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LETTER

Shifts in biomass and productivity for a subtropical dry forest in response to simulated elevated hurricane disturbances

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Supplementary material for this article is available online

Abstract

Caribbean tropical forests are subject to hurricane disturbances of great variability. In addition to natural storm incongruity, climate change can alter storm formation, duration, frequency, and intensity. This model-based investigation assessed the impacts of multiple storms of different intensities and occurrence frequencies on the long-term dynamics of subtropical dry forests in Puerto Rico. Using the previously validated individual-based gap model ZELIG-TROP, we developed a new hurricane damage routine and parameterized it with site- and species-specific hurricane effects. A baseline case with the reconstructed historical hurricane regime represented the control condition. Ten treatment cases, reflecting plausible shifts in hurricane regimes, manipulated both hurricane return time (i.e. frequency) and hurricane intensity. The treatment-related change in carbon storage and fluxes were reported as changes in aboveground forest biomass (AGB), net primary productivity (NPP), and in the aboveground carbon partitioning components, or annual carbon accumulation (ACA). Increasing the frequency of hurricanes decreased aboveground biomass by between 5% and 39%, and increased NPP between 32% and 50%. Decadal-scale biomass fluctuations were damped relative to the control. In contrast, increasing hurricane intensity did not create a large shift in the long-term average forest structure, NPP, or ACA from that of historical hurricane regimes, but produced large fluctuations in biomass. Decreasing both the hurricane intensity and frequency by 50% produced the highest values of biomass and NPP. For the control scenario and with increased hurricane intensity, ACA was negative, which indicated that the aboveground forest components acted as a carbon source. However, with an increase in the frequency of storms or decreased storms, the total ACA was positive due to shifts in leaf production, annual litterfall, and coarse woody debris inputs, indicating a carbon sink into the forest over the long-term. The carbon loss from each hurricane event, in all scenarios, always recovered over sufficient time. Our results suggest that subtropical dry forests will remain resilient to hurricane disturbance. However carbon stocks will decrease if future climates increase hurricane frequency by 50% or more.

Introduction

Hurricane strength and frequency could be altered due to climate change (IPCC 2007), motivating a need to better understand large, infrequent disturbances such as hurricanes (Turner and Dale 1998), as well as their long-term effects on vegetation dynamics. Several studies have reported hurricane damage and recovery of vegetation for the wet subtropical forests of Puerto Rico (Brokaw and Walker 1991, Basnet *et al* 1992, Zimmerman *et al* 1996, Dallmeier *et al* 1998, Frangi and Lugo 1998, Foster *et al* 1999). Dry forests have been less exhaustively studied (but see: Van Bloem *et al* 2003, 2005, 2006). In addition, studies are often limited to a single hurricane. The infrequency of storms, the limited sampling size and, particularly, the relatively low number of locations with forest data before and after a storm limits these studies. It remains a challenge to compare storm effects on vegetation over multiple storms occurring over decades and centuries (Everham and Brokaw 1996).

The absence of detailed data that describes multiple vegetation responses from varying impacts and across longer time scales makes it difficult to evaluate the role hurricane disturbances play in forest dynamics. Do hurricane disturbances as natural events help maintain the ecological integrity of these forests? Could alterations in the average intensity or frequency of hurricanes lead to novel forest successions? Simulations from detailed individual-based models are tools for investigating these issues. Individual-based models can assess both individual- and ecosystem-level changes because they incorporate tree and climate interactions and allow for each tree to alter the local microenvironment (Whitmore 1982, Brokaw 1985, Silvertown and Smith 1988). This, in turn, influences tree growth, survival, and regeneration (Pastor and Post 1986, Shugart 2002).

Individual-based forest gap models have been applied to simulate vegetation dynamics in response to global change (Solomon 1986, Overpeck *et al* 1990, Shugart *et al* 1992, Shuman *et al* 2011) and can help refine carbon estimation and reporting schemes used by groups such as REDD+ (Reducing Emissions from Deforestation and Degradation). This study developed hypothetical hurricane simulations for a Puerto Rican subtropical dry forest within ZELIG-TROP, an individual-based forest gap model, to determine the effects of varying patterns of hurricane disturbances on tropical forest dynamics in a globally changing environment.

Hurricane Disturbances

There is still on-going debate and research about the current forecast and future predictions of hurricane intensity and frequency with respect to human induced climate change (Henderson-Sellers *et al* 1998, Vecchi *et al* 2008, Landsea *et al* 2010). Some studies predict that human-induced warming and increased sea-surface temperatures (SSTs) have caused an increase in tropical cyclone *intensity* (Goldenberg *et al* 2001, Emanuel 2005, 2006, Mann and Emanuel 2006, IPCC 2007, Bender *et al* 2010). These are contrasted by other studies that conclude intense hurricanes are not caused by human-induced warming (Vecchi and Soden 2007a, 2007b), but that cyclones are changing from natural causes, notably, oscillations between La Niña years and strong West African monsoon seasons (Donnelly and Woodruff 2007). In contrast to hurricanes increasing with climate change, Knutson *et al* (2008) and Zhao *et al* (2009) predicted a reduction in tropical cyclone frequency with climate change. Clearly, evaluating vegetation response to multiple hurricane scenarios by varying intensity and frequency is critical to our understanding of potential effects from changes in climate.

Several studies have modeled the effect of hurricane disturbances on the wet subtropical forest of Puerto Rico (i.e. Luquillo Forest) (Doyle 1981, O'Brien *et al* 1992, Boose *et al* 2004, Uriarte *et al* 2009). Individual-based model simulations showed stand densities and species richness increased when hurricanes were introduced compared to the absence of hurricanes (Doyle 1981) due the creation of treefall gaps. The periodicity and intensity of hurricanes played a role in the abundance of species (Uriarte *et al* 2009) and depending on the hurricane severity, the predicted forest structure and maturity status is highly varied (O'Brien *et al* 1992). While gap models have been developed for the wet montane forests of Puerto Rico, this is the first attempt to model hurricane effects for subtropical *dry* forests of Puerto Rico—a overlooked, threatened, and major biome of the world (Murphy and Lugo 1986a, Miles *et al* 2006). The present study is unique in that it utilizes local forest inventory measurements that were recorded before and after a hurricane event, allowing for the creation of realistic species-specific model damage classes as opposed to assigning a uniform disturbance mortality to all species, and uses a detailed forest gap model to examine hurricane effects and recovery in a changing environment that reflects plausible climate change projections.

Changes in forest biomass and productivity

There is strong evidence that global tropical forests are acting as carbon sinks, and sequestering carbon at ∽1 Pg C yr^{-1} (Baker *et al* 2004, Lewis 2006, Pan *et al* 2011). However, this idea that intact tropical forests are gaining carbon at appreciable rates has been confounded by recent measurements (Clark *et al* 2013, Wright 2013, van der Sleen *et al* 2015). The role of tropical forests acting as a carbon sink or source strongly warrants quantification (Gatti *et al* 2014). While the total carbon stock in dry tropical forest vegetation is relatively low (49.7 Pg, 8%–9% of total global carbon) (Schlesinger 1997), these forests have an average net primary productivity (NPP) of 6.20 Mg C ha^{-1} yr^{-1} that is second only to wet tropical forests (Schlesinger 1997). Due to higher NPP, a better quantification of shifts in carbon allocation and plant respiration through disturbance is especially important in dry tropical forests compared to other forests.

Removal of plant material such as coarse woody debris (CWD) during large disturbances is a major

Table 1. Return interval (years) for storm events in each of the five wind classes between 119 and >250 km h^{-1}, and for all storms to pass over the southwestern portion of Puerto Rico. The ten treatments deviating from the control include increasing intensity of only the severe storms while maintaining the historical total number of storms, increasing frequency of all storms, and increasing both the frequency of all storms and the intensity of severe storms by 25%, 50%, and 100%, and decreasing the frequency of all storms and intensity of severe storms only by 50%.

	Wind Speed Class					
Treatments	119–153 km h^{-1}	154–177 km h^{-1}	178–209 km h^{-1}	210–249 km h^{-1}	>250 km h^{-1}	All Storms
Historical/Control	40	32	158	158	158	13
Intensity +25%	43	35	126	126	126	13
Intensity +50%	47	38	105	105	105	13
Intensity +100%	59	48	79	79	79	13
Frequency +25%	32	25	126	126	126	11
Frequency +50%	26	21	105	105	105	9
Frequency +100%	20	16	79	79	79	7
Inten. and Freq. +25%	35	26	106	106	106	11
Inten. and Freq. +50%	29	24	80	80	80	9
Inten. and Freq. +100%	25	19	53	53	53	7
Inten. and Freq. −50%	79	63	316	316	316	26

component of the carbon cycle in tropical forests and is often ignored in carbon cycle estimates. Coarse woody debris has also been estimated to account for 5% to 40% of total carbon in tropical forests (Brown 1997), and in a similar dry tropical forest in Jamaica that is hit by hurricanes, where CWD stocks were estimated to be up to 600 g C m^{-2} (Tanner 1980). The amount and rate of production of CWD is highly variable within and between tropical locations, such that production ranges from 670 g m^{-2} yr^{-1} in wet tropical forests in Brazil (Clark *et al* 2002) to 90 g m^{-2} yr^{-1} in an undisturbed dry forest in Mexico (Eaton and Lawrence 2006).

Hurricanes are important for maintaining dry forest structure in Puerto Rico. However, hurricanes are episodic and range in damage severity and frequency, and the consequences of these events are important and difficult to predict. Furthermore, it is critical to understand large, infrequent distance effects on vulnerable dry tropical forests. This study will assess key ecosystem interactions and the changes in biomass and forest productivity in terms of NPP and aboveground carbon allocation for a subtropical dry forest after simulating increased and decreased hurricane intensities and frequencies in addition to natural gap dynamics.

Materials and methods

ZELIG-TROP model

We used the individual-based gap model ZELIG-TROP to simulate the effects of hurricane disturbances on subtropical dry forests. Earlier versions of the ZELIG model have been used to simulate many forested locations for different applications (Urban 1990, 2000, Urban *et al* 1991, 1993, Cumming and Burton 1993, Larocque *et al* 2006, 2011, Pabst *et al* 2008). ZELIG-TROP has been developed to represent tropical forests and was parameterized with species and site-specific parameters for the Guánica Forest, a subtropical dry forest in southwestern Puerto Rico, and validated by directly comparing model results to observed field data, reproducing a similar modeled forest structure to existing forests (Holm *et al* 2012). ZELIG-TROP uses mechanistic and dynamic relationships for annual computations of individual tree establishment and growth, survival, and death. A more detailed explanation on the site description, model input drivers and parameters, and description of model structure can be found in supplementary data A (available at stacks.iop.org/ERL/12/025007/mmedia).

Hurricane disturbance simulations and model modifications

Meteorological data for past tropical storms were retrieved from the Hurricane database HURDAT, controlled by the U.S. National Hurricane Center and the National Oceanic and Atmospheric Administration (NOAA). Hurricane return times (i.e. intervals between hurricane events in years) for the historical pattern of storms in each wind speed category were first implemented in the model (table 1) and used as the control simulation. In addition to the control simulation, we simulated ten forced hurricane scenarios, or treatments, (table 1) that were congruent with observed and predicted increases in storms (Sanford *et al* 1991, Goldenberg *et al* 2001, Emanuel 2005, Webster *et al* 2005, IPCC 2007, Bender *et al* 2010). We chose to take a comprehensive approach and simulated an array of plausible hurricane scenarios, partially due to the fact that studies remain inconclusive on the long-term changes in storm patterns (Henderson-Sellers *et al* 1998, Vecchi *et al* 2008, Landsea *et al* 2010). A more detailed explanation on the hurricane modeling can be found in supplementary data A.

The model simulated tree communities on 0.04-ha plots, and all simulations were run for 800 years and replicated for 20 plots, with random variation to climate input drivers (within observed standard deviations ranges) and stochastic mortality to generate average responses. Simulations were started from bare ground, with ZELIG-TROP running for a spin-up period of 200 years to allow the model to reach an equilibrium and mature forest state. The spin-up period used the historical hurricane regime, and all hurricane treatments were initiated and conducted during the last 600 years of simulations. Our version of the model allows for multiple hurricanes to hit during any given year, as has occurred in the past. When a hurricane event occurred the new 'hurricane disturbance' function was initiated in ZELIG-TROP during that yearly time step.

Abundance of individuals (stems ha^{-1}), aboveground biomass (AGB; Mg ha^{-1}), stand basal area (m^2 ha^{-1}), and NPP (Mg C ha^{-1} yr^{-1}) were reported on an annual time step for each storm scenario. AGB was calculated using a dry forest allometric equation specific to Puerto Rico (Brandeis *et al* 2006). We assumed that carbon was 50% biomass (Schlesinger 1997). Net change in biomass over the 600-year treatment period was calculated as the difference between total biomass gain between all hurricane events minus the total biomass lost during a one-year period after the hurricane event for all disturbances. To investigate the disturbance severity effect from the control we performed one-way analysis of variance (ANOVA) for each of the four scenarios, and to determine which specific scenarios differed we compared categorical means with Tukey *posteriori* tests.

Hurricane effects on individual trees in a forest are typically heterogeneous across the landscape and among species. Therefore novel model parameters for hurricane damage were derived from past local measurements taken in the Guánica Forest after Hurricane Georges hit Puerto Rico in 1998 (Van Bloem *et al* 2005, 2007). In previous disturbance modeling studies there has been difficulty in obtaining species-specific local measurements (Doyle 1981, O'Brien *et al* 1992), leading to a homogeneous application of disturbance effect. Effects on each individual also varied depending on its diameter, with smaller stems being less affected. There were six separate damage types that could possibly occur to each individual, for the 18 species in the model, based on local measurements. These damage classifications were 1) no apparent damage, 2) loss of foliage, 3) branch damage, 4) main stem snapped, 5) tree uprooted, or 6) dead. For further explanations on how the damage types were modeled see supplementary data A.

We included new model additions to calculate net primary productivity (NPP) and additional carbon partitioning components, or carbon accumulation. In this study annual carbon accumulation (ACA) was defined as the total amount of carbon that was partitioned or accumulated into the live autotrophic aboveground components of the forest, minus the loss due to death of the tree or tree parts. Therefore, ACA was defined as the sum of carbon into plant parts, or the annual addition of 1) new wood biomass through diameter increment, 2) leaf production and leaf growth, 3) biomass from new basal sprouts, and 4) new saplings during the annual time step minus the autotrophic loss from 1) coarse woody debris (CWD), and 2) litterfall (all units in g C m^{-2} yr^{-1}). ACA can be considered here as partitioning of NPP into several components, and similar to NPP in that it already accounts for maintenance and growth respiration. A more thorough and detailed description of both NPP and ACA model additions can be found in supplementary data B.

Results

Effects of hurricane disturbance on forest structure

After simulating the historical hurricane regime (i.e. control run), basal area and stand density increased to values that more closely resembled the observed forest compared to original no-disturbance simulations (table 2) (Holm *et al* 2012). Thus, simulations incorporating hurricane disturbances appropriately represented the real-world forest dynamics. AGB increased from 69.0 to 75.3 Mg ha^{-1}, a slightly further separation from the observed value (64.8 Mg ha^{-1}), but still a realistic AGB representation. Upon simulating hurricane regimes in which the intensity of severe storms increased, all forest values stayed very similar to historical storm levels (∽1%–7% relative effect of treatment), with stand density showing the largest response. After increasing hurricane frequency, either with or without increasing intensity, all forest structure response variables (i.e. basal area, stand density, AGB) decreased compared to the historical hurricane disturbance. The relative effect of each treatment ranged from decreasing forest structure by 4%–41%, with higher effects seen with increasing hurricane frequency.

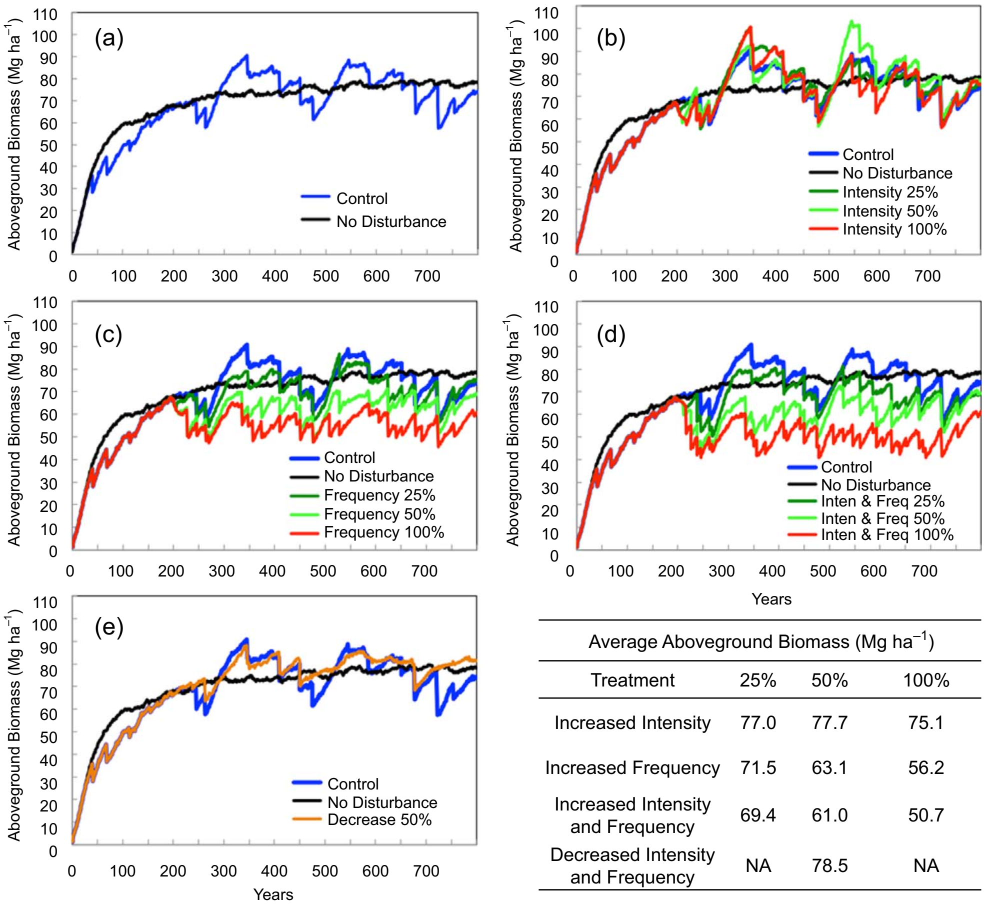
AGB in the control simulation oscillated between 57 and 90 Mg ha^{-1} (figure 1(*a*)), with a hurricane event causing a sudden decrease in AGB followed by a steady increase during the recovery process. Increasing the frequency of storm events from the control led to a significant decrease in average biomass ranging from 5.2%–29.0% ($F_{(79,2.7)} = 72.15$, $p < 0.001$, $r^2 = 0.74$; figure 1(*c*)), explaining 74% of the variation in AGB, and following a Tukey's ad hoc test all treatments had means that were significantly different from each other. An analysis of variance showed that increasing storm intensity from the control did not significantly change AGB: ($F_{(79,\ 2.7)} = 0.487$, $p = 0.692$, $r^2 = 0.019$). Increasing the intensity of severe storms only increased or decreased average AGB by 0.3%–3.1% around the control. However, increasing the intensity of severe hurricanes caused the AGB biomass to oscillate from

Table 2. Average basal area, stand density, aboveground biomass, and NPP for the observed Puerto Rico forest, simulations with no disturbance, historical hurricane events, and ten hurricane treatments (standard deviation in parentheses) from 600 years, after an initial spin-up of 200 years starting from bare ground. Relative effect of each treatment from the control (%), with a negative value meaning the treatment caused a decrease in value. $N = 20$ model runs for each treatment.

Treatments	Basal Area (m^2 ha^{-1})	Stand density (stems ha^{-1})	AGB (Mg ha^{-1})	NPP (Mg C ha^{-1} yr^{-1})	Relative Effect of Treatment % (Basal Area)	Relative Effect of Treatment % (Stand density)	Relative Effect of Treatment % (Biomass)	Relative Effect of Treatment % (NPP)
Observed Values (1981–2009)[a]	20.2 (2.3)	9322 (1553)	64.8 (11.9)	4.5[b]	NA	NA	NA	NA
No Disturbance[a]	19.2 (1.7)	8506 (798)	69.0 (2.8)	NA	NA	NA	NA	NA
Historical Hurricanes	20.0 (2.1)	9936 (1175)	75.3 (7.8)	3.04 (0.19)	NA	NA	NA	NA
Hurricane Intensity +25%	20.4 (2.4)	10226 (1563)	77.0 (9.3)	3.08 (0.23)	1.7	2.9	2.2	1.2
Hurricane Intensity +50%	20.5 (2.7)	10744 (1714)	77.7 (10.3)	3.11 (0.26)	2.6	7.8	3.1	2.1
Hurricane Intensity +100%	19.7 (2.8)	10137 (1456)	75.1 (10.2)	3.06 (0.24)	−1.5	2.0	−0.3	0.6
Hurricane Frequency +25%	18.9 (1.8)	9516 (1076)	71.5 (6.7)	5.10 (0.36)	−5.6	−4.3	−5.2	50.6
Hurricane Frequency +50%	16.5 (1.4)	8214 (606)	63.1 (5.3)	4.73 (0.31)	−19.0	−19.0	−17.6	43.4
Hurricane Frequency +100%	14.6 (1.1)	7248 (365)	56.2 (4.2)	4.39 (0.27)	−31.0	−31.3	−29.0	36.4
Intensity and Frequency +25%	18.3 (1.9)	9247 (1096)	69.4 (6.9)	5.00 (0.37)	−9.1	−7.2	−8.2	48.7
Intensity and Frequency +50%	16.0 (1.6)	8199 (658)	61.0 (5.9)	4.67 (0.34)	−22.3	−19.2	−20.0	42.2
Intensity and Frequency +100%	13.2 (1.3)	7021 (465)	50.7 (4.7)	4.21 (0.30)	−40.9	−34.4	−39.0	32.2
Intensity and Frequency −50%	20.8 (1.4)	10231 (779)	78.5 (5.0)	5.39 (0.25)	4.0	2.9	4.2	55.7

[a] Holm *et al* (2012)

[b] Clark *et al* (2001)



Average Aboveground Biomass (Mg ha^{-1})

Treatment	25%	50%	100%
Increased Intensity	77.0	77.7	75.1
Increased Frequency	71.5	63.1	56.2
Increased Intensity and Frequency	69.4	61.0	50.7
Decreased Intensity and Frequency	NA	78.5	NA

Figure 1. Average aboveground biomass (Mg ha^{-1}) over 800 years, for a total of 11 hurricane treatments and a no-disturbance scenario after spinning up the model for 200 years starting from bare ground. (*a*) Control based on historical hurricane patterns, (*b*) control and increasing storm intensity, (*c*) control and increasing storm frequency, (*d*) control and increasing both storm intensity and frequency, (*e*) control and decreasing both storm intensity and frequency. Average control simulation and observed measured AGB were 75.3 and 64.8 Mg ha^{-1}, respectively.

47 to 101 Mg ha^{-1} (figure 1(*b*)), creating large transient losses and gains in AGB, compared to the control and increased frequency scenarios. The combination of increasing both hurricane frequency and intensity of severe storms generated the greatest decrease in AGB: 8.2%, 20.9%, and 39.0% loss for increasing frequency and intensity by 25%, 50%, and 100% respectively (figure 1(*d*)). The storm scenario that decreased the frequency and intensity of hurricanes by 50% was the only scenario that led to an increase in AGB, but only by 4.2% (i.e. 78.5 Mg ha^{-1}) (figure 1(*e*)).

While there were large annual and decadal fluctuations in biomass, over the centennial time scale these forests remained in a dynamic equilibrium stable- table-state and the net change in total biomass was minimal to non-existent (supplementary table C1). Over a 600-year time period the net change in total biomass was only predicted to increase from 6.2 to 28.6 Mg ha^{-1} depending on treatment. Biomass recovery following all hurricanes, over the 600-year period, was higher than the biomass lost during hurricane events; therefore, forest recovery and the dynamic equilibrium forest state was not limited by severe hurricane damage. The model predicted the historical hurricane regime to maintain the forest in a stable state, with a minimal net change in biomass of 7.5 Mg ha^{-1}. When comparing all hurricane treatments, the scenarios that increased storm intensity had larger net change in total biomass, or differences between overall AGB gains and losses.

Effects of hurricane disturbance on net primary productivity (NPP)

The average NPP under historical hurricane disturbance (i.e. control) was 3.04 Mg C ha^{-1} yr^{-1}. Increasing the intensity of severe storms only had a very slight effect on average NPP, increasing by only 0.6%–2.1%. Similar to biomass results, an analysis of variance found no significant effect of increase in intensity ($F_{(79,\ 2.72)} = 0.588$, $p = 0.625$, figure 2(*a*)). While the effect of increase in frequency of storm events was significant, and substantially increased NPP ($F_{(79,\ 2.72)} = 713.9$, $p < 0.001$, figure 2(*b*)), with the treatment accounting for 17% of the variation in NPP. NPP increased by 50.6%, 43.4%, and 36.4% with increasing frequency of 25%, 50%, and 100% (table 2). Additionally, increasing both hurricane frequency and intensity significantly increased NPP values over the control ($F_{(79,\ 2.7)} = 589.79$, $p < 0.001$, $r^2 = 0.96$, figure 2(*c*)), due to the strong effects from more

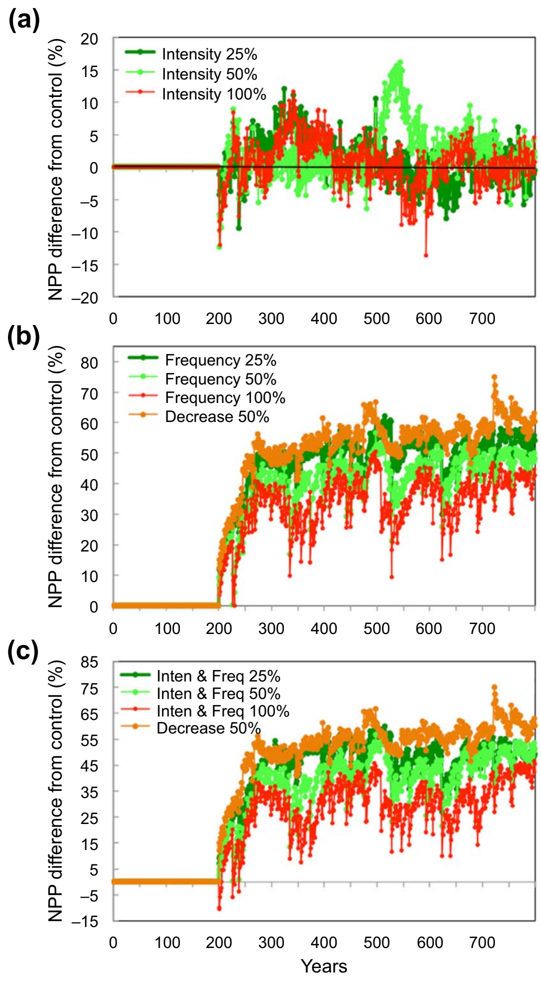


Figure 2. Net primary productivity predictions as a percent difference from the control hurricane treatment, for ten hurricane treatments, as described in table 1.

frequent storms. Decreasing the frequency and intensity of severe storms by 50% from the control levels produced the largest, significant, average NPP value, 5.39 Mg C ha^{-1} yr^{-1}, a 55.7% increase in NPP from the control ($F(_{39,\ 4.1}) = 1163.08$, $p < 0.001$, $r^2 = 0.97$, figure 2(*c*)).

Compared to the control, NPP increased as a result of all elevated hurricane regimes. Higher levels of NPP and higher frequency of storms were negatively correlated, such that the highest level of NPP was seen with the smallest simulated increase in storm frequency, 25% (figure 3). The lowest NPP was predicted when only the intensity of storms was increased, and there was no trend between the intensity treatments. NPP increased as a function of increasing AGB (Mg ha^{-1}) (figure 3); further highlighting that hurricane regimes play a major role in NPP levels.

Effects of disturbance on components of carbon accumulation

ACA was predicted to be negative during both the control simulation and the treatments that increased storm intensity (figure 4(*a*) and (*b*)), due to loss of carbon through litterfall and CWD; with CWD being a large contribution in ecosystems that routinely get hit by disturbances and repeatedly left out of modeled carbon balance calculations. Conversely, ACA was positive and the forest gained carbon during treatment simulations that increased the frequency of storms and also decreased the intensity and frequency of storms (figure 4(*c*) and (*d*)). In all four hurricane treatments the ACA component which produced the largest gain in carbon sequestration was annual leaf production, followed by diameter increment, basal-sprouting of new stems, and lastly regeneration of new trees. The ACA component that produced the largest loss in carbon was leaf litterfall followed by CWD.

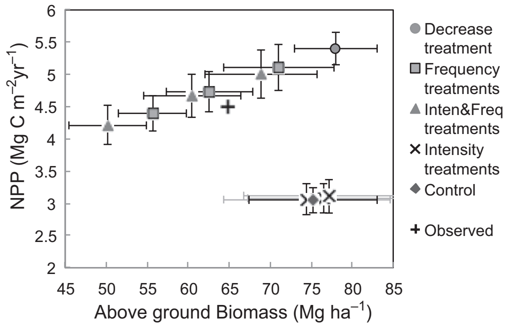


Figure 3. Pattern of change in average NPP (Mg C ha^{-1} yr^{-1}) as a function of average AGB (Mg ha^{-1}) over 600 years, for the control scenario, ten hurricane treatments under altered hurricane regime conditions, and observed values.

Increased hurricane frequency (figure 4(*c*)) and decreased hurricane intensity and frequency (figure 4(*d*)) displayed significantly different patterns from the control (figure 4(*a*)). There was sign-shift from negative to positive ACA due to a significant increase in carbon gain from leaf production (∽93% and 120% increase respectively) and a 16% reduction in CWD in the increased frequency treatment, compared to the control simulation. Basal sprouting also increased by 13% in both scenarios. The only notable variations between the control and increased intensity scenario were the increase in basal-sprouting by 7.6%, larger spikes in CWD due to more severe storms, and close to no change in average annual ACA (−111.9 vs. −115.8 g C m^{-2} yr^{-1}) (table 3). The pattern and variation in ACA was strongly driven by changes in CWD. There were occurrences of high inputs of CWD (>400 g C m^{-2} yr^{-1}) during increased intensity treatments, more so than any of the other treatments. Average annual CWD made up 11.4% to 16.5% of total ACA depending on the hurricane scenario (table 3).

Litterfall in subtropical dry forests is highly variable and fluctuates depending on climate and disturbances, ranging from 127.75 to 500.00 g m^{-2} yr^{-1} (table 4). In September 1998 Hurricane Georges hit the Guánica Forest and caused a large increase in litterfall to 500 g m^{-2} yr^{-1}. In September, four days before the hurricane hit, the litterfall was 238.7 g m^{-2} yr^{-1}. Annual litterfall was lowest in model runs during the absence of

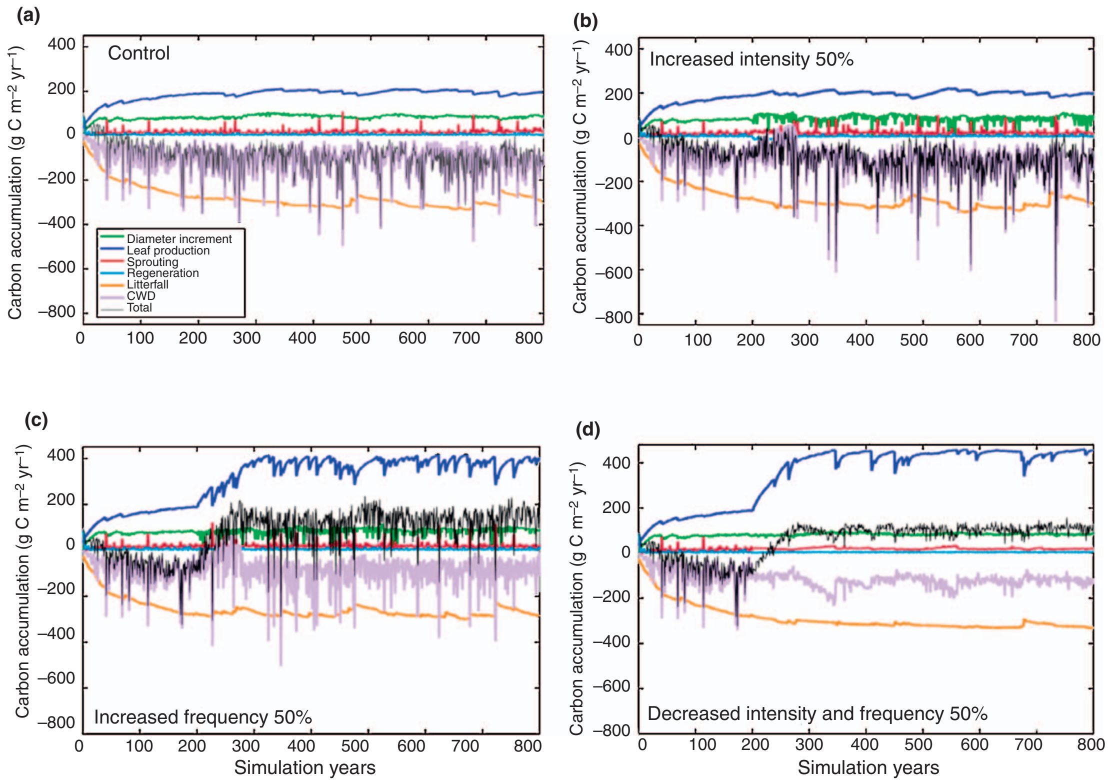


Figure 4. Simulated annual carbon accumulation (ACA), and six components of ACA for four hurricane treatments, over the full 800-year simulation. ACA components and aboveground carbon partitioning consists of leaf production, diameter increment, basal-sprouting, regeneration for new saplings, biomass loss to coarse-woody debris, and leaf loss (all in g C m^{-2} yr^{-1}). (*a*) Control treatment, (*b*) increased hurricane intensity by 50%, (*c*) increased hurricane frequency by 50%, and (*d*) decreased hurricane intensity and frequency by 50%.

Table 3. Simulated average autotrophic live carbon accumulation (ACA; g C m^{-2} yr^{-1}), coarse woody debris (CWD; g C m^{-2} yr^{-1}) and percent of total ACA from the final 600 years of simulation from the control hurricane treatment, and three adjusted hurricane scenarios for Guánica Forest.

Treatment	ACA (g C m^{-2} yr^{-1})	CWD (g C m^{-2} yr^{-1})	CWD % of total ACA	Leaf production % of total ACA
Control	−111.9	−116.3	16.1	27.3
Intensity + 50%	−115.8	−118.8	16.5	27.4
Frequency + 50%	128.7	−98.0	11.4	44.6
Decreased − 50%	104.9	−126.7	12.9	44.2

hurricane disturbances (191.17 g C m^{-2} yr^{-1}), 60% less than modeled historical disturbances patterns (299.45 g C m^{-2} yr^{-1}; figure 5(*a*)). Increasing the frequency of storms by 25%, 50%, and 100% all significantly reduced annual litterfall from the control ($F_{(79,\ 2.7)} = 81.5$, $p < 0.001$, $r^2 = 0.76$; figure 5(*a*)); with an inverse relationship seen between litterfall and increasing storm frequency (e.g. 291.31, 272.14, and 255.63 g C m^{-2} yr^{-1} litterfall respectively). Increasing the intensity of storms did not have a significant effect on annual litterfall compared to the control ($F_{(79,\ 2.7)} = 1.50$, $p = 0.221$, $r^2 = 0.06$). All treatments that increased hurricane disturbances led to a reduction in average litterfall, compared to the control, and in contrast a reduction in hurricane disturbances from control levels caused litterfall to significantly increase to 313.95 g C m^{-2} yr^{-1} ($F_{(39,\ 4.1)} = 10.22$, $p = 0.003$, $r^2 = 0.21$).

Leaf production in the subtropical dry forest did not mirror litterfall patterns. All treatments with increased hurricane frequency showed greater leaf production over treatments that only increased intensity of storms (figure 5(*b*)). When the forest was in a hurricane disturbance-free state, the annual leaf production was high, averaging 438.56 g C m^{-2} yr^{-1}, in contrast to the leaf production under the control hurricane treatment (i.e. 196.13 g C m^{-2} yr^{-1}). Leaf production under increasing hurricane frequency regimes was high (353.71 to 406.01 g C m^{-2} yr^{-1}, figure 5(*b*)), and led to large increased leaf production over the control ($F_{(79,\ 2.7)} = 2007.18$, $p < 0.001$, $r^2 = 0.99$). The annual leaf production during treatments of increased intensity of storms only differed by −1.18% to 0.56% from the control ($F_{(79,\ 2.7)} = 0.851$, $p = 0.470$, $r^2 = 0.03$).

Table 4. Observed and simulated average annual litterfall (g C m^{-2} yr^{-1}) for Guánica State Forest a subtropical dry forest in Puerto Rico.

Year	Average Litterfall (g C m^{-2} yr^{-1})	Source
1974	127.75	Cintron and Lugo 1990
1975	324.85	Cintron and Lugo 1990
1976	350.40	Cintron and Lugo 1990
1982	433.70	Murphy and Lugo 1986b
Sep. 1998	238.70	Van Bloem *et al* 2005
1999	500.00	Van Bloem *et al* 2005
2000	220.00	Van Bloem *et al* 2005
Hurricane Treatment	Average Litterfall (g C m^{-2} yr^{-1})	Source
No Disturbance	191.17	This study
Control	299.45	This study
Intensity + 25%	300.60	This study
Intensity + 50%	298.40	This study
Intensity + 100%	290.84	This study
Frequency + 25%	291.31	This study
Frequency + 50%	272.10	This study
Frequency + 100%	255.63	This study
Decreased − 50%	313.90	This study

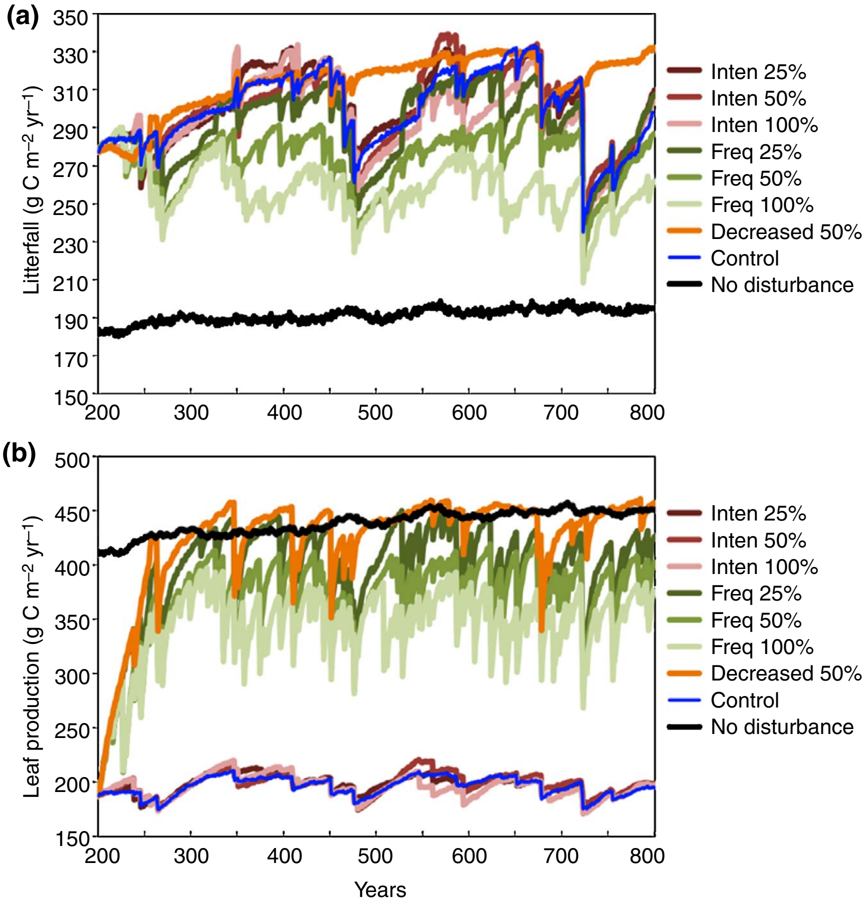


Figure 5. Simulated (*a*) average annual litterfall (g C m^{-2} yr^{-1}), and (*b*) average annual leaf production (g C m^{-2} yr^{-1}) for a subtropical dry forest in Puerto Rico, under scenarios with no disturbance, historical disturbance regime (i.e. control), and seven treatments with changes to hurricane intensity and frequency.

Discussion

Hurricane treatments

Our model predictions showed that increasing hurricane frequency had substantial effects on forest structure and production in the dry forest system of Puerto Rico. Increased hurricane intensity created larger fluctuations and variability in biomass levels, but had no long-term effects (i.e. centuries) on the average condition of AGB or productivity, a noteworthy result due to studies showing increasing storm intensity over the past decades and with similar expectations for future climate change scenarios. However, the model results presented here do not include the effects of changes to temperature and precipitation that might be associated with alternate hurricane regimes and changing climates.

Over the 600-year time period we saw close to no net change in AGB (supplementary table C1) as a result of elevated hurricane regimes, but in shorter observational intervals, there were extreme fluctuations in biomass (figure 1). This result supports field studies from other forest types that reported short-term reductions in biomass after Hurricane Hugo, but five years later AGB accumulated at faster rates than pre-hurricane rates, returning the forest to its pre-disturbed state (Frangi and Lugo 1998). Potential hurricane regimes with more frequent storms produced higher NPP values; likely due to more frequent thinning and recovery episodes, and recovery from less intense storms, compared to the treatments that increased the intensity of storms. The little to no predicted change in average biomass stocks over 600 years (once the forest reached a new quasi-stable state) shows a high degree of resilience in this tropical forest system.

A major difference in results between the wet and dry forests of Puerto Rico was that even after largely increasing hurricane regimes (i.e. increasing hurricanes intensity and frequency by 100%), the dry forest did not experience extreme basal area or biomass loss, where basal area, biomass, and leaf area came close to zero in the wet forest. The dry forest on Puerto Rico appears to be more resistant to large, infrequent disturbances like hurricanes (Van Bloem *et al* 2003). This resiliency in the model and in the actual ecosystems appears to be due to the inclusion of sprouting in simulations. Furthermore, our study agreed with the results in Boose *et al* (2004) that increased forest effects were dependent on effects of recent hurricanes and that shorter return intervals of storms have a larger effect on decreasing forest biomass. Verifying these results for additional dry tropical forests could be of interest, as post-hurricane sprouting and multistemmed growth habits of trees have been noted in other dry subtropical forests (Quigley and Platt 2003) and thus our results may be representative not only of Puerto Rican dry forests, but others in hurricane-prone locations. A more detailed explanation of the simulation modeling results in comparison to benchmarking field data can be found in supplementary data D.

Effects of disturbance on forest productivity

This study further validates the dynamic relationship between AGB and NPP. The pattern of higher NPP in stands with lower biomass (which is also seen in other tropical forests that are highly disturbed by windstorms (Johnson *et al* 2016)) is analogous to the patterns predicted by the self-thinning theory (Yoda *et al* 1963), as well as productivity being a function of stand structure (Sprugel 1984). During simulated increased storm frequencies and under self-thinning, there is a pronounced drop in forest stand density and AGB. With this decrease there is a corresponding increase in carbon uptake during the recovery process, and consequently a higher NPP. It has been observed in wet forests of Puerto Rico that debris after a hurricane will decompose quickly followed by a rapid regrowth of vegetation transferring the nutrients from the floor back into the aboveground growth, and primary productivity rates can be triple that prior to the hurricane (Scatena *et al* 1996). However, the pattern has not been observed in dry forests, where decomposition rates in the absence of recent storms are about ∽65% slower than in wet forests (Lugo and Murphy 1986, Ostertag *et al* 2003). Currently there is no decomposition function in the model used here.

During increased hurricane intensity scenarios, the model predicted a large recovery process after each extreme hurricane, but there was no substantial increase in NPP. A possible explanation may be found in the mode of recovery in Caribbean dry forests that favors basal sprouting and advance regeneration. Whereas other tropical forest types may undergo stand replacement or gap filling by pioneer species, in the Caribbean dry forest stand density is high and tree size (height and crown diameter) is low, so the proportion of stems lost is low (e.g. ∽13% after Hurricane Georges in Puerto Rico; Van Bloem *et al* 2005). Caribbean dry forests have low leaf area index (Murphy and Lugo 1986a) so light is not limited at the forest floor and the 'gap' that is created is already filled by juvenile trees or quickly filled by new sprouts. Low proportions of lost stems and high stand density suggest that little change would occur in NPP unlike other systems where a spike in NPP would occur from the re-establishment of pioneer species. We suggest that variations in NPP and AGB between the hurricane treatments were explained by differences in recovery trends. Our results suggest that reducing the frequency and intensity of hurricanes generated a forest with the largest AGB, due to decreased occurrence of damage and biomass loss (table C1), and also the largest NPP compared to all other hurricane regimes. We believe the increase in NPP was related to the greater canopy structure, leaf area index, and leaf production (figure 5(*b*)) as a result of reduced disturbance events.

Both litterfall and leaf production were crucial compensating elements of ACA, making up a large constituent of annual carbon partitioning (tables 3 and 4). The large contribution from leaf production in a system with more frequent, less severe disturbances played a major role in switching ACA from negative to positive. Measuring components of ACA can be challenging, especially in tropical terrestrial systems. A major carbon component that is frequently left out or overlooked is dead woodfall. The carbon transfer from large trees once they die can lead to negative ACA values. The carbon contribution from respiring and decomposing woodfall is a hard variable to measure in field studies, but the transfer of live carbon to dead can be monitored in individual based simulation models which track the fate of each tree, where biomass is known at the time of death. With increased occurrences of hurricanes hitting the dry forest, the size structure of the forest (e.g. total basal area, height) typically remained low, therefore keeping CWD low and contributed to the switch in ACA becoming positive.

In the present-day hurricane disturbance scenario, based on historical trends, the average ACA was negative (-111.9 g C m^{-2} yr^{-1}) and the dry tropical forest of Puerto Rico was losing autotrophic live carbon. This carbon loss was attributed to high woodfall, litterfall, and low leaf production. This study found that different hurricane disturbances produce substantial differences in annual litterfall, leaf production, and overall ACA, followed by smaller differences in diameter increment, basal-sprouting, and regeneration. We believe that the modeling approach demonstrated here can be used as a tool for entities such as United Nations supported REDD+ (Reducing Emissions from Deforestation and Degradation+; Miles and Kapos 2008, Venter *et al* 2009, Laurance 2007). For example, forest carbon accumulation rates after varying disturbance regimes could interact with forest-based carbon mitigation strategies that aim to reduce carbon emissions. For more information on suggestions for practical model application please see supplementary data E.

Conclusions

With the new hurricane disturbance routine implemented into the gap model ZELIG-TROP, we have the ability to assess long-term dry forest dynamics in response to large disturbances. With increasing hurricane intensity (even up to 100% increase) we did not see a large shift in AGB or NPP over time from the control treatment. Therefore, while there is evidence and predictions that hurricane intensity has been increasing in the Atlantic Basin over the past 30 years and into the future (Emanuel 2006, IPCC 2007) we predict the forest structure and productivity will not be largely affected in relationship to storm intensity alone. However, large fluctuations in AGB were observed with increased intensity treatments, and should be a point of concern with regard to short-term processes.

Treatments that increase the frequency of storms have a larger effect (both negative through biomass loss and positive through enhanced forest productivity) on the forest. More frequent storms also led to a switch in simulated ACA from negative to positive, with CWD and leaf production being major carbon components that should be included in modeling. We found that NPP always increased as a result of elevated hurricane regimes, with increases in hurricane frequency producing larger NPP due to its recovery pattern. This research provides examples that subtropical dry forests will respond with a great deal of resilience to changes in hurricane disturbance. Modeling efforts improve the capability to predict carbon stocks, emissions, and sequestration in dry tropical forests that can be used by initiatives like REDD+, where there is a need for a strong monitoring and verification system in order to succeed in reducing carbon emissions from forests.

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