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Tracking the Rates and Mechanisms of Canopy Damage and Recovery Following Hurricane Maria Using Multitemporal Lidar Data

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Abstract

Hurricane Maria, a Category 4 storm, snapped and uprooted canopy trees, removed large branches, and defoliated vegetation across Puerto Rico. The magnitude of forest damages and the rates and mechanisms of forest recovery following Maria provide important benchmarks for understanding the ecology of extreme events. We used airborne LiDAR data acquired before (2017) and after Maria (2018, 2020) to quantify landscape-scale changes in forest structure along a 439-ha elevational gradient (100–800 m) in the Luquillo Experimental Forest. Damages from Maria were widespread, with 73% of the study area losing ≥ 1 m in canopy height (mean = −7.1 m). Taller forests at lower elevations suffered more damage than shorter forests above 600 m. Yet only 13.5% of the study area had canopy heights ≤ 2 m in 2018, a typical threshold for forest gaps, highlighting the importance of damaged trees and advanced regeneration on post-storm forest structure. Heterogeneous patterns of regrowth and recruitment yielded shorter and more open forests by 2020. Nearly 45% of forests experienced initial height loss > 1 m (2017–2018) followed by rapid height gain > 1 m (2018–2020), whereas 21.6% of forests with initial height losses showed little or no height gain, and 17.8% of forests exhibited no height changes larger than ± 1 m in either period. Canopy layers < 10 m tall accounted for most increases in canopy height and fractional cover between 2018 and 2020, with gains split evenly between height growth and lateral crown expansion by surviving individuals. These findings benchmark rates of gap formation, crown expansion, and canopy closure following hurricane damage and highlight the diversity of ecosystem impacts from heterogeneous spatial patterns and vertical stratification of forest regrowth following a major disturbance event.

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Highlights

1. Hurricane Maria gave forests a haircut by toppling trees and shearing branches.
2. Regrowth after Maria was patchy, with equal areas of height gain and no change.
3. 3-D measures of forest recovery after hurricanes can improve ecosystem models.

Introduction

Natural disturbances restructure forest ecosystems by altering the distributions of tree size, age, and species composition. In tropical and subtropical forests, cyclones are among the largest and most damaging disturbances. Cyclones occur with greater frequency than microburst ''blow-down'' events (Espírito-Santo and others 2014) and cause widespread damage to coastal and inland tropical forests each year (for example, Chen and others 2015). Cyclonic storms are projected to increase in intensity (Knutson and others 2010; Knutson and others 2020) and frequency (Emanuel 2013; Bhatia and others 2018; but see Knutson and others 2015) as a result of warming ocean temperatures (Hoyos and others 2006) and rising atmospheric moisture content from climate change (Trenberth and others 2018). Understanding the patterns and processes of forest disturbance and recovery following major cyclone events is therefore a priority to improve Earth system model predictions of the carbon, water, and energy balance of tropical forest regions (Seidl and others 2011; U.S. DOE 2018).

Hurricane Maria was the most powerful storm to hit Puerto Rico since 1928, making landfall just two weeks after Hurricane Irma on September 20, 2017. The Category 4 storm had maximum sustained winds of 210 km h^{-1} (NOAA 2017), and the Luquillo Mountains in northeast Puerto Rico received $>$ 1200 mm of rainfall in just 48 h (Hall and others 2020). The combination of strong winds and drenching rains damaged infrastructure, causing the largest electricity blackout in US history (Román and others 2019), and triggering more than 40,000 landslides across the island (Bessette-Kirton and others 2019). About half of the Luquillo Experimental Forest area had at least one landslide per km^2 from Hurricane Maria (Van Beusekom and others 2018).

Studies of initial forest damage at the individual-tree scale suggest that wind and rain from Hurricane Maria were more damaging to the forests of Puerto Rico than previous hurricanes (Tanner and others 1991; Everham and Brokaw 1996; Lugo 2008; Uriarte and others 2019). Hurricane damages to individual trees typically range from defoliation and branch fall to uprooting or stem breakage, with variability among tree species based on structural traits such as wood density, tree height, buttressing, and crown size (Zimmerman and others 1994; Canham and others 2010). At our study site, Hurricane Maria caused more stem breaks, even for species with high wood density, than Category 3 Hurricanes Hugo in 1989 or Georges in 1998 (Uriarte and others 2019). The selective removal of taller individuals and canopy tree species with lower wood density favors palms and understory vegetation (Drew and others 2009; Uriarte and others 2019), leading to forests with lower canopies and higher stem densities (Ibanez and others 2018). Delayed mortality of individuals damaged by Hurricane Maria, a process documented in past storms (Walker 1995), could accentuate a long-term shift to fast-growing pioneer species and species most resilient to high winds, such as palms (Drew and others 2009). Combined, Hurricanes Irma and Maria also caused a pulse of litter deposition that equaled or exceeded total annual litterfall, with a doubling of woody material (Liu and others 2018).

Initial assessments of island-wide damages from Hurricane Maria using Landsat and Sentinel-2 satellite imagery data confirmed widespread defoliation (Van Beusekom and others 2018; Feng and others 2020; Hall and others 2020). Patterns of defoliation manifested as a sharp decline in vegetation greenness, especially in the Luquillo Experimental Forest (Van Beusekom and others 2018; Feng and others 2020), and an increase in the subpixel fraction of non-photosynthetic vegetation, particularly in taller forests and areas that experienced high rainfall before and during Hurricane Maria (Hall and others 2020). These studies also captured the heterogeneity of forest damages across Puerto Rico, consistent with the interactions between hurricane wind, rainfall, and local factors such as forest structure and topography (Tanner and others 1991). However, passive optical satellite data are primarily sensitive to changes in fractional vegetation cover (Hu and Smith 2018), and therefore do not differentiate defoliation from structural damages, or provide definitive evidence regarding the mechanisms of canopy recovery following hurricane disturbance (for example, Feng and others 2020).

Structural changes in the forest canopy from hurricane winds promote forest regeneration through recruitment, regrowth, or release (Everham and Brokaw 1996; Uriarte and others 2004; Uriarte and others 2005; Drew and others 2009; Shiels and others 2015). Pioneer woody species can recruit from the seed bank immediately after the formation of a canopy opening, overtake existing non-pioneer trees based on rapid height growth, and dominate the adult community for many years following disturbances (Shiels and others 2010). Smaller gaps in tropical forests typically lead to a combination of canopy infilling and promotion from below via recruitment and sprouting, although the lateral growth of neighboring trees in tropical forests may be more limited (Hunter and others 2015) than in temperate ecosystems (Runkle and Yetter 1987; Young and Hubbell 1991). In larger gaps, including in simulated hurricane experiments, defoliated or damaged stems often remain standing, limiting light penetration to the forest floor and potentially altering recovery pathways compared to non-hurricane gaps (Dietze and Clark 2008). Damaged individuals can respond quickly after disturbance and flush new leaves or resprout within 7–10 weeks to rebuild the tree canopy, a process sometimes referred to as direct regeneration (Yih and others 1991; Zimmerman and others 1994; Tanner and others 2014). Disturbance can also release surviving individuals in the canopy or understory from light, nutrient, or water competition, leading to rapid height growth (Uriarte and others 2004; Shiels and others 2010). Whether forests recover via recruitment, regrowth, or release has distinct impacts on forest structure and function following hurricane damages.

Small-footprint airborne LiDAR data provide three-dimensional (3-D) information on forest structure needed to understand the mechanisms that contribute to the structural reorganization of forests from hurricane damage and recovery. Previous studies demonstrate the ability to quantify fine-scale changes in canopy structure using repeat LiDAR surveys of the same area (for example, Marvin and Asner 2016; Leitold and others 2018). Pre- and post-hurricane LiDAR data provide a unique canopy perspective to investigate landscape-scale patterns of damage from an extreme event. For example, the spatial and vertical distributions of residual canopy tree cover following a hurricane influence light availability and growing conditions for release and recruitment in the forest understory (Comita and others 2009). Repeat measurements with high-density airborne LiDAR data in the post-hurricane period capture height growth, crown expansion, and delayed treefall.

We analyzed a time series of airborne LiDAR data to quantify changes in forest structure from damages and recovery from Hurricane Maria in the Luquillo Experimental Forest. Based on the elevational gradient (100–800 m) in pre-storm forest structure and species composition (Gould and others 2006; Weaver 2010) and post-storm research at the plot scale (Uriarte and others 2019), we hypothesized that forest damage from Hurricane Maria would vary by forest type, with less damage in palm-dominated forests at higher elevations. However, the 3-D forest recovery following hurricane damages is poorly understood, based in part on competing processes of vegetation recovery and delayed mortality. Our two specific aims were therefore to (1) quantify landscape-scale variability in structural damage from Hurricane Maria, and (2) track the rates and mechanisms of changes in canopy structure during the first 2.5 years following the storm. Airborne data from NASA Goddard's LiDAR, Hyperspectral, and Thermal (G-LiHT) Airborne Imager were acquired over 439 ha, providing estimates of height changes across broad gradients of initial forest structure and composition. Understanding changes in forest structure from hurricane disturbance and forest recovery is necessary to capture the long-term effects of hurricanes on tropical forest ecosystems and improve Earth system models.

Methods

Study Area

The study area covers an elevational gradient on the northwest-facing slopes of the Luquillo Experimental Forest (coterminous with El Yunque National Forest) in northeastern Puerto Rico (Figure 1). The climate is tropical maritime, with average annual rainfall of 3860 mm and average temperature of 22 °C in winter and 30 °C in summer (Quiñones and others 2018). Elevation is the primary control on temperature and rainfall distributions, with differences of about 5 °C in mean annual temperature and > 3000 mm in mean annual precipitation from the coast to the top of the Luquillo Mountains (González and others 2013). The subtropical wet and rain forest formations within the study area are distributed by elevation in four main vegetation zones: (1) secondary wet forests in the lowlands; (2) tabonuco montane wet

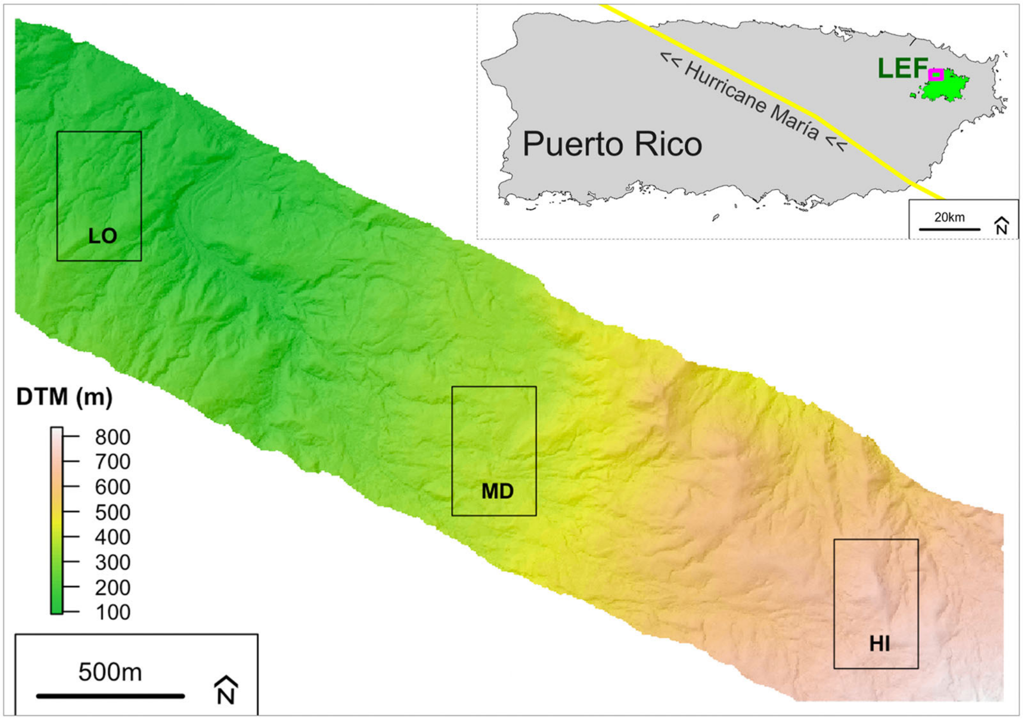

Figure 1. Digital terrain model (DTM) of the 439-ha study area showing the 100–800 m elevational gradient and the three 16-ha focus areas at low (LO), mid (MD), and high (HI) elevations. The inset panel (top right) shows the location of the study area (in magenta) within the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico and the path of Hurricane Maria (in yellow) across the island (NOAA 2017).

forests between 150–600 m dominated by tabonuco (*Dacryodes excelsa*) and motillo (*Sloanea berteriana*) trees with tall canopies reaching 30 m; (3) sierra palm (*Prestoea montana*) forests above 450 m that are common on steeper slopes and saturated soils; and (4) palo colorado (*Cyrilla racemiflora*) cloud forest between 600 and 900 m with tree heights reaching 15 m (Gould and others 2006; Quiñones and others 2018); our study area did not cover the elfin woodland vegetation type that is found on the tallest peaks above 900 m elevation. Hurricane Maria made landfall in Puerto Rico on 20 September 2017 as a Category 4 hurricane (Figure 1), damaging forests across the whole island, including the Luquillo Experimental Forest (Hall and others 2020).

Airborne LiDAR Data

Airborne LiDAR data over the Luquillo Experimental Forest were collected using the G-LiHT Airborne Imager (Cook and others 2013) in three separate campaigns. Data were acquired in March 2017 (pre-hurricane), April 2018 (7 months post-hurricane), and March 2020 (2.5 years post-hurricane), with time intervals between LiDAR data collections of 13 months (2017–2018) and 23 months (2018–2020). All three airborne surveys used the same G-LiHT v2 instrumentation, including two VQ-480i scanning LiDARs (Riegl Laser Measurement Systems, Horn Austria). Data were acquired from a nominal flying altitude of 335 m AGL and 130 knots, which produced approximately 10 cm laser footprints (1550 nm) and an average sampling density of 12 laser pulses m^{-2}. Pre- and post-flight boresight alignment of the LiDAR sensors ensured vertical accuracies of < 10 cm (1 sigma) for all three campaigns. G-LiHT terrain and canopy height products are openly available online from the G-LiHT data portal (https://glihtgsfc.nasa.gov).

The total area covered by all three LiDAR surveys was 439 ha, and subsets of the study area were designated using two different approaches (Figure 1). First, the study area was subdivided into 100-m terrain elevation classes to compare pre-hurricane forest structure, hurricane damages, and post-hurricane recovery along the gradient from 100 to 800 m elevation. All G-LiHT DTM elevations were referenced to the EGM96 vertical datum. Second, we selected three focus areas at low (LO), mid (MD), and high (HI) elevations for analyses of changes in forest canopy structure over time, based on a consistent sample size. The mid-elevation (~ 380 m) focus area corresponds to the 16-ha Luquillo Forest Dynamics Plot (LFDP), part of the Long-Term Ecological Research Program (LTER). This 16-ha rectangular area (500 m × 320 m) was replicated for the LO (~ 170 m elevation) and HI (~ 700 m elevation) focus areas, with the location of the LO and HI sites selected at random within the LiDAR coverage areas with the lowest and highest elevations. The dominant vegetation type in the LO and MD focus areas is tabonuco forest, while the HI focus area contains sierra palm and palo colorado forests.

Analysis

LiDAR point clouds from the three airborne surveys (2017, 2018, and 2020) were processed using a consistent methodology (Cook and others 2013) to evaluate changes in canopy height and canopy closure during the study period. Digital terrain models (DTM) and canopy height models (CHM) were generated separately for 2017, 2018 and 2020 at 1-m spatial resolution. The decision to process LiDAR data from each campaign separately, rather than using a single reference DTM derived from all three campaigns, was based on the high LiDAR point density (Leitold and others 2015) and the potential influence of landslides and erosion from the hurricane on the underlying topography (Van Beusekom and others 2018; Bessette-Kirton and others 2019). Changes in canopy height were calculated as the simple difference between CHM layers in 2017–2018, 2018–2020 and 2017–2020 at 1-m resolution. Canopy cover was estimated at each 1-m vertical increment above the ground as the percent ground area covered by vegetation at that height; cumulative canopy cover profiles were derived from these estimates at the scale of the 16-ha focus areas (LO, MD, HI) and the full study area. Similarly, canopy gap fraction was calculated at the native 1-m resolution of the LiDAR CHM layers as a measure of canopy openness—the percent ground area *not* covered by vegetation—at each 1-m vertical height bin in the canopy within the 16-ha focus areas and the full study area.

Forest canopy change was analyzed on a pixel-by-pixel basis and classified as one of three change categories: (a) *loss* pixels had canopy height change < -1 m between surveys, (b) *gain* pixels had canopy height change > 1 m, and (c) *zero* pixels had canopy height change between -1 m and + 1 m, that is, a conservative estimate of near-zero changes in canopy height. Canopy height changes associated with hurricane damage (2017–2018) and post-hurricane recovery (2018–2020) created nine potential trajectories: loss–loss, loss–zero, loss–gain, zero–loss, zero–zero, zero–gain, gain–loss, gain–zero, and gain–gain. The magnitudes of forest canopy changes in each trajectory are reported on a per-area basis within the whole study area, in 100-m elevation bands (100–800 m), and in three 16-ha focus areas (LO, MD, HI). In each time interval, 1-m^2 loss pixels were summed to estimate the fraction of forest area with canopy height losses. Previous studies have clustered loss pixels into individual canopy turnover events (Leitold and others 2018). Annualized rates of canopy turnover within our study area are therefore also reported using these more conservative thresholds for height loss (> 3 m) and minimum size (> 4 m^2) for clusters of canopy turnover (Leitold and others 2018). Change pixels were grouped into vertical canopy height bins (1-m increments) and cohorts (5-m increments) to examine height changes and cumulative canopy cover within the forest profile during the study period. The relationship between pre-hurricane initial canopy height and post-hurricane height change was examined using ordinary least-square linear regression.

Patterns of vertical versus lateral (horizontal) growth in the canopy between 2018 and 2020 were analyzed using a threshold for maximum vertical height gain during this interval derived from two approaches. First, height gains within surviving canopy tree crowns were assessed in the three focus areas (LO, MD, HI). Crown objects in the 2018 and 2020 canopy height models for trees at or exceeding the pre-storm mean canopy height were identified using the ForestTools package (Plowright 2020) of the R statistical software (R Core Team 2020). These canopy tree objects (containing one or more tree crowns) were used as inputs for the watershed segmentation algorithm to delineate the horizontal extent of all canopy tree crowns, not to separate individuals within the canopy stratum. Overlapping 2018 and 2020 canopy tree objects were used to estimate height gains within and adjacent to the 2018 crown extents (Figure 2). Gains within the 2018 extent of crown objects were attributed to vertical growth, while height gains around crown edges were attributed to lateral expansion. Across the three focus areas, 85.1%–89.3% of height gains within the extent of 2018 crown objects were ≤ 4 m (Figure 3). Second, published values of the maximum height growth of pioneer tree species were consulted for comparison. Vertical growth of up to 4 m was considered possible between 2018 and 2020, based on the maxi-

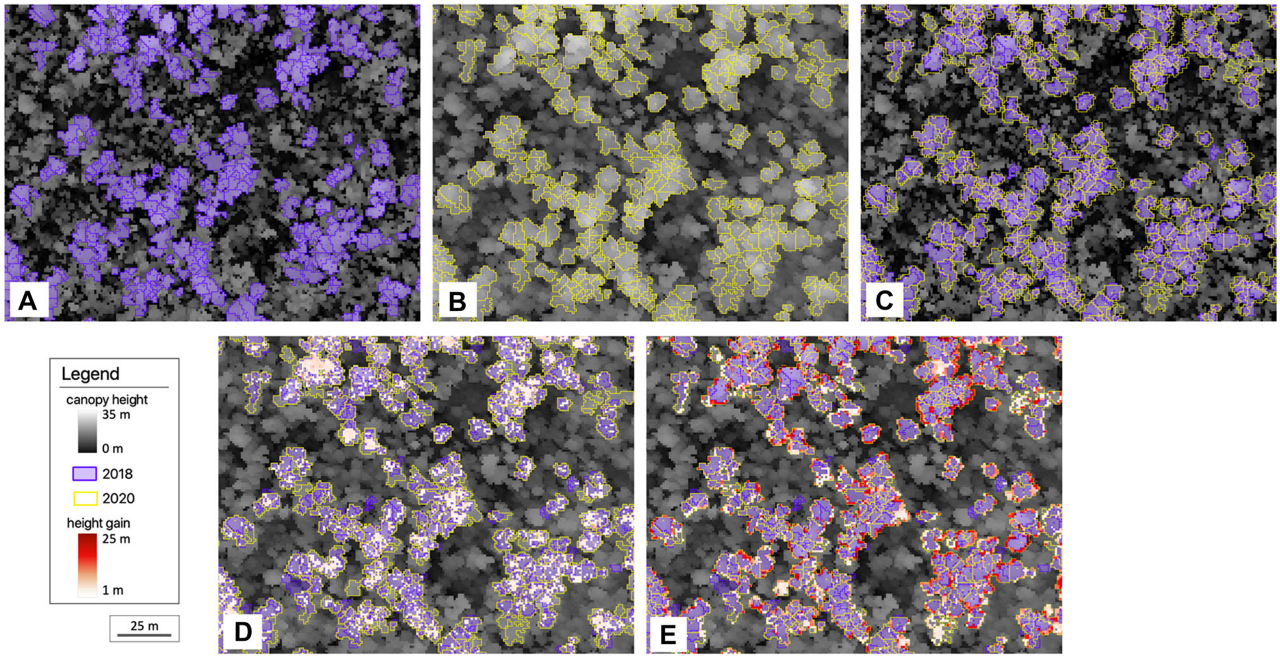

Figure 2. Height gains within and between surviving canopy tree crowns were used to attribute changes to vertical or lateral crown expansion. An example subset of the MD focus area shows the horizontal extent of surviving canopy tree crown objects (≥ 19.7 m, the pre-hurricane mean canopy height in MD) identified in the (**A**) 2018 and (**B**) 2020 canopy height models; (**C**) the union of these two sets of polygons was used to separate 2018–2020 height gain (**D**) within the extent of 2018 tree crown objects (i.e. *vertical growth*) and (**E**) outside the extent of 2018 but within the extent of 2020 tree crown objects (i.e. *lateral growth*).

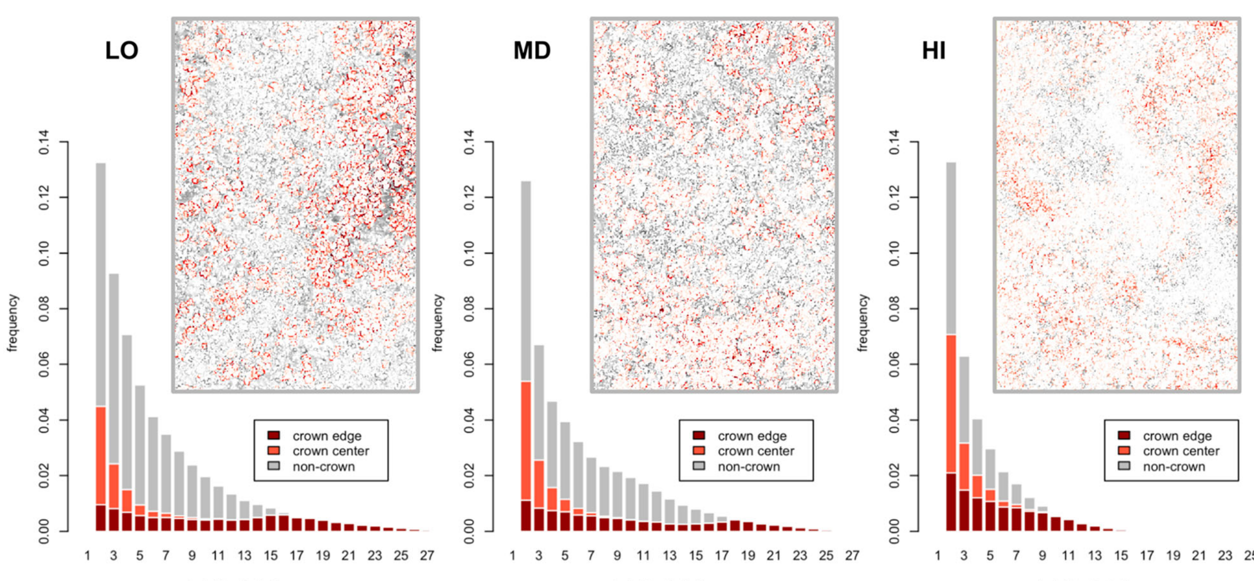

Figure 3. In each 16-ha focus area (LO, MD, HI), 2018 and 2020 canopy tree crown objects (see Figure 2) were used to quantify the distributions of post-hurricane height gains (2018–2020) within crown objects (''crown center'', light red), adjacent to crown objects (''crown edge'', dark red), or associated with shorter vegetation (''non-crown'', gray). Height growth attributed to vertical gains within the horizontal extent of existing crown objects in 2018 (''crown centers'') was primarily ≤ 4 m during this interval in all three focus areas (85.1%, 88.3%, and 89.3% for LO, MD, HI, respectively).

mum elongation of *Cecropia*, a dominant pioneer species in the understory (height growth up to 2.16 m y^{-1} following disturbance, see Silander 1979; also, Brokaw 1998). Based on consistent estimates of vertical height growth for canopy trees and pioneer trees in the forest understory, a height gain threshold of 4 m was used to differentiate canopy closure via vertical growth (height gain ≤ 4 m) versus horizontal infilling by adjacent trees (height gain > 4 m), and to report the percentages of the total area of canopy height gain attributed to each process.

Results

Pre-Hurricane Forest Structure

In March 2017, closed-canopy tropical forests covered the entire study area (Figure 4, Figure S1). The distribution of canopy heights was unimodal, with mean (± SD) canopy height of 18.2 ± 6.1 m (Table 1, Figure 5). Forests were tallest at lower elevations between 100 and 500 m, with mean top of canopy heights near 20 m. Forests above 600 m elevation had shorter trees with mean canopy heights of 13.8 ± 3.8 m at 600–700 m and 10.9 ± 3.4 m at 700–800 m. At all elevations, canopy cover was approximately 99% at 2 m and 98% at 5 m heights above the ground. For taller forests between 100 and 500 m, canopy cover was approximately 91% at 10 m above the ground.

Hurricane Damage (2017–2018)

Forests were substantially shorter and more open seven months after Hurricane Maria (Table 1). Mean canopy height decreased by 7.1 m (39%) across the study region, with average losses ranging from 5.8 to 9.6 m between 100 and 600 m elevation and 2.4–3.2 m above 600 m elevation. Mean height losses were strongly correlated with pre-storm mean canopy height (R^2 = 0.80, p = 0.0063), as taller forests suffered larger height losses from Hurricane Maria. Declines in mean canopy height were largest at lower elevations (Table 1), such that the tallest forests following the storm were at intermediate elevations (Figure 4). The distribution of canopy heights at low and middle elevations was bimodal in 2018, with one prominent mode corresponding to understory vegetation and advanced regeneration (1–2 m) and a second at the mean canopy height of 11.1 ± 7.6 m (Figure 5).

Overall, approximately 73% of the study area lost at least 1 m of canopy height between the 2017 and 2018 LiDAR acquisitions (Table 2). Forests in the LO focus area had more damage, (80% ≥ 1 m canopy height loss), whereas only 54% of forests in the HI focus area had ≥ 1 m height loss from the storm (Figure S2). Based on a more conservative approach to cluster height losses into canopy turnover events using height-loss (> 3 m) and size (> 4 m^2) thresholds from previous studies, canopy turnover from Hurricane Maria was 53.5% y^{-1}, 30

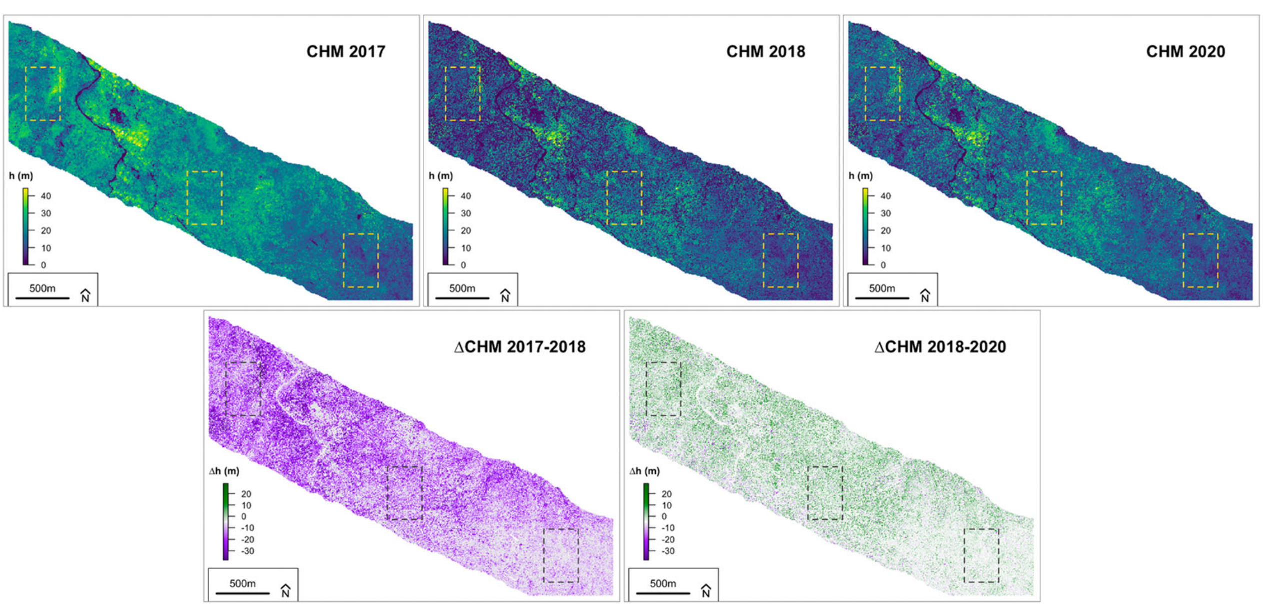

Figure 4. Canopy height models (CHM) at 1-m resolution of the study area in 2017, 2018, 2020 (top row), and canopy height change layers between 2017–2018 and 2018–2020 (bottom row). See supplemental Figure S1 for the canopy height and change layers for each 16-ha focus area (dashed rectangles).

Table 1. Canopy Height and Canopy Height Changes Between 2017 and 2020 for the Full Study Area, the 16-ha Focus Areas (LO, MD, HI), and Each 100-m Elevation Band

	CHM 2017		CHM 2018		CHM 2020		Δ CHM 2017–2018		Δ CHM 2018–2020	
	Mean (m)	SD (m)	Mean (m)	SD (m)	Mean (m)	SD (m)	Mean (m)	%	Mean (m)	%
Full Area	18.2	6.1	11.1	7.6	13.3	6.8	−7.1	−39.0	2.2	19.8
LO	18.9	5.8	10	7.5	13.1	6.8	−8.9	−47.1	3.1	31.0
MD	19.7	4.1	13.2	7.6	15.8	6	−6.5	−33.0	2.6	19.7
HI	11.8	3.7	9.3	4.3	10.4	3.8	−2.5	−21.2	1.1	11.8
100–200 m	20.3	6.7	10.7	8.5	13.5	7.8	−9.6	−47.3	2.8	26.2
200–300 m	20	5.9	10.9	8.3	13	7.5	−9.1	−45.5	2.1	19.3
300–400 m	19.7	4.5	13.5	7.7	15.8	6.5	−6.2	−31.5	2.3	17.0
400–500 m	19.8	4.3	13.3	7.6	15.7	6.2	−6.5	−32.8	2.4	18.0
500–600 m	17.9	4.5	12.1	6.8	13.9	5.8	−5.8	−32.4	1.8	14.9
600–700 m	13.8	3.8	10.6	4.9	11.7	4.3	−3.2	−23.2	1.1	10.4
700–800 m	10.9	3.4	8.5	4	9.4	3.6	−2.4	−22.0	0.9	10.6

Mean and standard deviation (sd) canopy heights and canopy height changes were derived from the 2017, 2018, and 2020 Canopy Height Models (CHM) at 1-m spatial resolution. Focus area locations are shown in Figure 1.

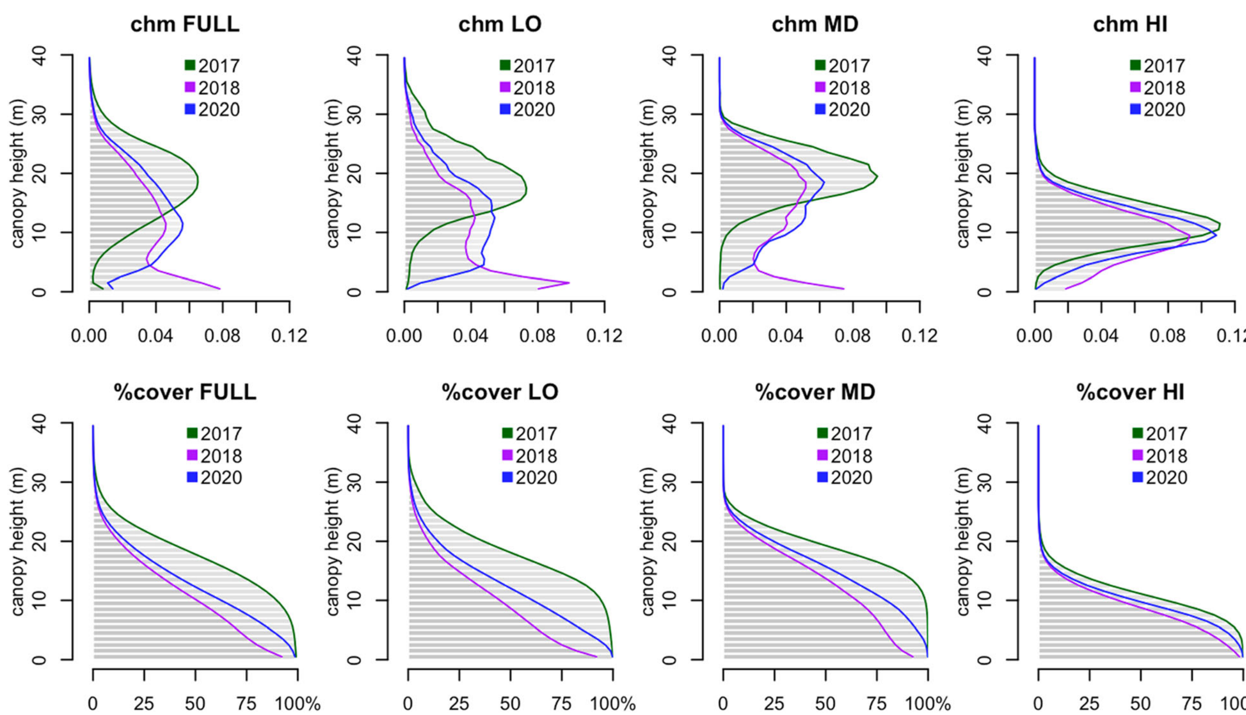

Figure 5. Vertical profiles of top of canopy height (''chm'', top row) and cumulative canopy cover (''%cover'', bottom row) in 2017 (green), 2018 (magenta), and 2020 (blue) across the full study area (FULL) and in 16-ha focus areas at low (LO), mid (MD) and high (HI) elevation.

times higher than background canopy turnover in Amazon forests (1.8% y^{-1}, Leitold and others 2018).

Height losses between 2017 and 2018 were concentrated in the dominant canopy layer around 20 m height, proportional to the distribution of pre-storm canopy heights (Figure 5). Branch loss and snapped or uprooted canopy trees therefore altered the vertical profile of canopy material, revealing layers of understory vegetation at lower canopy heights. The forest canopy in 2018 was significantly more open than before Maria, with

Table 2. Canopy Change Trajectories for the Full Study Area and the Three 16-ha Focus Areas (LO, MD, HI) Expressed as the Percentage of Each Area in Nine Different Change Categories: Loss–Loss, Loss–Zero, Loss–Gain, Zero–Loss, Zero–Zero, Zero–Gain, Gain–Loss, Gain–Zero, And Gain–Gain

	Full area	2018–2020			LO	2018–2020			MD	2018–2020			HI	2018–2020		
		Loss	Zero	Gain		Loss	Zero	Gain		Loss	Zero	Gain		Loss	Zero	Gain
2017–2018	Loss	6.37%	21.59%	44.62%	Loss	6.00%	19.81%	55.84%	Loss	4.90%	22.09%	46.41%	Loss	2.89%	22.21%	28.73%
	Zero	2.86%	17.82%	3.25%	Zero	2.08%	9.95%	2.79%	Zero	2.65%	18.81%	2.86%	Zero	3.15%	34.12%	5.23%
	Gain	0.95%	2.06%	0.43%	Gain	0.83%	2.09%	0.60%	Gain	0.60%	1.52%	0.27%	Gain	0.76%	2.55%	0.36%

Gains and losses were separated from zero (no-change) areas based on height changes larger than ± 1 m.

13.5% of top of canopy heights ≤ 2 m above the ground, a typical height threshold for gaps in field studies (Brokaw, 1982), 25.7% ≤ 5 m, and 38.1% ≤ 10 m across the entire study area. Forests at lower elevations (100–600 m) were significantly more open than forests above 600 m elevation, with approximately 15% canopy openings ≤ 2 m above the ground in lower elevation forests and 5% canopy openings ≤ 2 m at higher elevation (Figure 5). Forests at lower elevations also had lower canopy cover throughout the vertical profile following the storm (for example, 72% at 5 m, and 53% at 10 m).

Post-Storm Recovery (2018–2020)

By March 2020, mean (± SD) canopy height had increased from 11.1 ± 7.6 m in 2018 to 13.3 ± 6.8 m across the study area (Table 1). Average vertical height gains were greater at lower elevations (2–3 m) than above 600 m (~ 1 m), yet the tallest forests, on average, remained at intermediate elevations (Figure 4). Canopy closure increased rapidly between 2018 and 2020 at 2 m above the ground (97.5%), but open conditions persisted at 5 m (89%) and 10 m (65%) canopy heights (Figure 5). Approximately 50% of the landscape gained at least 1 m in canopy height during this 2.5-year interval (Table 2, Figure S2).

Between the 2018 and 2020 LiDAR acquisitions, approximately 10% of the study area lost > 1 m height (5% y^{-1}). Clusters of canopy turnover based on the more conservative 3-m height loss and 4-m^2 minimum size thresholds was 2.3% y^{-1}, more consistent with background turnover rates in other tropical forests (Leitold and others 2018). Over 40% of the landscape had no detectable height change larger than ± 1 m in the 2.5 years following the hurricane (Figure 6, Table 2), with canopy heights in these no-change areas concentrated around the pre-hurricane dominant tree height (mean heights of 16.8 m for the full study area, 18.8 m for LO, 20.7 m for MD, and 11.7 m for HI). Over the full study period (2017–2020), there was a net loss of canopy material at all canopy heights (Figure S2).

Change Trajectories

Three change trajectories of canopy damage and recovery were dominant at all elevations (Figure 6, Table 2). Nearly 45% of the study area followed the loss–gain trajectory, consistent with large height losses from the storm and rapid height gains between 2018 and 2020. The proportion of the loss–gain trajectory decreased with elevation from 56%

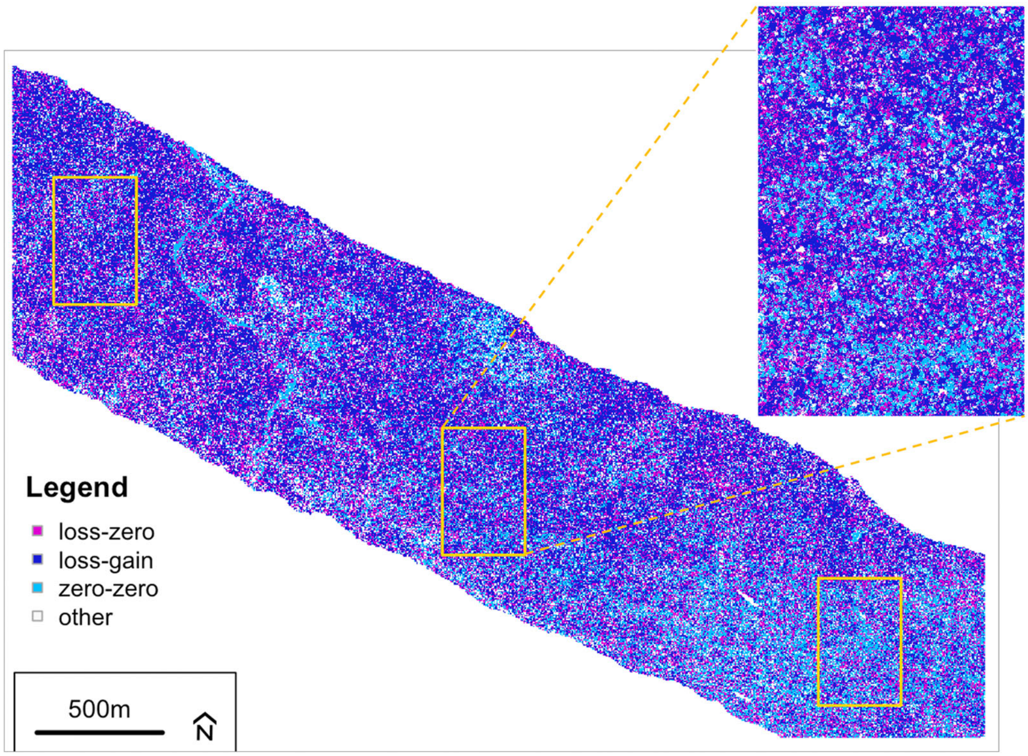

Figure 6. Map of the full study area showing the three dominant canopy change trajectories: loss–gain (44.6%), loss–zero (21.6%), and zero–zero (17.8%) at 1-m pixel resolution. All other change trajectories are shown in white (16%, see Table 2). The yellow rectangles indicate the locations of the three focus areas at low elevation (LO, top left), mid elevation (MD, center, and enlarged inset panel), and high elevation (HI, bottom right).

(LO) to 29% (HI). The second most important trajectory was the loss–zero pathway (22%), suggesting delayed canopy recovery in areas of severe storm damage. The proportion of forest areas with loss–zero trajectories was similar across the elevation gradient in the full study area. The third most dominant trajectory was the zero–zero pathway (18%), forest canopy trees that neither lost height from the storm nor gained height from release in the post-storm environment. This trajectory was most common at high elevation (34%), where shorter trees, greater dominance of palms (Uriarte and others 2019), and more regular exposure to strong winds may have resulted in both less storm damage and slower rates of post-storm height growth. Overall, the loss–gain and loss–zero trajectories were widely distributed across the study area, whereas the zero–zero trajectory exhibited clearer patterns at the individual tree crown and landscape scales (Figure 6).

The vertical distribution of canopy height changes provided important insight into the mechanisms of forest damage and recovery from Hurricane Maria (Figure 7). Across the entire study area, both height losses and zero (no-change) areas from 2017 to 2018 were proportional to the pre-storm distribution of canopy heights. In the loss areas, canopy material was concentrated below 5 m in height or distributed more uniformly between 5 and 30 m than in the pre-storm structure. Gains in canopy height between 2018 and 2020 created closed-canopy conditions at or below 5 m height and reestablished a dominant mode of canopy height at 12 m by 2020. Areas of no-change and loss between 2018 and 2020 occurred at all height levels, suggesting a highly heterogeneous canopy response.

The vertical redistribution of canopy material was similar in the LO and MD focus areas (Figure 7), and broadly consistent with the patterns observed across the entire study area. No-change areas between 2017 and 2018 in the LO and MD focus areas tended to be in taller canopy positions, on average. These taller canopy areas also suffered greater damages, with a bi-modal distribution of canopy heights in the loss category and the most open environments below 5 m. Shorter canopy environments closed rapidly between 2018 and 2020, with little or no replacement of gap areas

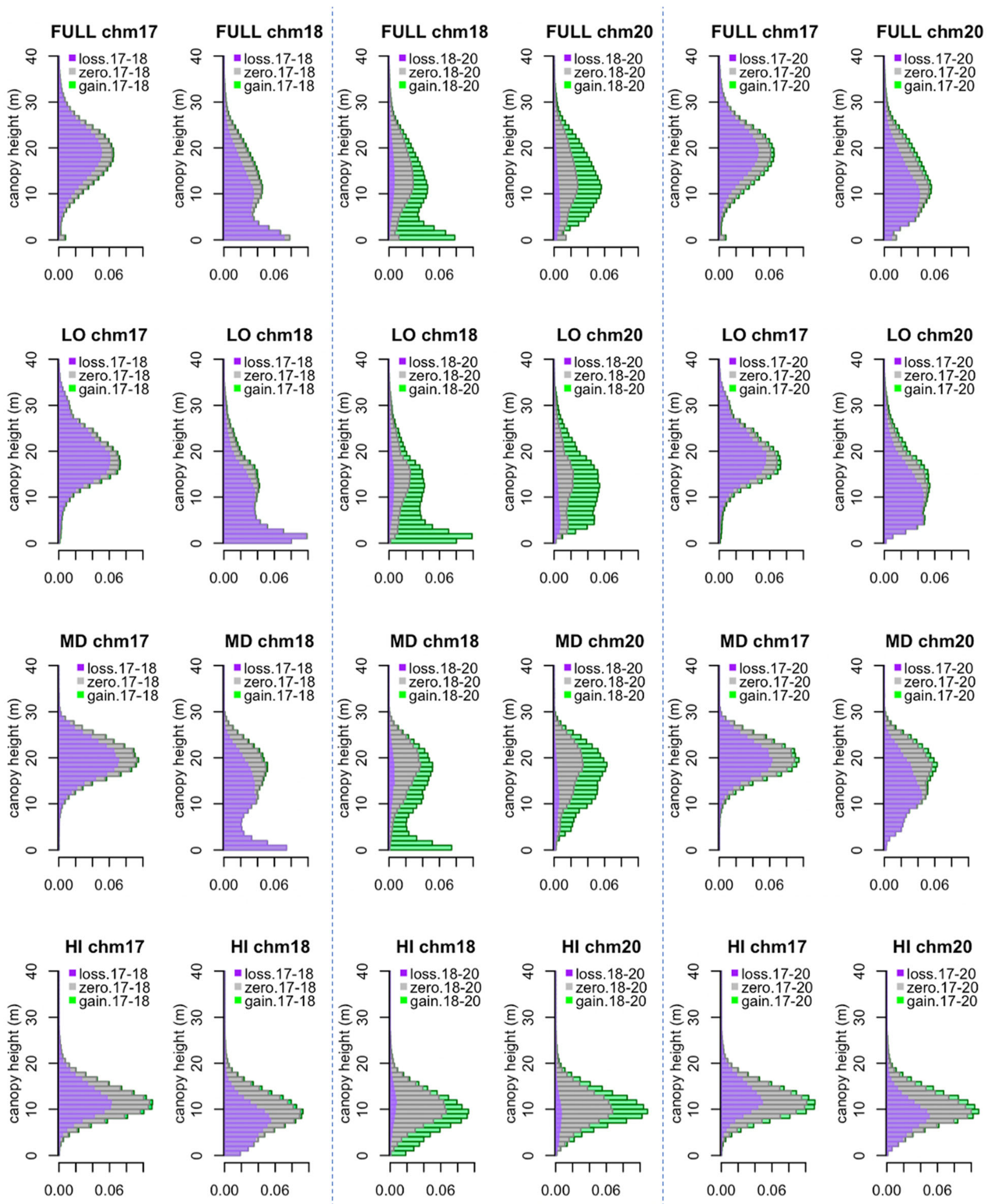

Figure 7. Canopy height distributions colored by change class, where paired figures in each time period illustrate the ''from-to'' movement of canopy material. Horizontal stacked bars in each 1-m height bin are colored according to the proportion of the study area associated with height loss (purple), height gain (green), and zero change (gray) categories for each time interval, 2017–2018 (left column), 2018–2020 (middle column), and 2017–2020 (right column).

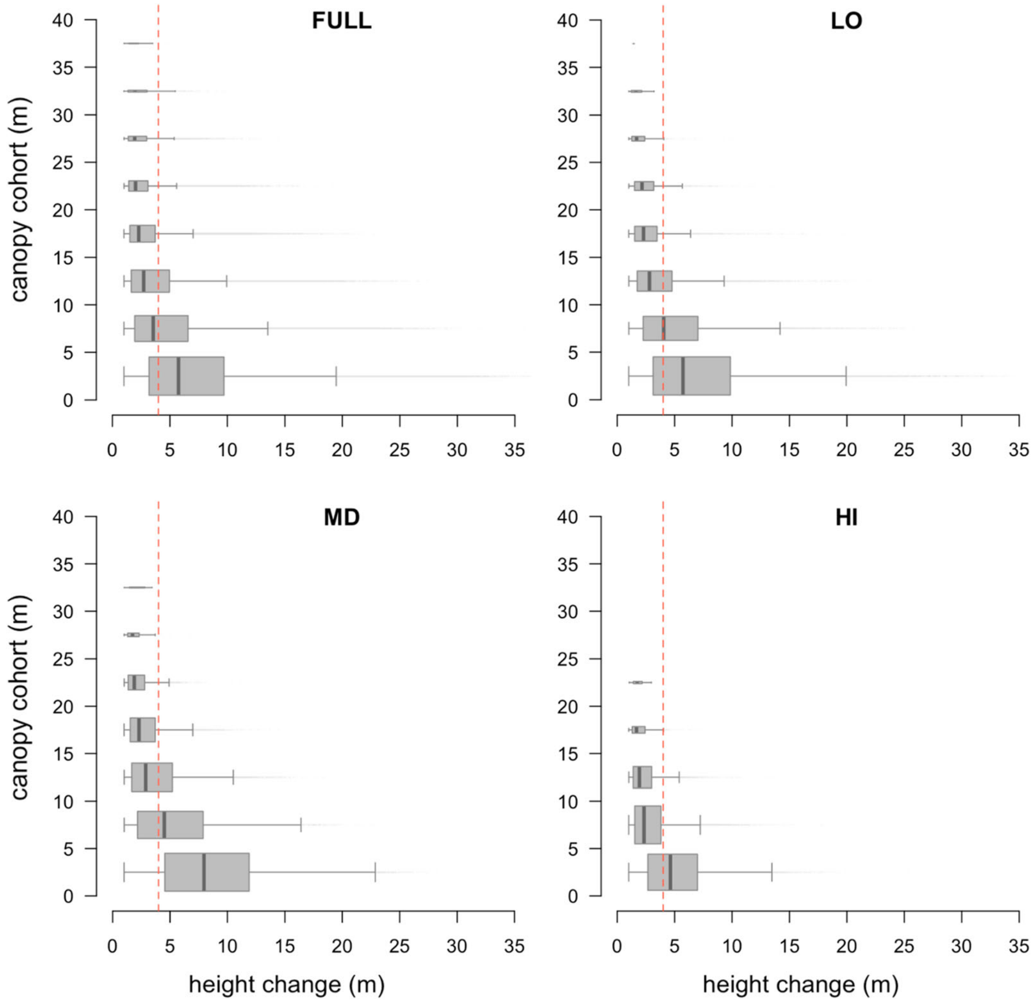

Figure 8. Canopy infilling between 2018 and 2020 was vertically stratified, with more overtopping (> 4 m) than vertical height growth (< 4 m) lower in the canopy profile. Box plots summarize canopy height gains between 2018 and 2020 for 5-m cohorts in forest areas with loss–gain trajectories in the full study area (FULL) and three 16-ha focus areas (LO, MD, HI). The vertical dotted red lines indicate the threshold (4 m) separating vertical growth from horizontal infilling by neighboring trees, and box widths denote the proportion of all height gains in each 5-m cohort.

with canopy height ≤ 2 m through further loss events.

Less damage at the HI focus area resulted in a more uniform vertical redistribution of canopy material. Canopy losses between 2017 and 2018 were proportional to the pre-storm canopy height distribution, but lower overall damages (Table 1, Figure S1) resulted in fewer canopy openings near the ground in 2018. Unlike the other focus areas, the most rapid growth response was near the mean canopy height. These factors limited overall changes in the vertical distribution of canopy material between 2017 and 2020 compared to portions of the study area at lower elevations.

Vertical height growth from established or new individuals and lateral growth of existing tree crowns contributed equally to canopy height gains between 2018 and 2020 for forest areas with loss–gain trajectories during the study period (Figures 7, 8). Most height gains occurred in canopy positions < 10 m in 2018. The shortest cohort (0–5 m) was more likely to be overtopped by neighboring trees (66%) than retain a canopy position through rapid height growth of new or established individuals (34%). For taller forests at LO and MD elevations, the canopy cohort from 5 to 10 m exhibited roughly equal proportions of height growth and infilling. For canopy positions > 10 m in 2018, 73–88% of height gains were small, indicative of regrowth or expansion within existing crowns (≤ 2 m y^{-1}), with limited expansion of tree crowns by surviving individuals in the pre-storm canopy cohorts.

Discussion

Small footprint airborne LiDAR data captured widespread changes in forest structure from Hurricane Maria and rapid forest recovery along an elevational gradient of subtropical wet forest in Puerto Rico. Almost three-quarters of the study area lost canopy height from crown damage or treefall events. Yet, the pattern of hurricane damages was heterogeneous. Losses occurred at all canopy heights, and approximately one quarter of forests suffered little or no damage, including many taller and more exposed canopy positions. These findings reinforce the need to consider species-specific attributes (for example, Uriarte and others 2019) and topographic effects (Van Beusekom and others 2018; Muscarella and others 2020) to better understand the selective pressure of hurricanes on forest structure and composition. Nearly 2.5 years after the storm, forests were markedly shorter and more open, despite rapid vegetation growth in the forest understory. Surprisingly, more than 40% of forest canopy positions exhibited little or no height growth after the storm. Together, these no-change trajectories (loss–zero, zero–zero, gain–zero) were as abundant as forest areas with large height losses and subsequent height gains. Future work to combine LiDAR and inventory data may help reveal whether individuals with little or no height growth experienced lower productivity due to canopy damage, abiotic factors such as heat stress, or a shift in carbon allocation from height growth to other demands, such as fine root production (Silver and Vogt 1993; Vargas and others 2009; Van Beusekom and others 2020). Overall, these data provide important benchmarks of changes in forest structure from an extreme event, including critical inputs for ecosystem models regarding gap formation, initial and delayed structure changes, and the importance of surviving trees (with or without storm damage) on forest composition and productivity.

Hurricane Damage

Landscape-scale patterns of forest damage from repeat LiDAR data expand upon the understanding of hurricane damages from plot-scale studies. Brokaw and Grear (1991) estimated hurricane damage in 1-ha plots at three elevations in the Luquillo Mountains after Hurricane Hugo, documenting similar decreases in top of canopy height and variability in hurricane damages by forest type (21.1–9.3 m in tabonuco and 10.1–7.7 m in palo colorado forests). LiDAR data in this study covered a much larger area (439 ha), capturing the spatial distributions of large and small height losses and the extent of forest patches with little or no damage from the hurricane (Figure 4), including well-drained sites at higher elevations. These findings clarify our understanding of fine-scale variability in hurricane damages across the landscape (Weaver 2010) and motivate additional work on the complex interactions among rainfall, wind, and forest structure that create a mosaic of disturbance impacts from hurricanes.

Patterns of damage in this study differ from those in studies of initial forest damages from Hurricane Maria using moderate resolution (30 m) optical satellite imagery (Van Beusekom and others 2018; Feng and others 2020; Hall and others 2020). Airborne LiDAR data provide precise, 3-D information at 1-m spatial resolution regarding the heterogeneity in canopy height loss, vertical distribution of vegetation within the forest profile, and fractional canopy cover. By contrast, estimates derived from optical satellite data show more uniform damages across the Luquillo Experimental Forest (Feng and others 2020; Hall and others 2020), despite general agreement for greater initial changes in sub-pixel estimates of non-photosynthetic vegetation at low and mid elevations than for high-elevation forest types. Differences between LiDAR-derived changes in forest structure and optical measures of fractional vegetation cover suggest that initial defoliation is an imperfect proxy for structural damages from hurricane disturbance.

The spatial and vertical distributions of canopy openings following a major hurricane have not previously been quantified using LiDAR data. We estimated that Hurricane Maria generated canopy openings $\leq$ 2 m from branch loss and treefall events covering 13.5% of the study area, on average. Previous work at the plot scale reported even larger increases in gap area (vegetation height $\leq$ 2 m) from Hurricane Hugo in 1989 (Brokaw and Grear 1991), with estimates of pre- and post-hurricane percent gap area of 0.4% versus 26% in tabonuco forest and 2% versus 27% in palo colorado forest, respectively. Results from this study for comparable forest types in the MD and HI focus areas had somewhat lower pre-hurricane gap area (0.05% and 0.14%) and substantially lower post-hurricane gap area (12.6% and 4.7% in tabonuco and palo colorado forests, respectively). Adding constraints for the minimum gap size, rather than summing all 1-m^2 resolution pixels with canopy heights $\leq$ 2 m, would further reduce the estimate of gap formation from Hurricane Maria in our study area despite widespread evidence of crown damages and openings in the mid and upper canopy.

Three methodological factors may contribute to the large differences in estimated post-storm gap area between field and LiDAR studies. First, the time since the hurricane may influence the estimates of gap area (9–20 weeks in Brokaw and Grear versus 7 months in this study), as resprouting and reflushing of canopy leaves may rapidly restore canopy cover (Tanner and others 1991). Second, observer and laser-based estimates of forest structure differ substantially, even for common parameters such as tree height (for example, Hunter and others 2015). Brokaw and Grear (1991) collected field-based observations on a 5-m grid, with visual assessments of gap versus no-gap, compared to spatially and vertically explicit measures of forest structure at 1-m resolution, with objective, laser-based estimates of canopy material. Third, estimates in this study reflect landscape-scale responses to hurricanes, not individual plots, given the extensive survey of 439 ha. However, direct comparisons between damage from different hurricanes are also confounded by other factors, including differences in pre-hurricane forest structure and composition. For example, selective removal of specific size and species classes from sequential storms (for example, Uriarte and others 2019) may reduce vulnerability at the stand scale in the short term.

One of the unique measurements from the time series of LiDAR data in this study is the direct comparison of initial and delayed canopy turnover following the storm. Previous studies have considered the long-term effects of other disturbance types using LiDAR data, including selective logging (Rangel Pinagé and others 2019) and drought in Amazon forests (Leitold and others 2018), but delayed structural damages from extreme events such as hurricanes have not been previously reported. We found limited evidence for delayed structural damages following the storm. Although initial canopy turnover was 30 times higher than background turnover rates in Central Amazon forests (Leitold and others 2018; Rangel Pinagé and others 2019), canopy turnover between 2018 and 2020 in this study was comparable to background rates in those studies, and lower than annualized estimates of branch and treefall events in Western Amazon forests (Marvin and Asner 2016).

At least three factors may contribute to the rapid return to background turnover following Hurricane Maria. First, structural damages within the first 7 months following the storm were included in the assessment of hurricane turnover, such that short-term delays in canopy turnover were attributed to initial forest damages. Second, canopy damages from Hurricane Maria reduced the mean crown size for surviving individuals; the per-tree change in fractional canopy cover would therefore be smaller in the second time interval (2018–2020). Third, the survival rate of damaged individuals may be higher than expected, given the magnitude of initial canopy damages. Previous studies suggest that rates of tree mortality from hurricanes are low ($<$ 10% in Puerto Rican forests, see Frangi and Lugo 1991; Walker 1991; Zimmerman and others 1994; Uriarte and others 2019), even when entire forest stands suffer defoliation (Liu and others 2018) and large amounts of damage occur in the form of snapped or uprooted trees (Walker 1991; Basnet 1993; Vandermeer and others 1995). Overall, these findings suggest that hurricanes are a pulse disturbance, with direct impacts on individual tree and forest canopy structure, and long-term contributions from damaged canopy individuals to forest structure and function.

Canopy Recovery

Hurricane Maria created open-canopy conditions throughout the forest vertical profile, increasing light availability to spur rapid regrowth. Overall, nearly half of the forest area gained $>$ 1 m in height between 2018 and 2020. These height gains led to closure of canopy openings $<$ 10 m height from a combination of height growth of existing or new individuals and lateral crown expansion by surviving canopy trees or advanced regeneration. Repeat LiDAR measurements therefore suggest that rapid increases in leaf area captured by satellite vegetation indices (for example, Feng and others 2020) were concentrated in lower canopy layers, rather than from the rapid recovery of taller canopy trees.

We estimated that vertical and lateral growth contributed equally to canopy closure during this period, based on a threshold of maximum potential height growth (2 m y^{-1}), with marked differences in height growth distributions between taller and shorter cohorts. Importantly, the upper forest canopy remained open in 2020, with 65% canopy cover at 10 m compared to closed-canopy conditions at that height before the hurricane. Evidence for limited crown expansion from taller individuals (for example, Figure 8) is consistent with previous reports of limited canopy tree plasticity adjacent to new gaps in other tropical forests (Hunter and others 2015; Kellner and Asner 2014). Rates of crown expansion may have been further suppressed by crown damage from Hurricane Maria, triggering epicormic resprouting from branch and stem positions lower in the forest vertical profile (Bellingham and others 1994; Bellingham and others 1996). Overall, this balance between vertical and horizontal growth has important implications for the size structure and species composition of hurricane-impacted forests (Uriarte and others 2009; Uriarte and others 2019). Our focus on canopy closure and increases in top of canopy height excluded important dynamics associated with recruitment and growth of understory vegetation that did not secure a canopy position following hurricane disturbance (Yih and others 1991; Vandermeer and others 1995; Uriarte and others 2004; Dietze and Clark 2008; Shiels and others 2010). Subsequent studies that consider the full LiDAR point cloud may offer insights regarding the spatial distribution and density of understory vegetation changes in response to initial changes in canopy structure from Hurricane Maria.

Even with high-density airborne LiDAR data, differentiating vertical growth from lateral expansion following Hurricane Maria remains a challenge. For example, we excluded subtle losses and gains of fine branches within tree crowns (< 1 m height changes), potentially leading to an underestimate of height growth or release of surviving individuals. In addition, the use of a single threshold to separate height growth from crown expansion offers an initial estimate, whereas continuous distributions of height gains at all height levels illustrate the difficulty in separating specific mechanisms (for example, Figures 3, 8). Ideally, such a height threshold would be context-specific, based on observed differences in initial canopy height distributions and the presence or absence of advanced regeneration. Future studies that leverage other technologies may provide more confident separation of the mechanisms that contribute to structural changes in the post-hurricane environment. For example, terrestrial LiDAR scanners with higher point density and narrower beam divergence permit the separation of woody and leaf material, even for canopy vegetation in tall tropical forests (Boni Vicari and others 2019). Similarly, volumetric analyses of tree objects (for example, Ferraz and others 2016; Ferraz and others 2020), rather than the watershed approach used in this study, might also prove useful for evaluating the different processes of infilling within the original, pre-storm volumes occupied by canopy trees. Finally, field data also provide important constraints on the relative abundance of tree species that resprout following crown damage to guide the interpretation of LiDAR-derived estimates of changes in canopy structure.

Key Lessons for Ecosystem Models

LiDAR-derived estimates of forest damage and recovery in this study provide four novel benchmarks for parameterization or validation of disturbance processes in ecosystem models. First, the current generation of ecosystem models represent the proportion of forest areas in different age classes since the last disturbance (for example, Fisher and others 2018). Spatial and temporal variability in gap formation is therefore a critical parameter to ensure that long-term simulations capture the impact of hurricane disturbance. Here, we estimated that 13.5% of the study area had vegetation $\leq$ 2 m following the storm; model-dependent translation of this LiDAR-derived estimate would likely be lower, given minimum patch sizes in some models that build on the pseudo-spatial representation of forest structure first developed in the Ecosystem Demography model (for example, Moorcroft and others 2001; Fischer and others 2016; Longo and others 2020; Koven and others 2020). Parameterization of new patches in size and age-structured models is an essential first step to improve the accuracy of post-disturbance recruitment following extreme events such as hurricanes. Second, trajectories of forest growth in ecosystem models typically vary based on plant functional types or plant traits, rather than disturbance. In this study, we estimated the proportion of the forested landscape that followed nine specific height gain and loss pathways from storm damage and initial forest recovery. These proportions, and the associated metrics of forest damage and recovery in each pathway, offer insights regarding damage-dependent rates and mechanisms of forest recovery, even for forests with similar species compositions and site conditions. Third, rates of canopy closure following hurricane disturbance at different heights within the forest vertical profile provide empirical values to constrain models that assume either perfect plasticity of canopy material or some modified plasticity (for example, Purves and others 2008; Koven and others 2020). Open canopy conditions in 2020 demonstrated that light penetration and growth of understory vegetation or shorter canopy cohorts constituted an important fraction of post-storm recovery. Initial findings of equal contributions from vertical and lateral growth also confirmed the influence of light penetration for promotion of shorter cohorts. Finally, this study provided clear evidence for the long-term impact of damaged individuals on the structure and function of tropical forests following hurricane disturbance. Limited height growth, crown expansion, and turnover of surviving canopy trees during 2018–2020 underscore the longevity of damaged individuals in post-hurricane forest environments. Ultimately, it may be possible to use LiDAR-derived measures of forest structure to directly parameterize plant structural traits in ecosystem models and account for reductions in productivity and evapotranspiration for damaged individuals. Combined, these metrics of forest disturbance provide new constraints on forest growth and carbon cycling following hurricane damages, opening new avenues for future research.

Ecosystem Science with Repeat LiDAR

The growing availability of repeat LiDAR and other 3-D data paves the way for a wide array of ecosystem studies, and especially research to link disturbance processes with associated changes in the land–atmosphere exchange of carbon, water, and energy. Repeat measures of vegetation structure offer insight into the timing and potential cause of tree death or sublethal changes in forest structure, such as branch loss (for example, Leitold and others 2018). LiDAR may be a more direct approach to quantify processes such as branch loss (Scaranello and others 2019) that are generally ignored in conventional forest inventories because they are laborious to estimate, even with high levels of uncertainty (Van der Meer and Bongers 1996; Palace and others 2008). Annual airborne LiDAR data collections are available for a range of ecosystems within the US National Ecological Observation Network (NEON), and a growing number of other long-term research sites have repeat LiDAR (for example, G-LiHT) or similar 3-D data derived from overlapping photographs (structure from motion). These repeat LiDAR and optical remote sensing measurements capture both fine-scale changes associated with vegetation phenology (for example, Park and others 2019) and regional phenomena, such as drought-induced tree mortality (for example, Asner and others 2015; Stovall and others 2019). Tower-based camera systems, such as PhenoCam (Richardson and others 2018), or autonomous laser scanning systems (Eitel and others 2016) can pinpoint the day or even the hour of disturbance events, including confirmation of collateral damages that can be difficult to reconstruct using less frequent LiDAR or field measurements. Together, these 3-D data support new investigations into carbon turnover, the timing and duration of subsequent changes in forest structure, and the associated impacts on productivity, demography, runoff, and nutrient cycling across ecosystems. This type of monitoring activity is critical to benchmark background rates of disturbance and detect signatures of increasing disturbance frequency, such as subtle shifts in tree mortality associated with climate change (for example, Brienen and others 2015), or the severity of ecosystem impacts from single events, such as hurricanes.

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DATA AVAILABILITY

LiDAR data in this study are online at https://gliht.gsfc.nasa.gov. Data files used in the analysis are available from the NGEE Tropics Data Collection at http://dx.doi.org/10.15486/ngt/1797399.

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