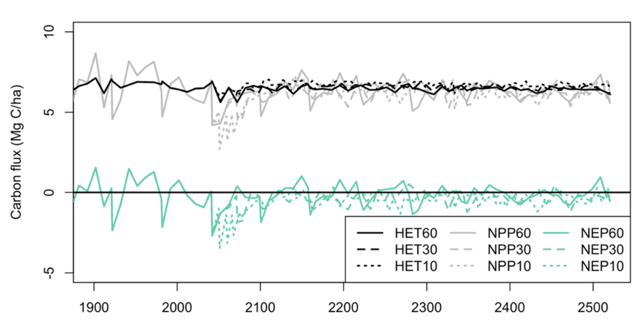

Figure 6. Forest ecosystem C fluxes (Mg C/ha/y) across hurricane frequency treatments including heterotrophic respiration (HET; red), net primary productivity (NPP; green), and net ecosystem productivity (NEP; blue; calculated as the difference between NPP and HET; negative NEP indicates the ecosystem is a C source).

Changes in Carbon Fluxes

Mean NPP during the 500-year treatment period ranged from 6.2 ± 0.06 MgC/ha/y to 6.3 ± 0.04 Mg C/ha/y and did not differ significantly among treatments (Table 4, Figure 6). Mean heterotrophic respiration under the historical hurricane frequency was 6.4 ± 0.02 Mg C/ha/y, and there was a significant increase of 0.1 ± 0.06 Mg C/ha/y and 0.3 ± 0.06 Mg C/ha/y at 30- and 10-year frequencies, respectively (Table 4; $p < 0.05$). Mean NEP was negative across all treatments (that is, the forest was a net C source), and NEP decreased significantly from -0.2 ± 0.08 Mg C/ha/y to -0.4 ± 0.04 Mg C/ha/y with increasing hurricane frequency (Table 4; $p < 0.001$). Consistent with the large decrease in forest biomass, there was a significant reduction in autotrophic soil respiration as hurricane frequency increased (Table 4; $p < 0.001$).

Discussion

Our results suggest that the long-term effects of increased hurricane frequencies on humid tropical forest C stocks and fluxes will alter the role of tropical forests in the global C cycle. Increasing hurricane frequency led to large losses of forest biomass and corresponding increases in heterotrophic respiration that limited gains in soil C storage. The net result was an increase in C losses from this tropical forest and an increase in a tropical forest C source.

Increasing hurricane frequency led to large, long-term losses of forest biomass, highlighting the vulnerability of aboveground C stocks to changes in the disturbance regime. Tropical forests worldwide are facing increasing pressures from intensifying disturbance regimes (Dale and others 2001; McDowell and others 2020). Aboveground biomass loss caused by hurricane disturbances has been widely documented in tropical forests, with dramatic reductions (> 25–50%) occurring after major storms (that is, cat. 3–5; Tanner and others 1991; Scatena and others 1996; Hall and others 2020). If periods of increased hurricane frequency are sustained over time, shorter periods between hurricanes will strongly limit the ability for forest biomass to recover to pre-disturbance levels, and effectively reduce the maximum forest biomass that can be attained (Lin and others 2020). Long-term empirical studies documenting the effects of increasing hurricane frequency are lacking, but comparisons across regions suggest that forests that experience more frequent hurricanes tend to have lower canopy height and biomass (Gouvenain and Silander Jr. 2003; Lugo 2008; Lin and others 2011; Xi 2015; Hogan and others 2018; Ibanez and others 2019; Simard and others 2019; Lin and others 2020).

The duration of the transition period in response to increased hurricane occurrence was determined by the magnitude of the change in frequency, with more frequent hurricanes resulting in a faster transition to a new, dynamic, steady state condition. DayCent does not capture changes in plant community composition. In theory, however, the shorter recovery time between hurricanes could set in motion a gradual shift in forest structure in a direction that is consistent with these results (Xi 2015; Lin and others 2020). This process, driven by changes in abiotic conditions, could result in a disproportionate loss of large trees that represent a significant contribution to tropical forest C stocks, mainly due to the accumulation of woody biomass (Sist and others 2014; Feng and others 2018). The downing of large trees during storms could feedback to the forest C cycle through the loss of C uptake as well as the addition of coarse woody debris to the forest floor (Lodge and others 1991; Lodge and others 1994; Zimmerman and others 1995; Liu and others 2018). However, we did not see a statistically significant change in NPP. The marginal decrease in mean LAI with increasing hurricane frequency combined with the lack of a significant treatment effect on NPP suggests that the photosynthetic capacity of the forest is resilient to changes in hurricane frequency. These findings are consistent with shorter-term observational evidence of the resilience of tropical forest LAI and NPP to hurricane regimes across a range of frequencies (Lodge and McDowell 1991; Scatena and others 1993; Scatena and others 1996; Wang and Hall 2004; Lin and others 2011; Lin and others 2020).

Total soil C stocks increased as hurricanes became more frequent. Soils serve as a reservoir for some of the C lost from plant biomass due to hurricane disturbance (Sanford and others 1991; Silver and others 1996; Gutiérrez del Arroyo and Silver 2018). This response was driven by the acceleration of the C flux from biomass to litter inputs, with both background litterfall and hurricane-induced litterfall increasing significantly with hurricane frequency. The importance of disturbance-induced pulses of organic matter as a source of soil C in tropical forests is widely recognized (Sanford and others 1991; Lodge and others 1994; Gutiérrez del Arroyo and Silver 2018). In the model, litterfall represents the principal source of organic matter inputs for the formation of soil C. However, the long-term increase in soil C was able to account for only a small fraction of the losses in biomass C stocks due to increasing hurricane frequency.

Patterns in soil C fractions that differ in turnover times provide the opportunity to better understand belowground dynamics (Berardi and others 2020). Model results suggested that pools of all soil C fractions grew larger with increasing hurricane frequency. The magnitude of change was proportional to the initial size of the C stock. For example, the largest treatment effects were found for the passive soil C fraction, which was also the fraction with the highest soil C content. By the end of the experimental simulations, the increase in the passive soil C fraction explained most of the total soil C increase, with only a small contribution from the slow-cycling C fraction. The orders of magnitude of soil C fractions were consistent with field studies that have shown the importance of slow-cycling C in tropical forests (Marín-Spiotta and others 2008; Cusack and others 2010; Hall and others 2015; Gutiérrez del Arroyo and Silver 2018). There is uncertainty about the long-term stability of the slower cycling C fractions, especially in warm and wet ecosystems such as tropical forests (Hall and others 2015; Kleber and others 2015). However, the results from the current research suggest an increasing importance of the passive C fraction as one of the major C reservoirs in these forests.

One of the greatest concerns about the compounding effects of climate change is that increased disturbance frequency could alter the net C balance of tropical forests and decrease their capacity for serving as C sinks (Lewis 2006; Wood and others 2012; Brienen and others 2015; Feng and others 2018; McDowell and others 2020). The large changes in the distribution of forest C stocks caused by increasing hurricane frequency was accompanied by significant changes in some C fluxes. For example, heterotrophic respiration increased with more frequent hurricanes. The stimulation of microbial respiration with higher rates of litter inputs limited the rate of soil C accumulation. Litter inputs increased by 2.0 to 6.0% with an increase in hurricane frequency to 30 and 10 years, respectively, while heterotrophic respiration, an index of decomposition, increased by 1.6 to 4.7%, respectively. Given that NPP did not vary significantly by treatment, the forest net C balance became more negative (a larger C source) with increasing hurricane frequency. The increase in heterotrophic soil respiration resulted in a twofold decrease in NEP of these forests. Thus, the forest became a larger C source as hurricane frequency increased and lost the temporary C sink that periodically occurred during the background (60-y) hurricane frequency scenario. The results presented here point to the long-term vulnerability of the tropical forest C sink—in addition to the vulnerability of its biomass C stocks—within the context of increasing hurricane frequency (Holm and others 2017; Feng and others 2018).

Increasing hurricane frequency led to greater overall losses of forest biomass and the tropical forest C stocks when compared to other climate change-related disturbance such as warming and drought (O'Brien and others 1992; Feng and others 2018). Significant declines in biomass with increasing hurricane frequency have also been projected for subtropical dry forests in Puerto Rico, but the magnitude of biomass losses were much lower relative to those reported here due to the lower background biomass of subtropical dry forests (Holm and others 2017). The complementary modeling studies of Doyle (1981) and O'Brien and others (1992) applied demographic models to better understand the dynamic relationship between hurricane frequency and forest composition at the LEF, highlighting the potentially catastrophic consequences of high hurricane frequencies. The results from the DayCent model demonstrated the dramatic changes in forest structure that can be expected with increased hurricane frequencies, with cascading long-term effects on biogeochemical processes that drive ecosystem function.

Our findings underscore the significant impact of heightened hurricane frequency on the delicate balance of the global C cycle. Such occurrences cause extensive tropical forest biomass losses and elevated heterotrophic respiration rates, ultimately leading to a reduction in soil C storage capacity. As a result, affected tropical forests transition from C sinks to C sources, with severe implications for the planet's climate. These results emphasize the urgent need for increased efforts to mitigate the factors contributing to more frequent and intense hurricanes and implement measures to safeguard the crucial role of tropical forests in C sequestration.

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OPEN ACCESS

DATA AVAILABILITY

https://github.com/miguelcleon/HurricaneFrequency_TropicalForest_Carbon_with_DayCent

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