



The impact of hurricanes Irma and Maria on the forest ecosystems of Saba and St. Eustatius, northern Caribbean

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ABSTRACT

In September 2017, Irma became the first recorded category 5 hurricane to hit the Caribbean Windward Islands. The second category 5, Maria, followed two weeks later. In November 2017, we assessed the structural impact of this disturbance on highly valued Caribbean forest ecosystems. We recorded the status of 935 tree stems on Saba and St. Eustatius in stands at different elevations. Tree damage was substantial on both islands, with 93 percent of stems being defoliated, 84 percent having lost primary and/or secondary branches and 36 percent having structural stem damage. Average tree mortality was 18 percent, with mortality being nearly twice as high on St. Eustatius than on Saba. Surprisingly, we found that neither individual stem size nor community size distributions mediated the forests' response to the hurricanes. Our results show that these hurricanes comprised a density-independent disturbance, which may become more common as the frequency of strong hurricanes is projected to increase.

Abstract in Dutch is available with online material.

Key words: defoliation; density-independent disturbance; forest community structure; island ecology; tree mortality; tree size distribution; tropical cyclones.

CARIBBEAN FORESTS ARE HIGHLY VALUED ECOSYSTEMS, PROVIDING important ecosystem services such as the regulation of soil, water, and nutrient cycles (Myers *et al.* 2000, Maass *et al.* 2005, Brookhuis & Hein 2016). Although hurricanes are a natural disturbance within the Caribbean (Lugo & Frangi 2016), there is growing concern that projected increases in the frequency of strong hurricanes (Knutson *et al.* 2015) may affect forest ecosystem functioning (Lugo 2000, Luke *et al.* 2016a). Multiple studies found that larger trees suffered more damage from hurricanes (Walker 1991, Ostertag *et al.* 2005, Vandecar *et al.* 2011, Lewis & Bannar-Martin 2012, Tanner *et al.* 2014) and that denser stands may be more susceptible to hurricane damage (Foster 1988), possibly due to limited branching opportunities in such stands (Tanner *et al.* 1991). However, these patterns have not been observed consistently in Caribbean forests (Bellingham 1991, Van Bloem *et al.* 2005, Canham *et al.* 2010, Webb *et al.* 2014). Hence, more observations are needed to help define the range of responses of forest ecosystems to hurricane disturbances (Xi 2015).

In September 2017, the Caribbean Windward Islands experienced an extreme disturbance. Hurricane Irma was the first category 5 hurricane on record to pass over these islands, and it was followed by the second category 5, Maria, two weeks later (Fig. 1A; Shuckburgh *et al.* 2017). In this study, we assess these hurricanes' impacts on the forests of Saba and St. Eustatius, two islands in the northern Caribbean that are relatively small (13 and 21 km², respectively) and that were in close proximity (50–

60 km) to the eye of Irma when it passed (Fig. 1B). Though not as close and therefore reduced in strength (Fig. 1C), Maria brought strong wind gusts and substantial amounts of precipitation to the islands (~100 mm, Madden 2017, Royal Netherlands Meteorological Institute 2017). Our aims were to: (1) assess canopy damage, (2) test whether the extent of damage differed between the two islands, (3) test whether stem size and stand density affected the susceptibility to damage at the individual and stand level.

METHODS

STUDY AREAS.—Saba (17°38' N, 63°14' W) and St. Eustatius (17°28' N, 62°58' W) are the northernmost islands of the Cenozoic lesser Antilles volcanic island arc (Macdonald *et al.* 2000). Their lower mountain slopes are covered by dry evergreen forests, (semi-)evergreen, and deciduous seasonal forests, whereas (secondary) rain forest can be found on the highest elevations (Stoffers 1956, Rojer 1997a,b, De Freitas *et al.* 2014, 2016, Van Andel *et al.* 2016). Furthermore, the crater of the Quill volcano on St. Eustatius harbors a unique type of evergreen forest (Stoffers 1956, De Freitas *et al.* 2014, Van Andel *et al.* 2016). In the 60 yr before hurricanes Irma and Maria, a total number of 18 (for St. Eustatius) to 23 (for Saba) hurricanes came in proximity of the islands, of which seven caused considerable damage (De Freitas *et al.* 2014, 2016, Appendix S1). The most recent of these latter hurricanes were Luis in 1995 (for Saba), George in 1998, and Lenny in 1999 (De Freitas *et al.* 2014, 2016), but no

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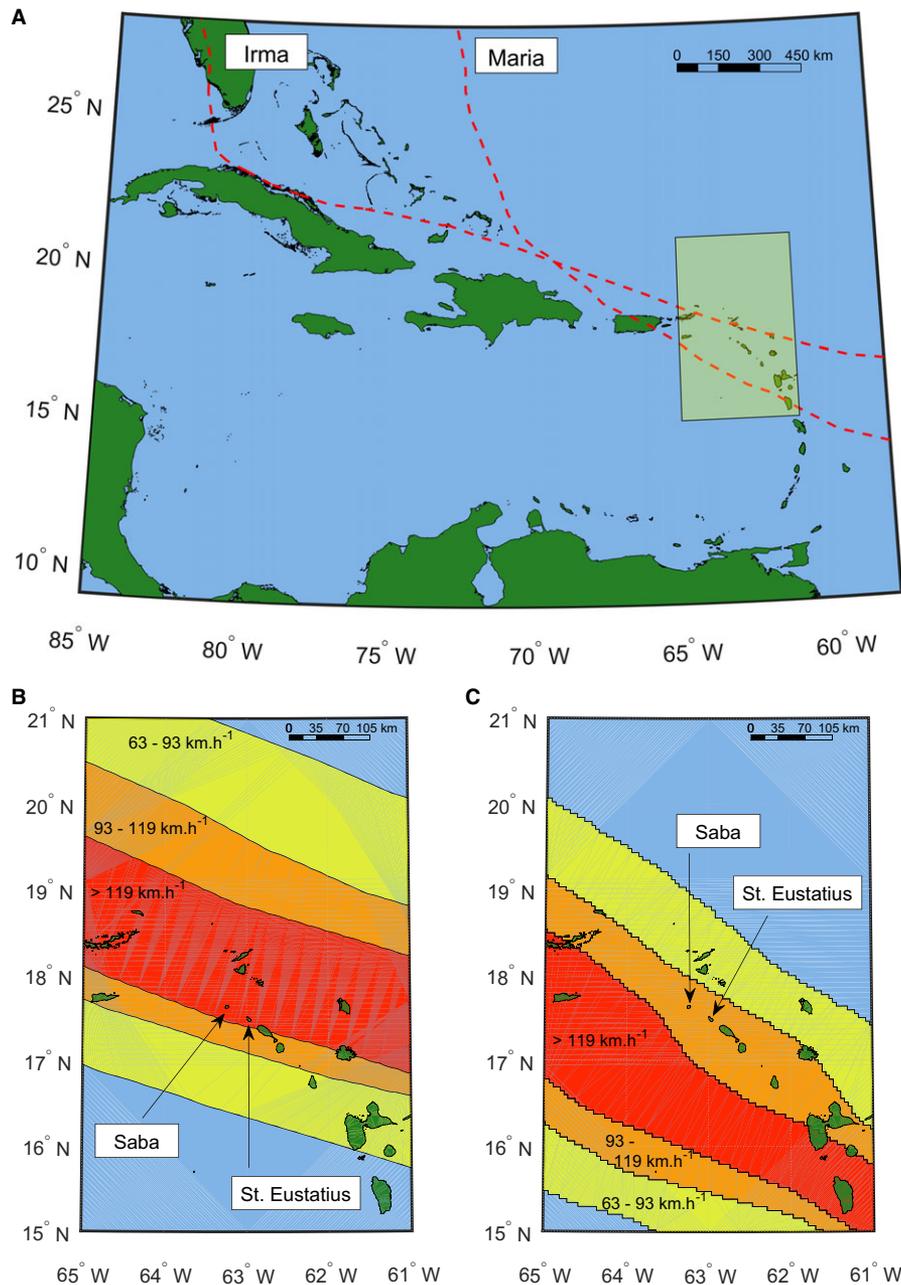


FIGURE 1. Trajectories of the 2017 hurricanes Irma and Maria through the Caribbean and associated wind speeds when passing Saba and St. Eustatius. (A) Map of the larger Caribbean region, the small window covers the area shown in bottom panels. (B) Trajectory of hurricane Irma on 6 September from 05:00 until 18:00 h. During this entire time period, the hurricane was categorized as a Category 5. (C) Trajectory of hurricane Maria, from 19 September, 00:00 h until 20 September, 06:00 h. During this entire time period, the hurricane was categorized as a Category 5, with the exception of one observation (19 September, 06:00 h), when the hurricane was categorized as Category 4. At this time, the eye of the hurricane was positioned around 62°W. Data source: NOAA, National Hurricane Center.

systematic surveys of impacts on the islands' forests were documented afterward.

FIELD SURVEY.—Field surveys were undertaken from 18–29 November 2017, approximately 2 mo after the hurricanes. This interval was long enough for regrowth of leaves, but not for

branches (Walker 1991). To account for different vegetation types, sampling locations were stratified across the following elevation classes: class 1: <250 m (St. Eustatius only), class 2: 250–450 m, class 3: 450–650 m, and class 4: 650–800 m (Saba only). Within class 2, plots within the volcanic crater of St. Eustatius were considered a separate class (2c). Sampling plots

measured 10 m × 10 m. We sampled eight plots on Saba (three plots of class 2 and 3, two plots of class 4) and 20 plots on St. Eustatius (five plots for each of the classes 1, 2, 2c, and 3). In each plot, we recorded the basal area and status of all tree stems with a diameter at breast height (dbh) exceeding 5 cm (Boucher *et al.* 1990). A stem's status was described by recording: (1) signs of recent defoliation (Walker 1991), (2) recent loss of secondary and/or primary branches (Reilly 1991), (3) whether the stem had been uprooted or snapped (Boucher *et al.* 1990), (4) mortality (Boucher *et al.* 1990). The first characteristic was determined by estimating the percent of canopy loss (or defoliation). If a tree showed signs of losing more than 75 percent of its leaves, its status was recorded as defoliated. Although many trees quickly regrew leaves, these leaves often grew in unusual places (*e.g.*, epicormic shoots, Bellingham 1991) or only on a small fraction of the estimated pre-hurricane tree canopy. The second characteristic was determined by examining recent scars on the stem (indicating loss of primary branches) and branches (indicating loss of secondary branches). Regarding the fourth characteristic, we followed previous studies (Boucher *et al.* 1990, Koptur *et al.* 2002) by assuming that all living trees would have started to

produce leaves and/or shoots two months after the hurricanes. Hence, trees without green leaves or shoots were recorded as deceased. This method may overestimate mortality in cases where new growth took longer than two months. However, previous studies reported that hurricanes caused higher rates of mortality that lasted for multiple years (Lugo & Scatena 1996, Tanner *et al.* 2014). As our method did not capture such effects, it could also underestimate hurricane-induced mortality. In total, we recorded the status of 935 stems on both islands (272 on Saba, 663 on St. Eustatius).

ANALYSES.—Hurricane damage was described by the frequencies of defoliation, loss of (primary or only secondary) branches, snapping/uprooting of stems, and mortality. To test whether these impacts differed between islands, and across elevations within each island, we employed chi-square tests. For the within-island comparisons, a Bonferroni correction was employed. As stem densities did not follow a normal distribution (one-sample Kolmogorov–Smirnov test, $D_{28} = 0.96$, $P < 0.001$), and normality could not be obtained through transformation, subsequent analyses involved non-parametric tests. First, to test whether tree size mediated the response to the hurricanes, we compared the

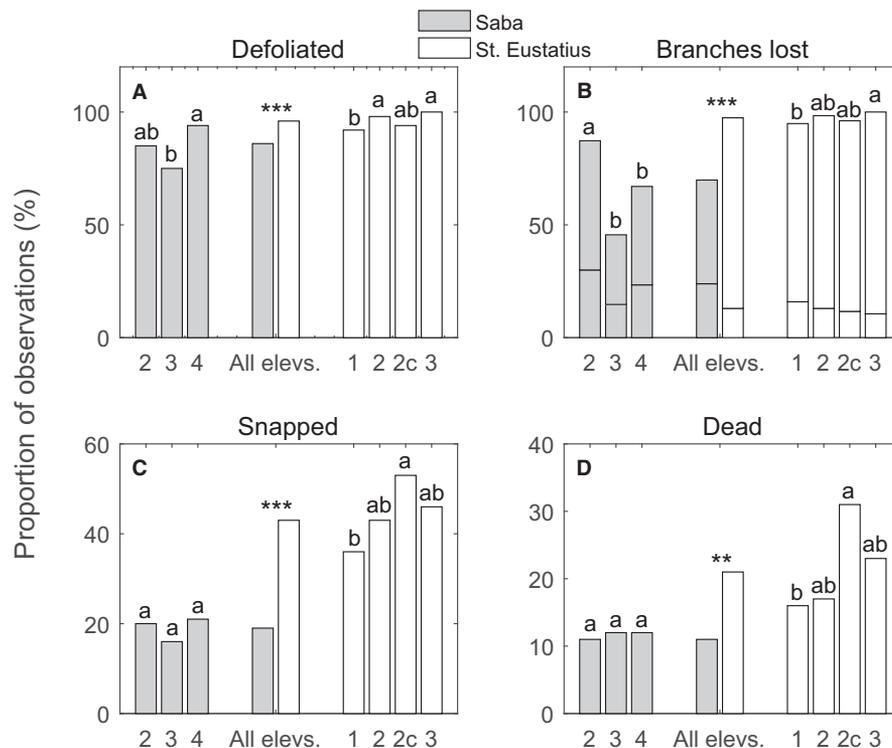


FIGURE 2. Status of forest trees on the Caribbean islands Saba ($N = 272$) and St. Eustatius ($N = 663$), as observed two months after the passing of hurricanes Irma and Maria. Status was assessed among four elevation classes: 1: <250 m (St. Eustatius only), class 2: 250–450 m (St. Eustatius' crater plots indicated as 2c), class 3: 450–650 m, and class 4: 650–800 m (Saba only). Status was assessed for four impact categories of increasing severity: (A) defoliation (more than 75 percent of leaves lost); (B) loss of branches (trees that lost only secondary branches indicated in the bottom segments of the bars, trees that lost primary branches lost as well indicated in the top segments of the bars); (C) snapping of the main stem; (D) mortality. For all impact categories, forest trees on St. Eustatius were affected more frequently; asterisks indicate significant differences between islands for each impact category (chi-square tests: *: $P < 0.05$; **: $P < 0.01$ ***: $P < 0.001$). Different lowercase letters indicate significant differences between elevations (chi-square test with Bonferroni correction, $P < 0.05$).

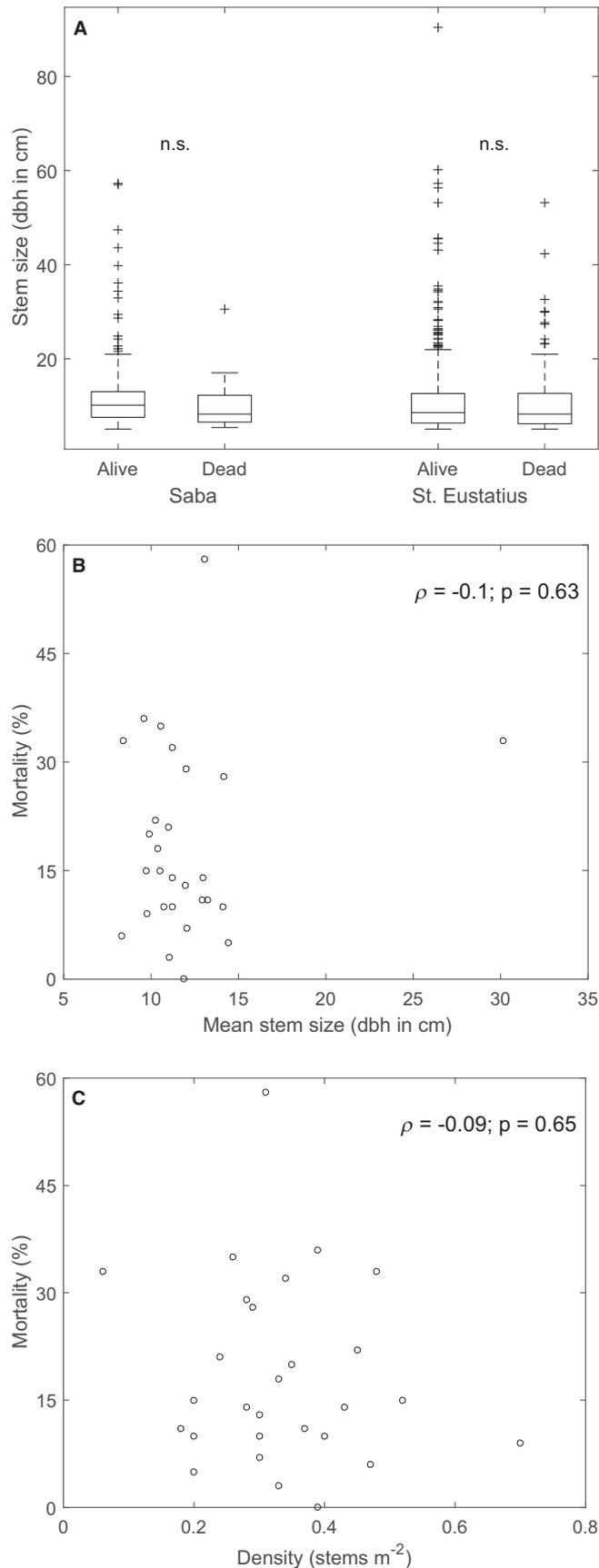


FIGURE 3. (A) Boxplots showing forest tree size distributions of alive and dead stems on the Caribbean islands Saba ($N = 272$) and St. Eustatius ($N = 663$), as observed two months after the passing of hurricanes Irma and Maria. (B) There was no significant relationship between the average stem size in plots and the proportion of deceased trees in these plots. (C) There was no significant relationship between stem density in plots and the proportion of deceased trees in these plots.

median stem size and stem size distributions of alive and deceased trees, using Mann–Whitney U -tests and two-sample Kolmogorov–Smirnov tests. We made these comparisons for each island and also compared size distributions within the separate elevation classes (Appendix S1). Second, to test whether stem size structure at the plot level affected the response to hurricanes, we correlated average stem size and stem density with the frequency of mortality. The chi-square and Mann–Whitney U -tests were performed in SPSS (IBM corporation, 2016, SPSS v. 24.0, Armonk, New York, USA); all other statistical analyses were executed in Matlab (Mathworks, 2016, Matlab v.9.0, Natick, Massachusetts, US).

RESULTS

Hurricane impacts were substantial on both islands: 93 percent of trees showed signs of severe (>75 percent) defoliation, 11 percent had lost secondary branches, 73 percent had lost both secondary and primary branches, 36 percent had been uprooted or snapped and stem mortality was 18 percent (Fig. 2). However, damage to individual trees was observed more frequently on St. Eustatius than on Saba (Fig. 2; Appendix S1). Specifically, more St. Eustatius trees exhibited defoliation (chi-square test: $\chi^2_1 = 32.4$, $P < 0.001$). St. Eustatius trees had also lost branches more frequently, particularly primary branches (chi-square test: $\chi^2_2 = 191.9$, $P < 0.001$). St. Eustatius forests also exhibited more frequent occurrences of severe (snapped/uprooted) tree damage (chi-square test: $\chi^2_1 = 47.2$, $P < 0.001$) and tree mortality (chi-square test: $\chi^2_1 = 10.9$, $P = 0.001$). On each island, variation across elevations was relatively small compared to the differences between islands (Fig. 2). On Saba, intermediate elevations showed slightly less defoliation and loss of branches (Fig. 2A, B; chi-square tests: defoliation: $\chi^2_2 = 11.1$, $P = 0.004$ branches lost: $\chi^2_1 = 35.3$, $P < 0.001$). On St. Eustatius, snapping and mortality was observed more frequently in the crater (chi-square tests: snapped: $\chi^2_3 = 9.2$, $P = 0.026$ dead: $\chi^2_1 = 11.3$, $P = 0.01$).

Pre-hurricane stem size distributions were positively skewed, and size distributions were similar across elevation classes on both islands (Appendix S1). Surprisingly, there were no significant differences between surviving and deceased stems in terms of median stem size (Fig. 3A; Mann–Whitney U -tests: Saba: $U = 35273$, $P = 0.81$; St. Eustatius: $U = 3120$, $P = 0.14$) or size distribution (two-sample Kolmogorov–Smirnov tests, Saba: $D_{241,31} = 0.22$, $P = 0.12$; St. Eustatius: $D_{527,136} = 0.05$, $P = 0.90$). These results suggest that there was no association between stem size and hurricane-induced mortality. This finding

was corroborated by our plot-level analysis of forest structure and impacts (Fig. 3B, C). Neither average stem size (Fig. 3B) nor stem density (Fig. 3C) explained the observed variation in mortality (non-parametric correlations: average stem size: $\rho = -0.10$, $df = 26$, $P = 0.63$; stem density: $\rho = -0.09$, $df = 26$, $P = 0.65$), or any of the other impact categories (Appendix S1).

DISCUSSION

For Saba and St. Eustatius, we observed that the hurricanes Irma and Maria were indiscriminate as a cause of death in terms of tree size (Fig. 3). Although this finding is in agreement with some observations of Caribbean forest responses to hurricanes (Bellingham 1991, Van Bloem *et al.* 2005, Metcalfe *et al.* 2008, Canham *et al.* 2010), it stands in contrast with others (Walker 1991, Ostertag *et al.* 2005, Vandecar *et al.* 2011, Lewis & Bannar-Martin 2012, McGroddy *et al.* 2013). Tree stability models suggest that associations between tree size and mortality may depend on storm strength, with storms of intermediate strengths being the most discriminate (Godfrey & Peterson 2017). Hence, the strength of the disturbance considered in this study may explain the size- and density-independency of observed responses. Indeed, the average mortality rates observed in this study (11–21 percent, Fig. 2) were relatively high compared to the studies that did report an association between tree size and damage (~2–9 percent in Walker 1991, Ostertag *et al.* 2005, Vandecar *et al.* 2011, Lewis & Bannar-Martin 2012, McGroddy *et al.* 2013). Within regions, an association between size and tree damage has been observed at intermediate post-cyclone mortality rates, but not when mortality was either higher (Metcalfe *et al.* 2008) or lower (Van Bloem *et al.* 2005), corroborating the above notion.

Given the proximity of the islands studied and their positions within the hurricane tracks (Fig. 1), differences in forest responses were surprisingly large (Fig. 2). The number of plots sampled was relatively small, but additional analyses suggested that our conclusions would not have altered substantially if more plots were sampled (Appendix S1). Previous studies have noted how differences in vegetation may mediate forest responses to hurricanes (Carrington *et al.* 2015, Luke *et al.* 2016b). If differences in vegetation were an important driver mediating forest responses in our study sites, however, we would expect larger differences between elevations within each island (Fig. 2). Instead, we suggest that it is more likely that the observed differences were driven by local wind patterns. Wind flows and gusts during hurricanes are complex, can occur in the lee of elevated landscape features, and are difficult to predict at the relevant spatial scales for the islands studied (10^2 – 10^3 m; Xi 2015, Gardiner *et al.* 2016). Repeated, multi-island surveys following hurricanes will be needed to establish whether certain island topographies create an inherent vulnerability to disturbance, or whether this is hurricane-specific.

It should be noted that our sampling design considered plots within the same elevation class as independent observations, which does not account for spatial patterns in forest impacts. This creates uncertainty when extrapolating the impacts of the hurricane to estimate total damage experienced by the forest

ecosystems of Saba and St. Eustatius, and therefore, such extrapolations should be interpreted with care. In future studies, characterization of spatial patterns in disturbance could be achieved through integration of ground surveys with remotely sensed data to identify spatial patterns in impacts (Rogan *et al.* 2011). Application of such approaches in multi-island studies provides a promising way to better understand how Caribbean forest impacts depend on the interaction between local topography and larger-scale hurricane characteristics.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.21cj2vp> (Eppinga & Pucko 2018).

SUPPORTING INFORMATION

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

APPENDIX S1. Additional background information about the study sites, survey data, and additional analyses.

TABLE S1. Overview of hurricanes passing within proximity of Saba and St. Eustatius between 1956 and 1999.

TABLE S2. Pair-wise comparisons of tree size distributions within each elevation class and the total tree size distribution for the island.

FIGURE S1. Frequency of undamaged trees on the Caribbean islands Saba and St. Eustatius, as observed two months after the passing of hurricanes Irma and Maria.

FIGURE S2. Relationships between average stem size in plots and tree density in plots and the proportion of stems that were defoliated, had lost branches, or were snapped/uprooted.

FIGURE S3. Results of a bootstrapping procedure assessing the relationship between number of plots sampled and the estimated errors for forest damage.

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