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RESEARCH ARTICLE

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Globally consistent impact of tropical cyclones on the structure of tropical and subtropical forests

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Abstract

1. Tropical cyclones (TCs) are large-scale disturbances that regularly impact tropical forests. Although long-term impacts of TCs on forest structure have been proposed, a global test of the relationship between forest structure and TC frequency and intensity is lacking. We test on a pantropical scale whether TCs shape the structure of tropical and subtropical forests in the long term.
2. We compiled forest structural features (stem density, basal area, mean canopy height and maximum tree size) for plants ≥10 cm in diameter at breast height from published forest inventory data (438 plots ≥0.1 ha, pooled into 250 1 × 1-degree grid cells) located in dry and humid forests. We computed maps of cyclone frequency and energy released by cyclones per unit area (power dissipation index, PDI) using a high-resolution historical database of TCs trajectories and intensities. We then tested the relationship between PDI and forest structural features using multivariate linear models, controlling for climate (mean annual temperature and water availability) and human disturbance (human foot print).
3. Forests subject to frequent cyclones (at least one TCs per decade) and high PDI exhibited higher stem density and basal area, and lower canopy heights. However, the relationships between PDI and basal area or canopy height were partially masked by lower water availability and higher human foot print in tropical dry forests.
4. *Synthesis*. Our results provide the first evidence that tropical cyclones have a long-term impact on the structure of tropical and subtropical forests in a globally consistent way. The strong relationship between power dissipation index and stem density suggests that frequent and intense tropical cyclones reduce canopy cover

through defoliation and tree mortality, encouraging higher regeneration and turnover of biomass. The projected increase in intensity and poleward extension of tropical cyclones due to anthropogenic climate change may therefore have important and lasting impacts on the structure and dynamics of forests in the future.

KEYWORDS

basal area, canopy height, hurricanes, power dissipation index, stem density, tropical dry forest, tropical humid forest, typhoons

1 | INTRODUCTION

Tropical cyclones (TCs), also referred to as hurricanes in the Atlantic and Northeast Pacific and typhoons in the Northwest Pacific, are unavoidable, large-scale disturbances (Everham & Brokaw, 1996; Turner, Baker, Peterson, & Peet, 1998; Turner & Dale, 1998; Whigham, Dickinson, & Brokaw, 1999). Disturbances are "relatively discrete events in time that disrupt ecosystem, community, or population structure and change resource or substrate availability or the physical environment" (White & Pickett, 1985). Due to their large footprints (TCs signatures extend over hundreds of kilometres and their tracks cover thousands of km, see Chan & Chan, 2015; Knaff, Longmore, & Molenar, 2014) and high intensity (sustained wind speeds of up to 300 km/hr), TCs can cause extensive damages to natural ecosystems and human societies (Costanza et al., 2008; Lugo, 2008; Yih, Boucher, Vandermeer, & Zamora, 1991). This was recently highlighted by the devastating impacts of Cyclone Winston (2016), Hurricane Irma (2017) and Typhoon Haiyan (2013), some of the most intensive systems ever recorded (Le Page, 2016).

The effects of disturbances on the composition, structure and functioning of ecosystems depend on the disturbance regime, which is for TCs mainly characterized by their frequency, size and intensity (Turner et al., 1998; Whelan, 1995; White & Jentsch, 2001; White & Pickett, 1985). The disturbance regime exerted by TCs is highly spatially heterogeneous. For example, forests in the Northwest Pacific and Northwest Atlantic experience frequent, intense and large TCs while forests in South America and Africa experience few TCs (Chan & Chan, 2015; Schreck, Knapp, & Kossin, 2014). Therefore, on a pantropical scale forests may experience TC disturbance regimes ranging from infrequent TCs to frequent and intense TCs (Figure 1).

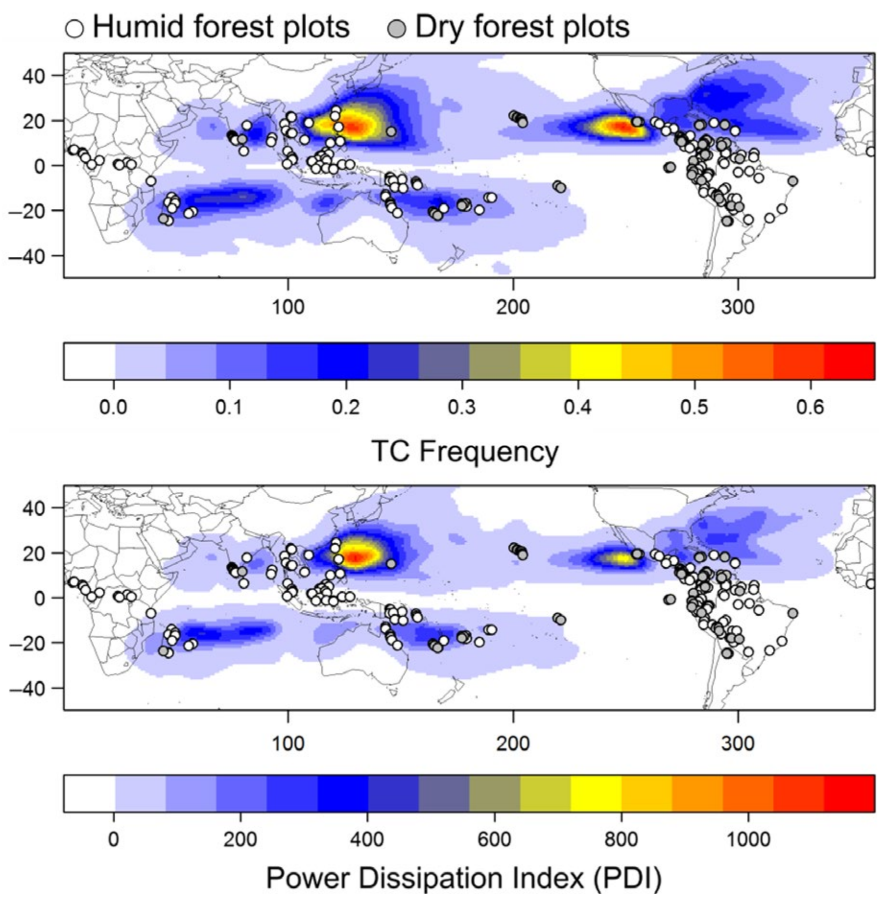

FIGURE 1 Global distribution of the frequency and energy released (power dissipation index) by tropical cyclones, and locations of forest structure datasets [Colour figure can be viewed at wileyonlinelibrary.com]

On a landscape scale, the TC impacts vary with topographical exposure and other abiotic and biotic factors (e.g., Basnet, Likens, Scatena, & Lugo, 1992; Boose, Serrano, & Foster, 2004; Everham & Brokaw, 1996; Metcalfe, Bradford, & Ford, 2008; Turton, 2008; Webb, Seamon, & Fa'aumu, 2011). However, in regions where TCs are frequent, successive TCs with different trajectories and wind directions should in the long term affect the entire landscape (Turner, Gardner, & O'Neill, 2001).

TCs can considerably impact the structure of forests (Everham & Brokaw, 1996; Turner, Dale, & Everham, 1997; Whigham et al., 1999). Visible short- to medium-term effects (Lugo, 2008) include direct damage to trees, ranging from defoliation to snapped and uprooted trunks, and have been widely reported (Basnet et al., 1992; Brokaw & Grear, 1991; Curran, Gersbach, Edwards, & Krockenberger, 2008; Everham & Brokaw, 1996; Franklin, Drake, McConkey, Tonga, & Smith, 2004; Metcalfe et al., 2008; Turton, 2008; Zimmerman et al., 1994). The gaps and defoliation generate space and allow more light penetration on the forest floor, enhancing regeneration (e.g., Bellingham, Tanner, & Healey, 1995; Turner et al., 1998; Uriarte et al., 2004; Whitmore, 1974).

Because TCs tend to disproportionally affect big trees and encourage regeneration (Beard et al., 2005; Everham & Brokaw, 1996; Franklin, 2007; Hjerpe, Hedenas, & Elmqvist, 2001; Murphy, Metcalfe, Bradford, & Ford, 2014; Murphy et al., 2008; Roth, 1992), forests affected by frequent cyclones would be expected to have lower canopies and higher stem densities. Comparative regional studies support these expectations for Madagascar vs. African rainforests (De Gouvenain & Silander, 2003), New Caledonia vs. other Southwest Pacific humid forests (Ibanez et al., 2017), Caribbean vs. Neotropical dry forests (Quigley & Platt, 2003; Van Bloem, Murphy, & Lugo, 2007). Furthermore, stem density increased with TC frequency in lowland rainforests of five South Pacific archipelagos (Keppel et al., 2010), and was higher in Neotropical dry forests that experienced TCs in the last 25 years compared to regions with no TCs (Gillespie, Zutta, Early, & Saatchi, 2006). However, a pantropical test for these invisible, medium- to long-term effects (Lugo, 2008) on forest structure is still lacking.

The availability of high-resolution historical databases of TCs trajectories and intensities such as the International Best Track Archive for Climate Stewardship (IBTrACS; Knapp, Kruk, Levinson, Diamond, & Neumann, 2010) allows to objectively quantify the cyclone regime at any location (e.g., Schreck et al., 2014). The frequency or the intensity of TCs (i.e., the maximum sustained wind speed) is often used to estimate the level of disturbance induced by TCs in a given area. However, it has been suggested that this level of disturbance (or the destructiveness) is better described by the energy transferred by TCs to the land surface, as this parameter combines the frequency, intensity, size and translation speed of TCs (Camargo & Sobel, 2005; Emanuel, 2005).

In this study, we test on a pantropical scale the long-term, invisible effects (sensu Lugo, 2008) of TCs on the structure of tropical forests. We test it by analysing the effects of the frequency and intensity of TCs on structural features of forests (stem density, basal area and canopy height), relative to other climatic variables (mean annual temperature [MAT] and water availability) and human disturbances (human foot print index) that are known to affect forest structure (e.g., Klein, Randin, & Körner, 2015; Moles et al., 2009; Tao, Guo, Li, Wang, & Fang, 2016; Zhang, Nielsen, Mao, Chen, & Svenning, 2016). We hypothesize that TC are an important disturbance that has long-term effects on the structure of tropical forests and that, therefore, areas exposed to frequent and intense TCs would exhibit higher stem densities and lower canopy heights. Our findings are highly relevant to understanding how forecasted changes in the behaviour of TCs (Christensen et al., 2013; Walsh et al., 2016) may impact forest ecosystems.

2 | MATERIALS AND METHODS

2.1 | Structural features

We compiled the location, stem density (number of stems per ha), basal area (the total cross section area in m^2/ha, which is a good proxy of above-ground biomass; e.g., Slik et al., 2010), maximum size (maximum DBH, diameter at breast height, cm), mean canopy height (m) and maximum height for plants with stem diameter ≥10 cm at ~1.3 m above the base (DBH) from published inventories for plots ≥0.1 ha in size (Ibanez et al., 2018). Relevant literature was identified using key word searches in ISI Web of Science (https://webofknowledge.com/) and Google Scholar (http://scholar.google.com/). Our final dataset was derived from 88 scientific papers published between 1983 and 2017. Montane forest plots (as defined by authors of source data, i.e., "pre-montane," "lower-montane," "montane" and "upper-montane") were not considered in the analysis (Aiba and Kitayama, 1999; Clark et al., 2015, Culmsee et al., 2011; Davidar, Mohandass, & Vijayan, 2007; Noumi, 2013, Rakotomalaza and Messmer, 1999, Yamada, 1975). We also only considered plots where authors did not report evidence of recent natural (e.g., TCs) or anthropogenic disturbances (e.g., removal of trees). When canopy height was reported with lower and higher bounds (e.g., 20–30 m), we used the mean value (e.g., 25 m).

2.2 | Cyclones

The frequency and energy released by TCs were computed over the 1981–2016 period from the IBTrACs database, an exhaustive and global database (https://www.ncdc.noaa.gov/ibtracs/, see Knapp et al., 2010). We assumed these values, derived from a 35-year period, to be representative of the relative TC regime in different regions over the Holocene on a global scale. Although some geomorphological records in TC-prone regions show centennial to millennial variations in local TC frequency and intensity during the Holocene, these variation are pseudo-cyclic and do not indicate long-term trends (e.g., Burn & Palmer, 2015; Haig, Nott, & Reichart, 2014; Nott & Forsyth, 2012; Toomey, Donnelly, & Woodruff, 2013). Instead, global patterns of TCs across different regions vary less on a centennial scale but respond more strongly to major changes in global climate over longer time-scales, such as the Pliocene glaciations (e.g., Yoo, Galewsky, Camargo, Korty, & Zamora, 2016).

The IBTrACs database provides information on the position, maximum sustained wind speed and translation speed (an indicator of the duration of disturbance impact, as slower moving cyclones imply longer presence of damaging winds) of each inventoried cyclone at 6-hr intervals. We used these data to calculate the average frequency and energy released by TCs was computed as a proxy of the level of TC disturbance.

For each grid cell with a spatial resolution of 1° latitude × 1° longitude (≈12,345 km^2 at the equator, Figure 1), the energy released by TCs was computed as the power dissipated by friction in the surface layer (Emanuel, 2005) following Menkes et al. (2016) and Vincent et al. (2012). At each point, the maximum 10-min sustained wind speeds at 10 m above the ground (V) was extracted from the database. Only events reaching V > 17 m/s at some point were considered, i.e., tropical storms and category one to five TCs according to the Saffir–Simpson Hurricane Scale (Simpson, 1974). Following Vincent et al. (2012), the spatial pattern of each TC at each time step was computed using the Willoughby, Darling, and Rahn (2006) idealized vortex. We then computed the power dissipation index (PDI) as the integration over the entire lifetime (τ) and spatial extent (r_0) of TCs as follows:

$$\mathrm{PDI} = 2\pi \int_0^{\tau} \int_0^{r_0} \alpha |V|^3 r dr$$

where α ($\alpha = C_D\rho$ with C_D being the surface drag coefficient and ρ the surface air density) is considered a constant (see Emanuel, 2005). The PDI was then integrated over each 1° latitude × 1° longitude grid cells and averaged to get the average yearly PDI. As expected, TC frequency and PDI were strongly correlated (see Figure S1.1).

2.3 | Bioclimatic variables

Plots were classified as dry or humid forest plots following authors' classifications, with tropical dry forests being identified by the common occurrence of drought-deciduous canopy species. For each plot, we extracted the corresponding TC frequency and energy released by TCs (PDI). We also computed the MAT, mean annual precipitation (MAP), annual potential transpiration (PET) and a water availability index as MAP-PET. MAP and MAT where extracted from the WorldClim 2.0 database (http://www.worldclim.org/version2, Fick & Hijmans, 2017) and PET from the CGIAR-CSI database (http://www.cgiar-csi.org/, Trabucco & Zomer, 2009).

2.4 | Human disturbances

Human activities have had a major impact on forests and may affect forest structure directly, e.g., by cutting trees for wood (Crowther et al., 2015; Hansen et al., 2013), or indirectly, e.g., by edge effects related to fragmentation (Laurance, 1997). To take into account the effects of these disturbances, we extracted the human foot print index (HFP, Human Footprint 2009, http://wcshumanfootprint.org/, Venter et al., 2016), as a proxy of potential human disturbances. This index measures the cumulative impact of direct pressures on natural ecosystems from human activities and includes the extent of built environments, crop land and pasture land, the human population density, the night-lights and the circulation ways (railways, roads and navigable waterways).

2.5 | Analysis

All analyses were performed using R.3.3.0 (R Core Team, 2016). All explanatory variables (except TC frequency and PDI) were extracted on 10-min (~340 km^2) spatial resolution maps. To avoid pseudo-replication, we averaged structural and climatic features within 1 × 1 degree grid cells (i.e., the spatial resolution of the PDI maps) and forest type (dry and humid forests). We used a total of 438 plots (355 in humid forests, 83 in dry forests) that were pooled into 250 grid cells (203 in humid forests, 47 in dry forests, Figure 1 and Figure S1.2). Multicollinearity was <0.5 (Spearman's rho) for all explanatory variables (Table S1.1).

We first tested whether structural features differed between areas experiencing low- (freq. <0.01 TC/year, i.e., less than one TC per century is expected based on the 35-year IBTrACs dataset), medium- (0.01 ≥ freq. < 0.1 TC/year, i.e., 1–10 TCs per century) or high- (freq. ≥0.1 TC/year, i.e., at least one TC per decade) TC frequency. This was done separately for dry and humid forests (see distribution of TC frequency Figure S1.1). The significance of the differences was tested using one-way pairwise Wilcoxon rank sum tests with corrections for multiple testing (Holm's correction).

We used multivariate linear regressions to test the relative importance of PDI and other relevant parameters; MAT, water availability (MAP-PET) and human disturbances (HFP). Response variables describing the structure of forests were log-transformed to increase normality (Figure S1.3). Because basal area and maximum size, and canopy height and maximum height, were highly linearly correlated for both forest types, we focussed on three relatively independent structural variables: stem density, basal area and canopy height (Figure S1.4). We used the *MuMIn* R package (Bartoń, 2016) and the *dredge* function to generate different sets of models representing all possible combinations and subsets of explanatory variables. We then selected the best models based on the Akaike information criterion (ΔAIC <2 from the best models, Bunnefeld & Phillimore, 2012). Explanatory variables were centred and scaled before fitting models to allow a fair comparison of their respective effects.

3 | RESULTS

Across the tropics and in both forest types, forests located in areas experiencing high TC frequency (>1 per decade) exhibited higher

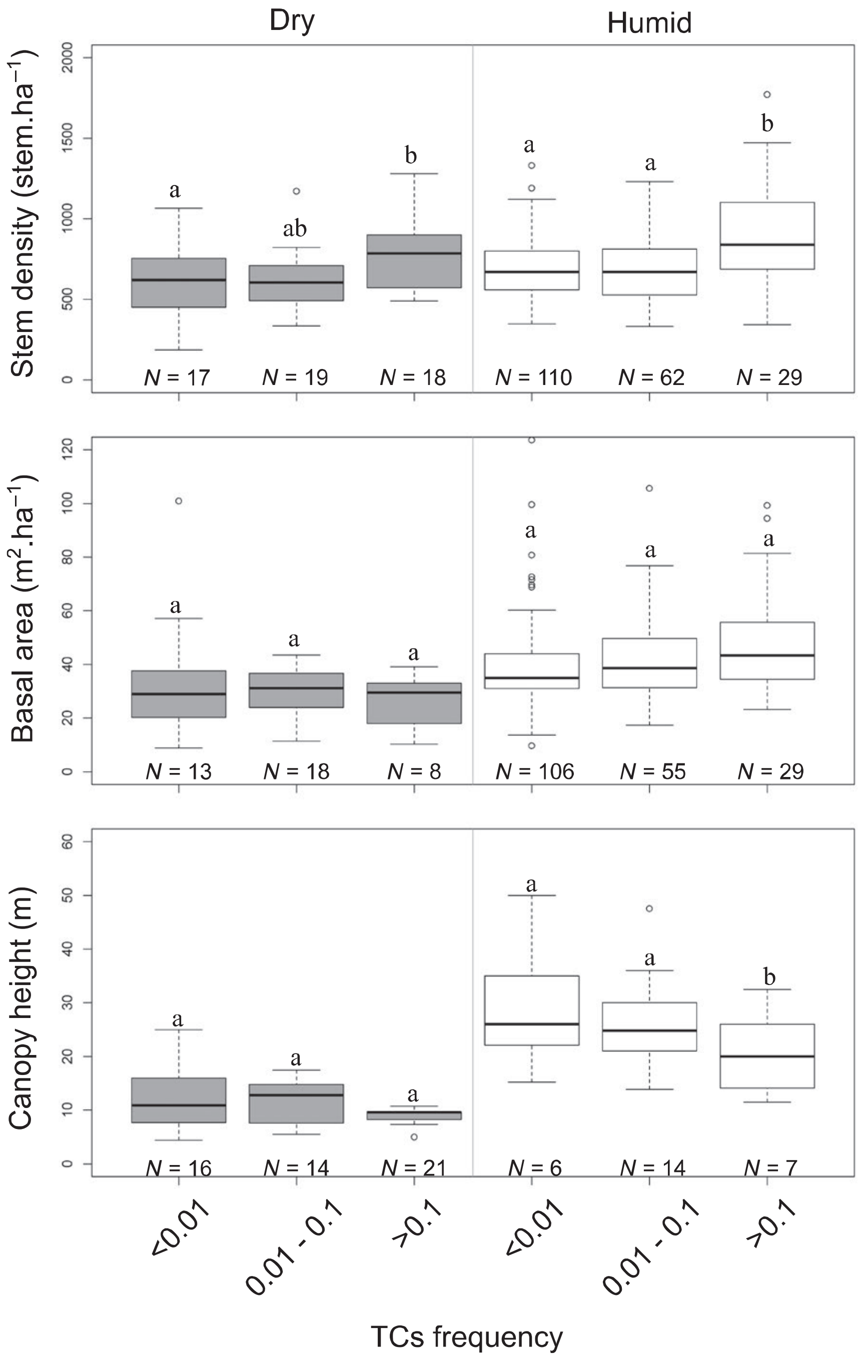

FIGURE 2 Comparison of structural features in dry and humid forests with different tropical cyclone (TC) frequencies (<0.01 = low frequency, less than one TC per century, 0.01–0.1 = medium frequency, at least one TC per century and >0.1 = high frequency, at least one TC per decade). Letters above groups indicate significant differences, i.e., forest classes sharing a letter are not significantly different (p > 0.05) using a pairwise Wilcoxon rank sum test

stem densities (Figure 2). The stem density in these regions was on average 798 ± 253 stems per ha in dry forests and 888 ± 340 stems per ha in humid forests, compared to 643 ± 195 stems per ha and 703 ± 194 stems per ha, respectively, in regions experiencing less than one TC per decade. In contrast, basal area did not differ significantly between the three cyclone frequency classes (low, medium and high) for both dry and humid forests. The canopy of humid forests (27 ± 8 m) was on average more than twice as high as in dry forests (12 ± 5 m). Humid forests exposed to frequent TCs were also significantly shorter (20 ± 6 m) than those exposed to low- and medium-TC frequencies (27 ± 8 m).

The amount of energy released by TCs (the so-called, PDI) was positively correlated to stem density and basal area (Table 1). PDI together with MAT explained 14% of stem density variance, but had no significant effect basal area (Table 1 and Figure 3). Canopy height had a significant positive relationship with water availability and a significant negative relationship with human foot print. Water availability was significantly lower (−177.7 ± 626.65 mm vs. 700.6 ± 1,030.1 mm; Wilcoxon rank test p < 0.001, Figure S1.4) and the human footprint significantly higher (12.1 ± 9.1 vs. 8.0 ± 6.4; Wilcoxon rank test p < 0.01, Figure S1.5) in dry forests compared to humid forests.

TABLE 1 Best multivariate linear regressions explaining structural features in tropical forests overall and in humid and dry forest separately

				Coefficient estimate and significance				Model performance	
Forest types	Structural features	*N*	Model ranks	PDI	MAT	MAP-PET	HFP	R^2	AICc
Both	Stem density	245	1	0.10***	−0.08***			0.14	119.24
			2	0.10***	−0.08***		0.01	0.14	121.24
	Basal area	229	1		−0.09***	0.05†		0.06	191.88
			2		−0.08**			0.05	192.92
			3		−0.08**	0.05	−0.01	0.06	193.44
			4	0.01	−0.08**	0.05†	−0.05†	0.06	193.77
	Canopy height	78	1		0.12*	0.19***	−0.20***	0.32	93.08
			2	−0.06	0.10	0.19***	−0.18**	0.33	94.02
			3	−0.09†		0.18***	−0.16**	0.30	94.52
Humid	Stem density	201	1	0.08**	−0.09***			0.17	74.03
			2	0.08**	−0.09***		0.02	0.17	75.50
	Basal area	190	1		−0.09***			0.08	119.41
			2	0.04	−0.09***			0.09	119.63
			3		−0.09***		0.03	0.08	120.68
			4	0.04	−0.09***		0.02	0.09	121.17
	Canopy height	51	1	−0.15***		0.07†		0.33	23.42
			2	−0.13**	0.06	0.07†		0.36	24.05
			3	−0.15***				0.29	24.10
			4	−0.13**	0.06			0.31	24.90
Dry	Stem density	44	1	0.13*				0.11	39.65
			2	0.11†		0.13		0.15	40.64
			3			0.18		0.07	41.28
	Basal area	39	1		0.18†		−0.15*	0.17	44.39
			2						45.13
			3				−0.10	0.07	45.38
			4		0.10			0.04	46.32
	Canopy height[a]	27	1			−0.22		0.12	25.62
			2						25.79
			3				−0.09	0.10	26.10
			4			−0.20	−0.08	0.19	26.51

Note. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$; $^{\dagger}p < 0.1$.
[a]Only the four models with the lowest AICc are shown.
PDI, power dissipation index; MAT, mean annual temperature; MAP-PET, mean annual precipitations – potential evapotranspiration; HFP, human foot print.

Within humid forests, which was less affected by human disturbance than dry forest, PDI was a significant predictor of stem density and canopy height (Table 1), explaining alone about 10% and 29% of total variation in stem density and canopy height respectively (Figure 3). MAT was the other significant predictor. Together with PDI it explained 17% and 9% of total variance of stem density and basal area (Table 1). PDI had positive relationships with stem density, while MAT had positive relationships with stem density and basal area. Canopy height tended to increase with water availability which explained together with PDI 33% of the observed variance. Within dry forest, PDI was the only significant predictor of stem density, explaining about 11% of its variance (Figure 3). HFP together with MAT explained about 17% of the variance in basal area, while none of the variables was significantly related to canopy height variations.

4 | DISCUSSION

Our results confirm that TCs are important disturbances that have a long-term, global-scale effects on forest structure, despite being

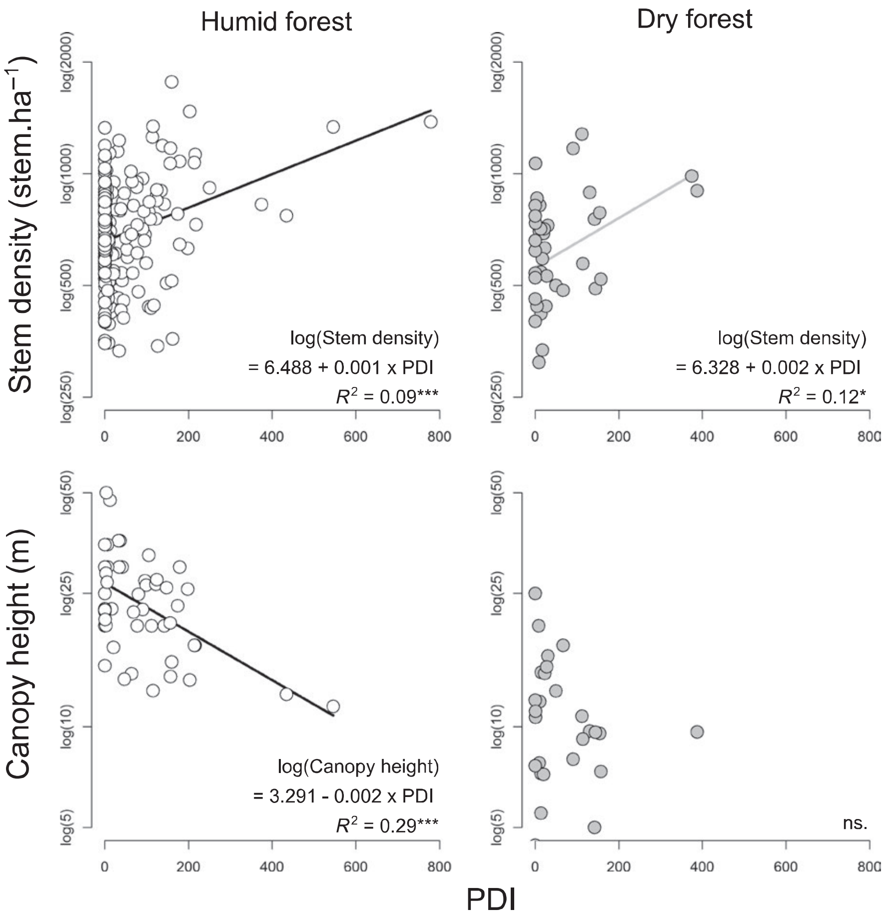

FIGURE 3 Relationships between the energy released by tropical cyclones (power dissipation index), stem density and canopy height (on log scales). Thick lines represent significant linear relationships (***p < 0.001, *p < 0.05)

relatively uncommon weather events (about 80–90 TCs per year, see Schreck et al., 2014; Maue, 2011). We show for the first time that stem density and canopy height are significantly related to the frequency of and energy released by TCs in a globally consistent way. Furthermore, our results indicate that these relationships were most pronounced for stem density and for humid forests, which are not limited by water availability and are less impacted by human disturbances (based on lower human foot print) than dry forests. Therefore, forecasted changes in the intensities, sizes and trajectories of TCs are likely to have important impacts on the structure of tropical and subtropical forests (Kossin, Emanuel, & Vecchi, 2014; Mei, Xie, Primeau, McWilliams, & Pasquero, 2015).

Our results explained a considerable proportion of the variation in stem density and canopy height in our dataset, suggesting that TCs are important large-scale disturbances that have long-term impacts on forests structure. Our analysis did not capture edaphic and topographic variation known to impact forest structure from local to regional scales, which makes the strong relationship we found between cyclone and forest structure even more remarkable. Indeed, soil depth, nutrient availability and topographical position are known to affect forest structure (e.g., Clark & Clark, 2000; Quesada et al., 2012; Schut et al., 2014; Slik et al., 2010; Webb, Stanfield, & Jensen, 1999).

The strong, universal relationship between TCs and stem density documented in this study is not surprising. TCs are disturbances that reduce the canopy cover of forests (Comita et al., 2009; Grove, Turton, & Siegenthaler, 2000; Hjerpe et al., 2001; Staben & Evans, 2008) and cause tree mortality (Webb et al., 2011; Zeng et al., 2009; Zimmerman et al., 1994). This results in increased light availability for several years in the undergrowth (Bellingham, Tanner, Rich, & Goodland, 1996; Lin et al., 2011; Luke, McLaren, & Wilson, 2014; Turton, 1992), creating suitable conditions for regeneration and the release of saplings (Luke et al., 2014; Nicotra, Chazdon, & Iriarte, 1999; Tanner, Rodriguez-Sanchez, Healey, Holdaway, & Bellingham, 2014). Therefore, frequent cyclones (e.g., one per decade) would be expected to maintain high light availability and, consequently, regeneration. Furthermore, higher mortalities and regeneration reported from TC-prone forests suggest that such forests may experience higher turnover and quicker dynamics than forests not or rarely affected by these disturbances (Swenson et al., 2012; Webb et al., 2011).

Given that TCs are known to trim forest canopies to lower heights (Brokaw & Grear, 1991; Lin et al., 2011), the moderate effect of TCs on canopy height may seem surprising. Our results suggest that canopy height first depends on hydraulic limitation and then by mechanical pruning by intense TC winds, as canopy height of dry forest (with MAP-PET being on average −177.7 ± 626.7 mm) was less than half that of humid forest (with MAP-PET being on average 700.6 ± 1,030.1 mm). This is in the line with recent global analyses showing canopy height to increase with water availability (Klein et al., 2015; Zhang et al., 2016) and the hydraulic limitation hypothesis (Ryan, Phillips, & Bond, 2006; Ryan & Yoder, 1997).

In humid forests, frequent TC disturbances may result in a greater investment in horizontal over vertical growth, as suggested by the negative relationship between the energy released by TCs with canopy height and its weaker, positive relationship with basal area. This deduction is supported by recent studies comparing height-diameter tree allometries across the tropics, which have shown that areas exposed to frequent strong winds, such as New Caledonia (Blanchard et al., 2016) or Dominica (Thomas, Martin, & Mycroft, 2015), have lower growth in height relative to diameter. These changes in tree allometry could result from repeated pruning of crown tips by TCs (Brokaw & Grear, 1991) or from evolutionary adaptations to TCs, which have been suggested to explain differential responses of neotropical palms (Areacaeae) to TCs (Griffith, Noblick, Dowe, Husby, & Calonje, 2008). The latter would imply TCs to have important evolutionary influences. Alternatively lower canopy heights may be due to resprouting, which is commonly observed in trees surviving TC damages (Bellingham, Tanner, & Healey, 1994; Scanlon, Petit, Tuiwawa, & Naikatini, 2018; Van Bloem et al., 2007; Zimmerman et al., 1994) and produces multistemmed trees that tend to be lower in height than single-stemmed trees (Givnish, 1984; Kruger, Midgley, & Cowling, 1997).

The expected changes in the frequency, intensity or geographical distribution of TCs due to anthropogenic climate change are therefore likely to impact the structure and dynamics of affected forests. While the influence of global warming on TCs remains uncertain (Walsh et al., 2016), there is an emerging consensus that TCs will increase in intensity (Christensen et al., 2013; Kang & Elsner, 2015; Mei et al., 2015), attain unprecedented sizes and intensities (Lin & Emanuel, 2016; Mei et al., 2015), and expand their trajectories poleward (Kossin et al., 2014). Our findings suggest that more intense TCs may alter tropical forest structure (density, height and basal area) and dynamics (higher turnover). Similar changes can be expected in forests at higher latitudes experiencing TCs for the first time. Furthermore, forests subjected to more intense cyclones may experience changes in species composition (Keppel et al., 2010; Webb et al., 2011) and increased vulnerability to drought and other threats, such as fire and invasion by weeds (Beard et al., 2005; Franklin, 2007; Hjerpe et al., 2001; Murphy et al., 2008).

The significant, negative relationship of human foot print with forest canopy height and basal area highlights that factors other than TC are impacting forest structure. This relationship could be the result of selective tree removal by humans or edge effects related to fragmentation (Laurance, Delamonica, Laurance, Vasconcelos, & Lovejoy, 2000; Lindenmayer, Laurance, & Franklin, 2012). While these potential causes are purely speculative, it is well documented that forests are being degraded and destroyed at alarming rates (Crowther et al., 2015; Hansen et al., 2013). A direct anthropogenic influence on forest structure (and hence dynamics) is further supported by the effects of the human foot print being stronger in tropical dry forests, which is known to be extremely disturbed and fragmented (Gillespie et al., 2014; Janzen, 1988; Miles et al., 2006).

5 | CONCLUSIONS

We provide the first evidence that the visible, short-term damages caused by TCs have less obvious, long-term effects on the structure of forests on a pantropical scale. The consistent finding of an increased stem density in regions experiencing a stronger TC disturbance regime suggests that TCs alter the structure of forests in a globally consistent manner. Furthermore, our results suggest that, within humid forests, TCs may have a stronger effect on canopy height than water availability. This implies that the predicted higher intensities and higher latitudes of cyclone impact in future will result in major and predictable changes in forest structure and, hence, global carbon stocks.

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AUTHORS' CONTRIBUTIONS

T.I., G.K. and P.B. conceived of the idea; T.I., G.K., T.W.G., G.R. and P.B. compiled the forest inventory data; C.M. and M.L. computed the tropical cyclone maps; T.I., G.K. and M.M. analysed the data; T.I. and G.K. interpreted the results and drafted the paper. All authors contributed to the writing of the paper.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4nn33b2 (Ibanez et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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