



Effects of hurricane disturbance on a tropical dry forest canopy in western Mexico[☆]

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ABSTRACT

Hurricanes are meteorological events with intense effects on coastal ecosystems where the change in wind kinetic energy is first concentrated. The quantification of forest change and the understanding of forest recovery trajectories after hurricane impact require a series of observations from before and after the event. Our objective was to quantify the immediate and delayed impacts of two successive large hurricanes, Jova (October 2011) and Patricia (October 2015) on the canopy structure and some ecosystem functions of the Chamela tropical dry forest on the Pacific coast of Mexico. This forest is not typically affected by large disturbance events, but has a background of extreme rainfall seasonality and corresponding phenological responses. We used a series of detailed historic and recent measurements of canopy structure and Photosynthetic Photon Flux Density (PPFD) coupled with a continuous series of remote sensing indices (NDVI) to help assemble a comprehensive view of the effects from hurricanes Jova and Patricia, category 2 and 4 in the Saffir-Simpson Hurricane Wind Scale, respectively. From ground-based LiDAR observations of canopy structure we estimated aboveground forest biomass at various times before and after the hurricanes. The net aboveground biomass loss from the two hurricanes combined (26.4 Mg ha^{-1}) was about 33.7% of the pre-hurricane value of 78.4 Mg ha^{-1} . Biomass loss from the first hurricane was about 8.6 Mg ha^{-1} (11.0% of the original). Damage from the second storm alone might have been as much as 22.7%, depending on the course of recovery between hurricanes. We also found a temporary decline in the fraction of Absorbed Photosynthetically Active Radiation (fAPAR). NDVI, well correlated to fAPAR, also showed this pattern after both hurricanes. Canopy structure was considerably altered by both hurricanes, including leaf area and persistent vertical and horizontal woody components. The effects of wind and precipitation differed in several ways: whereas biomass loss appears related to hurricane wind energy, the duration of extended greenness may be due to the extra aseasonal precipitation. Our data suggest that different aspects of ecosystem structure and function will recover at different time scales. The recovery of greenness occurs rapidly, on the order of weeks to months but canopy cover and production will recover more slowly. The re-establishment of persistent canopy structure and total biomass will likely take decades in the absence of other major disturbances or active forest management.

1. Introduction

Large disturbance from extreme weather events can have significant impacts on the structure, composition and function of terrestrial ecosystems. The effects of these events can be both obvious and subtle at immediate and delayed time scales (Foster et al., 1998; Lugo, 2008; Frank et al., 2015). The varied origin of these disturbances, their

different effects, their large size and infrequent occurrence make such events challenging to study (Turner and Dale, 1998; Altwegg et al., 2017). Hurricanes (typhoons, cyclones) are meteorological events that can have particularly intense effects in coastal ecosystem, where the change in wind kinetic energy is first concentrated. Hurricane impacts on forests have been studied in numerous coastal systems (e.g., Queensland: Webb, 1958; Puerto Rico: Zimmerman et al., 1996; Van

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Bloem et al., 2005; Holm et al., 2017; Solomon Islands: Bursalem et al. (2000); Florida: Diamond and Ross, 2016; Yucatan Peninsula: McGroddy et al., 2013). These studies agree that sources of damage from hurricanes involve a mixture of driving factors, often winds and rainfall (e.g., McNulty, 2002) and a whole range of concurrent/delayed responses and cascading effects (see Gavito et al., *this issue*; Martínez-Ruiz and Renton, and other papers in *this issue*). Understanding the trajectory of forest recovery requires a series of observations, preferably initiated promptly and continued until a return to pre-hurricane conditions. Quantifying the extent of change requires observations from both before and immediately after the event (Holm et al., 2017), which though rarely feasible, is of paramount importance to assess the role of hurricanes in forest dynamics.

Patterns of hurricane damage on forest canopy functions (e.g. increase in light transmittance) and recovery (e.g. decline of transmittance toward pre-disturbance levels) vary widely. Turton (1992) found an increase of median Total Site Factor (similar to transmittance) from 3.5% before Cyclone Winifred in northern Queensland to 5.7% after six months and then 2.9% after 11 months. Fernández and Fetcher (1991) in Puerto Rico measured 3% transmittance 14 months after Hurricane Hugo – mostly caused by recent growth of pioneer plants. Bellingham et al. (1996) showed a long gradual decline in transmittance from seven to 33 months after Hurricane Gilbert in Jamaica. Sherman et al. (2001), studying the effects of Hurricane Georges on Dominican Republic mangroves, found canopy transmittance 3% before the storm, 51% after 6 months and 47% after 18 months. In the Comita et al. (2009) study of Hurricane Georges in Puerto Rico, canopy openness dropped from about 35% after the storm to about 10% eight years later. More recently, Shiels and Gonzalez (2014) found canopy opening of 16% immediately after a trimming manipulation - this value declined to background levels in about three years. This experimental study had observations before, immediately after, and through the return to pre-disturbance conditions; such a full series of measurements is not usually available for comparison.

Hurricanes are a regular climatological feature of some coastal tropical forests such as tropical dry forests (TDF). TDF represents 42% of all intra-tropical vegetation worldwide (Murphy and Lugo 1995) and is characterized by a highly seasonal rainfall pattern, which controls many ecosystem processes (Martinez-Yrizar and Sarukhán, 1990; García-Méndez et al., 1991; Jaramillo and Sanford, 1995; Rentería and Jaramillo, 2011; Anaya et al., 2012). Hurricane events have the potential for major disruption of seasonal patterns in such ecosystems. The disruption of and return to the pre-hurricane state of canopy cover is often an indicator of forest resilience (in the sense of Hodgson et al. (2015)), which implies potential changes in biomass, litterfall rates and overall forest structure.

Changes in canopy cover strongly correlate with changes in the transmittance of light to the understory, and both can be measured using satellites or ground sensor-based observations (Parker et al., 2005). Many satellites acquire spectral images on a regular basis and have been sustained over many years. This capacity provides the possibility of capturing not only the extent of change due to the event but also the long-term pattern of recovery, albeit at large scales (Negrón-Juárez et al., 2010). For example, changes in canopy cover can be assessed using satellite images taken before and after the hurricane to calculate reflectance indices such as the Normalized Difference Vegetation Index – NDVI (‘greenness’) and the Enhanced Vegetation Index – EVI (e.g., Wang and D’Sa, 2010). On the other hand, ground-based observations can be useful to estimate the components of Photosynthetic Photon Flux Density (PPFD) (i.e. canopy reflectance, canopy penetration and ground layer reflectance) that are useful to estimate the PPFD fraction absorbed by the canopy (Parker et al., 2005).

Forest recovery in tropical ecosystems impacted by hurricanes involves the rapid return of leaf area to pre-disturbance levels –although much of this may involve sprouts of extant vegetation and vines. Change in biomass is often proposed as an indicator of disturbance

intensity (Frolking et al., 2009). Yet, biomass change can be difficult to measure (even if there is a pre-disturbance value) because damage (loss of branches and snapped trees) is difficult to assess with allometric approaches based on intact trees. However, biomass can be usefully estimated at large-scales with various remote sensing approaches. LiDAR (Light Detection And Ranging) has proved to be a good solution (Lefsky et al., 2002; Wulder et al., 2012; Zolkos et al., 2013) as it does not suffer from saturation effects of radar or reflectance-based methods (Frolking et al., 2009; Steininger, 2000). Airborne and space-borne LiDAR systems are limited in local detail and capacity to penetrate canopies, but ground-based systems such as the Portable Canopy LiDAR (PCL, Parker et al., 2004; McMahon et al., 2015; Stark et al., 2015) can provide interior canopy detail at high spatial resolution.

In this paper we aimed at understanding the effects of recent strong hurricanes on a TDF not typically affected by large natural disturbance events, but with a background of extreme rainfall seasonality and corresponding phenological responses that are characteristic of this water-limited ecosystem. Our specific objective was to quantify the immediate and delayed impacts of two successive large hurricanes, Jova (October 2011) and Patricia (October 2015) on the canopy structure and some ecosystem functions of the Chamela forest, a well-studied TDF on the Pacific coast of Mexico. We posed three main questions: i) what was the magnitude of the hurricane effects on the vertical structure, remotely perceived reflectance, and the net exchange of PPFD (here called the ‘balance’) of the canopy?, ii) was the change in these properties related to measures of the hurricane intensity?, and iii) what are the implications of these findings for the time scales of recovery?

2. Materials and methods

2.1. Study site

The study was conducted at the Estación de Biología Chamela (EBCh) in the Chamela-Cuixmala Biosphere Reserve (Ceballos et al., 1999). The field station is located 2 km inland from the Pacific coast of Mexico (19° 30'N, 105° 03'W). The climate is warm (mean annual temperature 24.6 °C; 1978–2000, EBCh weather station). Mean annual precipitation is 800.4 mm (1983–2015, Maass et al., *this issue*). Long-term annual runoff is 99.5 mm (Maass et al., *this issue*) and the runoff:precipitation ratio is 0.124 (= 99.5/800.4). Potential evapotranspiration (PET) of 1130 mm was estimated for this region from the gridded climatology of New et al. (1999). There is a strong seasonality in rainfall (Bullock, 1986; Maass et al., *this issue*) with a 6 to 8-month dry period extending normally from November to mid-June. Tropical cyclones and the El Niño – Southern Oscillation (ENSO) add extra intra- and inter-annual variation to the precipitation regime (Bullock, 1986; García-Oliva et al., 1991; Maass et al., *this issue*).

The regional vegetation is predominately tropical dry forest, a 4–15 m tall, highly diverse and dense vegetation type with a well-developed understory of shrubs (Lott, 1993; Lott et al., 1987; Segura et al., 2003). The forest is old-growth, with no evidence of human disturbance (Maass et al., *this issue*). Most woody species in the Chamela TDF drop their leaves between October and May as a response to seasonal drought (Bullock and Solis-Magallanes, 1990). Consequently, there is a markedly seasonal pattern of leaf cover (Bullock and Solis-Magallanes, 1990), leaf area index (Maass et al., 1995), litterfall (Martínez-Yrizar and Sarukhán, 1990) and surface litter (Anaya et al., 2012).

The landscape is dominated by low-elevation (< 200 m asl) steep hills with convex slopes (López-Blanco et al., 1999). This topography controls important variation in soil moisture availability and radiation input across the landscape (Galicia et al., 1999). Structural and functional characteristics of the Chamela forest have been monitored continuously for more than 30 years on five small (12–28 ha each) contiguous watersheds (Maass et al., 2002a; Martínez-Yrizar et al., *this issue*). In all five watersheds, permanent plots (80 × 30 m) were established for monitoring light, tree growth, litterfall and nutrient

Table 1

Pre-disturbance ecosystem structural and functional characteristics of the tropical dry forest on three elevation zones in Watershed 1 in Chamela, Jalisco, Mexico.

Parameter	Elevation zone		
	Lower	Middle	Upper
Elevation (m asl) ^a	70	130	150
Live basal area (m ² ha ⁻¹) ^b	10.7	8.1	7.9
Maximum tree height (m) ^c	25.0	14.0	9.0
Net primary production (Mg ha ⁻¹ yr ⁻¹) ^d	13.5	11.5	11.2
Mean annual litterfall (Mg ha ⁻¹ yr ⁻¹) ^e	4.2	3.2	3.3
Total aboveground biomass (Mg ha ⁻¹) ^e	93.2	76.3	69.1
Leaf Area Index (m ² m ⁻²) ^e	5.4	3.8	3.3

^a Galicia et al. (1999),

^b Segura et al. (2003),

^c Maass et al. (1995),

^d Martínez-Yrizar et al. (1996),

^e Jaramillo et al. (2003).

cycling. In Watershed 1, three plots were distributed along the altitude gradient, with one plot in the upper, middle, and lower elevations (hereafter referred to as the upper, middle, and lower plot). Many of the ecosystem studies have been organized focusing on the specific elevation zones along this gradient (e.g., Maass et al., 1995; Martínez-Yrizar et al., 1996). In Table 1 we present key ecosystem characteristics of our main study area, Watershed 1.

2.2. The hurricanes

Hurricane Patricia was clearly the more powerful of the two events, with higher wind speeds and much lower minimum pressure along the full hurricane track (Table 2). Hurricanes lost some power on coming ashore –Jova became a category 2 and Patricia reduced to category 4 when it hit the study area. The maximum mean winds of Patricia at landfall were 2.3 times that of Jova. Since pressure force is proportional to the square of wind velocity, Patricia may have had as much as 5.4 times the strength of Jova. Hurricanes rapidly lost wind velocity on coming ashore and disappeared as named storms within 12 (Jova) and 24 h (Patricia). In both cases, the wind directions veered markedly as the storm moved onshore: Jova abruptly (within 10 min) from around 280 to 70 degrees, Patricia more gradually, from 300 to 110 degrees. As the local coastline trends NW-SE, the winds in both cases were first aligned along the coast but changed after landfall to arising from inland. Both hurricanes were accompanied by much more than usual amounts of rainfall. Hurricane Jova produced 187.9 and Patricia 142.6 mm (213.3 mm if the 70.8 mm following one week later is included). The mean October precipitation for the base period –when seasonal rainfall typically begins to decline sharply, is 50.9 mm. For Jova the rain lasted about 2 days –for Patricia about one. The maximum

Table 2

Meteorological comparison between hurricanes Jova and Patricia. Characteristics referring to the storm history are given in bold. Other values were recorded at the RUOA station at the Chamela Biological Station (EBCh). Impact time and date are when the maximum wind speed was recorded at EBCh. Note the storms fell to categories 2 and 4 after landfall.

Characteristic	Jova	Patricia
Maximum Saffir–Simpson category	3	5
Maximum wind speed, km h ⁻¹	201	322
Minimum pressure, mb	955	880
Maximum mean wind, km h ⁻¹	55.8	130.1
Maximum gust, km h ⁻¹	102.4	202.6
Precipitation, mm	187.9	142.6 ^a
Impact date	12-Oct-11	23-Oct-15
Impact time	0820	1750

^a Plus 70.8 mm seven days after = 213.3 mm.

rainfall rates, of 7.1 and 7.9 mm (10 min)⁻¹ for Jova and Patricia, respectively, are not unusually high. Thus, both hurricanes produced not only high winds but also atypical amounts of rain for that season. Meteorological data at a 10-min frequency near the area of landfall of Hurricanes Jova (2011) and Patricia (2015) and within 2 km of the study area was provided through the RUOA (Red Universitaria de Observatorios Atmosféricos) meteorological station run by EBCh. Data along the track of each storm were acquired from the National Hurricane Center (2012, 2016).

2.3. Base conditions for evaluating hurricane effects

Distinguishing the effects of a large, infrequent event from the background variation of a seasonal ecosystem is challenging. Our approach was to develop an expectation of the structured variation from long-term data and then evaluate the deviation associated with the hurricanes against that basis. We used the period 2000–2009 as the basis for assessing the hurricane effects, because it: 1) had no on-shore cyclonic activity (such as was reported by Maass et al. (1995) for 1992 and 1998) [Note that Hurricane Dean in August 2007 originated in the Atlantic Ocean and did not directly hit the Chamela coast, but produced intense rainfall (Maass et al., this issue)], 2) coincided with our record of light observations for the intact canopy starting in 2000 (Parker et al., 2005) and continuing through mid-2017, and 3) included a continuous series of satellite reflectance indices. The mean annual precipitation for this hurricane-free period, 671.6 mm, was lower than the long-term value. However, the runoff:precipitation ratio of 0.121 (= 81.9/671.6) was nearly the same as the long-term value of 0.124. Measurement systems were not in place to acquire direct observations of hurricane impacts immediately following the first event (Jova) but for the subsequent one (Patricia), we initiated a series of canopy structure and light climate observations. Our approach used a detailed picture of post-Patricia recovery to infer the pattern and intensity of Jova damage.

2.4. The satellite sensor and its metrics

We used MODIS (Moderate-resolution Imaging Spectrometer) product MOD13Q1 Collection 6 for the Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI) spectral indices (Didan, 2015; ORNL DAAC, 2017) every 16 days. We centered a trapezoidal box of 17 × 17 250 m pixels on the Watershed 1 study area (19.5074 N, 105.0345 W). The land cover type in this area reported from the MODIS product was Woody Savannah for 95.2% (275/289) of the pixels. Dates where more than 30% of the pixels were of low quality, mostly due to clouds, were excluded from the analysis (1.8% of observations for the 2000–2009 and 2.0% for the 2000–2017 periods).

2.5. Canopy cover and PPFD balance

We used interpolated foliage cover information from a 42-month phenological study by Bullock and Solis-Magallanes (1990) as a general curve of annual foliage dynamics for the standard period –referred to hereafter as BSM90. This pattern was used by Parker et al. (2005) to estimate the seasonality of PAR balance. Many of the ground-based observations of PPFD balance reported here are referenced to this undisturbed pattern.

We measured components of the balance of Photosynthetic Photon Flux Density (PPFD) with different methods, all described in Parker et al. (2005). Canopy reflectance, R_c , was estimated as a function of solar angle and canopy cover using measurements derived from balloon- and pole-mounted sensors. Canopy penetrance, P_1 , and ground layer reflectance, R_g , were measured with a TRAC (3rd Wave Engineering, Nepean, Ontario, Canada), a hand-held instrument acquiring PPFD at 32 Hz from quantum sensors (Li-Cor 190SA, Li-Cor, Lincoln NB) facing both up and down (Chen, 1996). We made these

observations at each of three locations within each elevation zone of Watershed I under clear conditions at intervals of 2–3 weeks following Hurricane Patricia. Additional measurements at nearby open sites interspersed with the in-canopy observations were interpolated to estimate the simultaneous incident PAR flux. The ratio of the downwelling light at 1 m to the concurrent external value is termed “canopy penetrance”. The upwelling:downwelling ratio at this level is termed the “ground reflectance”. Ground reflection, though a small fraction of canopy penetrance in most systems, can nonetheless be a significant contribution to canopy absorption when canopy penetrance is high in the dry season. The amount of PPFD scattered back to the canopy is the fraction of penetrance reflected from the ground, i.e., $P_1 \cdot R_g$. Combining these, the fraction of PPFD absorbed by the canopy ($fAPAR$) is:

$$fAPAR = 1 - R_c - P_1 + (P_1 \times R_g)$$

2.6. Canopy structure measured with a portable LiDAR system

We made observations of canopy structure at six times in the same location along one of the main trails within the EBCh reserve (the Chachalaca trail), with the Portable Canopy LIDAR (PCL, Parker et al., 2004). The system is based on the LD90-3100 VHS FLP rangefinder (Riegl Measurement Systems, Horn Austria) which measures ranges at 2 kHz. The PCL provides estimates of overhead surface area density (SAD, $m^2 m^{-3}$) above 1 m height. These data are typically represented as a horizontal-vertical section of the canopy surface – a ‘slice’ of the canopy surfaces along sampling transects, or as the mean canopy height profile, CHP, the average vertical profile of SAD across horizontal locations. The vertical sum of SAD is an estimate of the canopy area index (CAI, $m^2 m^{-2}$). Additional measures include the mean surface height weighted by SAD (the center of gravity of canopy surface area, H_{wtd}), the mean height of the outermost surface (Local Outer Canopy Height, H_{loc}), the variation in the outer canopy height (rugosity) and the gap fraction (proportion of observations open to the sky at the zenith). Because the rangefinder has a narrow divergence, the gap fraction samples a very small area overhead – the spot size at 10 m is only 4 cm (Parker et al., 2004).

The sampled area was the 0–300 m section of the Chachalaca trail which runs through the middle and upper forest zones. The first third of the path faces south, the middle part has a northerly aspect and the final third is atop a flat hilltop. This transect was sampled well before there was any hurricane damage (August 2001), 15 months after Jova (January 2013), and four times beginning immediately after Patricia (November 2015, March 2016, December 2016 and August 2017). The entire transect was sampled in each case, except for the first occasion after Patricia (November 2015) when the final 200–300 m could not be accessed due to the many fallen trees and branches. In that case, the canopy height profile for the missing 200–300 m was estimated based on the relation between the 200–300 m and the 0–200 m portions of the samples before and after November 2015.

2.7. Biomass estimation

For estimating aboveground biomass from the canopy metrics, we made measurements in Watershed 1 using three parallel line transects 10 m apart on each elevation zone (upper, middle, lower). For this purpose, we used an Impulse LR 200 rangefinder (Laser Technology Inc., Englewood CO). This instrument and the PCL rangefinder have similar pulse characteristics and record surface ranges very similarly. The data were analyzed and metrics produced as described in Parker et al. (2004). Total aboveground biomass values for each elevation zone were extrapolated from Jaramillo et al. (2003). Several of the derived canopy metrics showed the expected increase with biomass corresponding to the elevational differences in ecosystem characteristics (Table 1). For biomass estimation, we fitted the following relation based on the SAD-weighted height (H_{wtd}):

$$Biomass = B_{max} \times [1 - \exp(-b \times H_{wtd})]$$

Total aboveground biomass is in $Mg ha^{-1}$ and H_{wtd} is in meters. The B_{max} is the asymptotic value of biomass and the b parameter is the exponential slope of the relation.

2.8. Data analyses

The relation between the MODIS NDVI and the BSM90 phenology was fitted with a fourth order polynomial and to estimate the leaf cover phenology for the NDVI dates. We used a similar function for the reverse prediction –that is, to estimate NDVI from leaf cover.

To estimate the biomass and the PPFD components for the entire study area we weighted our ground observations considering that the upper, middle and lower zones of Watershed 1 contributed 50, 40 and 10% of the total area, respectively. Note that since the Chachalaca trail area traverses the regionally dominant middle and upper elevation zones the mean metrics for this transect are regionally representative.

In the case of Hurricane Patricia, the MODIS spectral indices were interpolated between dates for direct comparison of the dates of the ground measurements of canopy light environment and biomass. Regressions were performed between those indices and both $fAPAR$ and canopy structural measures. We used the SAS package (SAS Institute, 2009) for dataset organization and statistical analyses.

3. Results

3.1. Phenology

The mean seasonal pattern of the MODIS indices (NDVI, EVI) and the phenological course of leaf cover fraction are very similar during the base period (Fig. 1). The rapid seasonal greening up starting in early June is reflected in all three patterns. The variations in the remote sensing observations, indicated by the error bars, are distinctly highest in the day 155–190 dry-to-wet transition period. The seasonal pattern of precipitation for this period is given in the lowest panel. Similar coincidences of patterns were observed over the entire (2000–2016) record (not shown here). Note that both hurricanes hit the region, Jova (day 285) and Patricia (day 296), in October, when NDVI remains near maximum but precipitation begins to decline sharply.

Leaf fraction (BSM90) was consistently and non-linearly related to the mean NDVI for the 2000–2009 period (Fig. 2). Two points outside the trend derived from the dry-to-wet season transitions where variances are highest (Fig. 1). The curve shown was fitted excluding the two transition season points –their inclusion affected the variance explained by the regression by only 3.3%. The relation between BSM90 and the EVI index (data not shown) was similarly consistent but had a broad asymptotic section at high values of EVI. Thus, we opted to use the NDVI relation as it provided greater discrimination over the range of BSM90.

The period following each hurricane showed two deviations of the actual NDVI from the base seasonal pattern (2000–2009) shown in Fig. 1. There was an initial short-term decline in the index, lasting around two 16-day satellite cycles following Jova and three cycles after Patricia (Fig. 3). Following that decline there was an increase in the deviation sustained for 17 (Jova) and 13 cycles (Patricia). The integral increases and declines are represented by brown and green areas respectively for each hurricane (Fig. 3). These are termed ‘integral deviations’ here. Estimates of those areas, calculated with the trapezoidal rule, are -0.98 and 19.38 for the immediate and delayed effects, respectively, for Hurricane Jova. For Hurricane Patricia the corresponding values are -2.28 and 32.07. These sections, in units of index-days, are identified here as being associated with wind and precipitation effects, respectively (Fig. 3).

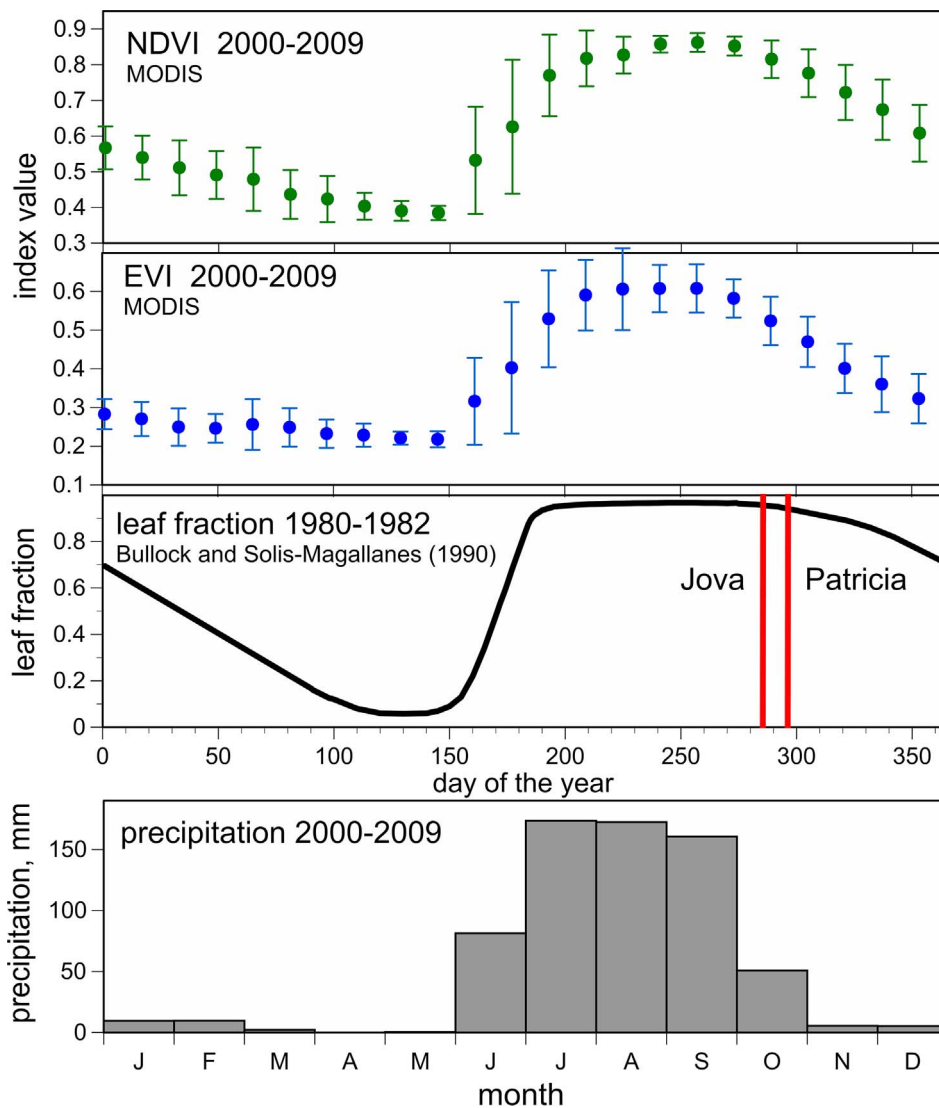


Fig. 1. Seasonal pattern of the MODIS NDVI (upper panel) and EVI (next to top) for the base period 2000–2009 and for the interpolated leaf cover fraction for 1980–1982, 'BSM90,' from Bullock and Solis-Magallanes (1990, next to bottom) and monthly precipitation for 2000–2009 (bottom). Error bars in the upper two panels are standard deviations. Hurricane impact dates are indicated with red vertical lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. PPFD balance

Following Hurricane Patricia, the mean values of PPFD canopy penetration (P_1) and ground reflectance (R_g) in Watershed 1 varied by season and with elevation (Fig. 4) – both parameters showed an increase in the dry seasons (days 150–250 and 460–600 after Patricia). Canopy penetration was lower and the dry season rise was delayed in the lower elevation plot (Fig. 4).

The elevation-weighted patterns of both canopy penetration and ground reflectance following Hurricane Patricia deviate in several ways from those expected under the 2000–2009 pre-disturbance period (Fig. 5). Canopy penetration was high after the storm, reflecting the loss of cover. Immediately following the event it was most likely at the maximum possible, around 0.5–0.6, but no observations were made until one month later. The initial high penetration period lasted less than 100 days, followed by a return to the normal seasonal pattern (a reduction and then increase of penetration). Note there is some suggestion of an overshoot in the penetration in the first year – a delay of about one month relative to the expected pattern (Fig. 5). After a year, the measured and expected patterns match more closely. In contrast, the pattern of ground reflectance following Hurricane Patricia does not follow the base case – it is persistently lower than expected and without much seasonal variation (Fig. 5). However, it shows a small but significant increase in time ($r = 0.45$, $df = 20$, $p < .05$).

A comparison of all components of the elevation-weighted PPFD balance for Watershed 1 showed several patterns (Fig. 6). As also seen in Fig. 4, canopy penetration and ground reflectance are highest in the dry season. Canopy reflectivity is highest in the dry season also, mostly because of leaf cover – the sun angle is less important in this predictor. The pattern of canopy absorption (fAPAR) resulting from combining these is thus mostly influenced by canopy penetration.

The temporal patterns of fAPAR and NDVI were similar in the 600 days following Hurricane Patricia (Fig. 7, upper panel); both exhibited a dry season decline and a subsequent rise with the onset of June rains in both years. The ground-measured fAPAR seemed to lag somewhat that of the NDVI, by about 25 days. The linear equation relating these is $fAPAR = 0.949 \cdot NDVI + 0.009$ ($r = 0.86$, $df = 20$, $p < .01$). Using this equation, we estimate the canopy fAPAR of the corresponding interval following Hurricane Jova (Fig. 7, lower panel). In that case, predicted canopy absorbance simply tracks the NDVI.

3.3. Canopy structure and dynamics

In the base period before both hurricanes, the vertical canopy structure of the forest in the three elevation zones within Watershed 1, including the maximum and mean heights (Fig. 8), parallels the estimates of tree top heights given in Table 1. The SAD-weighted height, H_{wtd} , is 4.36, 5.13, and 10.53 m for the upper, middle and lower

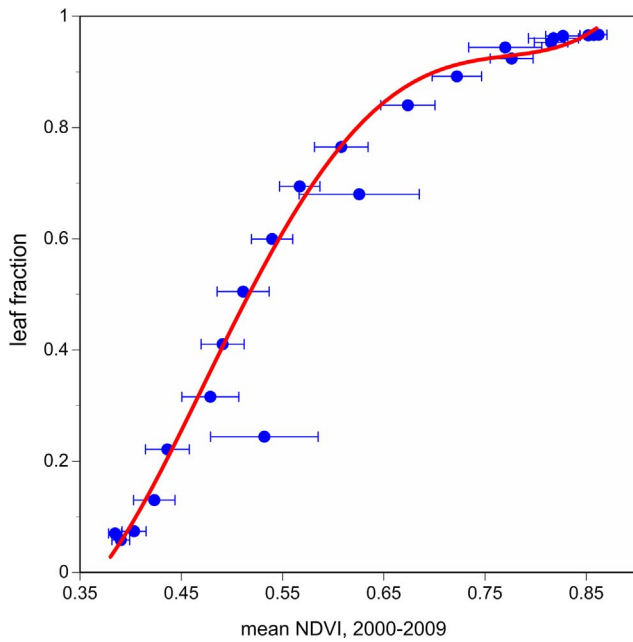


Fig. 2. Estimation of ground-based cover estimates (BSM90) from NDVI (see Fig. 1). The curve is a fourth order polynomial fit (see Section 2.8). The error bars of NDVI are standard errors.

elevation zones, respectively. The fitted relation (Fig. 9) to predict total aboveground biomass from the canopy metrics is $\text{Biomass} = 98.2 \cdot (1 - \exp(-0.285 \cdot H_{\text{wtd}}))$.

The forest canopy structure changed markedly in the middle and upper elevation zones of the Chachalaca trail following the two hurricanes (Fig. 10). Before the period of hurricanes (August 2001 in top row, Fig. 10), canopy structure was more-or-less continuous along all

sampled sections: the canopy top was smoother and there were few gaps. Following Jova and again after Patricia, there was a clear decline in both horizontal and vertical components of the surface area density. Visually, the decline seemed greater following Patricia than after Hurricane Jova (Fig. 10). Similarly, while canopy cover was nearly complete before the storms, it declined substantially after Jova and then, even more following Patricia.

Before both hurricanes in August 2001, the mean canopy height profile averaged across topographic positions shows a continuous vertical structure with a broad single peak at 5–7 m height (Fig. 11). However, not only were there distinct alterations following each of the two events, but also the separate trail sections were differentially affected. The north-facing, and particularly the hilltop areas experienced greater losses after Patricia than did the south-facing slope. After Hurricane Jova, canopy material was lost from all levels – the mean change in SAD following Jova was $50 \pm 20\%$ across all heights. However, after Patricia the damage was not evenly distributed vertically. The top section 4–11 m lost on average $83 \pm 16\%$ (se) whereas the bottom 1–3 m gained $61 \pm 68\%$.

A summary of canopy metrics derived from the Portable Canopy LiDAR measurements is shown in Fig. 12. Before hurricane disturbance, the canopy was tall ($H_{\text{loc}} = 6.8$ m), dense ($\text{SAI} = 7.2 \text{ m}^2 \text{ m}^{-2}$) and closed (gap fraction = 0.025). After Jova it lost height ($H_{\text{loc}} = 5.9$ m) and overall density ($\text{SAD} = 3.2 \text{ m}^2 \text{ m}^{-2}$) and opened substantially (gap fraction = 0.375). Following Patricia the canopy further decreased in height ($H_{\text{loc}} = 3.5$ m), density ($\text{SAD} = 1.7 \text{ m}^2 \text{ m}^{-2}$) and increased in openness (gap fraction = 0.633). In the 21 months following Patricia, there were only small but progressive increases in heights - gap fraction appeared to change little.

3.4. Loss and recovery of biomass and canopy structure

The linear recovery rate of biomass based on the PCL observations in the 21 months after Patricia was $1.83 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (Fig. 13).

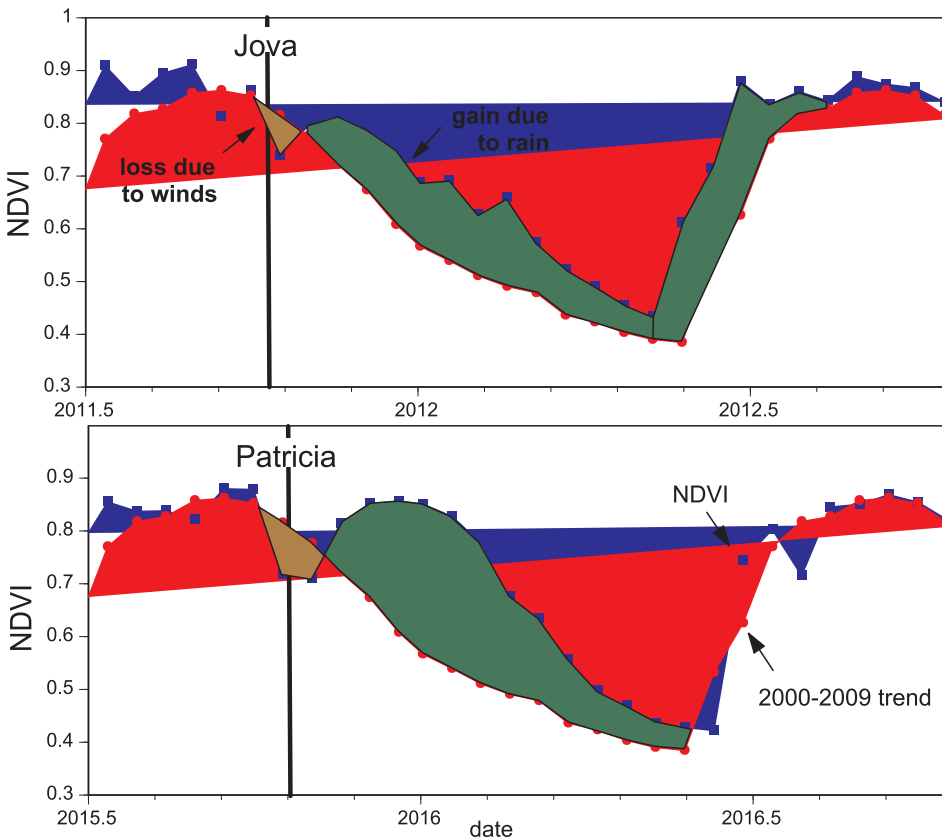


Fig. 3. Actual (blue symbols) and long-term (red) NDVI values in the Chamela study area for the 1.2 years following Hurricanes Jova (upper panel) and Patricia (lower). The brown and green shapes are the integrals of negative and positive index deviations following the storms. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

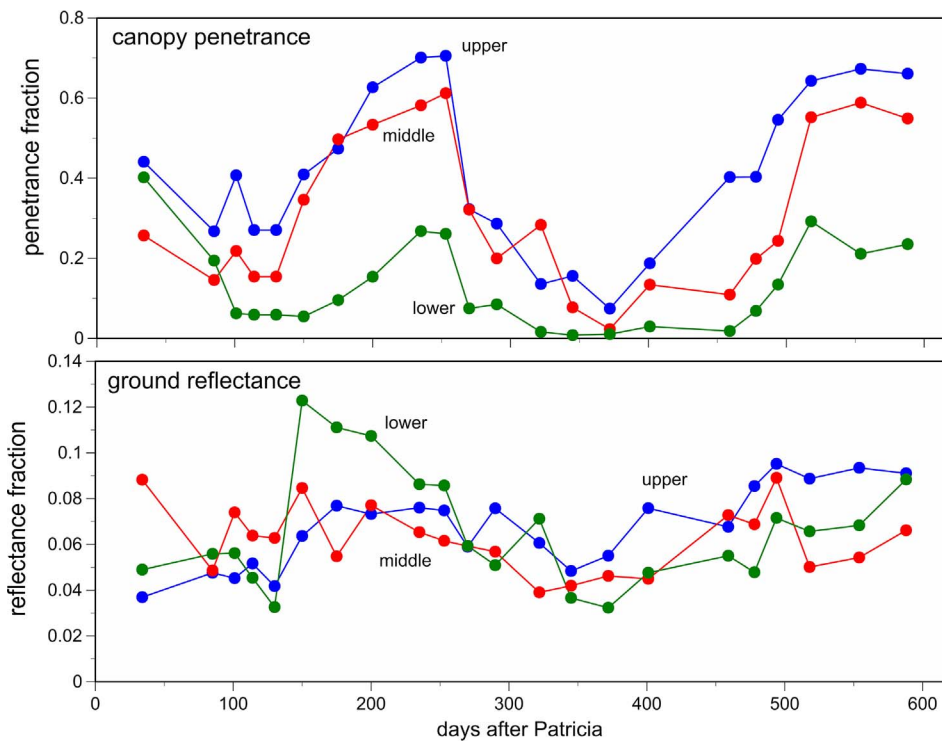


Fig. 4. Measured canopy penetration (upper panel) and ground reflectance (lower) in the three elevation zones of Chamela Watershed I in the first 600 days after Hurricane Patricia. Each point is the mean value from three locations in each zone at each sampling time.

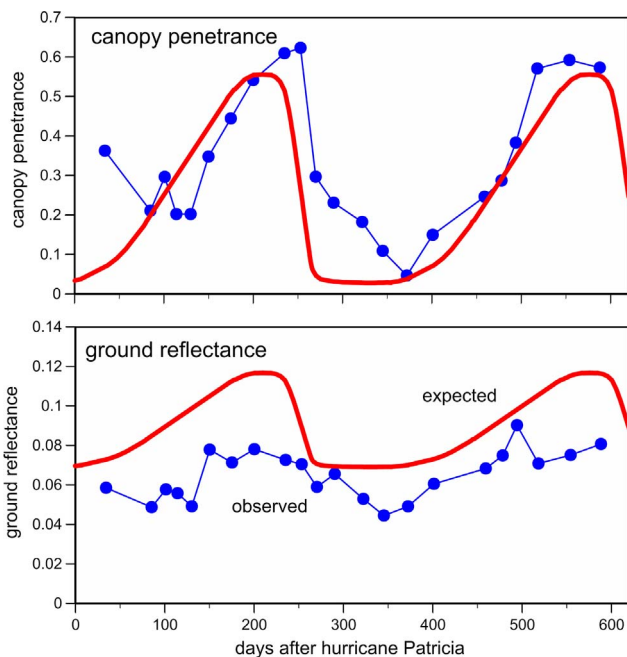


Fig. 5. Whole-watershed estimates of canopy penetration (upper panel) and ground reflectance (lower) compared with expected values, in the first 600 days following Hurricane Patricia.

Applying this recovery rate backward in time from the post-Jova measurement to the date of the storm suggests that the biomass after Jova was 69.8 Mg ha^{-1} , implying a loss of 8.62 Mg ha^{-1} or about 11.0% of the original 78.4 Mg ha^{-1} (Fig. 13). Biomass immediately after Patricia was 52.0 Mg ha^{-1} , a change from the base case of 26.4 Mg ha^{-1} , a loss of 33.7% (Fig. 13). However, the effect of Patricia is probably not the simple difference between these, i.e., $69.8 - 52.0 = 17.8 \text{ Mg ha}^{-1}$ (22.7%), because the forest likely recovered further between the hurricanes.

4. Discussion

4.1. Quantification of effects

Our detailed historic and recent measurements of canopy structure and PPFD coupled with a continuous series of remote sensing indices helped us assemble a more comprehensive view of the effects from both Jova and Patricia hurricanes in our study area. A comparison of canopy structural changes and the immediate and negative integral deviations suggested some of the direct effects were proportional to storm force – these should be taken into account to assess the effects from different hurricanes (Lugo, 2008). The ratio of the kinetic energies of Patricia and Jova was 5.44 ($= 130.1^2/55.8^2$). The corresponding ratios in the integral deviation immediately after the event was quantitatively similar, about 2.33 ($= 2.28/0.98$). The ratio of biomass loss from Jova (8.62 Mg ha^{-1}) and Patricia (as much as 17.8 Mg ha^{-1}) was also of this order ($2.06 = 17.8/8.62$). The net loss from the two hurricanes combined was 26.4 Mg ha^{-1} , about 33.7% of the pre-hurricane value of 78.4 Mg ha^{-1} . Note that the ratio of the Patricia/Jova October litterfall in Watershed 1 was 1.65 ($= 3.73/2.26 \text{ Mg ha}^{-1}$, middle plot only). This deposition of fine litterfall immediately following the hurricanes was exceptional high, compared to the low average value of 0.33 Mg ha^{-1} from the 29-yr pre-disturbance period (Martínez-Yrizar et al., this issue). The integral deviations and changes in both litterfall and biomass suggest the effects of hurricanes scale with wind force.

The effects of wind and precipitation differ in several ways. The ratio of the positive and sustained integral deviations (green areas in Fig. 3), 1.65 ($= 32.07/19.38$), differs from the ratio of the precipitation totals, 1.14 ($= 213.3/187.9$), which is closer to one. The similarity in precipitation amounts means it is difficult to evaluate whether the integral deviations scale with extra rain. The force of kinetic energy is delivered almost instantaneously, with immediate effects on leaf cover and persistent structure, whereas the rainfall was sustained over two (Jova) and one (Patricia) days. The rainfall rates themselves (maxima were 7.1 and 7.9 mm per 10 min), were high but not unusual and unlikely to have caused direct damage. Moreover, the rain effect is likely to be longer-term, with cumulative consequences for the recovery of

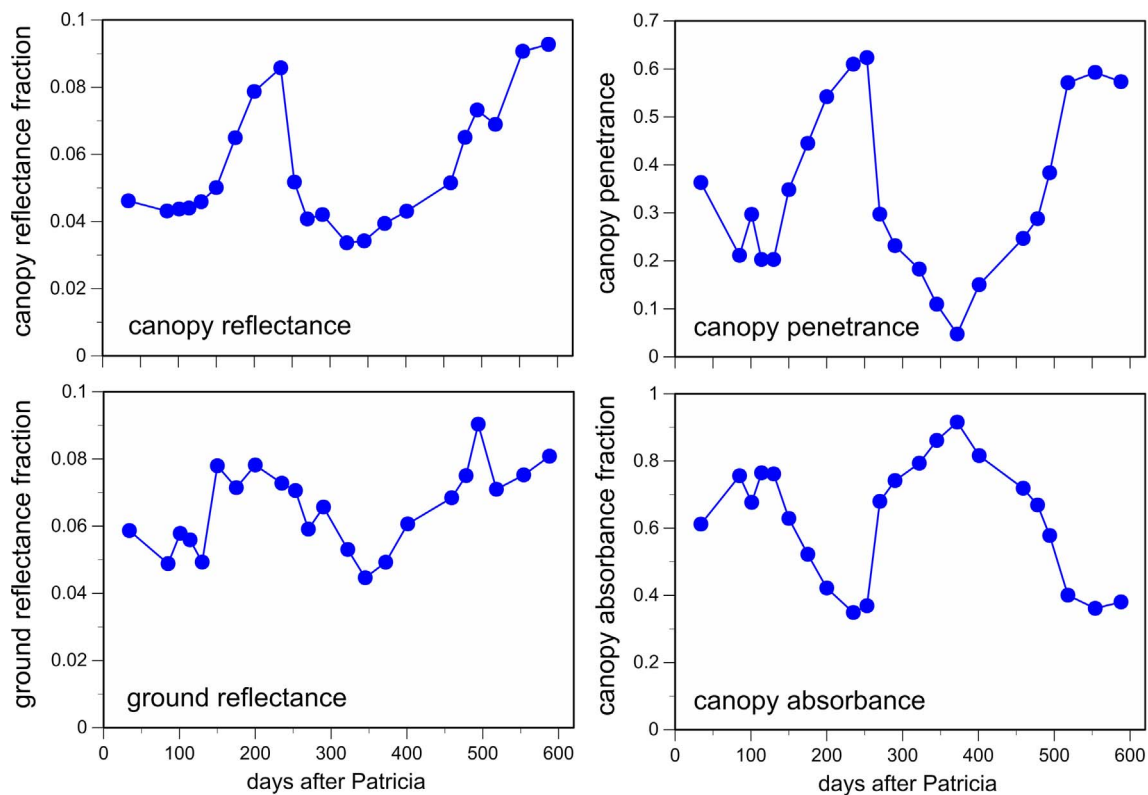


Fig. 6. Whole-watershed estimates of PPFD components in the Chamela forest in the first 600 days following Hurricane Patricia.

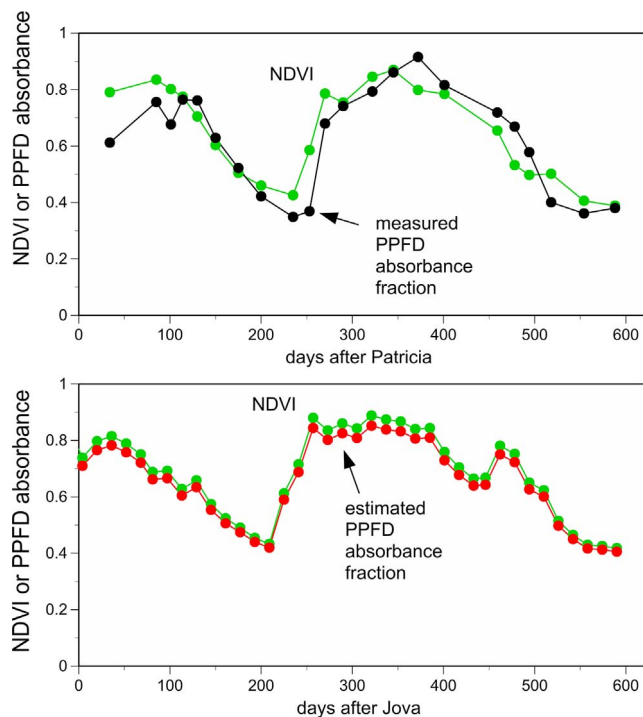


Fig. 7. Comparison of NDVI (green symbols) and estimated PPFD absorption (fAPAR) following Hurricanes Patricia (upper panel) and Jova (lower). The PPFD fraction after Hurricane Jova is estimated from the relation following Hurricane Patricia (see Section 3.2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

canopy structure.

Although we argue the integral deviations are clues to the timing and type of responses to the hurricanes, these values should be

considered in the context of their long-term variation. We found that the pattern of a distinct negative deviation occurring immediately after each storm, followed by a positive and extended deviation happened only after these two events in our MODIS record. In both hurricanes, the satellite-apparent structure indicates a short-term loss followed by a longer-term gain.

4.2. Ground and remotely sensed radiation

Hurricane Patricia altered the dynamics of some components of the PPFD balance relative to the expected pattern. First, there was an increase in light penetrance, probably relatively short-lived (e.g., Sherman et al., 2001), and a shift in the seasonality of pattern (Fig. 5). The penetrance rises due to lack of intercepting surfaces (both non-photosynthetic and leaves, e.g., Parker et al., 2005) the ground reflectance increases due to the reflectivity of dry soil and the lack of forest floor litter (Idso et al., 1975). We suspect a similar, although less marked, series of effects occurred following Hurricane Jova, but we have no basis for evaluating these changes.

In the 21 months after Jova the gap fraction declined from 0.223 to 0.375; in the same interval after Hurricane Patricia measured openness fell and then rose somewhat – it was essentially unchanged. Yet the NDVI following both events exceeded the base case, and, following Patricia, closely tracked the ground-measured fAPAR. Such reflectances are consistent with the high cover of the base case. The outer canopy was relatively flat in the base case but following the storm it became more complex (i.e., the rugosity increased). It is likely that the high NDVI under reduced cover is related to the geometry of post-storm leaf display and its appearance to remote sensors since the increase in lateral surfaces suggested by the higher rugosity may have been sensed as higher cover from a sensor viewing off-nadir.

The positive relation between PPFD absorption (fAPAR) and NDVI such as the one we found for the period following Hurricane Patricia has been previously reported (e.g., Goward and Huemmrich, 1992) – our relation is very similar to that of Sims et al. (2006). We used this

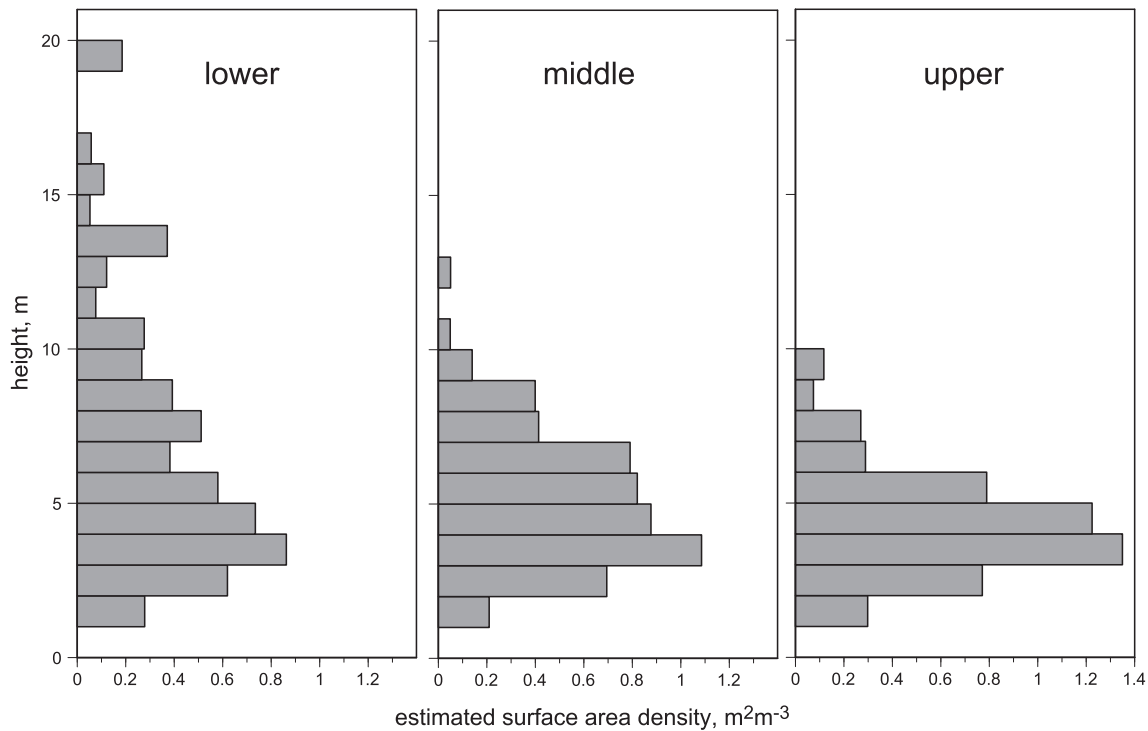


Fig. 8. Foliage-height profiles of canopies in the three elevation zones in 2001, well before the hurricanes.

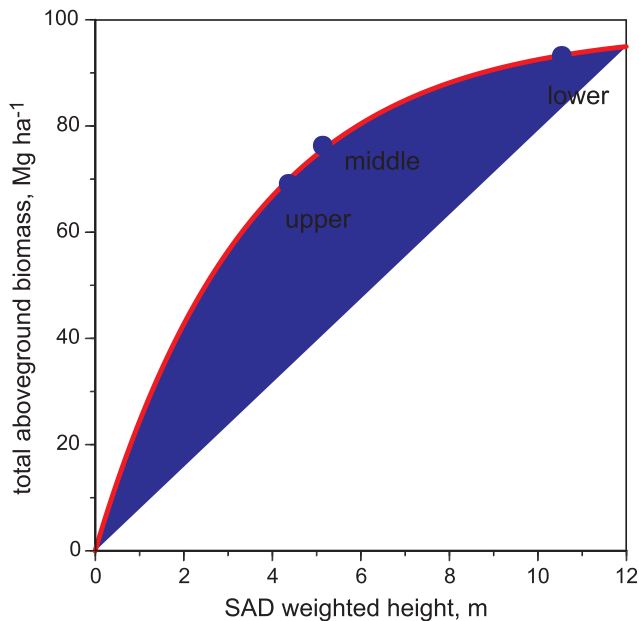


Fig. 9. Relation used to estimate total aboveground biomass from canopy height metrics, derived from observations made preceding the hurricanes (see Fig. 7).

relation to predict the fAPAR following Hurricane Jova. However, the slight lag of fAPAR with respect to NDVI is unexpected. The uncertainty in the NDVI values might help explain this apparent lag. For example, the reported 16-day NDVI is a composite of the best pixels in the interval (Solano et al., 2010). The index values and their dates may have uncertainty in this period. Moreover, the NDVI values we used are highly variable in the transition season.

In our study, our estimated biomass values (PCL-derived biomass), canopy rugosity and gap fraction were uncorrelated with NDVI ($p > 0.05$, $df = 4$) over the six times measured. NDVI and similar indices are poor predictors of biomass for systems with high LAI (e.g.,

Huete et al., 2002) and do not sense aspects of vegetation vertical structure (Steininger, 2000). Functional aspects such as fAPAR are related much more closely to NDVI (e.g., Goward and Huemmrich, 1992). However, it is unlikely that primary production immediately after the storm can be predicted from fAPAR.

4.3. Canopy damage characteristics

Topographic variation in canopy damage may be related to the nature of the hurricane winds (Section 2.2). In both storms the wind direction after landfall was from the north and east - the south-facing slopes were relatively protected. This is consistent with the observed differences in damage (Figs. 10 and 11). Variations in the storm energies may have caused qualitatively different canopy structure damage. The relatively weaker Jova event appeared to remove material from all vertical layers, as if in proportion to the amount displayed. The stronger Patricia storm removed material predominantly from the top layers - the shift of the peak SAD toward the ground may reflect the downing of branches and stems.

4.4. Limitations of the study and additional observations

The current case study was fortunate to have previous measurements, some additional new observations and a means to assemble them. However, the observational basis of the two hurricanes was not uniform. For Hurricane Jova we could not acquire direct ground observations of impacts immediately after the event. However, after Patricia we promptly began a series of canopy structure and PPFD environment measurements. We used information from the post-Patricia recovery not only to infer the pattern and intensity of Jova damage but also to compare the two storms. Inevitably, such an approach has limitations. First, the two hurricanes themselves were quantitatively different in strength and may have differed in other respects. Next, the storms were separated by only 4 years - some overlap in effects is possible. Ongoing recovery from the first hurricane (Jova) could make it hard to infer the specific effects of the second (Patricia). Finally, some of the effects are not strictly proportional to the causative agents - there

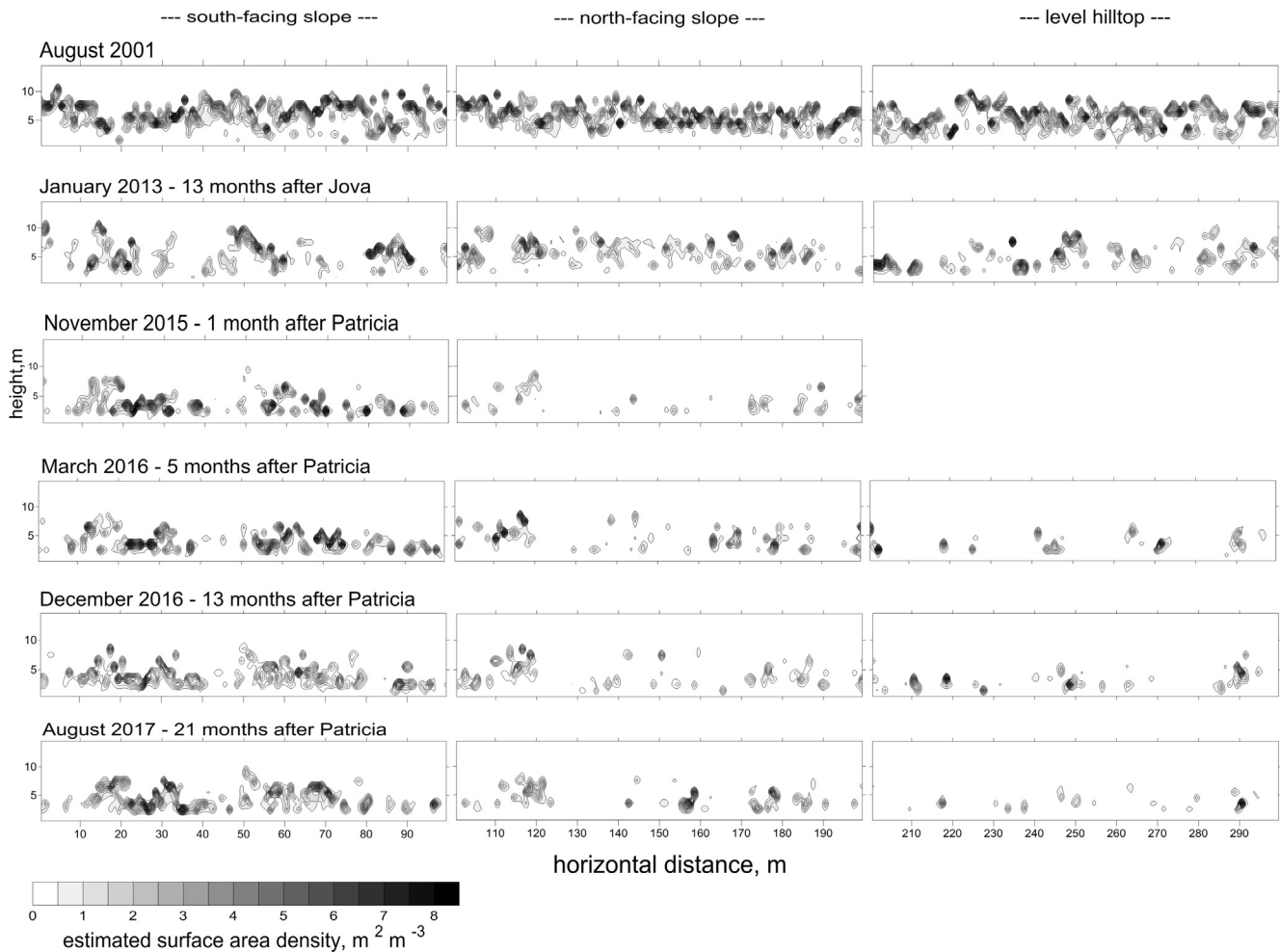


Fig. 10. Changes in canopy vertical-horizontal structure on the Chachalaca trail before and after Hurricanes Jova and Patricia in three successive 100 m sections. The sections of the trail differ in aspect. The vertical axis is exaggerated by 43% for clarity.

are differences in susceptibility among ecosystem parts (Lugo, 2008). For example, canopy woody structure and leaf area both include components which are easily dislodged (such as dead suspended material, e.g., Maass et al., 2002b), components that require more force to loosen (live leaves, small branches) or others that are very resistant (large branches, whole stems). Also there are differences among species that cause differential resistance to wind damage (Paz, this issue).

An additional complication for the attribution of effects is the nonlinear character of the spectral indices –both EVI and NDVI are arithmetically bounded (e.g., Liang, 2004), whereas the impact measures are not similarly constrained. We treated the recovery rates of biomass and canopy components as linear but that trajectory may well combine processes of different rates, for example, quick recovery of leaf area but a much slower recovery of supporting woody tissue. Likely these rates will be strongly influenced by the occurrence of precipitation falling during the post-hurricane wet-to-dry transition period (Bhasker et al., this issue; Martínez-Yrizar et al., this issue). We attributed the positive integral deviation in NDVI following the storms to foliar dynamics, but reflectance from bare branches and forest floor litter could have also contributed to those changes. We also assumed that the recovery processes from the two hurricanes was qualitatively similar –but the large differences in impact energy between them may have induced different trajectories. Recovery may have been more rapid after the less intense Hurricane Jova.

Even a single-event observation can be important for understanding the behavior of the ecosystem and for theory development (Altwegg et al., 2017). However, for a clear attribution of hurricane effects, it

would be optimal to have continuous observations of ecosystem characteristics in a multiyear framework that captures seasonal effects. This is rarely practical, especially at the scale of spatial representativeness and temporal frequency required. One must generally rely on existing relevant measurements and proxy observations to assemble a realistic picture. Of course, more data of the sort we report would have been useful but observations on additional processes would also be informative. For example, 1) what were the components of early regeneration (vines, sprouts and normal flushing, e.g. Miller, 1999) – this could indicate which responses were temporary and which might persist, 2) how much of the extra precipitation was retained in the soil and how did that change (a model would be useful)? – this could inform the understanding of the persistence of the positive integral deviation, 3) how did the character of the forest floor (bare soil, litter) change? – this might clarify the soil reflectance contribution to the NDVI and 4) what were the components of the immediate litterfall (non-senescent green leaves vs. dead leaves and non-leaf material)? – such information could help to understand the different qualitative effects of the hurricanes.

4.5. Implications for forest recovery

The two hurricanes produced qualitatively similar but quantitatively different immediate and delayed effects in the tropical dry forest of Chamela in Mexico. For both hurricanes, first Jova and then Patricia, high winds on landfall caused a distinct but very short-term decline in canopy greenness (NDVI) very likely related to the unprecedented high rates of hurricane-induced litterfall (Martínez-Yrizar et al., this issue).

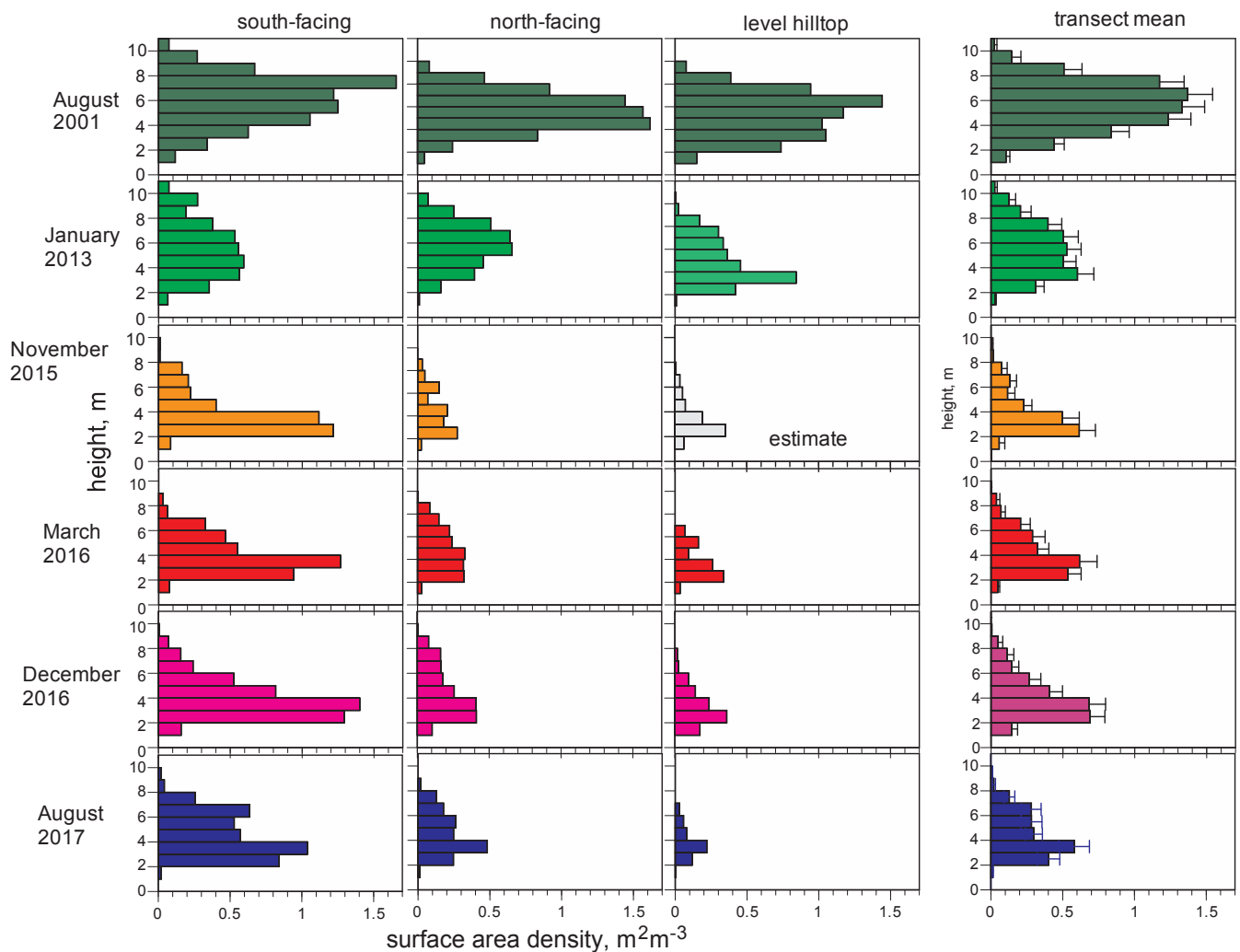


Fig. 11. Foliage-height profiles of the canopy along the Chachalaca trail at 5 times (rows) before and after Hurricanes Jova and Patricia. The first three columns give the profiles for each 100 m trail section – the last column is the mean (with standard errors) of those. The value for the third, level section in November 2015, was estimated (see Section 2.6).

Canopy structure was considerably altered by both hurricanes, including loss of leaf area and persistent vertical and horizontal woody components. Furthermore, the accompanying unusually high and aseasional rainfall (3.7 and 4.2 times the monthly normal) after the passage of the hurricanes produced a sustained increase in canopy NDVI relative to the expected seasonal pattern, lasting for about 8 (Jova) and 6 (Patricia) months.

The steep decline in the NDVI integral deviation right after both Jova and Patricia hurricanes likely relates to the loss of canopy leaves and structure from wind effects. However, the later steep increase in these measures sustained over many months is probably linked to the initial canopy recovery driven by the extra precipitation, which increased soil moisture above normal for this season, even with the losses in runoff (Maass et al., this issue). Therefore, following the immediate wind-driven loss of canopy cover and structure the primary visible change is the production of new foliage, much from vines and sprouts, driven by the aseasional extra rainfall, which provides the basis for sustained production and greenness. Because it is displayed over the ragged surface of the damaged canopy, such new leaf area may be more apparent to remote sensing instruments. We found a slow recovery of canopy structural features (height and surface density) in the 21 months following Hurricane Patricia. We suspect that subsequent changes will include the production of additional foliage, especially of trees, with rapid recovery in cover, leaf area index and litter production (see Martínez-Yrizar et al., this issue). Recovery of the persistent canopy

features may require decades if the assumptions of linear rates apply –perhaps even much longer.

In both hurricanes, almost all canopy leaf area fell as litter – the time required to recover the source of production is unknown (but see Martínez-Yrizar et al., this issue). However, the recovery of other aspects of canopy structure may be similarly estimated from the post-Patricia series. The post-Patricia biomass recovery rate of $1.83 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ is substantially less than the $7.85 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ($= 11.55 \text{ NPP} - 3.70 \text{ litterfall}$) estimated for base conditions by Martínez-Yrizar et al. (1996). Following Patricia the weighted height (H_{wtd}) increased by 0.146 m yr^{-1} , the outer canopy height (H_{loc}) by 0.139 m yr^{-1} and the canopy area index (CAI) by $0.735 \text{ m}^2 \text{ m}^{-2} \text{ yr}^{-1}$. If, as in the case of biomass, we apply these rates backward from the first measurement after Jova (see Fig. 13) we can estimate that H_{wtd} was 4.40 m and H_{loc} was 5.71 m immediately after the first event. If we project these rates forward from the onset of Patricia we can estimate the time required to recover the pre-hurricane values: 23.9, 20.4 and 7.4 years for H_{wtd} , H_{loc} and CAI respectively. Using this linear approach, it would require 14.4 years after Hurricane Patricia to recover the original aboveground biomass.

In summary, different aspects of ecosystem structure and function will recover at different time scales. The recovery of greenness occurs rapidly, on the order of weeks to months but canopy cover and production will recover more slowly. The re-establishment of persistent canopy structure and total biomass will likely take decades in the

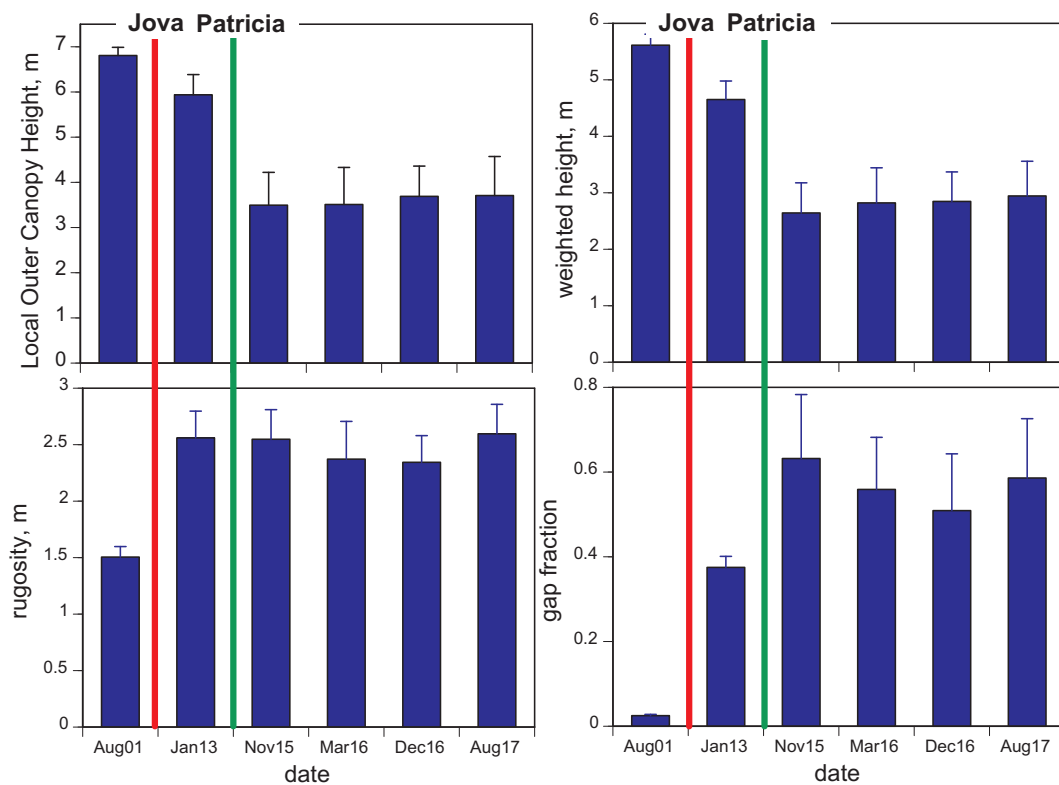


Fig. 12. Summary canopy metrics of the Chachalaca trail transect derived from the PCL measurements made before and after Hurricanes Jova and Patricia.

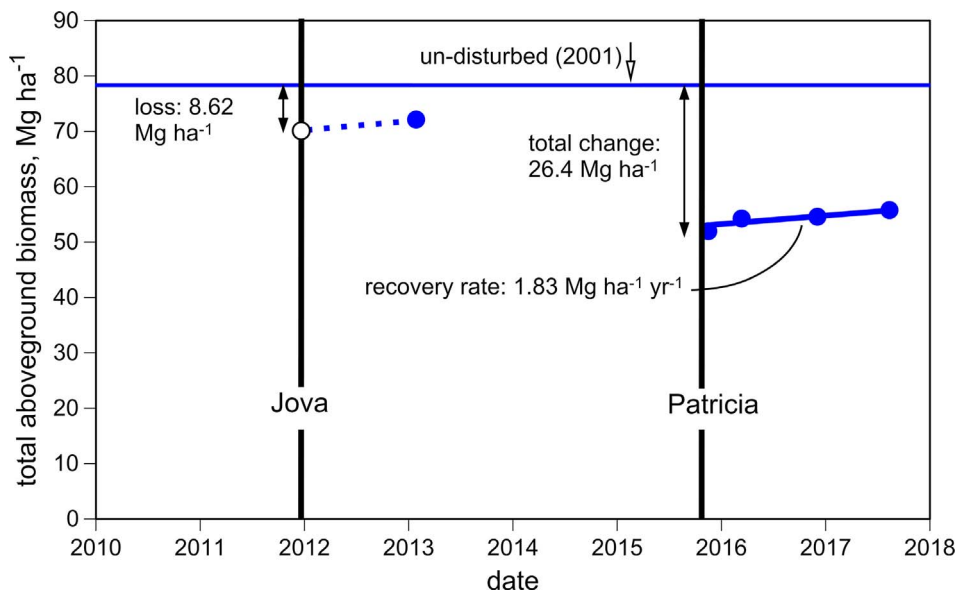


Fig. 13. Graphical depiction of the method for estimating Hurricane Jova biomass loss based on the pattern of recovery from Hurricane Patricia.

absence of other natural (e.g. hurricanes, droughts, and fires) or anthropogenic disturbances (e.g. logging) or management strategies that may alter the forest recovery pathway.

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References

- Altwegg, R., Visser, V., Bailey, L.D., Erni, B., 2017. Learning from single extreme events. *Phil. Trans. R. Soc. B* 372, 20160141. <http://dx.doi.org/10.1098/rstb.2016.0141>.
- Anaya, C.A., Jaramillo, V.J., Martínez-Yrizar, A., García-Oliva, F., 2012. Large rainfall pulses control litter decomposition in a tropical dry forest: evidence from an 8-Year

- study. *Ecosystems* 15, 652–663. <http://dx.doi.org/10.1007/s10021-012-9537z>.
- Bellingham, P.J., Tanner, E.V.J., Rich, P.M., Goodland, T.C.R., 1996. Changes in the light availability below the canopy of a Jamaican montane rainforest after a hurricane. *J. Trop. Ecol.* 12, 699–722.
- Bhaskar, R., Arreola, F., Mora, F., Martínez-Yrizar, A., Martínez-Ramos, M., Balvanera, P., this issue. Does response diversity influence resilience to extreme events in tropical dry secondary forests?
- Bullock, S.H., 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. *Archiv. Meteorol. Geophys. Bioclimat. (B)* 36, 297–316.
- Bullock, S.H., Solís-Magallanes, J.A., 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22, 22–35.
- Bursalem, D.F.R.P., Whitmore, T.C., Brown, G.S., 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *J. Ecol.* 88, 1063–1078.
- Ceballos, G., Szekely, A., García, A., Rodríguez, P., Noguera, F., 1999. Programa de Manejo de la Reserva de la Biosfera Chamela-Cuixmala. Instituto Nacional de Ecología, SEMARNAP, pp. 141.
- National Hurricane Center, 2012. Tropical Cyclone Report - Hurricane Jova (EP102011).
- National Hurricane Center, 2016. Tropical Cyclone Report - Hurricane Patricia (EP202015).
- Chen, J.M., 1996. Optically based methods for measuring seasonal variation in leaf area index of boreal conifer forests. *Agr. For. Meteorol.* 80, 135–163.
- Comita, L.S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C.D., Zimmerman, J.K., 2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *J. Ecol.* 97, 1346–1359.
- Diamond, J.M., Ross, M.S., 2016. Canopy gaps do not help establish pioneer species in a South Florida dry forest. *J. Trop. Ecol.* 32, 107–115. <http://dx.doi.org/10.1017/S0266467416000109>.
- Didan, K., 2015. MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006. NASA EOSDIS Land Processes DAAC. <http://dx.doi.org/10.5067/MODIS/MOD13Q1.006>.
- Fernández, D.S., Fetcher, N., 1991. Changes in light availability following Hurricane Hugo at three elevations in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 23, 393–399.
- Foster, D.R., Knight, D.H., Franklin, J.F., 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1, 497–510. <http://dx.doi.org/10.1007/s100219900046>.
- Frank, D., Reichstein, M., Bahn, M., Thonicke, K., Frank, F., Mahecha, M.D., Smith, P., van der Velde, M., Vicca, S., Babst, F., Beer, Ch., Buchmann, N., Canadell, J.G., Ciais, P., Cramer, W., Ibrom, A., Miglietta, F., Poulter, B., Rammig, A., Seneviratne, S.I., Walz, A., Wattenbach, M., Zavalá, M.A., Zscheischler, J., 2015. Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. *Global Change Biol.* 21, 2861–2880. <http://dx.doi.org/10.1111/gcb.12916>.
- Frolking, S., Palace, M.W., Clark, D.B., Chambers, J.Q., Shugart, H.H., Hurtt, G.C., 2009. Forest disturbance and recovery. A general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure. *J. Geophys. Res.* 114, G00E02. <http://dx.doi.org/10.1029/2008JG000911>.
- Galicia, L., López-Blanco, J., Zarco-Arista, A.E., Filip, V., García-Oliva, F., 1999. The relationship between solar radiation interception and soil water content in a tropical deciduous forest in Mexico. *Catena* 36, 153–164.
- García-Méndez, G., Maass, J.M., Matson, P., Vitousek, P., 1991. Nitrogen transformations and nitrous oxide flux in a tropical deciduous forest in México. *Oecologia* 88, 362–366.
- García-Oliva, F., Ezcurra, E., Galicia, L., 1991. Pattern of rainfall distribution in the Central Pacific Coast of Mexico. *Geografiska Annaler. Series A. Phys. Geogr.* 73, 179–186.
- Gavito, M., Sandoval-Pérez, A. L., del Castillo, K., Cohen-Salgado, D., Colarte-Avilés, M. E., Mora, F., Urquijo-Ramos, C., Santibañez-Rentería, A., Siddique, I., this issue. Resilience of soil nutrient availability and organic matter decomposition to hurricane impact in a tropical dry forest ecosystem.
- Goward, S.N., Huemmrich, K.F., 1992. Vegetation canopy PAR absorbance and the normalized difference vegetation index. An assessment using the SAIL model. *Remote Sens. Environ.* 39, 119–140.
- Hodgson, D., McDonald, J.L., Hosken, D.L., 2015. What do you mean, 'resilient'? *Trends Ecol. Evol.* 30, 503–506.
- Holm, J.A., Van Bloem, S.J., Larocque, G.R., Shugart, H.H., 2017. Shifts in biomass and productivity for a subtropical dry forest in response to simulated elevated hurricane disturbances. *Env. Res. Lett.* 12, 02500. <http://dx.doi.org/10.1088/1748-9326/aa583c>.
- Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., Ferreira, L.G., 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens. Environ.* 83, 195–213.
- Idso, S.B., Jackson, R.D., Reginato, R.J., Kimball, B.A., Nakayama, F.S., 1975. The dependence of bare soil albedo on soil water content. *J. Appl. Meteorol.* 14, 109–113.
- Jaramillo, V.J., Sanford, R.L., 1995. Nutrient cycling in tropical deciduous forests. In: Bullock, S.H., Mooney, H.A., Medina, E. (Eds.), *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, pp. 346–361.
- Jaramillo, V.J., Kauffman, J.B., Rentería-Rodríguez, L., Cummings, D.L., Ellingson, L.J., 2003. Biomass, carbon, and nitrogen pools in Mexican tropical dry forest landscapes. *Ecosystems* 6, 609–629.
- Lefsky, M.A., Cohen, W.B., Harding, D.J., Parker, G.G., Acker, S.A., Gower, S.T., 2002. Lidar remote sensing of above-ground biomass in three biomes. *Global Ecol. Biogeogr.* 11, 393–399.
- Liang, S., 2004. *Quantitative Remote Sensing of Land Surfaces*. John Wiley and Sons, Hoboken, NJ.
- López-Blanco, J., Galicia, L., García-Oliva, F., 1999. Hierarchical analysis of relief features in a small watershed in a tropical deciduous forest ecosystem in Mexico. *Geografía Física e Dinámica Cuaternaria* 22, 33–40.
- Lott, E.J., 1993. Annotated checklist of the vascular flora of the Chamela Bay Region, Jalisco, Mexico. *Occasional Papers California Acad. Sci.* 148, 1–60.
- Lott, E.J., Bullock, S.H., Solís-Magallanes, A., 1987. Floristic diversity and structure of upland and arroyo forest at coastal Jalisco. *Biotropica* 19, 228–235.
- Lugo, A.E., 2008. Visible and invisible effects of hurricanes on forest ecosystems, an international review. *Austr. Ecol.* 33, 368–398.
- Maass, M., Ahedo-Hernández, R., Araiza S., Verduzco A., Martínez-Yrizar A., Jaramillo V., Parker, G., Pascual F., García-Méndez G., Sarukhán J., this issue. Long-term (33 years) rainfall and runoff dynamics in a tropical dry forest ecosystem in western Mexico: management implications under extreme hydrometeorological events.
- Maass, J.M., Vose, J.M., Swank, W.T., Martínez-Yrizar, A., 1995. Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. *For. Ecol. Manage.* 74, 171–180.
- Maass, J.M., Martínez-Yrizar, A., Patiño, P., Sarukhán, J., 2002b. Distribution and annual net accumulation of above-ground dead phytomass and its influence on throughfall quality in a Mexican tropical deciduous forest ecosystem. *J. Trop. Ecol.* 18, 1–15.
- Maass, J.M., Jaramillo, V., Martínez-Yrizar, A., García-Oliva, F., Perez-Jimenez, A., Sarukhán, J., 2002a. Aspectos funcionales del ecosistema de selva baja caducifolia en Chamela, Jalisco. In: Noguera, F.A., Vega, J.H., García-Aldrete, A.N., Quesada, M. (Eds.), *Historia natural de Chamela*. Instituto de Biología, UNAM, México D.F., pp. 525–542.
- Martínez-Ruiz, M., Renton, K., this issue. Habitat heterogeneity facilitates resilience of diurnal raptor communities to hurricane disturbance.
- Martínez-Yrizar, A., Jaramillo, V. J., Maass, M., Búrquez, A., Álvarez-Yépiz, J. C., Parker, G., Araiza, S., Verduzco, A., Sarukhán, J., this issue. Resilience of the Chamela tropical dry forest productivity to hurricanes.
- Martínez-Yrizar, A., Maass, J.M., Perez-Jimenez, J.A., Sarukhán, J., 1996. Net Primary productivity of a tropical deciduous forest ecosystem in western Mexico. *J. Trop. Ecol.* 12, 169–175.
- Martínez-Yrizar, A., Sarukhán, J., 1990. Litterfall patterns in a tropical deciduous forest in Mexico over a five-year period. *J. Trop. Ecol.* 6, 433–444.
- McGroddy, M., Lawrence, D., Schneider, L., Rogan, J., Zager, I., Schmoek, B., 2013. Damage patterns after Hurricane Dean in the southern Yucatán: has human activity resulted in more resilient forests? *For. Ecol. Manage.* 310, 812–820. <http://dx.doi.org/10.1016/j.foreco.2013.09.027>.
- McMahon, S.M., Bebb, D.P., Butt, N., Crockett, M., Kirby, K., Parker, G.G., Riutta, T., Slade, E.M., 2015. Ground based LiDAR demonstrates the legacy of management history to canopy structure and composition across a fragmented temperate woodland. *Forest Ecol. Manage.* 335, 255–260.
- McNulty, S.G., 2002. Hurricane impacts on US forest carbon sequestration. *Environ. Pollut.* 116, S17–S24. [http://dx.doi.org/10.1016/S0269-7491\(01\)00242-1](http://dx.doi.org/10.1016/S0269-7491(01)00242-1).
- Miller, P.M., 1999. Coppice shoot and foliar crown growth after disturbance of a tropical deciduous forest in Mexico. *Forest Ecol. Manage.* 103, 191–201.
- Murphy, P.G., Lugo, A.E., 1995. Dry forest of Central America and the Caribbean. In: Bullock, S.H., Mooney, W., Medina, E. (Eds.), *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, pp. 9–34.
- Negrón-Juárez, R., Baker, D.B., Zeng, H., Henke, T.K., Chambers, J.Q., 2010. Assessing hurricane-induced tree mortality in U.S. Gulf Coast forest ecosystems. *J. Geoph. Res.* 115. <http://dx.doi.org/10.1029/2009JG001221>.
- New, M., Hulme, M., Jones, P.D., 1999. Representing twentieth century space-time climate variability. Part 1, development of a 1961–90 mean monthly terrestrial climatology. *J. Clim.* 12, 829–856.
- ORNL, D.A.A.C., 2017. MODIS Collection 6 Land Products Global Subsetting and Visualization Tool. ORNL DAAC, Oak Ridge, Tennessee, USA. <http://dx.doi.org/10.3334/ORNLDAAC/1379>.
- Parker, G.G., Harding, D.J., Berger, M., 2004. A portable LIDAR system for rapid determination of forest canopy structure. *J. Appl. Ecol.* 41, 755–767.
- Parker, G.G., Tinoco-Ojanguren, C., Martínez-Yrizar, A., Maass, M., 2005. Seasonal balance and vertical pattern of photosynthetically active radiation within canopies of a tropical dry deciduous forest ecosystem in México. *J. Trop. Ecol.* 21, 283–295.
- Paz, H., this issue. Using functional traits to understand resistance and resilience of trees to hurricanes: The case for a tropical dry forest in the Pacific coast of Mexico.
- Rentería, L., Jaramillo, V., 2011. Rainfall drives leaf traits and leaf nutrient resorption in a tropical dry forest in Mexico. *Oecologia* 165, 201–211.
- SAS Institute, 2002–2009. SAS 9.2. SAS Institute Inc., Cary NC, USA.
- Segura, G., Balvanera, P., Duran, E., Perez, A., 2003. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. *Plant Ecol.* 169, 259–271.
- Sherman, R.E., Fahey, T.J., Martinez, P., 2001. Hurricane impacts on a mangrove forest in the Dominican Republic, damage patterns and early recovery. *Biotropica* 33, 393–408.
- Shiels, A.B., Gonzalez, G., 2014. Understanding the key mechanisms of tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects. *For. Ecol. Manage.* 332, 1–10. <http://dx.doi.org/10.1016/j.foreco.2014.04.024>.
- Sims, D.A., Luo, H., Hastings, S., Oechel, W.C., Rahman, A.F., Gamon, J.A., 2006. Parallel adjustments in vegetation greenness and ecosystem CO₂ exchange in response to drought in a southern California chaparral ecosystem. *Remote Sens. Environ.* 103, 289–303.
- Solano, R., Didan, K., Jacobsen, A., Huete, A., 2010. MODIS vegetation indices (MOD13) C5 – User's Guide. University of Arizona, Tucson, pp. 38.
- Stark, S.C., Enquist, B.J., Saleska, S.R., Leitold, V., Schietti, J.S., Longo, M., Alves, L.F., de Camargo, P.B., de Oliveira, R.C., 2015. Linking canopy leaf area and light environments with tree size distributions to explain Amazon forest demography. *Ecol. Lett.* 18, 636–645. <http://dx.doi.org/10.1111/ele.12440>.

- Steininger, M.K., 2000. Satellite estimation of tropical secondary forest above-ground biomass: Data from Brazil and Bolivia. *Int. J. Remote Sens.* 21, 1139–1157.
- Turner, M.G., Dale, V.H., 1998. Comparing large infrequent disturbances, what have we learned? *Ecosystems* 1, 493–496.
- Turton, S.M., 1992. Understory light environments in a north-east Australian rain forest before and after a tropical cyclone. *J. Trop. Ecol.* 8, 241–262.
- Van Bloem, S.J., Murphy, P.G., Lugo, A.E., Rivera Costa, M., Ruiz Bernard, I., Molina Colon, S., Canals Mora, M., 2005. The Influence of hurricane Winds on Caribbean dry forest structure and nutrient pool. *Biotropica* 37, 571–583.
- Wang, F., D'Sa, E.J., 2010. Potential of MODIS EVI in Identifying Hurricane Disturbance to Coastal Vegetation in the Northern Gulf of Mexico. *Remote Sens.* 2, 1–18. <http://dx.doi.org/10.3390/rs2010001>.
- Webb, L.J., 1958. Cyclones as an ecological factor in tropical lowland rainforest, north Queensland. *Aust. J. Bot.* 6, 220–230.
- Wulder, M.A., White, J.C., Nelson, R.F., Næsset, E., Ørka, H.O., Coops, N.C., Hilker, T., Bater, C.W., Gobakken, T., 2012. Lidar sampling for large-area forest characterization, a review. *Remote Sens. Environ.* 121, 196–209.
- Zimmerman, J.K., Willig, M.R., Walker, L.R., Silver, W.L., 1996. Introduction, disturbance and Caribbean ecosystems. *Biotropica* 28, 414–423.
- Zolkos, S.G.M., Goetz, S.J., Dubayah, R., 2013. A meta-analysis of terrestrial aboveground biomass estimation using lidar remote sensing. *Remote Sens. Environ.* 128, 289–298.