Environmental Research Letters

LETTER • **OPEN ACCESS**

Topography, drainage capability, and legacy of drought differentiate tropical ecosystem response to and recovery from major hurricanes

To cite this article: Mei Yu and Qiong Gao 2020 *Environ. Res. Lett.* **15** 104046

Environmental Research Letters

OPEN ACCESS

RECEIVED
28 February 2020

REVISED
3 August 2020

ACCEPTED FOR PUBLICATION
11 August 2020

PUBLISHED
28 September 2020

LETTER

Topography, drainage capability, and legacy of drought differentiate tropical ecosystem response to and recovery from major hurricanes

Mei Yu and Qiong Gao

Department of Environmental Sciences, University of Puerto Rico, Rio Piedras, San Juan, PR, 00936, United States of America

E-mail: meiyu@ites.upr.edu

Keywords: major hurricane, tropical forest, coastal mangrove, ecosystem resistance, ecosystem resilience, intensified climate variability, legacy of climate event

Supplementary material for this article is available online

Abstract

High-carbon sequestrations of tropical montane forests and coastal mangroves have been greatly disturbed by intensified extreme climate events such as alternating hurricanes and droughts. However, few studies of the hurricane impact have taken into consideration the legacy of past climate events and analyzed the heterogeneity of hurricane impacts between montane forests and coastal mangroves. Here, we studied the impact of Hurricanes Irma and Maria in 2017 on coastal mangroves and upland forests in Puerto Rico after a severe drought during 2015–2016. We investigated the island-wide immediate impact on greenness using fused vegetation index from Sentinel-2 and Landsat-8, and the impact on and the recovery of 62 homogeneous vegetation patches by deriving an impact index and one-year recovery ratio (RR). A linear mixed-effect model was applied to explore roles of hurricane wind, rainfall, topography, and biological components in the impact and the recovery. Island-wide, the immediate impact is highly spatial-heterogeneous. Although most of the island was browned, a green-up strip in the dry south showed benefits from the hurricane rain which relieved the prior drought stress. Coastal mangroves experienced the greatest impact and slowest recovery with relative recovery of 0.44 compared to recovery greater than 0.70 for upland forests, and evergreen forests sustained significantly more damage than deciduous forests. The recovery of evergreen forests was on average 11 days earlier and faster than that of mangroves. Mangrove recovery was mostly limited by inundation-related factors such as elevation, slope, and drainage capacity. While higher elevation relates to slower recovery for upland forests, it favors mangrove recovery. Particularly, mangrove recovery is facilitated by river presence, explaining 65% variation in RR. The differentiated response, recovery, and underlying mechanisms highlighted a complicated array of external forces, geophysical/ biological modulators, and legacy of past climate events in determining and understanding hurricanes' impact on tropical ecosystems.

1. Introduction

Tropical forests have the largest plant C pool (Pan *et al* 2013) and the highest net primary productivity (Chapin *et al* 2012), and thus play important roles in sequestrating C globally and modulating changes in climate. In tropical coast, the forested wetlands dominated by mangroves sequester especially large amounts of carbon with exceedingly high water use efficiency and low decomposition rate, despite their limited spatial extent (Kirwan and Megonigal 2013, Hutchison *et al* 2014). However, the sustainability of carbon sequestration capability of tropical coastal wetland is challenged by boosted coastal development, accelerated rising sea level (Church *et al* 2013, Krauss *et al* 2014, Lovelock *et al* 2015), and intensified climate variability (Cai *et al* 2014, 2015, Yi *et al* 2015) such as frequent severe droughts and hurricanes.

Tropical cyclones, especially major hurricanes, are the most important pulse disturbance affecting coastal ecosystems in tropical and temperate regions (Lugo 2000, 2008, Fisk *et al* 2013), and have both short- and long-term impacts on ecosystem structures, compositions, and functions such as C fluxes (Beard *et al* 2005, Vargas 2012, Fisk *et al* 2013, Hutley *et al* 2013). For example, Hurricanes Hugo in 1989 and Georges in 1998 hit the tropical montane forests in Puerto Rico and induced both imminent and delayed massive tree mortality (Lugo 2000). The hurricanes in 2005 and 2008 were thought to cause the significant loss of saltmarsh in the Gulf of Mexico in 2004–2009 (Dahl and Stedman 2013). High winds and excessive rainfall are often the major forces associated with hurricanes. For instance, a single event of tropical cyclones can bring 5%–40% annual rainfall to the Caribbean and US southeastern coast (Scatena and Larsen 1991, Michener *et al* 1997). In addition, storm surges and heavy runoff inundate the coastal lowland, and the inundation can last for weeks and cause significant changes in coastal vegetations (Michener *et al* 1997, Lugo 2008). Therefore, a complex array of external forces, e.g. wind, rainfall, discharge, storm surge, flooding, landslide, and hurricane-induced drought (Miller *et al* 2019) imposes diverse effects on ecosystems from upland to lowland. Recovery of the heavily affected ecosystems can last for decades and might take various directions (Lugo 2008).

Compared to upland forests, mangroves live in low, saline, and anaerobic environments, and survive this environment by excluding 80%–99% of salts in their roots, and by storing salts in or secreting salts through their leaves. Therefore, mangroves expend extra energy on salt exclusion and water uptake (Reef and Lovelock 2015, Lovelock *et al* 2016). Under the salty and anaerobic environment, the recovery of defoliated mangroves will be much harder than a neighboring upland forest, which can re-sprout quickly after hurricanes. On the other hand, to cope with anoxia, all mangroves have aerial roots of various types to take in oxygen for metabolism and nitrification of ammonium in soil (Clough 2013). Mangroves can tolerate an anaerobic environment to some degree. For example, partial sediment burial might induce morpho-anatomical adaptations, such as developing new roots, for enhanced survivorship (Okello *et al* 2020), and rising sea level might lead to increased mangrove contribution to soil organic carbon (Chen *et al* 2020). However, hurricane-induced prolonged inundations with severe damage such as mass defoliation may immerse their aerial roots and induce mortality before new roots come out.

In general, tropical forest ecosystems such as wet and rain forests were not considered as moisture-limited; however, intensified climate variability has brought out more frequent and severe drought events which were reported to modulate C dynamics and induce tree mortality (Gatti *et al* 2014, Doughty *et al* 2015). For example, drought suppressed photosynthesis in the Amazon and altered carbon allocation to reduce the maintenance and defense against herbivores and diseases which might be linked to increased mortality after drought (Doughty *et al* 2015). As found in the tropical forests of El Yunque in the Caribbean during 1989–1998 (Beard *et al* 2005), droughts caused more severe damage to fine roots than hurricanes did, and the recovery of fine roots after droughts was much slower than that after hurricanes. For coastal wetlands, severe drought exacerbated the negative effects of saltwater intrusion on the *Pterocarpus* freshwater swamp and induced massive mortality of seedlings and saplings (Yu *et al* 2019).

Although impacts of hurricanes on tropical forests and mangroves are well discussed in the literature (Michener *et al* 1997, Beard *et al* 2005, Lugo 2008), few studies have considered tropical upland forests and coastal lowland mangroves as a spatial continuum, and linked the impacts of the sequence of El Niño drought, major hurricanes, and post-hurricane drought. As a tropical mountainous island in the Caribbean, Puerto Rico is prone to storms and hurricanes (López-Marrero *et al* 2019), and the intensified climate variability promotes the probability of consecutive extreme climate events (Cai *et al* 2014, 2015, Runkle *et al* 2018). Puerto Rico underwent a severe drought in 2015–2016 (Mote *et al* 2017) and the annual rainfall in 2015 was about 45% lower than the long-term average in the wet forest (Gutiérrez-Fonseca *et al* 2020). This drought largely reduced the community-wide reproduction in the Guánica dry forest (Lasky *et al* 2016), increased the litter fall of the tropical montane forest due to physiological stress (Gutiérrez-Fonseca *et al* 2020), increased the C emission through soil respiration (O'Connell *et al* 2018), and induced low recruitment of the *Pterocarpus* freshwater swamp through elevated salinity (Yu *et al* 2019). Following the severe drought, Puerto Rico experienced major hurricanes Irma and Maria in 2017, which defoliated the ecosystems, snapped or uprooted trees from top-mountain rainforests, wet forests, low-mountain moist forests, dry forest, and coastal mangroves. The ground survey in the montane forest reported that Hurricanes Irma and Maria broke three times the stems and doubled the mortality compared to previous storms (Uriarte *et al* 2019). The major hurricanes after severe drought leave an important opportunity to investigate the ecosystem resistance and resilience from upland forests to lowland mangroves under consecutive extreme climate events.

In this study, we address the spatial distributions of the impact of 2017 hurricanes and the recovery after in Puerto Rico in the context of major hurricanes after severe drought. We assume the prior severe drought might reduce plant activities including slowing down individual tree growth (Doughty *et al* 2015, Schwartz *et al* 2019), lower the survivorship of seedlings and saplings (Yu *et al* 2019), and induce fine-root mortality (Beard *et al* 2005), and thus might amplify ecosystem responses to subsequent major hurricanes. We hypothesize that the impact and recovery are functions of hurricane wind and rainfall, topography, and biological components such as vegetation type and functional traits (Lugo 2008). Specifically, we hypothesize that coastal mangroves are less resistant and resilient, in terms of *in situ* survivorship during a short time period, than upland vegetation due to their saline and anaerobic environment that exerts stresses on the metabolism and growth of defoliated mangroves. Among upland vegetation, we hypothesize that higher-elevation forests experience more severe damage and slower recovery than lower-elevation ones due to stronger wind and the fact that higher-elevation plants in wet and moist environments are more sensitive to and more likely to suffer from the pre-hurricane drought. For coastal mangroves, drainage capacity reduces probability and period of inundation, and we hypothesize that mangroves in higher places, on steeper slopes, or having a river flowing through to drain experience less damage and faster recovery than those with poor drainage.

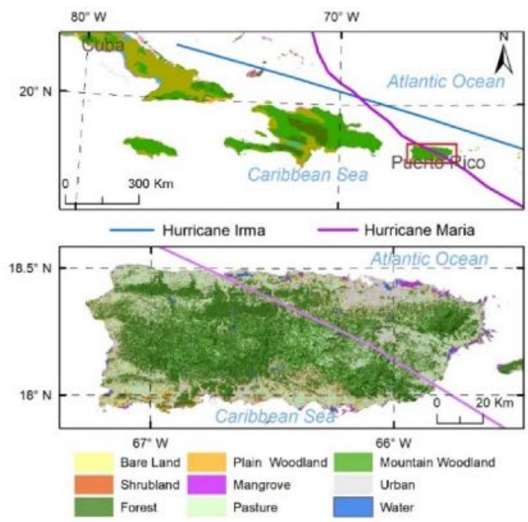

Figure 1. Location of Puerto Rico in the Caribbean (top) and land cover in 2010 (bottom). Hurricane Irma (blue line) passed to the northeast on September 6, 2017 while Hurricane Maria (purple line) made a landfall and traversed the island from southeast to northwest on September 20, 2017.

2. Methods

2.1. Study area

Puerto Rico is a mountainous tropical archipelago in the northeastern Caribbean (18°15'N and 66°30'W, figure 1), with elevations from slightly lower than sea level to more than 1000 m in the central mountains (figure 2(a)). The northeasterly trade wind brings moisture from the Atlantic Ocean and deposits more than 4000 mm of annual rainfall in windward mountains about 1000 m above sea level but less than 1000 mm in the southwestern leeward coast. Forest distribution varies from cloud forest and wet forest in windward mountains, to moist forest in lowland, to dry forest in leeward, and to mangrove and *Pterocarpus* swamp in coastal wetlands (Miller and Lugo 2009). After a severe drought in 2015–2016, Hurricane Irma passed near the northeast of the island on September 6, 2017 with sustaining wind speed of 298 km h^{-1}, and Hurricane Maria traversed the island on September 20 with sustaining wind speed of 249 km h^{-1} at its landfall. The largely reduced transpiration due to mass defoliation and the increases in Bowen ratio changed the regional hydrology, and incurred post-hurricane drought (Miller *et al* 2019).

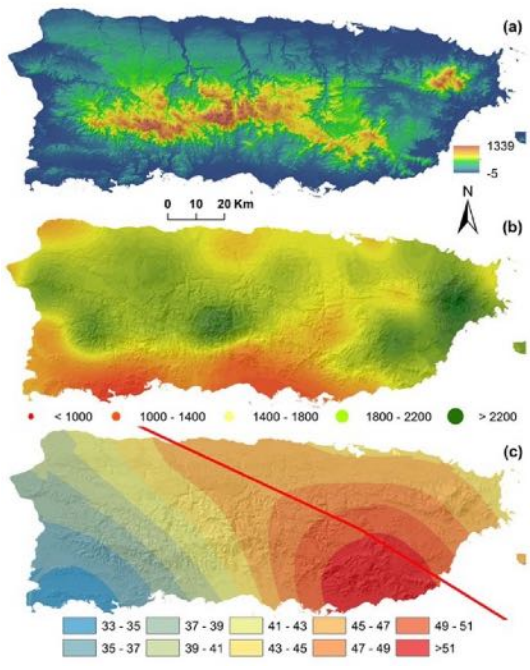

Figure 2. Elevation in m (a), normal annual rainfall in mm (1980–2010) (b), and wind gusts in m s^{-1} during Hurricane Maria (c).

2.2. Data preparation

We retrieved the hurricane data from the NOAA National Hurricane Center (Pasch *et al* 2019), including hurricane paths, rainfall, and gust wind during Maria recorded at stations in Puerto Rico. We calculated the distances to paths of Maria and Irma, and interpolated the rainfall and gust wind by cokriging (figure 2, appendix S1 (available online at stacks.iop.org/ERL/15/104046/mmedia)). We acquired satellite-based vegetation index from Landsat-8 (Wulder *et al* 2019) and Sentinel-2 (Chastain *et al* 2019, Pahlevan *et al* 2019) via Google Earth Engine (Gorelick *et al* 2017). Normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) were derived after cloud detection and shadow removal (Housman *et al* 2018).

To disentangle impact on various vegetation, we obtained large homogeneous patches without land-cover changes since 2000, guided by Land Cover

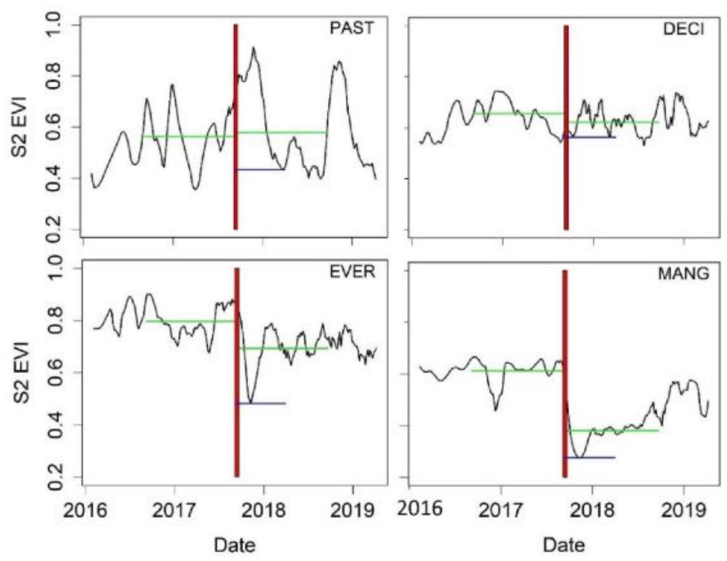

Figure 3. Typical dynamics of Sentinel-2 EVI time series for pasture (PAST), deciduous forest (DECI), evergreen forest (EVER), and mangrove and associates (MANG). The red vertical bar depicts the period between the two hurricanes (September 6 to 20, 2017). The horizontal green lines to the left and right of the red bar illustrate the 1-year mean before and after the hurricanes, respectively. The black line indicates the minimum EVI after the hurricanes, from September 6, 2017–March 31, 2018.

Maps of 2000, 2010 and aerial images of 2010 (Gould *et al* 2008, Wang *et al* 2017, Yu *et al* 2017). These include 13 mangrove and associate (*Pterocarpus*), 19 evergreen forest, 11 deciduous forest, and 19 pasture patches used as a reference vegetation type in comparison to woody vegetation. Sentinel-2 EVI and NDVI with 5-day revisit are used to capture the high-frequency changes of vegetation greenness from January 2016–March 2019.

2.3. Data analysis

2.3.1. Changes in vegetation index one month before and after the hurricanes over the island

To assess the immediate impacts, we compared NDVI before the hurricanes (Aug. 1–Sep. 5, 2017) and after (Sep. 21–Oct. 31, 2017) via median-composite of fused NDVIs from Landsat-8 and Sentinel-2 (Zhang *et al* 2018). The period of Aug–Oct is within the wet season, when deciduous forests have their leaves. The ratio of NDVI after to NDVI before reflects the relative changes in greenness and the immediate impacts. We further computed the relative changes regarding various life zones, direction to Maria's path (right of the path versus left, considering the counterclockwise spin and stronger winds to the right of hurricane eye), and distance from the path.

2.3.2. Analysis of impact of hurricanes on vegetation patches and their recovery

Different types of vegetation show different resistance and resilience, and we used the homogeneous and stable vegetation patches to assess the impact from the mountains to the coast. After filling missing data and filtering random noise of vegetation indices for each patch (Zeileis and Grothendieck 2005), we obtained the typical patterns of Sentinel-2 EVI time series as shown in figure 3.

For each time series, we computed three statistics: mean from September 6, 2016–September 5, 2017 as MEAN BEFORE, mean from September 21, 2017–September 20, 2018 as MEAN AFTER, and minimum from September 6, 2017–March 31, 2018 as LOW AFTER with consideration of the delayed mortality (figure S2). The LOW AFTER divided by MEAN BEFORE is computed as relative low (RL) to quantify the impacts of the hurricanes and post-hurricane drought/inundation (equation (1)), whereas the MEAN AFTER divided by MEAN BEFORE is regarded as recovery ratio (RR, equation (2)). The RL reflects the proportion of greenness remaining after the perturbations, which is conceptually similar to the resistance index proposed to depict drought impacts using tree rings (Lloret *et al* 2011). We used one-year mean before or after the perturbations as references to reduce seasonal effects. The RR reflects the proportion of average greenness that vegetation is able to reach after one year, and it is conceptually similar to the resilience index in the literature (Lloret *et al* 2011). As RR depends also on severity of the impact (Relative Low), we computed relative recovery ratio (RRR, equation (3)) as the difference between MEAN AFTER and LOW AFTER over that between MEAN BEFORE and LOW AFTER. This index depicts the percentage of lost greenness that vegetation regained during the year after perturbations (figure S2).

$$Relative\ Low:\ RL = \frac{Low_{After}}{Mean_{Before}} \quad (1)$$

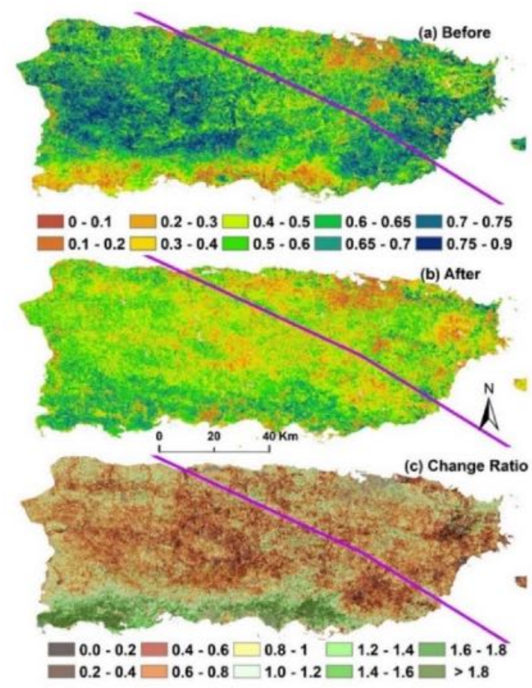

Figure 4. NDVI derived from Landsat-8 and Sentinel-2 over the main island of Puerto Rico (a) before Hurricanes Maria and Irma (Aug. 1–Sep. 5, 2017) and (b) after the Hurricanes (Sep. 21–Oct. 31, 2017). (c) Ratio of the change in NDVI (ratio of NDVI after to NDVI before, less than 1 indicating decrease in NDVI while greater than 1 indicating increase in NDVI after the hurricanes). The purple line shows the path of Hurricane Maria on September 20, 2017.

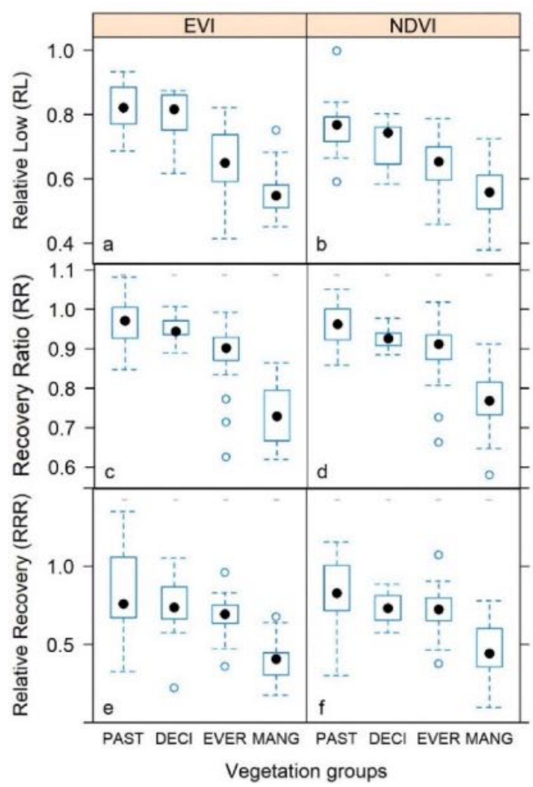

Figure 5. Boxplots of the relative low after the hurricanes (RL), recovery ratio (RR), and relative recovery ratio (RRR) of MANG–mangroves, EVER–evergreen forests, DECI–deciduous forests, and PAST–pastures.

$$Recovery\ Ratio:\ RR = \frac{Mean_{After}}{Mean_{Before}} \quad (2)$$

$$Relative\ Recovery\ Ratio:\ RRR = \frac{Mean_{After} - Low_{After}}{Mean_{Before} - Low_{After}}. \quad (3)$$

RL or RR reflects partly the ecosystem resistance or resilience, and depends on the local strength of the hurricanes (Gardiner *et al* 2008, 2019) reflected as wind and rainfall, geophysical variables such as topography (Achim *et al* 2003, Ribeiro *et al* 2016), and vegetation types (Peltola *et al* 2000, Peterson *et al* 2019, Shibuya and Ishibashi 2019). To quantify their effects, we log-transformed and regressed RL and RR on mean DEM (Digital Elevation Model) and slope, mean gust, mean rainfall during Maria, and mean distances to the paths of Maria and Irma, respectively. Linear mixed-effect model was applied for evergreen, deciduous forest, and pasture patches, with vegetation type as the grouping variable. Considering that mangrove patches have much lower DEM and slopes than others, and that drainage is especially important for coastal swamps, we added a binary variable RIVER to indicate whether there is a river flowing through to drain the swamp, and performed a multiple regression for mangroves. Statistical analyses were done with R (R Core Team 2017) and spatial analyses with ArcGIS (10.6, ESRI, Redland, CA). Details of the methodology are in appendix S1.

3. Results

3.1. Island-wide changes in vegetation index one month before and one month after the hurricanes

Although the vegetation index largely decreased island-wide one month after the hurricanes, the changes are highly spatially heterogeneous (figure 4). The montane forests close to the hurricane path encountered the most relative decrease. Change ratios are 0.63 ± 0.33, 0.66 ± 0.37, 0.71 ± 0.23, 0.71 ± 0.53, and 0.81 ± 0.26 in lower mountain wet forest (highest zone with 880 m a.s.l.), subtropical rain forest, subtropical wet forest, lower mountain rain forest, and moist forest, respectively (figures S1(a) and (b)). In contrast to greenness reduction in the aforementioned zones, we found a strip of leeward vegetation along south coast within dry forest zone (figures 2(b) and S1(c)), with increased greenness (figure 4(c)) as indicated by 1.50 ± 0.78 (figure S1(a)). The pattern of change ratio showed decreased impact (increased change ratio) with distance from the hurricane path (figures S1(d) and (e)). However, abrupt

Table 1. Mean ± SE and pairwise comparison of relative low (RL), recovery ratio (RR), and relative recovery ratio (RRR) among vegetation types. MANG–mangroves, EVER–evergreen forests, DECI–deciduous forests, and PAST–pastures.

	MANG	EVER	DECI	PAST
Relative low (RL)				
S2 EVI	0.56 ± 0.09 [a]	0.65 ± 0.11[b]	0.80 ± 0.08 [c]	0.82 ± 0.07 [c]
S2 NDVI	0.55 ± 0.10 [a]	0.64 ± 0.09[b]	0.71 ± 0.07 [c]	0.76 ± 0.08 [c]
Recovery ratio (RR)				
S2 EVI	0.74 ± 0.08 [a]	0.88 ± 0.09 [b]	0.95 ± 0.04 [c]	0.97 ± 0.06 [c]
S2 NDVI	0.76 ± 0.09 [a]	0.89 ± 0.08 [b]	0.93 ± 0.03[bc]	0.96 ± 0.05 [c]
Relative recovery ratio (RRR)				
S2 EVI	0.41 ± 0.16 [a]	0.68 ± 0.14[b]	0.73 ± 0.22 [b]	0.82 ± 0.31[b]
S2 NDVI	0.47 ± 0.18 [a]	0.72 ± 0.15 [ab]	0.73 ± 0.10 [ab]	0.98 ± 0.77 [b]

change in elevation in the east (figure 2(a)) modulated this pattern (figures S1(d) and (f)): The high El Yunque National Forest (figures 2(a) and S1(c)) located 50–60 km east of the path suffered more damage than those areas near the path (figures S1(d) and (f)). Direction also plays an important role because of the counterclockwise spin and northwestward movement of Maria: stronger wind and lower change ratio were found in the east (right) of the path than in the west (left), especially for areas greater than 30 km away from the path (figure S1(d)).

3.2. Differentiated hurricane impact on various vegetation types

For 62 homogeneous vegetation patches, mangroves have the lowest and evergreen forests have the second lowest average RL, whereas pastures have the highest average RL (figures 5(a) and (b)). Averaged over NDVI and EVI, mangroves, evergreen, deciduous forests, and pastures have mean RL of 0.56, 0.65, 0.76, and 0.79, respectively. The pairwise t-test (table 1) showed mangroves have significantly lower RL than others, and evergreen forests have significantly lower RL than deciduous forests and pastures.

The timing of LOW AFTER as the number of days after Maria indicates period of dying-out of leaves and bears the information about duration of hurricane-induced stresses (figure 6). Due to the large variation within vegetation groups, we did not find significant difference in the mean timing among groups. The averaged delay of LOW AFTER is 53.3 (11/12/2017), 53.9 (11/13/2017), 69.8 (11/29/2017), and 110.7 (1/9/2018) days for mangroves, evergreen forests, deciduous forests, and pastures, respectively. The much longer delays for the latter two may relate to post-hurricane drought and onset of dry season starting in late December. EVI is more sensitive to changes in greenness for high leaf biomass, and is more suitable for tropics than NDVI (Huete *et al* 2002). The delays detected by EVI showed stronger contrast among vegetation groups than those by NDVI (figure 6). The longest delay, 140.8 d (2/8/2018), for pastures shows that the impact on the lower profile herbaceous is mostly caused by the droughts. The shortest delay of 47.9 d (11/7/2017) for evergreen forests and 11 days more (11/18/2017) for mangroves

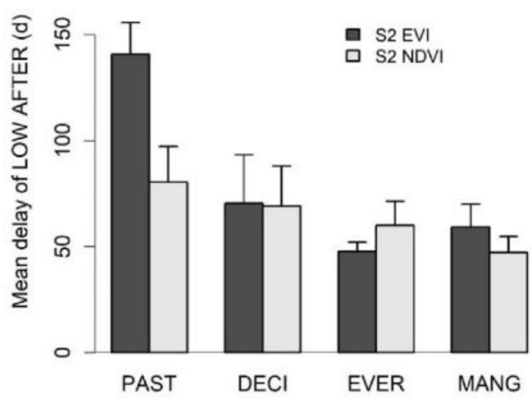

Figure 6. Mean plus standard error of the number of days after September 20, 2017 for LOW AFTER to occur. MANG–mangroves, EVER–evergreen forests, DECI–deciduous forests, and PAST–pastures.

imply the damage to these areas was mostly caused by the winds and/or inundation due to storm surge/runoff.

The application of linear mixed-effect model of RL (table 2) for non-mangroves showed that RL significantly depends negatively on elevation and gust strength, while positively on slope. Higher elevation and greater gust speed may indicate stronger sustained wind and greater rain during the hurricane, which tend to bring more damage. On the other hand, steeper slope might indicate easier drainage and attenuate wind speed when blowing from the opposite direction. The intercepts for the three vegetation groups follow the pattern of RL (figures 5(a) and (b)).

The regression of RL of mangroves (table 3) showed different patterns of the effects of geophysical variables (table 2). Although not significant, the coefficients of DEM become positive as higher elevation might indicate better drainage and less likely inundation. The absolute values of the coefficients of DEM are much larger than those in table 2 because elevation of mangroves is much smaller than that of other vegetation types. Slope is significant only for EVI, and the effect is similar to that of DEM with higher slope for better drainage. Gust is significant only for EVI and its effect is negative. In addition to

Table 2. Coefficients of linear mixed-effect model applied to log-transformed relative low (resistance, lowest divided by mean before hurricanes) and log-transformed recovery ratio (resilience, mean after hurricanes divided by mean before hurricanes) as functions of geophysical variables, with vegetation types as group variable. The first three rows are random intercepts added on to the fixed intercepts. Independent variables: DEM_A–mean DEM, SLOPE_A–mean slope, GUST_A–mean maximum gust during Hurricane Maria, DMARIA_A–mean distance to the path of Hurricane Maria. Independent variables were divided by their mean values across 62 patches. '*' indicates significance at 0.05 level.

	Relative Low		Recovery Ratio	
	S2 EVI	S2 NDVI	S2 EVI	S2 NDVI
EVER	2.109*	2.126*	2.096*	2.096*
DECI	2.242*	2.176*	2.133*	2.110*
PAST	2.379*	2.366*	2.222*	2.207*
DEM_A	−0.065*	−0.055*	−0.039*	−0.025*
SLOPE_A	0.103*	0.115*	0.070*	0.061*
GUST_A	−0.287*	−0.365*		
DMARIA_A			0.035*	0.037*
R^2	0.63	0.70	0.59	0.59

Table 3. Coefficients of multiple regression of log-transformed relative low and rate of recovery of mangrove patches from hurricanes on geophysical variables. DEM_A—mean DEM, SLOPE_A—mean slope, GUST_A—mean maximum gust during Hurricane Maria, DEM_S—standard deviation of DEM within patches, RAIN_A—rainfall during Hurricane Maria. RIVER is a logical variable, indicating whether there is a river running through the mangrove patch. '*' indicates significance at 0.05 level, and '†' significance at 0.10 level.

	Relative Low		Recovery Ratio	
	S2 EVI	S2 NDVI	S2 EVI	S2 NDVI
Intercept	2.64*	1.49*	2.269*	2.309*
DEM_A	16.5	14.5	55.493*	66.358*
DEM_S		2.63	3.384†	2.994†
SLOPE_A	1.59*	−0.19		
GUST_A	−0.97*	0.31	−0.685*	−0.761*
RAIN_A	−0.13*	−0.26*		
RIVER_TRUE			0.168*	0.201*
R^2	0.78	0.49	0.61	0.73
RIVER fraction			0.58	0.62

the variables for non-mangrove types (table 2), rainfall has significant negative effect on RL, as hurricane rainfall tends to inundate the mangrove system.

3.3. Heterogeneous post hurricane recovery

The one-year recovery from Sep. 21, 2017 to Sep. 20, 2018 (figures 5(c) and (d), table 1) indicates distinctiveness between mangroves and other vegetation groups. Mean RR of mangroves is 0.75, whereas mean RR of other groups is near or above 0.90. Pairwise t-test indicates that mean RR of mangroves is significantly lower than those of other groups with EVI and NDVI. With EVI, mean RR of evergreen forests is significantly lower than that of deciduous forests and pastures.

When RR of non-mangrove vegetation patches were regressed on the covariates (table 2), we found that the RR significantly decreased with elevation and increased with slope and distance to the path of Maria for both vegetation indices. Vegetation in high elevation experienced greater damage during the hurricanes, and coarser soil and poorer nutrient status may also limit their recovery. Steeper slopes and greater distance from hurricane path tend to give a better base for recovery because of the lighter damage with steeper slopes and greater distance. The intercepts for the three vegetation groups also follow the pattern of RR (figures 5(c) and (d)).

Regression of RR of mangrove patches (table 3) showed that high elevation significantly favored recovery of mangroves because of the better drainage. The standard deviation of DEM also shows positive impact, so that complex topography helps the recovery. The gust speed tends to negatively affect the recovery. Among the 13 mangrove patches, we found that 5 patches have rivers flowing through. Our regression indicates RIVER significantly and positively impacts recovery of mangrove forests. ANOVA showed that RIVER explained on average 65% of the sum of squares.

The RRR (figures 5(e) and (f), table 1), averaged over EVI and NDVI, is 0.44, 0.70, 0.73, and 0.90 for mangroves, evergreen forests, deciduous forests, and pastures, respectively. Thus, RRR further distinguishes mangrove recovery from other vegetation groups. The pairwise t-test (table 1) showed that mangrove indeed has significantly lower RRR than others.

4. Discussion

Tropical forests and mangroves are vulnerable to changes in press drivers such as warming, drying, or rising sea level, and pulse drivers such as hurricanes, which introduces large uncertainties to their C sequestration capacity and feedback to global climate. Intensified climate variability (Cai *et al* 2014, 2015) is likely to bring more frequent extreme-climate events, such as severe drought and subsequent major hurricanes, to Puerto Rico. From May 2015 to November 2016, the U.S. Drought Monitor recorded the longest drought in Puerto Rico since 2000 (www.drought.gov/drought/states/puerto-rico). This pre-hurricane drought would suppress plant growth, such as reduced individual tree growth in the El Yunque montane forest in high altitude, and lead to mortality of fine roots (Beard *et al* 2005, Schwartz *et al* 2019), and thus may have amplified the response of vegetation to the hurricanes in 2017. On the other hand, the excessive moisture carried by the hurricanes immediately relieved the drought stress on the vegetation in dry forest and pasture in the southwest of the island, which encountered less direct impacts from hurricane winds (figure 2(c)).

Our analyses support our hypotheses on the great differences in resistance and resilience between lowland mangroves and upland forests to major hurricanes (figure 5). Coastal wetlands encountered the worst damage and the slowest recovery, and evergreen forests experienced the second worst damage. The recovery of evergreen forest started earlier and was faster than that of mangroves (figures 5(e), (f) and 6). The mechanism of impact and recovery involves hurricane strength (wind and rainfall), topography, and biological components such as ecosystem properties (tables 2 and 3).

Coastal mangroves are most vulnerable, and less resistant and resilient to hurricane impacts (figure 5). The RRR, which considers the variation in damage, clearly showed much slower recovery of mangroves (0.44) than other vegetation (>0.7). In addition to negative effect of hurricane winds, the impact and recovery of mangroves are affected by inundation-related factors such as rainfall, elevation, slope, and drainage capacity. After hurricanes, the saline and anerobic environment exerted high ecophysiological stress on defoliated mangroves (Medina 1999, Reef and Lovelock 2015). As they must devote much more energy to maintaining the balance of water, salt, oxygen, and nutrients than other terrestrial plants, mangrove ecosystems are much more sensitive to disturbances and less resilient. After Hurricane Andrew in 1992, up to 80%–95% of mangroves in the Everglades were damaged (Smith *et al* 1994), and mangrove forests in southeast Florida encountered greater changes in structure and higher mortality than adjacent upland forests (Baldwin *et al* 1995). After Hurricane Maria, most of red mangroves (*Rhizophora mangle*) in Punta Tuna Reserve close to the landfall died (personal communication). Inundation due to storm surge, downpour rainfall, and excessive runoff submerged the aerial roots and blocked root respiration. Prolonged inundation tends to increase the mortality of mangroves, especially black mangroves (*Avicennia germinans* L.), which grow in higher salinity and need more metabolic energy to maintain the root function. Evaporation of inundating water increased salinity of basin mangroves, hurting their recovery. Field observations in Puerto Rico after the hurricanes exhibited massive mortality of black mangroves on the northern coast due to the extended inundation and disfunction of pneumatophores. With only 1.1 m in mean elevation of the mangrove patches, inundation after hurricanes is the major threat to survival and recovery. Efficient drainage is the key for mangroves to survive the inundation. Our analyses of RL and RR showed that hurricane gust speed and downpours tend to weaken the resistance and recovery, but steeper slope and higher elevation help reduce the damage or favor the recovery (table 3). Particularly, our model predicted that riverine type together with elevation promote recovery of mangroves (table 3), all supporting the hypothesis of the importance of drainage capacity to mangrove recovery.

Evergreen forests are more susceptible to hurricane damage than deciduous forests and pastures (figure 5). Evergreen forests grow in ample rainfall, and thus are located mostly in the north and higher elevations (mean of 404.4 m for the patches) closer in distance to Maria's path (mean of 25.1 km, figure 2(c)). Deciduous forests lie in lower elevations (150.8 m), further from the path (38.2 km), and to the left of the path, and thus experienced less wind speed (figure 2(b)). Evergreen trees have thicker leaves with stronger ties to branches, and are less likely to shed leaves; thus, they experience more drag force and damage during hurricanes than deciduous trees. All these factors fortified the comparison between evergreen and dry forests in terms of resistance to hurricane winds. In Guánica, dry forests in the south of Puerto Rico, the tree mortality after Hurricane Georges was lower than what was expected according to the mortality of wet forests in the Luquillo Experimental Forests after Hurricane Hugo due partially to the lower stature and structure of dry forest trees (Van Bloem *et al* 2005, 2006). Also, due to more severe damage, the evergreen forests recover much slower than the deciduous forests (table 2). From the landscape perspective, higher elevations encountered more erosion during hurricanes and the nutrient loss associated with excessive runoff might exacerbate the nutrient-poor status in higher elevations. In the Luquillo Experimental Forests, the montane elfin forests at the top showed much slower recovery than the wet forests at lower elevations after Hurricane Hugo (Walker *et al* 1996, Lugo 2008). Similarly, canopy recovery of montane forests was behind that of lowland forests in Jamaica (Wunderle *et al* 1992).

For both deciduous forests and pastures, drought is a more important threat. Hurricane rain benefits the deciduous forest (figure 3). However, ground observations indicate the boosted greenness might also be attributed to prosperous vines and understory seedlings or herbaceous plants, which take advantages of the light and nutrient resources of the opened canopy. Our analysis indicated that the minimum vegetation indices of deciduous forests and pastures appear on average 70 and 111 d, respectively, after the hurricanes in comparison with the mean delay of 54 d for evergreen forests. After Hurricane Hugo, wide sprouting and new leaves occurred within 7 weeks in the Luquillo Experimental Forests (Walker 1991), which is close to our finding of 54 d. An annual major dry period for deciduous forests appears from December to April (Rivera 2009), and leaves emerge before the rainy season starts (Murphy and Lugo 1986). The minimum greenness of deciduous forests and pastures occurred during the post-hurricane drought and the onset of the dry season due to the water scarcity.

We interpreted our results under the context of consecutive pre-hurricane drought (Schwartz *et al* 2019, Yu *et al* 2019), hurricane, and post-hurricane drought. The prior drought stress might exacerbate hurricane impacts in terms of severe damage in lowland swamps and high-altitude forests, or be relieved by hurricane rains for dry forest and pastures. The legacies of past disturbances were also highlighted in the studies at the Luquillo Experimental Forests after Hurricane Hugo (Beard *et al* 2005) and Hurricane Georges (Ostertag *et al* 2005). In addition to the legacies, our conclusions emphasize that a complicated array of external forces, including but not limiting to wind, rainfall, storm surge, and inundation, and the modulators of topography and biological components featured by vegetation type, structure, and functional traits (Lugo 2008) altogether form the basis to determine and understand the impacts of hurricanes on tropical ecosystems and their recovery. Use of higher-resolution images, such as Landsat or Sentinel 2 images, was suggested to reduce large subpixel atmospheric effects such as those from coarse-resolution MODIS, which together with possible sensor degradation (Zhang *et al* 2017) might lead to the debates on drought effects detection in the Amazon (Asner and Alencar 2010, Atkinson *et al* 2011, Schwartz *et al* 2019). We also took advantage of the high revisit-frequency of Sentinel 2 satellites to derive time series of greenness for analyzing the hurricanes' impact. However, our observed damage and recovery address only changes in greenness without discrimination of species composition or structural change such as vine prosperity (Chinea 1999). Ecosystem structures take much longer to recover than ecosystem functions such as photosynthesis and decomposition, and thus structural changes are better indicators of hurricane disturbance(Beard *et al* 2005). Resistance at species level is also related to wood texture, with hardwood species experiencing less damage than softwood (Ostertag *et al* 2005). Future studies on forest resistance and resilience to hurricane disturbance, based on hyperspectral or LiDAR images coupled with ground surveys, will be able to detect canopy structural changes and distinguish at the species level.

Acknowledgments

This research is supported by NASA EPSCoR NNX15AK43A and NOAA Puerto Rico Sea Grant. We thank Chao Wang for his help with initial VI data preparation in GEE. The EVI and NDVI data are extracted from publicly available datasets at USGS (https://lpdaac.usgs.gov/) and Google Earth Engine (https://developers.google.com/earth-engine/datasets).

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://developers.google.com/earth-engine/datasets/catalog/COPERNICUS_S2.

ORCID iD

Mei Yu https://orcid.org/0000-0002-0283-9649

References

R Core Team 2017 R: A language and environment for statistical computing. R Foundation for Statistical Computing

Achim A, Nicoll B, Mochan S and Gardiner B 2003 Wind stability of trees on slopes *Int. Conf. 'Wind Effects on Trees'* (Karlsruhe: University of Karlsruhe)

Asner G P and Alencar A 2010 Drought impacts on the Amazon forest: the remote sensing perspective *New Phytol.* **187** 569–78

Atkinson P M, Dash J and Jeganathan C 2011 Amazon vegetation greenness as measured by satellite sensors over the last decade *Geophys. Res. Lett.* **38** L19105

Baldwin A, Platt W, Gathen K, Lessmann J and Rauch T 1995 Hurricane damage and regeneration in fringe mangrove forests of Southeast Florida, USA *J. Coast. Res.* **SI 21** 169–83

Beard K H, Vogt K A, Vogt D J, Scatena F N, Covich A P, Sigurdardottir R, Siccama T G and Crowl T A 2005 Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts *Ecol. Monogr.* **75** 345–61

Cai W J *et al* 2015 Increased frequency of extreme La Nina events under greenhouse warming *Nat. Clim. Change* **5** 132–7

Cai W J *et al* 2014 Increasing frequency of extreme El Nino events due to greenhouse warming *Nat. Clim. Change* **4** 111–6

Chapin F S, Matson P A and Vitousek P M 2012 *Principles of Terrestrial Ecosystem Ecology* Second edn (Berlin: Springer)

Chastain R, Housman I, Goldstein J, Finco M and Tenneson K 2019 Empirical cross sensor comparison of Sentinel-2A and 2B MSI, Landsat-8 OLI, and Landsat-7 ETM+ top of atmosphere spectral characteristics over the conterminous United States *Remote Sens. Environ.* **221** 274–85

Chen J, Huang Y, Chen G and Ye Y 2020 Effects of simulated sea level rise on stocks and sources of soil organic carbon in Kandelia obovata mangrove forests *Forest Ecol. Manage.* **460** 117898

Chinea J D 1999 Changes in the herbaceous and vine communities at the Bisley Experimental Watersheds, Puerto Rico, following Hurricane Hugo *Can. J. Forest Res.* **29** 1433–7

Church J A *et al* 2013 Sea level change *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, ed T F Stocker, D Qin, G-K Plattner, M Tignor, S K Allen, J Boschung, A Nauels, Y Xia, V Bex and P M Midgley (Cambridge: Cambridge University Press) pp 1137–216

Clough B 2013 Continuing the journey amongst mangroves *International Society for Mangrove Ecosystems (ISME)* Okinawa, Japan;) (Yokohama: International Tropical Timber Organization (ITTO)

Dahl T E and Stedman S M 2013 Status and trends of wetlands in the coastal watersheds of the conterminous United States 2004 to 2009 U.S. Department of the Interior, Fish and Wildlife Service and National Oceanic and Atmospheric Administration, National Marine Fisheries Service

Doughty C E *et al* 2015 Drought impact on forest carbon dynamics and fluxes in Amazonia *Nature* **519** 78–82

Fisk J P, Hurtt G C, Chambers J Q, Zeng H, Dolan K A and Negrón-Juárez R I 2013 The impacts of tropical cyclones on

the net carbon balance of eastern US forests (1851–2000) *Environ. Res. Lett.* **8** 045017
Gardiner B, Achim A, Nicoll B and Ruel J-C 2019 Understanding the interactions between wind and trees: an introduction to the IUFRO 8th Wind and Trees Conference (2017) *Forestry Int. J. Forest Res.* vol 92 pp 375–80
Gardiner B, Byrne K, Hale S, Kamimura K, Mitchell S J, Peltola H and Ruel J-C 2008 A review of mechanistic modelling of wind damage risk to forests *Forestry Int. J. Forest Res.* **81** 447–63
Gatti L V *et al* 2014 Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements *Nature* **506** 76–80
Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D and Moore R 2017 Google Earth Engine: planetary-scale geospatial analysis for everyone *Remote Sens. Environ.* **202** 18–27
Gould W A, Alarcon C, Fevold B, Jimenez M, Martinuzzi S, Potts G, Quinones M, Solorzano M and Ventosa E 2008 The Puerto Rico gap analysis project (San Juan, PR) International Institute of Tropical Forestry, USDA Forest Service
Gutiérrez-Fonseca P E, Ramírez A, Pringle C M, Torres P J, Mcdowell W H, Covich A, Crowl T and Pérez-Reyes O 2020 When the rainforest dries: drought effects on a montane tropical stream ecosystem in Puerto Rico *Freshwater Sci.* **39** 197–212
Housman I W, Chastain R A and Finco M V 2018 An evaluation of forest health insect and disease survey data and satellite-based remote sensing forest change detection methods: case studies in the United States *Remote Sens.* **10** 1184
Huete A, Didan K, Miura T, Rodriguez E P, Gao X and Ferreira L G 2002 Overview of the radiometric and biophysical performance of the MODIS vegetation indices *Remote Sens. Environ.* **83** 195–213
Hutchison J, Manica A, Swetnam R, Balmford A and Spalding M 2014 Predicting global patterns in mangrove forest biomass *Conserv. Lett.* **7** 233–40
Hutley L B, Evans B J, Beringer J, Cook G D, Maier S W and Razon E 2013 Impacts of an extreme cyclone event on landscape-scale savanna fire, productivity and greenhouse gas emissions *Environ. Res. Lett.* **8** 045023
Kirwan M L and Megonigal J P 2013 Tidal wetland stability in the face of human impacts and sea-level rise *Nature* **504** 53–60
Krauss K W, Mckee K L, Lovelock C E, Cahoon D R, Saintilan N, Reef R and Chen L 2014 How mangrove forests adjust to rising sea level *New Phytol.* **202** 19–34
Lasky J R, Uriarte M and Muscarella R 2016 Synchrony, compensatory dynamics, and the functional trait basis of phenological diversity in a tropical dry forest tree community: effects of rainfall seasonality *Environ. Res. Lett.* **11** 115003
Lloret F, Keeling E G and Sala A 2011 Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests *Oikos* **120** 1909–20
Lovelock C E, Krauss K W, Osland M J, Reef R, Ball M C *et al* 2016 The physiology of mangrove trees with changing climate *Tropical Tree Physiology - Adaptations and Responses in a Changing Environment*, ed G Goldstein and L S Santiago (Berlin: Springer) pp 149–79
Lovelock C E *et al* 2015 The vulnerability of Indo-Pacific mangrove forests to sea-level rise *Nature* **526** 559–63
Lugo A E 2000 Effects and outcomes of Caribbean hurricanes in a climate change scenario *Sci. Total Environ.* **262** 243–51
Lugo A E 2008 Visible and invisible effects of hurricanes on forest ecosystems: an international review *Austral Ecol.* **33** 368–98
López-Marrero T, Heartsill-Scalley T, Rivera-López C F, Escalera-García I A and Echevarría-Ramos M 2019 Broadening our understanding of hurricanes and forests on the Caribbean island of Puerto Rico: where and what should we study now? *Forests* **10** 710
Medina E *et al* 1999 Mangrove physiology: the challenge of salt, heat, and light stress under recurrent flooding *Ecosistemas De Manglar En América Tropical*, ed A Yáñez-Arancibia and A L Lara-Domínguez UICN/ORMA, Costa Rica, NOAA/NMFS Silver Spring MD USA. 380 (El Haya: Instituto de Ecología A.C) pp 109–26
Michener W K, Blood E R, Bildstein K L, Brinson M M and Gardner L R 1997 Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands *Ecol. Appl.* **7** 770–801
Miller G L and Lugo A E 2009 Guide to the ecological systems of Puerto Rico (San Juan, PR) International Institute of Tropical Forestry, USDA Forest Service
Miller P W, Kumar A, Mote T L, Moraes F D S and Mishra D R 2019 Persistent hydrological consequences of Hurricane Maria in Puerto Rico *Geophys. Res. Lett.* **46** 1413–22
Mote T L, Ramseyer C A and Miller P W 2017 The Saharan air layer as an early rainfall season suppressant in the eastern Caribbean: the 2015 Puerto Rico drought *J. Geophys. Res. Atmos.* **122** 10966–82
Murphy P G and Lugo A E 1986 Ecology of tropical dry forest *Annu. Rev. Ecol. Syst.* **17** 67–88
Okello J A, Kairo J G, Dahdouh-Guebas F, Beeckman H and Koedam N 2020 Mangrove trees survive partial sediment burial by developing new roots and adapting their root, branch and stem anatomy *Trees* **34** 37–49
Ostertag R, Silver W L and Lugo A E 2005 Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest *Biotropica* **37** 16–24
O'Connell C S, Ruan L and Silver W L 2018 Drought drives rapid shifts in tropical rainforest soil biogeochemistry and greenhouse gas emissions *Nat. Commun.* **9** 1348
Pahlevan N, Chittimalli S K, Balasubramanian S V and Vellucci V 2019 Sentinel-2/Landsat-8 product consistency and implications for monitoring aquatic systems *Remote Sens. Environ.* **220** 19–29
Pan Y, Birdsey R A, Phillips O L and Jackson R B 2013 The structure, distribution, and biomass of the world's forests *Annu. Rev. Ecol. Evol. Syst.* **44** 593–622
Pasch R J, Penny A B and Berg R 2019 NATIONAL HURRICANE CENTER TROPICAL CYCLONE REPORT - HURRICANE MARIA (AL152017) September 16-30, 2017 (National Hurricane Center)
Peltola H, Kellomäki S, Hassinen A and Granander M 2000 Mechanical stability of scots pine, Norway spruce and birch: an analysis of tree-pulling experiments in Finland *Forest Ecol. Manage.* **135** 143–53
Peterson C J, Ribeiro G H P D M, Negrón-Juárez R, Marra D M, Chambers J Q, Higuchi N, Lima A and Cannon J B 2019 Critical wind speeds suggest wind could be an important disturbance agent in Amazonian forests *Forestry Int. J. Forest Res.* **92** 444–59
Reef R and Lovelock C E 2015 Regulation of water balance in mangroves *Ann. Bot.* **115** 385–95
Ribeiro G H P M *et al* 2016 Mechanical vulnerability and resistance to snapping and uprooting for central Amazon tree species *Forest Ecol. Manage.* **380** 1–10
Rivera O A M 2009 *Vascular Flora of the Guanica Dry Forest, Puerto Rico* (Mayaguez: University of Puerto Rico)
Runkle J, Kunkel K, Stevens L, Champion S, Easterling D, Terando A, Sun L, Stewart B and Landers G 2018 NOAA NOAA State Climate Summaries http://pubs.er.usgs.gov/publication/70197909
Scatena F N and Larsen M C 1991 Physical aspects of Hurricane Hugo in Puerto Rico *Biotropica* **23** 317–23
Schwartz N B, Budsock A M and Uriarte M 2019 Fragmentation, forest structure, and topography modulate impacts of drought in a tropical forest landscape *Ecology* **100** e02677
Shibuya M and Ishibashi S 2019 Stand-level windthrow patterns and long-term dynamics of surviving trees in natural secondary stands after a stand-replacing windthrow event *Forestry Int. J. Forest Res.* **92** 473–80

Smith T J III , Robblee M B, Wanless H R and Doyle T W 1994 Mangroves, hurricanes, and lightning strikes: assessment of Hurricane Andrew suggests an interaction across two differing scales of disturbance *Bioscience* **44** 256–62

Uriarte M, Thompson J and Zimmerman J K 2019 Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms *Nat. Commun.* **10** 1362

Van Bloem S J, Lugo A E and Murphy P G 2006 Structural response of Caribbean dry forests to hurricane winds: a case study from Guanica forest, Puerto Rico *J. Biogeogr.* **33** 517–23

Van Bloem S J, Murphy P G, Lugo A E, Ostertag R, Costa M R, Bernard I R, Colon S M and Mora M C 2005 The influence of hurricane winds on Caribbean dry forest structure and nutrient pools *Biotropica* **37** 571–83

Vargas R 2012 How a hurricane disturbance influences extreme CO 2 fluxes and variance in a tropical forest *Environ. Res. Lett.* **7** 035704

Walker L R 1991 Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico *Biotropica* **23** 379–85

Walker L R, Zimmerman J K, Lodge D J and Guzmangrajales S 1996 An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico *J. Ecol.* **84** 877–89

Wang C, Yu M and Gao Q 2017 Continued reforestation and urban expansion in the new century of a tropical island in the Caribbean *Remote Sens.* **9** 731

Wulder M A *et al* 2019 Current status of Landsat program, science, and applications *Remote Sens. Environ.* **225** 127–47

Wunderle J M Jr , Lodge D J and Waide R B 1992 Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica *Auk* **109** 148–66

Yi C, Pendall E and Ciais P 2015 Focus on extreme events and the carbon cycle *Environ. Res. Lett.* **10** 070201

Yu M, Gao Q, Gao C and Wang C 2017 Extent of night warming and spatially heterogeneous cloudiness differentiate temporal trend of greenness in mountainous tropics in the new century *Sci. Rep.* **7** 41256 10.1038/srep41256

Yu M, Rivera-Ocasio E, Heartsill-Scalley T, Davila-Casanova D, Rios-López N and Gao Q 2019 Landscape-level consequences of rising sea-level on coastal wetlands: saltwater intrusion drives displacement and mortality in the twenty-first century *Wetlands* **39** 1343-55

Zeileis A and Grothendieck G 2005 Zoo: S3 infrastructure for regular and irregular time series *J. Stat. Softw.* **14** 1–27

Zhang H K, Roy D P, Yan L, Li Z, Huang H, Vermote E, Skakun S and Roger J-C 2018 Characterization of Sentinel-2A and Landsat-8 top of atmosphere, surface, and nadir BRDF adjusted reflectance and NDVI differences *Remote Sens. Environ.* **215** 482–94

Zhang Y, Song C, Band L E, Sun G and Li J. (2017). Reanalysis of global terrestrial vegetation trends from MODIS products: Browning or greening?. Remote Sensing of Environment. **191** 145–55