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Hurricanes, Storm Surge, and Pine Forest Decline on a Low Limestone Island

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Abstract

Hurricanes are a frequent disturbance in the western Atlantic impacting coastal forest structure and persistence. This study addressed the hypothesis that periodic hurricane-associated winds and storm surges can interact with sea-level rise to cause the demise of coastal pine forests, based on the response of the Florida Keys' last extensive tract of slash pine (*Pinus elliottii* var. *densa*) following Hurricane Irma (September 2017). Irma's winds reached Category 4 strength in the study area on Big Pine Key, and storm surge flooded the island's low limestone surface with salt water for the third time in 20 years, including Hurricanes Georges in 1998 and Wilma in 2005. Total mortality was 32% and was concentrated in the largest trees. Broken and uprooted trees that died immediately were distributed randomly across the elevation gradient, but trees without major stem damage that succumbed later occupied lower elevations. The extensive salt water flooding at low elevations was likely an agent of the mortality of slash pine, a fresh water–dependent species. Mortality due to Hurricane Irma contributed to a 1998–2018 decline in pine tree density and biomass of 74% and 80%, respectively. These dynamics were characterized by pine recruitment that was minimal in comparison with the three hurricane-driven mortality episodes. The data suggest that the 6 cm sea-level rise over the period exacerbated storm surge mortality by ponding salt water over more of the land surface, and the resulting scarcity of mature trees contributed to recruitment failure. In effect, the population declined at each disturbance, sea-level rise magnified these losses, and the local resilience of the population, i.e., its capacity to recover, was exceeded.

Keywords Sea-level rise · Hurricanes · Resilience · Pine rocklands · Islands · Storm surge

Introduction

Within the world's hurricane belts, coastal landscapes on low oceanic islands are periodically impacted by tropical cyclones that bring violent winds and salt water flooding. Where hurricanes are frequent, they exert a critical control on the life cycle of island forests, including both intertidal forested wetlands and any well-drained forests that may be embedded within the wetland matrix. The capacity of either of these forest types to respond to storm surge and wind damage is likely affected by rising seas associated with climate change (Williams et al. 1999). In fragmented upland forests, this threat is especially pressing, as the demographic response may be compromised by a reduction in habitat extent brought on by sea-level rise.

In the lower Florida Keys, forests of South Florida slash pine (*Pinus elliottii* var. *densa*) historically occupied most areas more than a few decimeters above the high tide line, but in recent decades these stands have been severely reduced due to development pressures and rising seas (Snyder et al. 1990; Ross et al. 1994). As recently as the late 1980s, extensive pine forests were present on five islands, but today they maintain their characteristic structure—an open, monospecific pine canopy, an understory dominated by palms, and a rich herbaceous ground layer—on only one island, Big Pine Key. Stand structure is a key determinant of the ecosystem functions and environmental benefits of coastal pine forests. Structural characteristics govern timber production and carbon sequestration and often control the composition of

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understory vegetation, wildlife habitat quality, recreational opportunities, and esthetic values. Stand structure links closely with the disturbance history of a site (Pickett et al. 1989), which in pine forests of the southeastern USA typically includes frequent fires of low intensity and recurrent hurricanes and tropical storms. The impacts of these disturbances are modified by interactions with global change factors; for instance, the recent rapid rate of sea-level rise is already accentuating the effects of hurricanes by bringing storm surges further inland and decreasing the drainage capacity of a site during the post-storm period (Ross et al. 2009).

By incorporating juvenile trees that represent the stand's future and mature trees that govern its present, stand structure can provide an effective measure of forest condition. This is especially true of stands dominated by a single foundation tree species (Ellison et al. 2005). Below, we describe the structural dynamics in one such forest, slash pine (*P. elliottii* var. *densa*) stands impacted by recent disturbances, including a direct hit from Hurricane Irma in September 2017. The paper follows on an earlier manuscript (Sah et al. 2010) that addressed pine mortality associated with a set of moderate-to-low intensity-prescribed fires (1998–2001) and the storm surge occasioned by the close passage of Hurricane Wilma (October 2005). In that paper, we found that fire-initiated mortality on our sites on Big Pine Key, FL, USA, was concentrated among small trees, but storm surge killed mostly large individuals; the joint effect of the two disturbances was to narrow the size structure on sites affected by both. In this study, we examine changes to pine forest structure during the subsequent decade (2008–2018). Hurricane Irma was the most notable event during the period, bringing not only storm surge but the force of destructive winds to the entire island, and we focus on the structural impacts of the storm that were evident 9 months later. We explicitly quantify wind speeds and direction, extent of storm surge flooding, and amount of rainfall received during and in the months following the storm, as these physical factors are the major determinants of ecological response across the landscape and differentiate one hurricane from another. To better assess the long-term trajectory for the pine forest, we also expand our temporal scope to the entire 1998–2018 period. From this broader perspective, we ask whether the press of sea-level rise on low limestone islands exacerbates the demographic impacts of hurricanes' physical forces, i.e., violent winds and salt water flooding.

Methods

Study Area The study was conducted in the Florida Keys, an archipelago of limestone islands curving south and west from an origin near the southeastern tip of the Florida mainland to its terminus in Key West, about 220 km distant (Fig. 1). The limestone backbone of the island chain is a fossil coral reef; surrounded by salt water, the high permeability of the coral rock usually results in a brackish groundwater. However, in the islands closest to Key West (the lower Keys), the coralline rock dips beneath a surficial oolitic limestone. Compared with the coralline rock, the permeability of the oolite is low, allowing fresh groundwater lens to form on the larger and more elevated islands (Halley et al. 2004). This variation in hydrogeologic characteristics has long been reflected in the vegetation of the lower Keys, where forests of the fresh water–dependent slash pine once dominated the landscape. However, as sea level rose, the freshwater resources of the less elevated lower Keys islands became depleted (Ogurcak and Price 2019), and the pine forests transitioned to hardwood hammocks and other more salt-tolerant vegetation that prevailed elsewhere (Ross et al. 1994). Today, extensive pine forests persist only on the highest and largest of the lower Keys islands, Big Pine Key.

Experimental Design In 1998, we initiated a set of experimental treatments to explore the effects of fire season on Big Pine Key forests. The experiment involved a total of 18 1-ha plots. Three plots were established in relatively homogeneous blocks of pine forest in six parts of the island, and three treatments—Summer Burn (June–August), Winter Burn (December), and No Burn Control—were randomly assigned to plots within each block. Burn treatments were carried out as planned in two blocks per year during 1998 and 1999, except that one Winter Burn treatment was not implemented. Fires planned for 2000 were delayed until 2001, when all sites were burned during summer (Snyder et al. 2005).

In Spring 1998–2000, the diameter of all pine trees ≥ 5 cm DBH were determined prior to treatment, and stem locations were mapped by the interpoint and right-angle prism methods (Boose et al. 1998; Reed et al. 1989). Several months after sampling began in the plots to be burned in 1998, Hurricane Georges made landfall in the lower Keys at Category 1 strength (Pasch et al. 2001). Pine mortality due to the storm was spotty, and any trees killed in Georges were not included in the initial structural data. Tree survival and diameter were determined again following the experimental treatments in all 18 plots. In 2008, we resurveyed trees in all plots and completed an analysis and interpretation of stand dynamics through that time (Sah et al. 2010).

For our most recent monitoring activities, we selected eight plots from those described above. The selected plots represent a relatively wide range of elevations on either side of a modest "ridge" that bisects Big Pine Key, in four of the 1998 experimental blocks (Fig. 1). In January 2018, 4 months after Hurricane Irma, we re-surveyed trees in these eight plots, incorporating stems that had reached 5 cm DBH since 2008. We located and measured the DBH of both live and dead trees, noting whether dead trees had been hurricane-killed or had died prior to the storm, based on the condition of twigs and

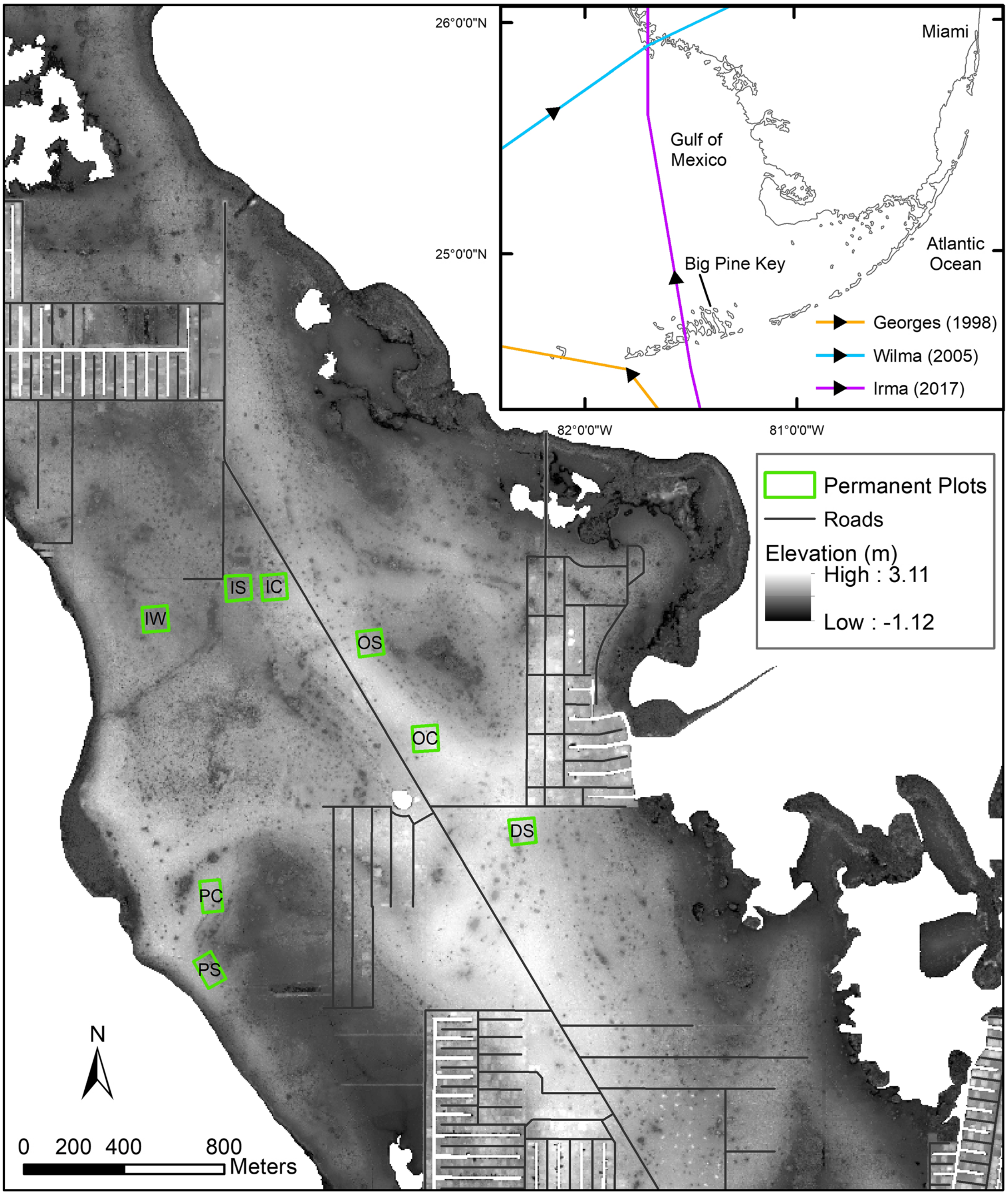


Fig. 1 Location of 1 ha permanent plots on Big Pine Key relative to island elevation as determined from LiDAR-derived DEM. Inset shows location of Big Pine Key in the lower Florida Keys relative to South Florida, as well as tracks of Hurricanes Georges (1998), Wilma (2005), and Irma (2017)

bark. For those that died since the hurricane, we recorded whether they were uprooted, suffered trunk breakage, or died standing with intact crown form. We also recorded the direction of treefall of all uprooted trees. For live trees, we noted the percentage of brown or red needles in the remaining crown. In July 2018, we resurveyed these trees, noting changes in condition during the intervening 6 months.

During the January 2018 survey, we also searched for evidence of storm surge visible from five evenly spaced transects that crossed each plot. When a pile of water-transported material was observed, its location, length, and width were recorded, and an average depth was determined by probing with an aluminum rod. The total area of wrack deposited per plot was estimated by assuming an elliptical shape for each pile.

The permanent plot framework in which our post-hurricane observations were integrated allowed us to examine storm responses within the context of long-term changes in pine population structure. Though our censuses were 10 years apart, they provided information on changes in tree biomass and patterns of recruitment at the stand level and growth and mortality based on repeated sampling of individual trees. Biomass was calculated using allometric equations developed for various tree components in a North Florida slash pine plantation (Gholz and Fisher 1982). Growth of individual trees was expressed as changes in diameter at breast height per year.

Growth, mortality, and recruitment processes are all affected by underlying site characteristics, as well as by disturbances that have affected each site. In Table 1, the elevation of each site is presented, along with the history of the fires and hurricanes experienced by the eight forests during 1998–2018. This physical and historical information serves as an important background for understanding the dynamics of the pine populations during the period and for projecting the pine rockland ecosystem's vulnerability going forward.

Data Analysis Irma's winds were reconstructed for multiple Big Pine Key field points based upon data from the HURDAT2 climatology (Landsea and Franklin 2013) used to approximate the parameters of the Holland (1980) analytical tropical-cyclone wind profile. This procedure is a reformulated version of the HURRECON model employed by Boose et al. (2004). HURDAT2 contains position, minimum central pressure, maximum wind, and radii of hurricane force (65 kt), 50 kt, and gale force (35 kt) winds NE, SE, SW, and NW of the center at nominal time intervals of 6 h, i.e., 00, 06, 12, and 18 UTC. In this analysis, the HURDAT values are interpolated to 3-h intervals. Landfalls at Cudjoe Key and Marco Island (1300 and 1930 UTC on the 10th of September) did not occur at even multiples of 6 h. They are retained, but not interpolated. The Holland profile provides a closed-form expression for the radial variation of axially symmetric pressure, from which winds at the field points can be computed using the gradient-wind relation, taking into account asymmetries due to Irma's translation. The profile depends upon maximum wind, V_{max}; radius of maximum wind, R_{max}; and the Holland "B parameter," which determines the sharpness of the eyewall wind maximum. Neither R_{max} wind nor B is tabulated in HURDAT2.

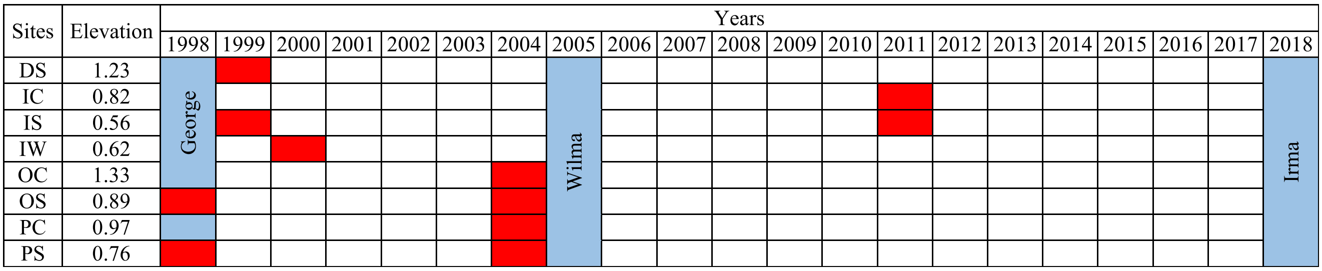
The motion is approximated by differencing the center positions and dividing by the time intervals between them. The resulting speed, C, is subtracted from V_{max}. It is then multiplied by the sine of the angle between Irma's motion vector and the radius to the field point and added to the modified profile wind value at that point. Thus, the wind at any given radius is strongest on the right side of the motion facing in the direction of motion and weakest on the left side. Finally, if a field point lies inside the eye, i.e.,$r < R_{max}$, the profile wind is replaced by $V_{max}-C$ and corrected for motion as described above.

Since neither R_{max} nor B is available from HURDAT2, R_{max} is obtained from available radar imagery since it is a nautical mile or two greater than the inner radius of the radar eye (Shea and Gray 1973). B is generally close to unity. It is adjusted subjectively to produce agreement with the HURDAT outer wind radii and to maintain time continuity throughout the reconstruction.

As the hurricane brought both strong winds and storm surge, mortality of trees that remained standing without evidence of major structural damage but had lost all needles by the July survey could be attributed either to wind or storm surge. We investigated the role of storm surge, using elevation as a proxy for the likelihood of flooding by saline water. Given the previously established relationship between tree size and mortality (Sah et al. 2010), it was also important to examine relationships between size and the three categories of hurricane mortality distinguished in this study. We obtained the elevation of each tree (NAVD88 m) as well as average plot elevation from a LiDAR-derived digital elevation model (DEM) that had a horizontal resolution of 1 m and vertical accuracy of 0.17 m at 95% confidence level (Robertson and Zhang 2007). The elevations of individual trees and average plot elevation was extracted from the DEM using Spatial Analyst in ArcGIS 10.4.

Spatial patterns in mortality and recruitment were assessed using regressions performed in R v.3.3.3 (R Core Development Team 2017). Using multinomial logistic regression (Venables and Ripley 2002), we assessed the relationships between tree size (DBH), elevation, location of the plots on the island (site), and tree mortality from Irma in each of the abovedefined damage categories (snapped, uprooted, and

Table 1 History of fires (in red) and hurricanes (in blue) experienced by forests in eight sites. Elevations are in meter (NAVD88)



Sites	Elevation	Years																				
		1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
DS	1.23	🟦 George	🟥						🟦 Wilma													🟦 Irma
IC	0.82	🟦							🟦						🟥							🟦
IS	0.56	🟦	🟥						🟦						🟥							🟦
IW	0.62	🟦		🟥					🟦													🟦
OC	1.33	🟦						🟥	🟦													🟦
OS	0.89	🟥						🟥	🟦													🟦
PC	0.97	🟦						🟥	🟦													🟦
PS	0.76	🟥						🟥	🟦													🟦

standing dead), using live trees as the reference. The preferred model was selected by comparing the Akaike information criterion (AIC) between nested models. *p* values for regression coefficients were determined using *Z* tests. We derived relative risk ratios by exponentiating model coefficients. Finally, we used the fitted function (Chambers and Hastie 1992) to derive predicted probabilities of each damage class based on models that independently considered the impact of elevation and DBH. To investigate variation in pine recruitment into the tree stratum, we conducted a linear regression with mixed effects, with average plot elevation and survey year as independent variables, using the lmer function in lme4 package; *p* values were calculated using Satterwaite approximations to degrees of freedom (Bates et al. 2015). Nested models were compared using krmodcomp function in package pbkrtest (Halekoh and Højsgaard 2014).

We used quantile regression to model the diameter growth of individual trees during 1998–2008 and 2008–2018. Whereas most regression applications focus on the rate of change in the mean of a response variable as a function of one or more predictors, quantile regression allows the analysis of distinct portions of a heterogeneous distribution (Cade and Noon 2003). We tested exponential models that predicted growth from the initial size of trees in two categories: moderate growth (0.50 quantile in the growth × DBH distribution, i.e., 50th percentile and above) and fast growth (0.90 quantile, i.e., 90th percentile and above).

Results

Approaching from the south after passing through the Florida Straits and grazing the north coast of Cuba, Hurricane Irma reached Big Pine Key on the morning of September 10, 2017. Maximum sustained winds at landfall were southerly, estimated at ~ 115 knots (130 mph) by the National Hurricane Center (Cangialosi et al. 2018). Modeled wind speeds, directions, and barometric pressures provide a clear picture of the conditions on the ground during the passage of the storm (Fig. 2a–c). Initial winds were from the east but swung rapidly to the south and finally west as the storm's center crossed the Keys about 16 km west of the island (Fig. 2b). However, the predominant direction of toppled trees was towards the west (60% of uprooted trees), suggesting that much damage to the forest occurred as winds were rising, at about 60 knots, but still easterly (Fig. 2d).

Storm surge drove water levels on Big Pine Key to 2.4 m above MHHW (Cangialosi et al. 2018), flooding the ground surface with salt water throughout the island. Piles of storm-transported wrack were present in all portions of the pine forest, but the most massive accumulations were concentrated in plots OS, OC, and DS in the eastern half of the study area (Fig. 1), where they covered as much as 1% of the ground surface. The deposits, which often exceeded 100 m^2 in area and 0.5 m in depth, were comprised mostly of organic material that originated on the island itself, especially pine litter, augmented by mangrove propagules in some cases. The distribution of wrack deposits suggests that storm surge crossed the island from the east, depositing transported material on the east slope of the island's central ridge as the water shallowed. Salt water then infiltrated into the aquifer and was still detectable during geophysical surveys conducted in May 2018 (Kiflai et al. In review).

Thirty-two percent of the pine trees in our plots died as a direct result of Hurricane Irma. The percentage of dead trees increased monotonically with size, from 24% for trees < 15 cm diameter to 52% for trees ≥ 25 cm DBH. Forty percent of killed trees were standing dead without notable structural damage, 38% had broken trunks, and 22% were uprooted, and these proportions did not vary substantially across size classes (Fig. 3).

The multinomial logistic regression model that best explained the patterns of tree mortality included elevation, DBH, plot, and the plot to elevation interaction as predictor variables (AIC = 2693, *n* = 1566). Tree size was a significant predictor of tree mortality for all damage categories, whereas elevation was only significant as a predictor for standing dead trees (Table 2); however, the DBH to elevation interaction was non-significant. Plot and the interactions of elevation with plot were significant for individual damage classes in several plots. The relative risk ratios and predicted probabilities for the damage categories indicated that for each unit increase in DBH, the likelihood of mortality in any of the three forms also increased (Table 2, Fig. 4a). Elevation had the opposite effect; as elevation increased, the probability of mortality decreased, but only in the standing dead class (relationships for snapped and uprooted classes were not significant) (Table 2, Fig. 4b). This finding suggests that the mortality of standing dead trees resulted from storm surge rather than wind.

The mortality event precipitated by Hurricane Irma was only one episode in a long-term decline in the population of *P. elliottii* var. *densa* in the study area (Fig. 5). During the two-decade period between 1998 and 2018, mean tree density declined from 515 to 133 stems ha^{-1} (74%), basal area across the eight stands declined from 8.0 to 1.87 m^2 ha^{-1} (77%), and aboveground biomass declined from 44 to 9 Mg ha^{-1} (80%) (Fig. 5). The decrease was evident during both the 1998–2008 and 2008–2018 periods, and all size classes were affected. While some of the variation among stands is attributable to the occurrence and intensity of the fires they experienced, the broad downward trend is unmistakable and extends beyond a single event or site.

With mortality rates averaging 64% per decade (Fig. 6), maintenance of a viable *P. elliottii* var. *densa* population requires, at minimum, (1) prolific recruitment and (2) rapid growth into the large size classes responsible for most pine

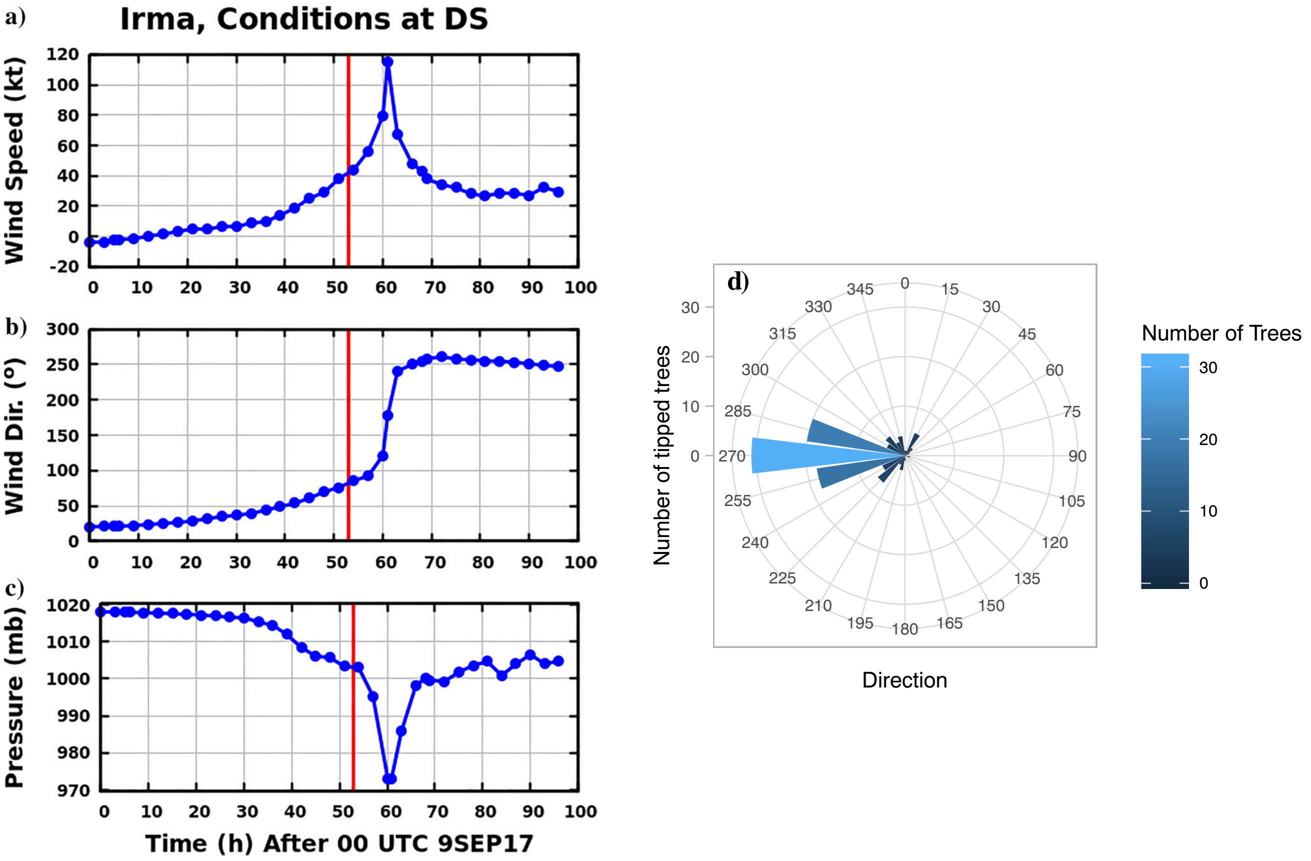


Fig. 2 Estimated meteorologic characteristics and treefall directions associated with the passage of Hurricane Irma over Big Pine Key. Meteorologic estimates are for Site DS. **a** Wind speed, **b** wind direction, **c** barometric pressure, and **d** rose diagram of fall directions (tree base to crown, n = 114) of all uprooted trees in 8 study plots. Red line indicates the time at which the majority of trees fell, based on fall direction

seed production (Platt et al. 1988). Over the course of the study, pine populations on Big Pine Key exhibited neither of these characteristics. Rates of ingrowth into the tree stratum observed in 2008 (19 trees ^{h}a^{-1} decade^{-1}) and 2018 (25 trees ha^{-1} decade^{-1}) were modest (Fig. 7), especially when considered against the high mortality that took place during

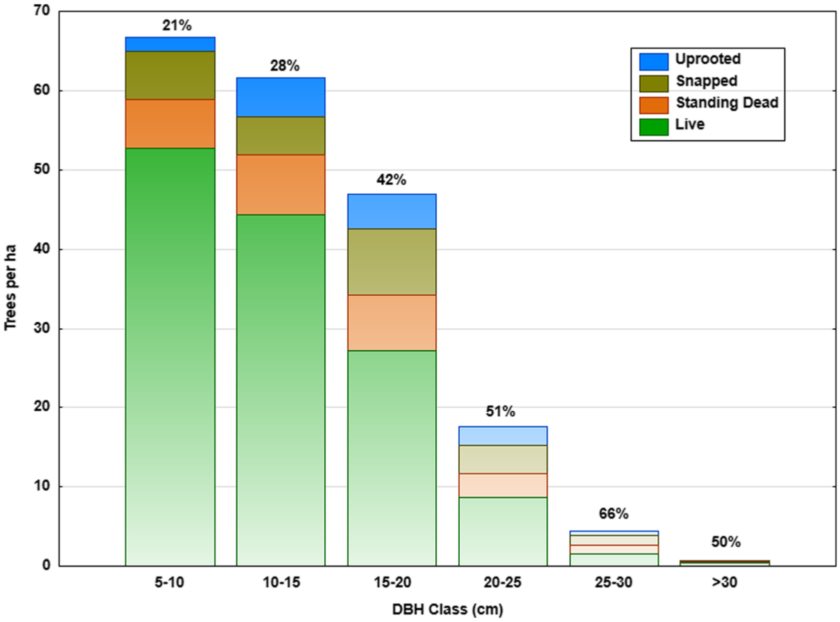


Fig. 3 Trees per ha live and dead in three categories of trees killed by Hurricane Irma in different size classes. Percentages at top of bars indicate percentage of dead trees of all three categories

Table 2 Relative risk ratios, i.e., the ratio of the probability of a tree being in each damage category (standing dead, snapped, and uprooted) relative to the baseline category (live), for a unit change in each predictor variable as determined from the multinomial logistic regression equation. Non-significant predictor variables are excluded for brevity. Plots are referenced to plot DS. Significance is reported for regression coefficients as follows: * $p < 0.01$, ** $p < 0.001$

Variable	Standing dead	Snapped	Uprooted
(Intercept)	4.67E+00	2.23E−01	2.54E−02
DBH	1.11E+00**	1.12E+00**	1.12E+00**
Elevation	2.57E−02**	2.25E−01	6.43E−01
Plot OC	4.34E−04*	5.28E−01	9.74E−01
Plot PC	4.32E−05**	1.71E−04**	1.86E−03
Elevation: plot IC	2.90E+01	3.27E+02*	3.03E+01
Elevation: plot OC	3.06E+02*	1.40E+00	1.54E+00
Elevation: plot PC	1.78E+03**	1.75E+03**	1.61E+02

the periods. Little period-to-period consistency in the relative density of juveniles among sites was evident, and inter-site differences were unrelated to elevation; inclusion of average plot elevation in a model with survey year and plot as predictors of ingrowth did not result in greater explanatory power.

Tree growth on Big Pine Key was quite slow, averaging 0.12 cm year^{-1} across all sizes and both sampling intervals (Fig. 8a–b). However, diameter growth was faster in small individuals than in large trees, and a handful of juveniles (5–10 cm DBH) increased in diameter by as much as 0.5 cm year^{-1}. Quantile regressions of growth on initial diameter were not significant for 2008–2018 but were significant for the 1998–2008 period. For the latter period, the regression model for trees in the 90th quantile indicated growth rates of 0.37 cm year^{-1} for trees 5 cm DBH in 1998 and 0.30 cm year^{-1} for 20 cm DBH trees. The regression for trees in the 50th quantile over the same period estimated growth rates of 0.21 cm year^{-1} and 0.17 cm year^{-1} for the same size classes (Fig. 8a). Based on these regression models, a tree that maintained itself in the 90th quantile throughout its development would take 45 years to grow from 5 to 20 cm diameter, and a tree in the 50th quantile would require nearly 80 years to reach the same size.

Discussion

In hurricane-prone portions of the Caribbean and North American coastal zone, massive cyclonic events are often remembered as important landmarks in the history of places; prominent examples are the Great Miami hurricane of 1926, Hurricane San Felipe in San Juan, P.R. in 1928, and Hurricane Katrina (2005) in New Orleans. Similarly, hurricanes frequently play a transformative though less well-remembered role in the forests they touch, one from which recovery may or may not eventually ensue. Of course, in neither city nor forest is history determined entirely by a single storm, as other pre-disposing events or conditions modify the impact of the hurricane, or the community's response afterward.

On Big Pine Key, Hurricane Irma rearranged the lives of several thousand human residents, but our focus here was on the mark it left on a pine forest that had experienced multiple hurricanes and fires during the previous two decades. Such disturbances are intrinsic to the ecology and evolutionary development of the dominant tree, *P. elliottii* var. *densa*, and their frequency and intensity during the period of study were well within the historical range of variation. However, one element that has changed from pre-settlement times is a reduction in the extent of pine forest, caused primarily by expansion of residential development. A second and probably more significant change is the accelerated rise in sea level since the mid-twentieth century (Church and White 2006), which reduced freshwater storage on the island while raising the level of the groundwater closer to the surface. As these changes may reduce the resilience of the foundational pine population, i.e., weaken its capacity to renew itself and thrive following

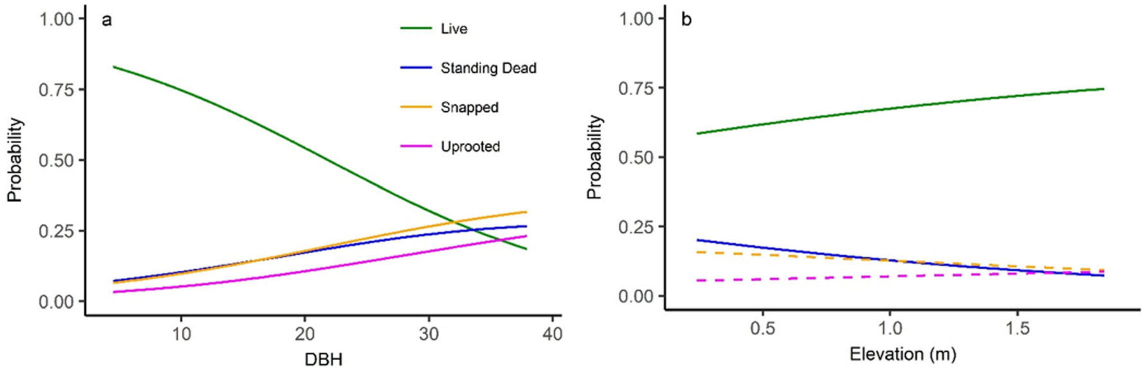


Fig. 4 Predicted probabilities of a tree falling into one of three damage categories (standing dead, snapped, uprooted) compared with being undamaged from the hurricane (live) as a function of **a** DBH and **b** elevation. Dashed lines in **b** indicate that elevation was not significant for that category at $p < 0.05$

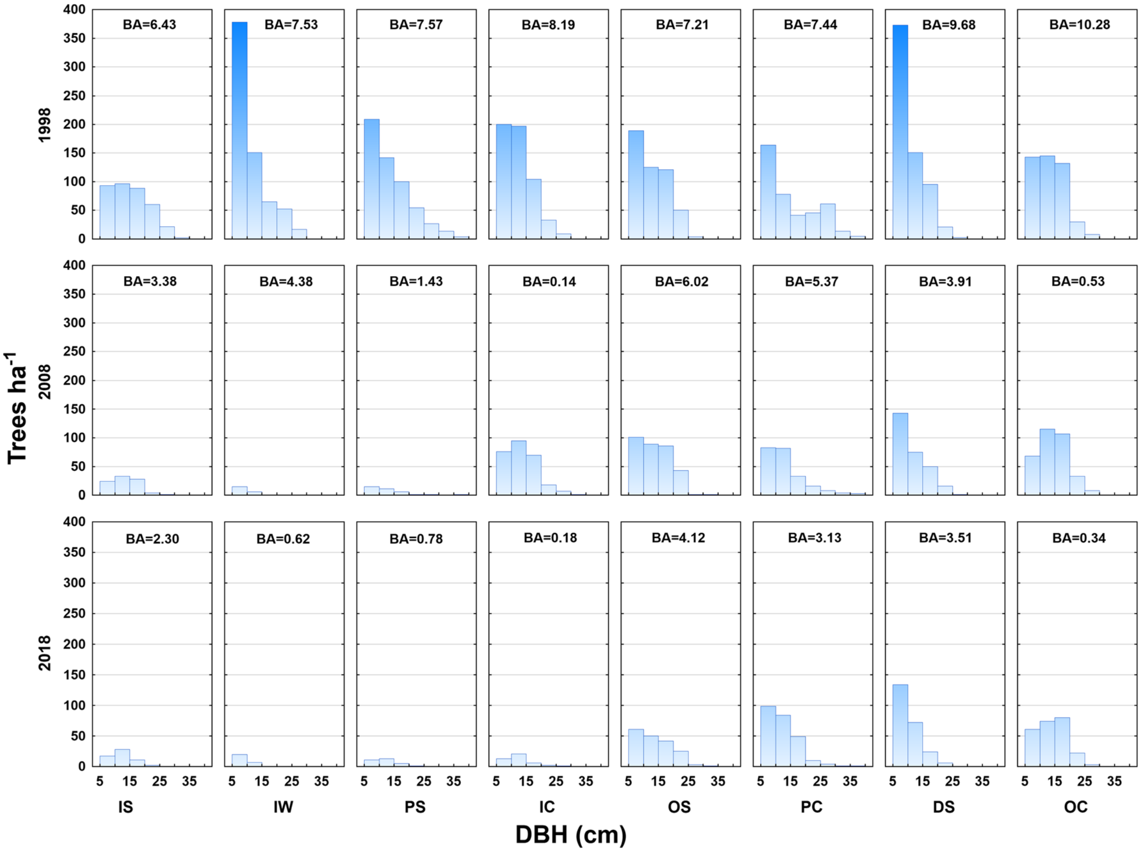


Fig. 5 Trees per ha by diameter class in all sites in 1998, 2008, and 2018. Sites are arranged from left to right in order of increasing elevation (for elevation values see Table 1). BA, basal area in $m^2 \cdot ha^{-1}$

Fig. 6 Decadal mortality percentage (1998–2008 and 2008–2018) by diameter class

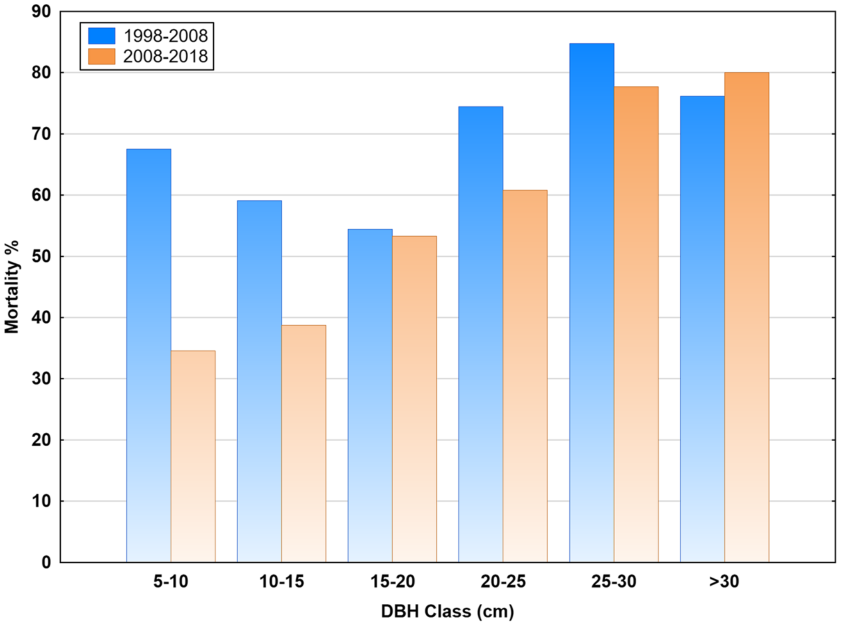
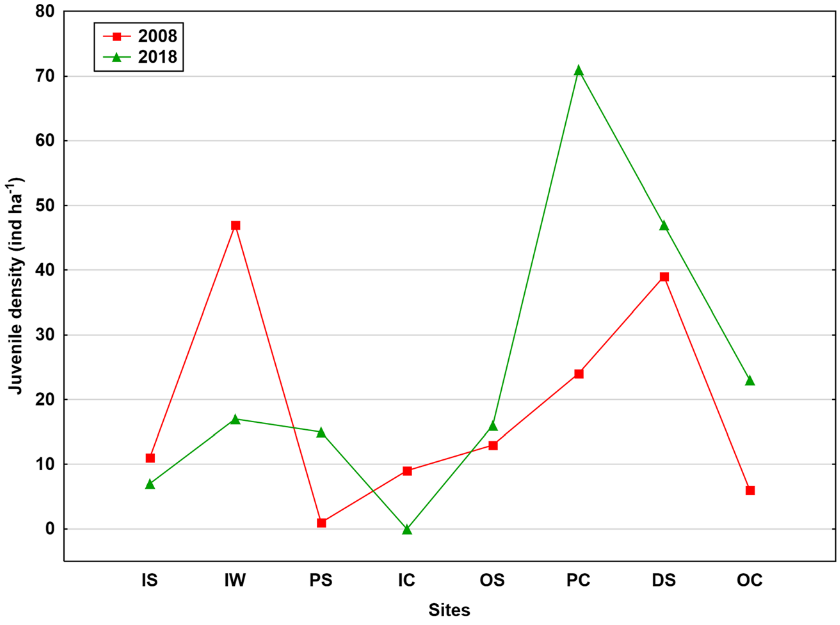


Fig. 7 Cumulative juvenile recruitment during 1998–2008 and 2008–2018, based on in-growth into the tree stratum (≥ 5 cm DBH) recorded in 2008 and 2018, respectively. Sites are arranged from left to right in order of increasing elevation (for elevation values see Table 1)



disturbance, they provide important context for assessment of the storm's influence and possible management responses.

The Influence of Hurricane Irma on Forest Structure

Effects of hurricanes can be direct or indirect, with some in the latter category unfolding over years or centuries. Our results paint a picture of the short-term changes in pine populations evident in the year after Hurricane Irma, but here we speculate as well on likely longer-term impacts.

Ten months after Hurricane Irma struck Big Pine Key, a majority of the pine mortality attributable to it came from individuals that suffered major structural damage. As in earlier studies of hurricane-damaged pine forests, a disproportionately high number of these snapped and uprooted trees came from the larger size classes (Gresham et al. 1991; Platt et al. 2000). Since these trees are the primary contributors to seed production, storm-induced episodes of large-tree mortality can have adverse consequences for future pine populations by affecting recruitment. In a 5-year study of pine regeneration in Everglades National Park, Ruiz et al. (2001) found that *P. elliottii* individuals ≥ 20 cm diameter were responsible for 92% of total cone production. Similarly, Platt et al. (1988) found that cone production was minimal in *Pinus palustris* trees < 20 cm DBH in southern Georgia forests, but increased sharply at larger tree sizes. In the aftermath of a hurricane, the loss of large trees results in an immediate reduction in seed production, one which is apt to persist for decades.

Broad geographic factors, local exposure, and substrate variation all affect the frequency of windstorms severe enough to uproot trees at a given location. Irma was a Category 4 hurricane at landfall, but our meteorological model suggests that the easterly winds that uprooted trees embedded in the limestone surface on Big Pine Key occurred earlier in the storm's passage, and were therefore only of Category 1 strength. Category 1 winds are expected to recur at a given South Florida location every 5 years, while winds of Category 4 strength occur every 15 years (Keim et al. 2007). Other factors that may affect the likelihood of a tree uprooting include its degree of exposure and rooting depth (Francis and Gillespie 1993). Wind exposure is typically high in South Florida pine forests due to the open, woodland structure they reach early in their development; this is especially true at present on Big Pine Key, where tree density is extremely low. In the rockland setting, the rooting system of pine trees is predominantly surficial, despite the presence of a central taproot that is able to penetrate the bedrock. We are not aware of any mechanical tests of the wind firmness of trees rooted in a rockland environment, where the plane of rupture typically occurs at a shallow depth within the limestone bedrock.

Soon after Hurricane Irma and increasingly over the next 10 months, relatively large dead pines that had sustained little apparent trunk or branch damage became common across the Big Pine Key landscape. Pine trees are reported to be sensitive to salt spray, with effects materializing within a few days or weeks following a storm (Wells and Shunk 1938; Little et al. 1958); thus, wind-driven aerosol salts may have been the cause for some mortality that occurred during the first month or so after the storm. However, our finding that standing dead trees were most abundant at low elevations suggests that the predominant cause of their death was storm surge flooding. Flood waters persist longest at such sites, as salt water recedes by overland flow and infiltrates into the lens at low points on the landscape. A similar pattern was noted in coastal South Carolina, where storm surge from Hurricane Hugo (1989) resulted in greater mortality of trees located in swales compared with ridges (Gardner et al.

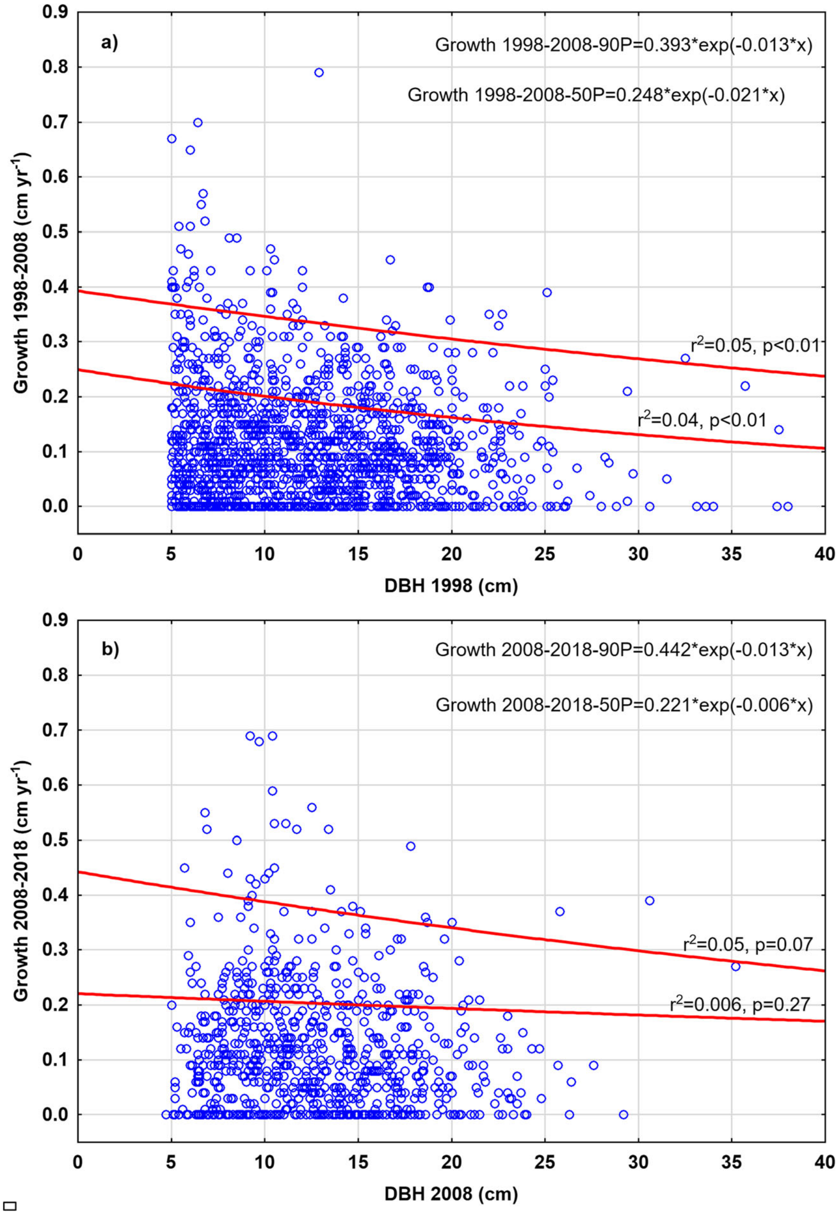


Fig. 8 Diameter growth in **a** 1998–2008 and **b** 2008–2018 and initial diameter relationship. Data was fitted by an exponential distribution to the 0.50 and 0.90 quantile data points represented by the lower and upper red lines in **a** and **b**

1991), presumably as a result of salt stress. Pine trees in the lower Florida Keys rely on groundwater to meet most of their fresh water requirements (Sternberg et al. 1991; Ross et al. 1994; Ogurcak 2015), and mortality may result if storm surge causes salt water to intrude into the fresh water lens for an extended period. In two Big Pine Key plots (OC and OS), large groups of standing dead trees were found in close proximity to debris piles that lodged at the western edge of an interior wetland that normally holds fresh water. Elsewhere on the island, post-hurricane geophysical surveys identified localized areas of saline groundwater, which were especially concentrated at lower elevation locations (Kiflai et al. In review).

Rainfall during and after a hurricane can lessen the impact of salt stress on vegetation. Precipitation may flush concentrated salts out of the soil, dilute surge waters, and limit the infiltration of saline water into the fresh water lens. Almost 32 cm of rain fell on Big Pine Key during the passage of Hurricane Irma (rainfall data for station TS607 on Big Pine Key, available at https://mesowest.utah.edu/). In contrast, only 5 cm of rain fell during Hurricane Wilma (2005), the last hurricane to have impacted these pine forests (Beven et al. 2008). However, an extended dry period that followed Wilma (Ross et al. 2009) was repeated in the 7 months after Hurricane Irma, during which rainfall was only 18 cm, compared with the 30-year average of 46 cm (1981–2010, Marathon Airport). In the years following Hurricane Wilma, cumulative mortality in pine stands located at elevations below 1 m exceeded 50% (Sah et al. 2010). Given similar post-hurricane climate conditions, additional mortality of pine trees attributable to storm surge from Irma is likely.

Changes in Pine Population Structure (1998–2018)

The pine population of Big Pine Key experienced a precipitous decline in density, basal area, and aboveground biomass during 1998–2018. As in any such population, this downward trajectory resulted from mortality rates that were not compensated by the growth of surviving trees and the recruitment of new individuals. We discuss these processes below.

The data presented here and in Sah et al. (2010) indicate that the disturbances listed in Table 1 were large contributors to the high mortality rates experienced during the last two decades. Hurricane Irma was a prime example, accounting for 74.4% of all pine deaths between 2008 and 2018, while an additional 17% was attributable to a 2011 prescribed fire that briefly escaped control. However, it should be recognized that neither the fire nor the hurricane frequency during the study period was abnormally high. For instance, the average of 1.38 fire events per stand over the 20-year study period (Table 1) is hardly excessive. In fact, it equates to a mean return interval of 14 years, which is less frequent than the 2–10-year interval understood to be the natural fire frequency in South Florida pine rocklands (Snyder et al. 1990), and this *infrequency* may represent a problem in itself. Moreover, the occurrence of two Category 1 (Georges and Wilma) and one Category 4 (Irma) hurricanes during these two decades is about what one should expect based on the historical record (Keim et al. 2007). However, though the frequency and intensity of recent hurricanes are well within the range of historical variation, our data suggest that the storm surge associated with these events is largely responsible for the decline in large trees evident in Fig. 5. By bringing the water table incrementally closer to the surface each year, sea-level rise has caused storm surge events to be more pervasive across the island, and the residual effects of the salt water to be more persistent. The limited viability of low elevation sites for pine trees on Big Pine Key has also been demonstrated with dendrochronological data (Harley et al. 2015). They found that the oldest trees on the island, over 200 years old, were found at the highest elevations, and suggested that low elevations were disturbed more often by storm surge, and consequently presented a younger age structure.

Disturbances are generally followed by a period of recovery, as small trees and new recruits occupy resources freed by the death of large individuals (Oliver 1980). However, with multiple disturbances occurring throughout the study period, our sampling for tree growth was far too infrequent to evaluate the extended responses associated with individual events. An additional issue in such an analysis is the need to distinguish positive effects over an extended period from the short-term stress that follows immediately after a disturbance, such as that experienced by pine trees impacted by Hurricane Wilma (Rebenack et al. 2018). Our data, which reflect a mixture of responses at both time scales, do reveal a current environment in which most *P. elliottii* var. *densa* individuals grow very slowly, and even trees that achieve excellent growth, i.e., match growth rates reported for mature trees of the same species on the Florida mainland (Platt et al. 2000), require a half-century or so to reach reproductive size.

By expanding the period during which pines are pre-reproductive or produce only a few cones, slow growth may impose an important constraint on regeneration in Keys pine forests. Other constraints include (a) the climatic and hydro-edaphic factors that limit seed germination and survival in the skeletal Keys soils, (b) the fire regime, especially the effect of fire, or the lack of it, on seedbed characteristics, and (c) fire as a direct agent of seedling mortality (Ross et al. 1992). Whether due to seed source limitation or the environmental factors listed above, a very modest number of seedlings have been able to pass through these filters to reach sapling size on Big Pine Key. In fact, ingrowth rates 17 and 13 times higher would have been necessary to match the mortality rates displayed in Fig. 6 during the 1998–2008 and 2008–2018 periods, respectively, thereby maintaining population size at the 1998 level.

Conclusions

The material presented above documents a 20-year decline in the condition of the *P. elliottii* var. *densa* population on Big Pine Key, where it is the foundation species in the single remaining, functional pine rockland ecosystem in the Florida Keys. Due to the site's protected status within the Key Deer National Wildlife Refuge, the extensive coastal development that has impacted other Florida coastal ecosystems has not been an important factor in the most recent decline. Rather, it has been driven by two endemic pulse disturbance types, hurricanes and fires, in conjunction with eustatic sea-level rise, a ramp disturbance that resulted in a local increase in adjacent marine water level of ~ 6 cm over the period. The two hurricanes that had such a large hand in the species' recent decline were of intensities that have occurred repeatedly throughout the island's history, presumably without catastrophic effects on the population. Why now? We suggest that (1) sea-level rise has exacerbated storm surge mortality by ponding salt water over more of the land surface, or for a longer duration, and (2) under current conditions, the pines are too slow growing and the regeneration too sparse to replace the lost individuals. In effect, the population steps down at each pulse disturbance, the ramp disturbance magnifies the size of the downward step, and the local resilience of the population, i.e., the capacity to retrace its steps, is exceeded.

In earlier times when the sea level was stable or slowly increasing, high elevation pine rocklands likely served as refugia able to supply the seeds needed to repopulate low elevation areas impacted by infrequent storm surge events. As sea level increased, however, overtopping storm surges came more frequently to any location, and the refuges became too small to serve the same function. The predicted increase in the frequency of strong hurricanes (Bender et al. 2010) may make the occurrence of extensive storm surge flooding even more common in the future, eliminating viable habitat entirely.

Is it possible for management action to forestall the decline we have documented? Like the rich *Pinus palustris-Aristida stricta* ecosystems to the north, the life cycle of the *P. elliottii*-dominated South Florida pine rocklands is marked by frequent hurricanes and tropical storms, but revolves around a pine-fire axis (O'Brien et al. 2008). The dominant pines require fire to prepare their proper seedbed, and the occurrence and behavior of fire in turn depends on well-distributed pine trees to provide the needle cast fuels that drive frequent, low-to-moderate intensity surface fires. In some instances, management action can mitigate, by planning and implementing prescribed fires or by planting trees to jump-start the regeneration process. These activities may become too costly or ineffective if the underlying environmental conditions deteriorate too far, but considering the value of the biological resources at risk, it is worthy to make the effort.

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