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ECOSYSTEMS

Chronic Winds Reduce Tropical Forest Structural Complexity Regardless of Climate, Topography, or Forest Age

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ABSTRACT

Tropical forests are the world's most structurally complex ecosystems, providing key functions like biomass accumulation, which is linked to this complexity. Tropical forests are also exposed to chronic, non-severe winds, yet their effect on forest structural complexity is understudied. Here we examine drivers of forest structural complexity in Puerto Rico with a particular focus on chronic wind exposure. We used airborne light detection and ranging data collected in 2016 to quantify canopy height and rugosity (variation in height) in 20,000, 0.28 ha forested sites stratified by forest age. We used random forest models to analyze variation in canopy height and rugosity as a function of chronic wind exposure, forest age, mean annual precipitation, elevation, slope (in degrees), soil type, soil available water storage, and exposure to a previous hurricane. Canopy height was driven by precipitation, forest age, and chronic wind exposure, decreasing by 2.12 m (16%) on average in wind-exposed forests across all forest ages. Canopy height increased by 4.0 m (41%) on average in forests aged 25–66 years, and by 4.0 m between sites with 1000 and 2000 mm y^{-1} precipitation. Canopy rugosity was driven by canopy height, precipitation, forest age, and elevation, increasing log-linearly with canopy height and precipitation, decreasing with elevation, and was highest in younger forests. Chronic wind exposure did not drive variation in canopy rugosity. Our results suggest that chronic wind exposure plays an integral role in limiting canopy height, potentially reducing aboveground carbon accumulation in older tropical forests.

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Key words: Tropical forests; Ecosystem function; Landscape ecology; Random forest; Canopy structure; Structural complexity; Disturbance; LiDAR; Old growth; Wind.

HIGHLIGHTS

- Chronic wind exposure significantly reduces tropical canopy height but not rugosity
- Canopy structural complexity increases log-linearly with water availability
- Canopy structural complexity in Puerto Rico peaks at 40 years of succession

INTRODUCTION

Tropical forests are among the world's most structurally complex and biodiverse ecosystems (Connell 1978; Jucker and others 2018b; Coddington and others 2023), accounting for half of the global terrestrial carbon sink (Pan and others 2011) and showing resilience to multiple disturbances (Poorter and others 2021b). This resilience is potentially linked to the structural complexity of tropical forest canopies (LaRue and others 2023b). Forest canopy structural complexity is a measure of the spatial variability in canopy elements and is an emergent ecosystem property arising from variation in tree crowns and bounded by canopy height (Atkins and others 2018a; Fahey and others 2019; Atkins and others 2022; LaRue and others 2023a). Canopy structural complexity increases have been positively linked to key ecosystem functions like biomass storage (Martinuzzi and others 2022), productivity (Gough and others 2019), biodiversity (Ishii and others 2004; Marselis and others 2019), resource use efficiency (Hardiman and others 2013; Atkins and others 2018b), and resilience to disturbances like fires and windstorms (Fahey and others 2015; Atkins and others 2020; Haber and others 2020). In temperate forests, taller canopies allow for higher structural complexity by increasing the vertical space available for tree crowns (Atkins and others 2022). Therefore, two canopy structural metrics specifically have been consistently linked to increased ecosystem functioning: canopy height and canopy rugosity—the surface variation in height (Gough and others 2019). We refer to these together as canopy structure (that is, height and complexity). Although canopy structure is gaining attention in the literature, most studies have focused on the effects of canopy structure on ecosystem function (LaRue and others 2023b), and yet we know less about what drives variation in canopy structure across environmental gradients, especially in tropical forests. This is an important knowledge gap, because understanding drivers of tropical canopy structure is critical to predicting their resilience to a changing climate (Johnstone and others 2016; Poorter and others 2021a).

Some drivers of structural complexity are established: for example, canopy height and structural complexity generally increase with water availability, soil fertility, and stand age, but decrease with elevation and severe disturbances (Fotis and others 2018; Hardiman and others 2018; Jucker and others 2018b; Ehbrecht and others 2021). Other drivers like moderate-severity winds have been suggested to dampen age effects, making old-growth stands structurally similar to younger forests (Fahey and others 2015; Haber and others 2020). However, there have been few large-scale studies evaluating drivers of tropical structure (Jucker and others 2018a; Swanson and Weishampel 2019) and even fewer examining non-severe wind effects, mostly due to a lack of available data over sufficiently broad environmental gradients (Jucker 2022). Filling this knowledge gap is now possible with airborne Light Detection and Ranging (LiDAR (Gorgens and others 2021)).

Chronic wind exposure—frequent exposure to non-storm winds—may be a key driver of tropical forest structure (Momberg and others 2021). At the individual tree level, chronic winds create a gravitational strain altering carbon allocation from height toward mechanical stability (Nicoll and others 2008; Niklas 2016; Malhi and others 2018), with wind speeds ≥ 30 km h^{-1} sufficient to induce such growth changes (Moulia and Combes 2004; Bonnesoeur and others 2016; Jackson and others 2019). At larger scales, models suggest wind-induced growth responses can shorten canopy heights and homogenize canopy structures (Gardiner and others 2016; Eloy and others 2017), and remote-sensing studies do find shorter canopies in wind-facing areas (Coomes and others 2018). Notably, these effects are distinct from severe, infrequent disturbances like cyclones, which are well studied (Xi 2015; Hogan and others 2018; Lin and others 2020) and cause widespread mortality leading to nutrient and biomass loss (Heartsill Scalley and others 2010; Zimmerman and others 2014). Unlike cyclones, few studies have focused on the role of chronic winds in driving canopy structural complexity in the tropics.

Here we evaluate the effect of chronic wind exposure on canopy structure (height and complexity) in tropical forests, while accounting for multiple other drivers across broad environmental gradients. To do this, we (i) quantified canopy height and structural complexity (that is, canopy rugosity) using airborne LiDAR across the island of Puerto Rico and (ii) used a random forest model to predict canopy metrics as a function of chronic wind exposure, forest age, mean annual precipitation (MAP), elevation, slope (in degrees), soil type, soil available water storage, and previous hurricane exposure. We hypothesized that canopy structure metrics will (a) decrease with chronic wind exposure; (b) increase with forest age; (c) decrease with elevation and slope; (d) increase with precipitation and soil available water storage; and (e) decrease with previous hurricane exposure.

METHODS AND MATERIALS

Study Site

Puerto Rico (Figure 1) is an ideal study system for examining the drivers of tropical forest canopy structure: it is a small island (9104 km^2) with 60% forest cover as of 2012 (Brandeis and Turner 2013; Hansen and others 2013). The forests span a large precipitation gradient (700–4500 mm y^{-1}), complex geology, rugged topography (0–1388 m a.s.l.), and Holdridge life zones ranging from subtropical dry forests to lower montane rain forests (Gould and others 2008). A history of agricultural land-use and recent reforestation has created an age gradient of emerging forests (< 15 years) to mature secondary forests (40–65 years) to old-growth forests (Lugo and Helmer 2004; Kennaway and Helmer 2007). Notably, forests in the wettest (> 3000 mm y^{-1}) and highest (> 1000 m) parts of the island are mostly old growth (Kennaway and Helmer 2007; Helmer and others 2008). Hurricanes make landfall on the island at ~ 50–150-year intervals during hurricane season August–November (Boose and others 2004), with the most recent ones before our dataset was collected (that is, 2016) occurring in 1998 (Georges) and 1989 (Hugo). Separately from stochastic hurricane winds, prevailing trade winds expose the island's forests to chronic gusts from the northeast to the southeast (Helmer and others 2002; Boose and others 2004), leading to topographic differences in chronic wind exposure (Figure 1, Figure S1).

DATA

Canopy Height and Canopy Rugosity

We used airborne LiDAR data from a 2016 flight collected by the USGS (Carswell Jr. 2016) with aggregate nominal pulse spacing of ≤ 0.35 m and pulse density of ≥ 8.0 pulses/m^2, sufficient to quantify vertical structure (Almeida and others 2019; LaRue and others 2020). We normalized point clouds and created a 1 m-resolution canopy height model by classifying and subtracting ground terrain from vegetation using LAStools (LAStools 2022) and the *lidR* package in R version 4.1.2 (R Core Team 2021; Roussel 2021). From the canopy

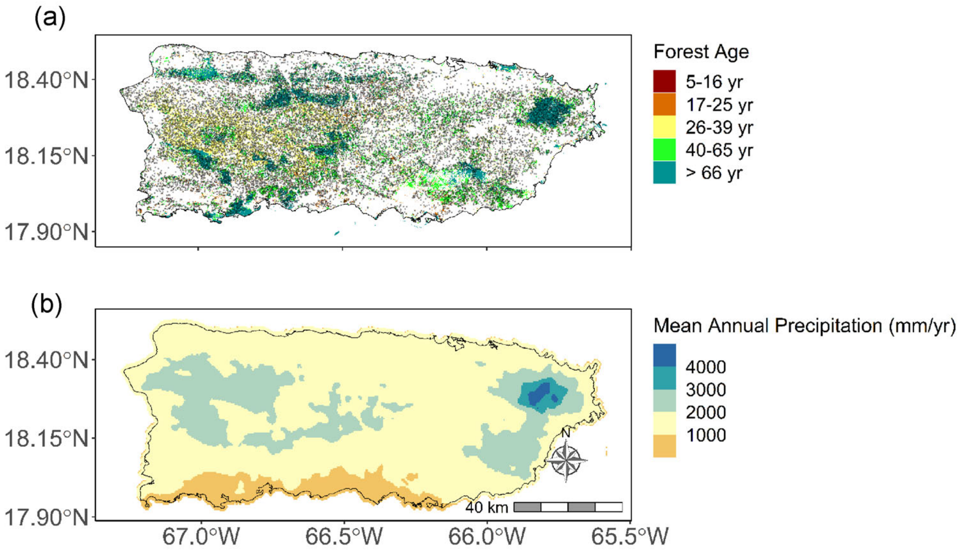

Figure 1. Study sites in Puerto Rico. Top panel: 17,593 forested sites (dots) randomly sampled and stratified by forest age class. Bottom panel: Mean annual precipitation (mm y^{-1}).

height model, we derived a1 m-resolution map of canopy rugosity—the standard deviation in canopy height (Atkins and others 2018a). Rugosity was calculated as the weighted mean in the center pixel of a 15 × 15 m moving-window grid using the focal function from the *raster* R package (Hijmans and others 2021) (Figure 2). Note that terrestrial laser studies often refer to this as top or surface rugosity (Atkins and others 2018a). We selected these variables to minimize redundancy and capture the structural metrics most associated with ecosystem function (Atkins and others 2018a; Gough and others 2019).

Chronic Wind Exposure

We created a map of chronic wind exposure by combining information on non-severe wind direction and topography. We extracted wind direction for the entire island of Puerto Rico from the Global Wind Atlas (GWA) version 3.0 (Technical University of Denmark 2020), which provides 3-km-resolution wind direction maps, and then checked the GWA results against wind direction and speed data (2000–2016) from nine weather stations across Puerto Rico from the Automated Surface Observing Systems network (Herzmann 2022) and the United States Forest Service (González 2017). We calculated the percentage of wind coming from 12, 30° sectors and considered a sector to represent chronic wind exposure if it accounted for > 10% of wind direction data and/or peak wind speeds (Boose and others 1994). We found that GWA and weather station data converged on prevailing wind directions, with only three sectors (60–90°, 90–120°, 120–150°) accounting for > 10% of wind direction data. The fastest wind speeds arrived from the same sectors (17–21 m/s, Figure S1), ensuring that our estimate of chronic wind exposure accounted for both direction and speed. To ensure our esti-

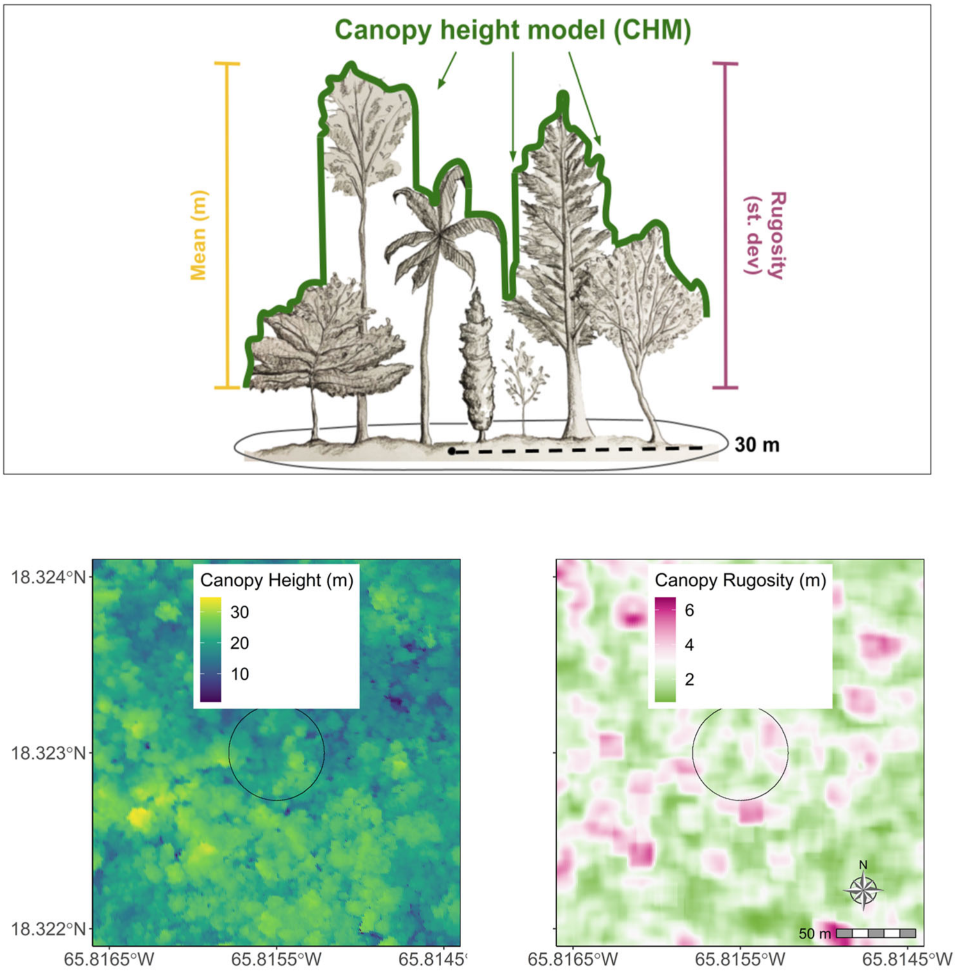

Figure 2. Top panel: Illustration of canopy structural complexity. Drawing: Nina Berinstein. Bottom panel: LiDAR-derived canopy height and canopy rugosity at an example 30 m-radius circular (0.28 ha) study site.

mate of chronic wind exposure was independent of tropical storm exposure, we checked whether prevailing wind directions differed during hurricane season (August–November) and whether winds during our study period reached sustained speeds > 33 m/s (that is, category 1 hurricane). Although wind directions did not differ between hurricane season and the rest of the year (Figures S1, S2), chronic wind speeds in our study were consistently below hurricane wind speeds (Figures S2, S3). Therefore, our estimate of chronic wind exposure captures exposure to wind speeds (17–21 m/s) that are sufficient to cause plant growth responses and minor damage (Moulia and Combes 2004; Bonnesoeur and others 2016) and yet are below tropical storm wind speeds that lead to blowdowns (Boose and others 2004).

We then used the EXPOS model (Boose and others 1994, 2004) to derive a map of chronic wind exposure across Puerto Rico based on angles of prevailing wind direction and topography using a digital elevation model (DEM) from the USGS (Carswell Jr. 2016). We chose the EXPOS model because it has been previously used in Puerto Rico to quantify wind effects on forests and works well at landscape scales (Boose and others 2004; Hall and others 2020). EXPOS takes a prevailing angle of wind, allows that wind to come into a study area, and bends over topographic barriers based on the DEM to calculate exposure. Slopes with wind-facing angles, as well as flat terrain, are exposed unless they are shaded by a topographic barrier upwind. Based on prior studies, we input prevailing directions in 30 m bins coming from 60 to 120° degrees to match our chronic wind estimates (weighting NE–E directions of maximum wind speeds) and used an inflection angle of 15° (Boose and others 1994; Batke and others 2014; Hall and others 2020) and a maximum upwind barrier distance of 5 km. Similar to a simple light exposure model, this yielded an island-wide 30-m-resolution map of binary chronic wind exposure (0 = protected, 1 = exposed, Figure S4).

Other Environmental Variables

In addition to chronic wind exposure, we included variables known to impact tropical forest structure for which spatially explicit data exist. We derived forest age class from historical land use maps and Landsat satellite data (Helmer and others 2008) and extended with a 2012 forest cover map (Hansen and others 2013), using 2016 (the year of the LiDAR collection) as the baseline year, resulting in a 30 m-resolution map of five forest age classes: 5–16, 17–25, 26–39, 40–65, and ≥ 66 years (Martinuzzi and others 2022). In addition, we obtained 30-year mean annual precipitation (MAP) from PRISM (PRISM Climate Group 2002), soil type from the USGS (Reed and Bush 2005), soil-available water storage from 0 to 150 cm belowground from the 1 m-resolution USGS gSSURGO database (Soil Survey Staff 2021), and elevation (in m a.s.l.) and slope (in degrees) from a 5-m-resolution 2016 USGS DEM (Carswell Jr. 2016). We used EXPOS and storm track data from the National Hurricane Center from NOAA (https://www.nhc.noaa.gov/) to calculate topographic exposure to hurricanes Hugo in 1989 and Georges in 1998 as in Boose and others (2004).

STATISTICAL ANALYSES

Sampling Scheme

We randomly sampled ~ 20,000, 30-m-radius circular sites (0.28 ha) within forested areas stratified by forest age class using the *raster* package in R (Hijmans and others 2021). To avoid spatial autocorrelation in our response variables, we ran multiple Moran's I Monte Carlo permutation tests with 1000 simulations using the *spdep* package in R (Bivand and others 2022), increasing distances from 50 to 1000 m in 100-m intervals. We found that a 250 m minimum distance between sites significantly reduced spatial autocorrelation in canopy height (Moran's statistic = − 0.0003, rank = 901, p-value = 0.90) and canopy rugosity (Moran's statistic = − 0.0003, rank = 97.5, p-value = 0.83) compared to distances 50–150 m (p-values = 0.08–0.09 for height and 0.05–0.14 for rugosity). Distances > 250 m did not further reduce spatial autocorrelation. We removed sites with missing values and those spatially overlapping non-forested areas as defined in the forest cover map from Hansen and others (2013).

Within each 0.28 ha site, we calculated canopy height and rugosity by averaging 1 m resolution height and rugosity values. We calculated independent variables within each site by averaging values of MAP, elevation, slope, and soil-available water storage from the source maps. Exposure to chronic winds for each site, as well as to hurricanes Georges and Hugo, was assigned as 0 or 1 from the 30-m-resolution EXPOS maps (as discussed above). Forest age class and soil type for each site were assigned as the value of the center pixel from the source maps.

The final sample size was n = 17,593, spanning wide environmental gradients (0–1276 m elevation and 711–4490 mm y^{-1} precipitation). Wind-exposed and wind-protected sites were evenly distributed in the sample (8609 and 8959, respectively, Table S1, Figure S6). Additionally, stratifying sampling by forest age ensured most elevation and precipitation quantiles had > 400 sites from each age class. For example, there were 578 sites in areas > 3000 mm y^{-1} precipitation (Figure 1) and 694 sites in areas > 800 m elevation (Figure S4).

Random Forest Regression

We built multivariate models to predict canopy height and canopy rugosity as a response of our set of environmental variables. We used Pearson correlations to check collinearity among predictors, removing variables for which $r \geq 0.7$ (Dormann and others 2013). Exposure to hurricanes Hugo in 1989 and Georges in 1998 was highly correlated (Pearson $r = -0.84$, Figure S5), so we included only exposure to hurricane Hugo (Canham and others 2010). Note that exposure to both hurricanes Hugo and Georges was not significantly correlated with chronic wind exposure (Figure S5). We also considered annual number of clear days, maximum temperature, and topographic roughness as predictors (Gorgens and others 2021), but dropped them since they were highly correlated with precipitation, elevation, and slope, and did not change model R^2 (data not shown).

We predicted canopy height and canopy rugosity using random forest models (RF) with the *randomForestSRC* package in R (Breiman 2001; Ishwaran and Kogalur 2022). RF is a nonparametric, nonlinear statistical method appropriate for large ecological datasets where parameter distributions, outliers, and collinearity between covariates do not meet the assumptions of linear or generalized linear models (Breiman 2001; Ishwaran and Kogalur 2022). It is also an efficient way of testing interactive effects between covariates. Each RF model was run with 5000 trees using permutations, 10 random split points, and an average of 2400 terminal nodes. Based on studies of canopy rugosity in temperate forests, we included canopy height as a predictor of canopy rugosity (Atkins and others 2022). We ranked relative predictor importance using variable importance (VIMP) across all regression trees—that is, the difference between out-of-bag prediction error before and after permutation, sorting variables by impact on predictive error (Ishwaran and Kogalur 2022). We ran 10 RF models for each response variable and considered a variable as important if it was above the median VIMP value for all 10 models.

To generate model predictions, we used the *ggRandomForests* package to create partial dependence plots of each predictor (Friedman 2001; Ehrlinger 2016). Partial dependence calculates the predicted mean values of a response (for example, canopy height) for 25 values proportionally sampled along the distribution of a predictor (for example, MAP), while keeping all other predictors at their mean values. This is similar to marginal plots (Gorgens and others 2021). To test interactive effects between chronic wind exposure and other variables, we generated partial dependence coplots. These show the conditional effect of each predictor on the response variable based on the effect of another predictor (that is, chronic wind exposure) after controlling for all other effects (Ehrlinger 2016). Finally, we calculated pairwise interactions between predictors using Friedman's H-factor with the *pre* and *iml* packages in R (Friedman and Popescu 2008; Molnar and Schratz 2020; Fokkema and Christoffersen 2021).

RESULTS

Canopy height ranged between 2.0 and 35.7 m, with a mean of 11.6 m. Canopy rugosity ranged between 0.5 and 7.0 m, with a mean of 3.13 m. Random forest models explained a substantial amount of the variance in canopy height ($R^2 = 0.40$, RMSE = 0.2 m) and canopy rugosity ($R^2 = 0.38$, RMSE = 0.006 m). The most important predictors of canopy height were (in descending order) MAP, forest age, and chronic wind exposure, while for canopy rugosity they were canopy height, MAP, elevation, and forest age (Figure 3).

As expected, chronic wind exposure significantly reduced canopy height. Wind-exposed forests were 2.12 m (or 16%) shorter on average than wind-protected forests (Figure 4, Table S1, Figure S6). This effect was consistent regardless of forest age, MAP, or elevation, and increased in magnitude with forest age (Figure 4, Table S1). As expected, both MAP and forest age had a positive, though saturating, relationship with canopy height. Predictions showed the wettest forests (> 3000 mm y^{-1}) were 6.0 m (or 45%) taller on average than the driest forests (< 1000 mm y^{-1}), and forests older than 66 years were 5.6 m (or 42%) taller on average than the youngest forests.

Contrary to expectations, chronic wind exposure did not drive variation in canopy rugosity (Figures 2, 5). As expected, canopy rugosity increased log-linearly with both canopy height and MAP and

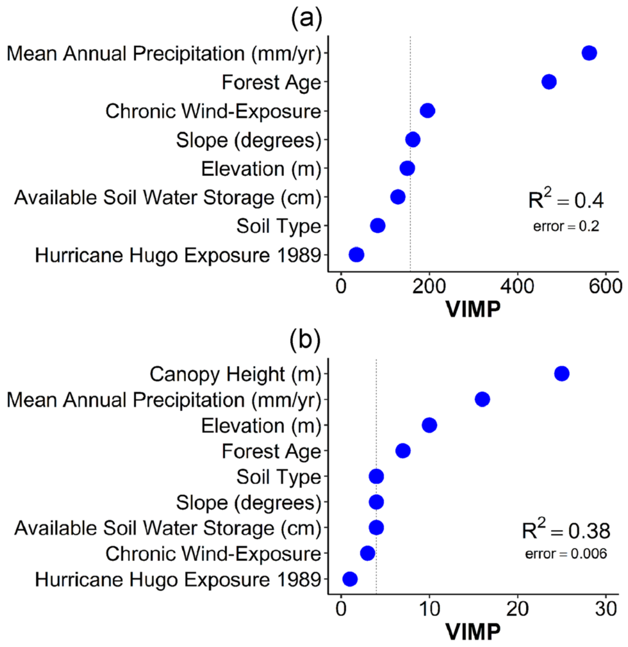

Figure 3. Ranking of variable importance (VIMP) according to island-wide random forest (RF) model results for **a** canopy height, and **b** canopy rugosity. VIMP is a unitless measure of impact on predictive error. Dashed lines represent the median VIMP value from 10 RF models.

decreased with elevation (Figure 5). Predictions showed forests taller than 10 m were 1.01 m (32%) more rugose than forests of < 10 m height, wet (> 2000 mm y^{-1}) forests were 0.69 m (20%) more rugose compared to dry forests (< 1000 mm y^{-1}), and forests at high elevation (> 1000 m) were 0.5 m (15%) less rugose than forests at lower (< 1000 m) elevation (Figure 5). Canopy rugosity did not increase with forest age, with the highest canopy rugosity in the youngest forest age classes (Figure 5, Table S1).

Finally, interactions played a minor role in explaining variance in canopy height (λ = 0.11, cv error = 21.2) and canopy rugosity (λ = 0.008, cv error = 0.68, Figure S7)—that is, most predictors had independent impacts on the response variables. For example, only 0.20 of MAP effects on canopy height stemmed from interactions with forest age and chronic wind exposure (Figure S7).

DISCUSSION

Our study sheds light on the role chronic wind exposure plays in determining the physical structure of tropical forests. Sampling across forest age classes and broad environmental gradients enabled us to simultaneously test multiple drivers of canopy structure. We found that precipitation and forest age, and to a lesser extent elevation, act as primary controls on forest canopy structure. At the same time, our results demonstrate a prominent role of chronic wind exposure as a constraint on canopy height across successional stages and broad gradients in water availability and elevation.

The negative effect of chronic wind exposure on canopy height in our study was evident regardless of other predictors, supporting previous remote-sensing studies showing shorter canopies in wind-exposed areas (Coomes and others 2018; Gorgens and others 2021). There are two potential mechanisms that may lead to shorter forests in wind-exposed areas: damage or acclimation. Damage involves the removal of tall trees, branches or crowns (Ibañez and others 2019), whereas acclimation involves changes to tree growth patterns. Specifically, trees display plastic responses to wind loading (Moore and others 2018). Experiments show even mild wind stress (~ 30 km h^{-1}) can lead trees to invest in mechanical stability at the expense of height (Moulia and Combes 2004; Nicoll and others 2008). Chronic winds in our study reach mean speeds 50–70 km h^{-1}, sufficient to induce acclimation responses and to reduce canopy height.

Alternatively, damage may be expected as a primary mechanism if canopy height is also lower in hurricane-exposed areas. However, previous hurricane exposure was not correlated with canopy structural complexity. The most recent hurricane that caused major forest damage in our dataset (that is, as of 2016) was H. Hugo in 1989 (Canham

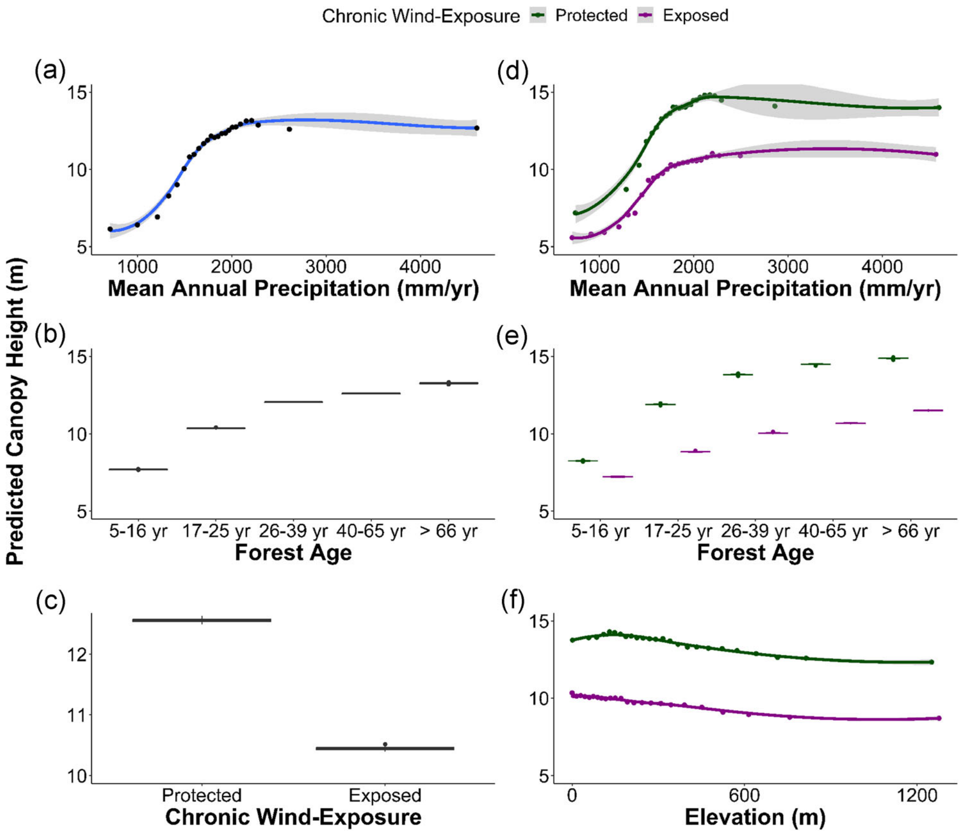

Figure 4. Predicted relationship between canopy height (y-axes) and its top predictors using partial dependence: **a** MAP (mm y^{-1}), **b** Forest age class and **c** Chronic wind exposure. **d–f**: Chronic wind exposure (legend) interactions with top predictors and elevation. Points represent mean predicted canopy height values from the random forest model for 25 values sampled proportionally along the distribution of each predictor of interest. Lines represent best fit, shaded regions, and error bars represent 95% confidence intervals around mean predicted values.

and others 2010). Although such stand-replacing hurricanes leave compositional legacies (Hogan and others 2016), forests in Puerto Rico can recover structurally within 20 years (Heartsill Scalley and others 2010). Therefore, our results suggest wind-induced acclimation may reduce landscape-scale canopy height. However, due to a lack of damage data from low-intensity storms—which may be prevalent (Figure S3)—we cannot discard the hypothesis that chronic wind exposure leads to canopy biomass loss.

We found that MAP was positively correlated with canopy height and canopy rugosity, but the relationship plateaued > 2000 mm y^{-1}. This partially supports global analyses showing a positive linear relationship between precipitation and structural complexity (Ehbrecht and others 2021). However, our study found a reduction in complexity in the wettest forests, probably due to the fact that global analyses have few data > 2500 mm y^{-1} while we were able to sample 799 sites in forests > 2500 mm y^{-1}. Our results agree with a study in the Amazon suggesting maximum canopy height occurs at 1500–3000 mm y^{-1} precipitation (Gorgens and others 2021). A previous study in Puerto Rico found that water-saturated microsites support lower forest biomass (Muscarella and others 2020). These findings make sense in terms of plant physiology—lack of water in soils reduces growth potential (Bauweraerts and others 2014), while water-saturated soils can lead to anoxic conditions that also reduce plant growth (Benkeblia 2021). Although the tropics are projected to experience more frequent and severe droughts (Cook and others 2020), our findings suggest that the wettest tropical forests may benefit from modest reductions in precipitation.

Contrary to expectations, canopy rugosity was not significantly affected by chronic winds. Instead, canopy rugosity was primarily driven by canopy height, increasing log-linearly until ~ 10 m height. Elevation was also an important driver of canopy rugosity with a linear negative relationship. These findings support previous studies showing struc-

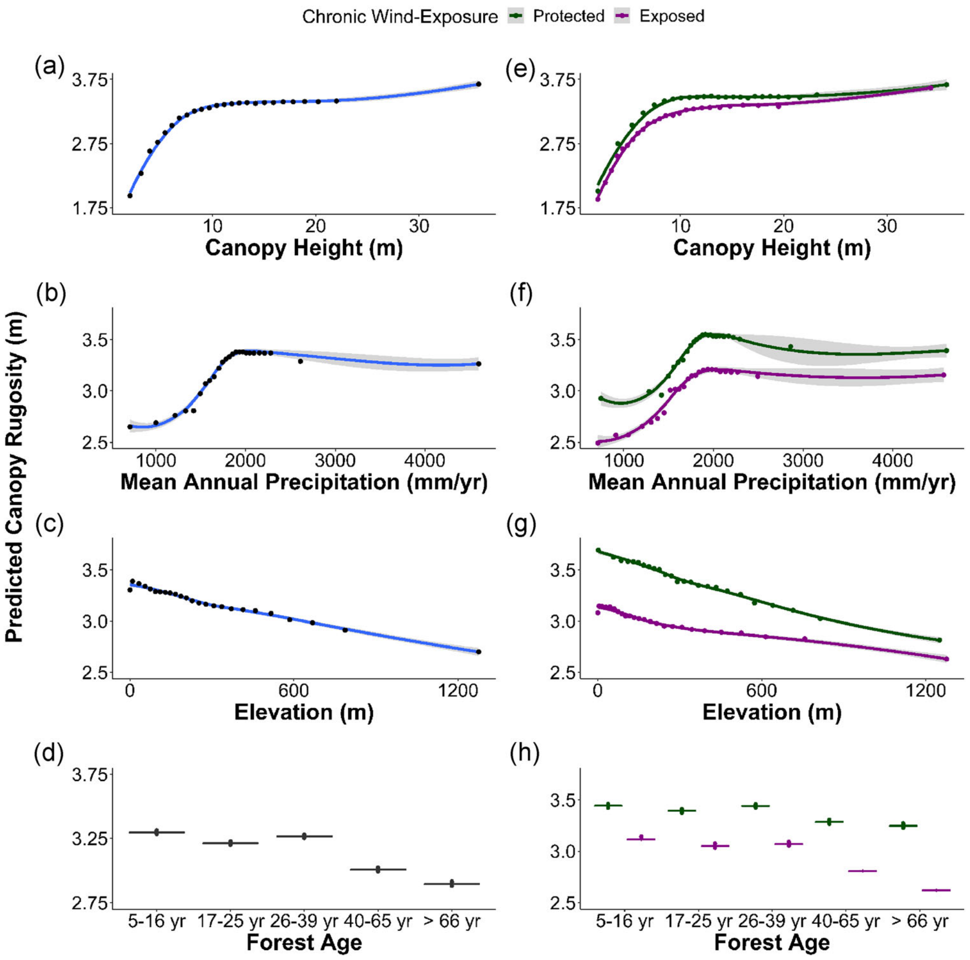

Figure 5. Predicted relationship between canopy rugosity (*y*-axes) and top four predictors of rugosity: **a** canopy height (m), **b** MAP (mm y^{-1}), **c** mean elevation (*m*) and **d** forest age class. **e–h**: chronic wind exposure (legend) interactions with top predictors. Points represent mean predicted canopy rugosity from the random forest model for 25 values sampled proportionally along the distribution of each predictor of interest. Lines represent best fit, shaded regions, and error bars represent 95% confidence intervals around mean predicted values.

tural complexity scales with height and that higher elevation forests tend to be less structurally complex (Jucker and others 2018b; Atkins and others 2022). However, studies generally find a power-law relationship between canopy height and rugosity (Gough and others 2020), whereas in our study the relationship ceased to be significant in canopy heights above 10 m. This may be a result of the context in Puerto Rico, where older forests are generally found in higher elevations with high precipitation (Crk and others 2009).

Canopy height in our study increased with forest age, yet most of the increase had occurred within 40 years of succession. Similarly, canopy rugosity in our study was highest in forests of intermediate age. This partially agrees with studies in temperate forests showing canopy structural complexity can plateau with age (Fahey and others 2015), although the timeline in our study is remarkably faster. Field-based studies in Puerto Rico demonstrate secondary forest structure resembles old-growth forests within 40 years of abandonment (Aide and others 1996; Martínez and Lugo 2008; Abelleira Martínez and others 2009). Secondary tropical forest height and biomass are usually projected to reach old-growth levels in ~ 66 years (Poorter and others 2016, 2021a), yet our results demonstrate timelines within half a century (Martin and others 2013), suggesting a fast structural recovery of tropical forests in the island. These findings may reflect the short stature of the oldest forests in our study compared to other tropical forests (Gorgens and others 2021).

Old-growth forests may be less structurally complex than younger forests because of wind exposure, differences in species compositions, or unfavorable environments (for example, anoxic conditions). Studies suggest old-growth forests in hurricane-prone areas are shorter than comparable forests due to intermittent stand-replacing damage (Ibañez and others 2019). However, our study is consistent with previous field-based studies finding no structural effect of previous hurricane exposure in Puerto Rico (Aide and others 1996). This may reflect the fact that while global studies tend to compare forests with frequent to no hurricane exposure (Ibañez and others 2019), all of Puerto Rico is exposed to hurricanes every ~ 50 years (Boose and others 2004). Another potential explanation for low structural complexity of old forests in our study is the relatively low-productivity areas where they tend to occur (Kennaway and Helmer 2007; Gould and others 2008). Lastly, differences in species composition across forest ages may account for the low structural complexity of older forests.

In Puerto Rico, species composition is strongly correlated with elevation and chronic wind exposure. In the Luquillo Mountains, for instance, forests are dominated by Tabonuco (*Dacryodes excelsa*) below 600 m and by Palo Colorado (*Cyrilla racemiflora*) in cloud forests 600–900 m (Weaver and Murphy 1990; Heartsill Scalley and others 2010). Sierra palm forest, dominated by *Prestoea acuminata* var *montana*, is found above 500 m and elfin woodland above 900 m (Weaver and Murphy 1990). Palms at high elevations are extremely resistant to winds, but generally yield shorter, simpler canopies than Tabonuco forests (Lugo and Frangi 2016). Because canopy height was the strongest predictor of canopy rugosity, the prevalence of shorter palms in older, wind-exposed forests in Puerto Rico may partially account for the negative correlation between forest age and canopy rugosity. Wind-exposed older forests in our study were the same height as unexposed younger forests—potentially due to the prevalence of shorter palms—which may indirectly lead to lower rugosity in older forests. This potential explanation would match findings in temperate forests demonstrating moderate-severity wind disturbances can make old-growth forests structurally similar to younger forests (Fahey and others 2015; Haber and others 2020).

In conclusion, canopy structural complexity is strongly linked to biomass accumulation and productivity (Gough and others 2019; Martinuzzi and others 2022), yet few studies have examined its drivers in the tropics. Moreover, although tropical forests can rapidly recover function after severe disturbances (Poorter and others 2021a), the potential role of low-severity disturbances is relatively unknown. Our study shows that chronic wind exposure reduces canopy height and potentially structural complexity across successional stages and environmental contexts. Therefore, chronic winds may act as a significant constraint on tropical forest productivity, possibly limiting carbon accumulation in wind-exposed areas.

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DATA AVAILABILITY

Data for analyses and figures can be found at Dryad: https://datadryad.org/stash/share/DjL6uLjBN-jvHrPqfXRy5_3xjVHhHvPsFk8Ytqo4GcM. No novel code was used for this manuscript.

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