

PRIMARY RESEARCH ARTICLE

Maintaining historic disturbance regimes increases species' resilience to catastrophic hurricanes

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Abstract

As habitat loss and fragmentation, urbanization, and global climate change accelerate, conservation of rare ecosystems increasingly relies on human intervention. However, any conservation strategy is vulnerable to unpredictable, catastrophic events. Whether active management increases or decreases a system's resilience to these events remains unknown. Following Hurricane Irma's landfall in our habitat restoration study sites, we found that rare ecosystems with active, human-imposed management suffered less damage in a hurricane's path than unmanaged systems. At the center of Irma's landfall, we found *Croton linearis* (a locally rare plant that is the sole host for two endangered butterfly species) survival and population growth rates in the year of the hurricane were higher in previously managed plots than in un-managed controls. In the periphery of Irma's circulation, the effect of prior management was stronger than that of the hurricane. Maintaining the historical disturbance regime thus increased the resilience of the population to major hurricane disturbance. As climate change increases the probability and intensity of severe hurricanes, human management of disturbance-adapted landscapes will become increasingly important for maintaining populations of threatened species in a storm's path. Doing nothing will accelerate extinction.

KEYWORDS

butterfly, conservation, endangered species, habit restoration, hurricane, population dynamics

1 | INTRODUCTION

Urbanization, habitat loss, and climate change are contributing to biodiversity losses across the globe (Dirzo et al., 2014). Against this background of multiple, interacting threats, conservation increasingly relies on hands-on actions to provide refugia where species have the best chance of survival. However, even the best designed conservation strategies are vulnerable to unpredictable, catastrophic events (Harris et al., 2018). Following the intense disturbance imposed by Hurricane Irma, we had the unique opportunity to test how habitat management interacted with the hurricane to affect population dynamics of a rare species found exclusively within a global biodiversity hot spot. We show quantitatively that

human-driven habitat management increases population resilience to an anthropogenically-driven, catastrophic, weather event.

The actions required to maintain appropriate refugia will depend on a species' life history and vulnerability to environmental change (Dawson, Jackson, House, Prentice, & Mace, 2011). For species that rely on disturbance to maintain key resources, this requires humans imposing disturbances that mimic natural ones, such as prescribed fire. Management-based disturbances, however, do not happen in isolation. For example, in pine savannahs of the southeastern United States, prescribed fire regimes periodically interact with hurricane disturbances (Beckage, Gross, & Platt, 2006). Observational and experimental studies of disturbance have a long history in ecology (Mackey & Currie, 2001), but the impacts of multiple, interacting

disturbances on population dynamics remain underexplored (Ehrlén & Morris, 2015). As frequency of major hurricanes increases with climate warming (Bender, Knutson, Tuleya, & Sirutis, 2010), understanding how populations are affected by the interaction between climate- and management-driven disturbance is necessary to design conservation strategies that promote species persistence.

Population dynamics of vulnerable species reflect the threats faced by entire ecological systems (Siddig, Ellison, Ochs, Villar-Leeman, & Lau, 2016). One group of organisms particularly susceptible to altered disturbance regimes is rare butterflies (e.g., Warchola, Crone, & Schultz, 2018). In the United States, half of the butterflies listed under the Endangered Species Act are endangered due to loss of historic disturbance regimes. Without disturbance, primary host plants are outcompeted as succession progresses. This process further reduces and fragments habitats that are already limited by accelerating land use change, and leads to extirpation of local populations (Haddad, 2018). The vulnerability of butterflies to loss of disturbance likely reflects vulnerabilities of other at-risk insect species about which we know almost nothing (Schultz, Haddad, Henry, & Crone, 2019). Directly managing disturbance is therefore critical to recovering rare insect populations and has the potential to increase population resilience and ability to adapt to new anthropogenically altered environments.

Working in the rarest forested ecosystem on the planet (only 9,700 ha remain), we studied the population dynamics of pineland croton (*Croton linearis*), which is the sole host plant for two endangered butterflies, Bartram's scrub-hairstreak (*Strymon acis bartrami*) and Florida leafwing (*Anaea troglodyte*). These three species are endemic to south Florida pine rockland forests, and depend on frequent, low-intensity fires. Pine rockland habitat is highly fragmented due to urban development (Figure S1) and requires active disturbance management; where humans do not manage pine rocklands, species are lost. We first tested how different disturbance-based management techniques (prescribed fire and its mechanical surrogate) affect croton population dynamics. Our study sites were then directly hit by Hurricane Irma on September 10, 2017. This allowed us to empirically test how previous disturbance-based management interacted with the hurricane's disturbance to affect plant population dynamics. Our replicated, experimental approach provides a robust test of the interacting effects of management and climate-driven disturbances (Altwegg, Visser, Bailey, & Erni, 2017), the results of which provide insight into how to manage disturbance-dependent systems in an era of rapid environmental change.

2 | METHODS

2.1 | Study system

We tested the effects of fire and mechanical restoration treatments and their interaction with Hurricane Irma on vital rates of pineland croton (hereafter referred to as croton). Croton is a perennial, dioecious shrub native to south Florida, The Bahamas, Cuba, Jamaica,

and the Turks and Caicos, where it grows on rocky or sandy substrates in disturbance prone environments. Little is known about the life history and demography of the plant. The largest individuals in south Florida can reach heights of close to 2 m in the absence of fire; however, their size is largely determined by time since fire. As ours is the first study to collect demographic data on the plant, there are no published estimates of croton longevity. Croton plants fruit year-round with a peak at the start of the rainy season. As with longevity, there is no information on the seed ecology of croton such as how seeds are dispersed, how long they persist in the seedbank, and what stimulates germination.

In south Florida, croton is locally rare, confined to pine rockland forests. Pine rocklands are characterized by open stands of South Florida slash pines (*Pinus elliottii* var. *densa*) and an open shrub/palm subcanopy, below which a rich herbaceous community thrives (Florida Natural Areas Inventory [FNAI], 2010). South Florida pine rocklands once extended along the Miami rock ridge, from North Miami Beach to Everglades National Park, and to a few islands in the Florida Keys. This entire distribution falls directly in the path of the most intense US hurricane landfalls (Ries, Neupane, Baum, & Zipkin, 2018). Ninety percent of the pine rockland on mainland south Florida and much of the habitat in the Keys has been cleared for development in the last 100 years (Figure S1). The largest remaining pine rocklands are protected within Everglades National Park (8,029 ha), Navy Wells—a Miami-Dade County Natural Area (150 ha), and the National Key Deer Refuge on Big Pine Key (559 ha). Given this large decline of pine rockland habitat, croton populations have declined and become increasingly fragmented. Pine rockland habitat loss affects not only croton but also the butterflies that rely on it. Declines in these butterfly populations are closely linked with the fragmentation and loss of croton populations in the landscape.

Even within protected areas, pine rocklands are threatened by loss of historic disturbance and subsequent forest succession which excludes croton. Historically, pine rocklands burned frequently, maintaining the forest in an early successional state (Robertson, 1962). Croton is well adapted to fire; based on anecdotal data, it appears to both seed and resprout following fires (C. Anderson, unpublished data). Without fire, pine rocklands convert to hardwood hammocks, and croton eventually disappears from the ecosystem. Since 1951, croton has gone from being one of the 10 most common plants in pine rocklands on Big Pine Key (Alexander & Dickson, 1972) to covering less than 0.01% of pine rocklands in 2014 (Bradley & Saha, 2009); this decline has occurred simultaneously with decline in fire across the island.

Because fire historically structured pine rockland ecosystems, it is the preferred management strategy for maintaining croton and habitat for Bartram's scrub-hairstreaks and Florida leafwings; however, there are multiple obstacles to implementing prescribed fire, especially at the wildland-urban interface and in instances where fuels have accumulated to levels that make it unsafe to burn. In these areas, mechanical clearing through mowing, brush hogging, etc., has been proposed as a possible habitat maintenance strategy. This is motivated by anecdotal observations by E. Henry of croton plants

sprouting and thriving in newly cleared fire breaks. While these observations are encouraging, evidence-based data are necessary for making informed management decisions.

2.2 | Mechanical clearing experiment

To test the effects of mechanical clearing on croton demography, we implemented a clearing experiment on Big Pine Key. In July 2015, we established four experimental blocks with two, half-hectare treatments each, a mechanical understory removal treatment and a no treatment control. We created two blocks each in both of the remaining pine rockland sites that support croton and Bartram's scrub-hairstreak populations on the island, one on the southern end of the island and one along the island's central ridge. We designed understory removal treatments to mimic the fire prescription for Big Pine Key which stipulates "a mosaic burn pattern consuming 50% of a burn unit." US Fish and Wildlife Service fire staff implemented clearing treatments by haphazardly driving a skid steer with a masticating head through the treatment unit, clearing and mulching the understory vegetation in a mosaic pattern covering 50% of the plot. The mulch was left in place after clearing.

Prior to treatments, we tagged croton plants in subplots in each replicate. To ensure that we tagged croton plants across the replicate, we identified croton sampling subplots by establishing a grid of parallel 50 m transects spaced 10 m apart in all treatment units (total of 10 transects). In each unit, we randomly selected five transects and established three, permanent 2.5 m radius subplots on each, in the middle and both ends of each transect. We marked subplots by hammering a 25 cm galvanized spike at the subplot center and attached a numbered, metal plant tag to identify the subplot number. In each subplot, we tagged all croton plants by wiring metal plant tags around the base of each plant. If we did not reach our goal of 30 plants tagged in the first five transects, we randomly sampled additional transects until we reached at least 30 plants. We tagged plants in 5–10 subplots in each unit, depending on croton density.

We tagged plants in July 2015 and implemented mechanical treatments in August of the same year. We resampled the croton subplots in July 2016 and July 2017. Each time we resampled, we located all previously tagged plants and recorded if they were alive or dead. When we could not relocate tagged plants, we recorded those individuals as dead. We also tagged new seedlings as well as plants that we missed in the previous round of sampling. New seedlings were easily distinguished from missed plants by their yellow-colored stems that were not noticeably woody. At each sampling round, we measured plant height, recorded plant sex, and counted fruits.

2.3 | Fire monitoring

Because logistical constraints prohibited burning on Big Pine Key during our study, we used long-term croton monitoring data from

Everglades National Park to examine the effects of fire on croton demography. Everglades National Park has the longest running prescribed fire program in the National Park Service. To facilitate the burn program, the pine rocklands in the park are divided into 15 fire units. In two of these fire units, every croton plant within a 20 m × 50 m plot was tagged with a metal plant tag and its location within the plot was mapped. The number of tagged croton plants in each fire unit ranged from 56 to 84. Everglades fire-effects staff have monitored these plants monthly over various time periods in the last 14 years. One of the units was monitored from July 2005 to July 2012. Monthly monitoring began again in this unit prior to a fire in 2016. The other unit was monitored monthly from January 2011 to July 2012 and from March 2014 to April 2015. The data collected each month were inconsistent; therefore, we used data from months where plant height, sex, and number of fruits were recorded, with the exception of pre- and post-2016 fire when fruit count data were not collected. Three different fires are represented in this dataset, in 2006, 2014, and 2016. The 2006 and 2016 fires burned the same fire unit, and the 2014 fire burned a different unit. We used these data to model annual transitions from pre- to post-fire. Our dataset includes the following transitions: July 2006–July 2007, March 2014–March 2015, and February 2016–March 2017.

We compared survival, growth, and recruitment rates in fire years in Everglades National Park to years in the same dataset in which there were no fires. For no-disturbance years, we selected years that were at least 3 years post-fire and were not affected by other disturbances such as frosts or hurricanes. There were 2 years that met these criteria, one for each of the fire units included in our fire dataset. These include the following transitions: April 2010–April 2011 and July 2011–June 2012. For the purposes of this paper, we consider these no-disturbance data to be analogous to control plots in the mechanical clearing experiment.

2.4 | Hurricane Irma

Hurricane Irma slammed into south Florida on September 10, 2017. The storm made its first United States landfall in Cudjoe Key, FL, 16 km west of our mechanical clearing experiment on Big Pine Key (Figure 1). This brought the eastern eyewall of the hurricane, and associated winds and storm surge, directly across our experiment. The National Weather Service estimated maximum wind gusts of 240 kph (Lovin, 2018) which, in some parallel with mechanical clearing, snapped pine trees in half. In addition to damage from strong winds, the entire island of Big Pine Key, including each of the tagged plants in our experiment, was completely washed over by storm surge with depths ranging from 4 m to just a few centimeters (Lovin, 2018). In Everglades National Park, the effects of Irma were less pronounced, mainly because storm surge did not affect pine rocklands in the park which are 30 km inland. The maximum wind gust recorded on Long Pine

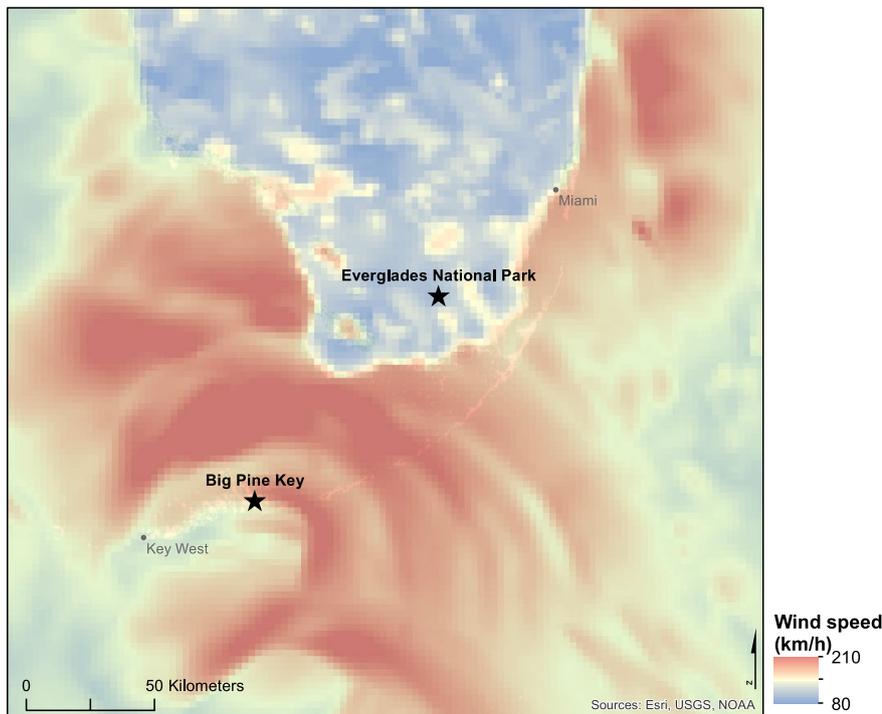


FIGURE 1 Maximum wind gusts as Hurricane Irma passed through south Florida and across our study sites (06:00–23:00 Eastern Daylight Time, September 10, 2017). Warm colors (red) are faster gusts; cool colors (blue) are slower. Wind data are modeled maximum hourly gusts from National Weather Service real-time mesoscale analysis

Key in Everglades National Park was 146 kph (Cangialosi, Latto, & Berg, 2018), which knocked down branches but did not snap tree trunks. Total rainfall at Big Pine Key was 318 mm and at Royal Palm in Everglades National Park was 287 mm (Cangialosi et al., 2018), a difference of 10%.

Following Hurricane Irma, we resampled all demography plots on Big Pine Key in July 2018, and we resampled croton plants in the fire unit that burned in 2016 in Everglades National Park in April 2018. This was the only fire unit within the park in which croton data had been collected within a year prior to Irma. At both locations, we recorded plant survival, height, sex, and fruit count. When we could not locate a tag, we assumed the plant was dead. This was most often due to portions of plots being buried under debris.

2.5 | Disturbance effects on vital rates

2.5.1 | Big Pine Key

To test for interactive effects of hurricane and management disturbance on individual vital rates, we built mixed effects models that included an interaction between treatment (mechanical, control) and Hurricane Irma fixed effects, with block and site included as random effects. For models with response variables of survival probability and probability of fruiting, we also included a fixed effect of \ln -transformed height in year t and assumed binomially distributed errors. To model growth, we used the change in \ln -transformed height from year t to $t + 1$ as the response variable and assumed normally distributed errors.

2.5.2 | Everglades National Park

Because we do not have data from a fire unit that was not burned prior to the hurricane, we do not have a crossed treatment \times Irma design in Everglades National Park. Instead of testing for significant disturbance interactions, we instead tested for differences between the three disturbance scenarios, no-disturbance, fire, and Irma + fire. Survival probability and growth are the only two vital rates for which we had data for this test. We used linear models as those described above for Big Pine Key, but did not have random effects to include.

2.6 | Integral projection model

We used integral projection models to estimate asymptotic values of lambda, the finite rate of increase in the population from one time step to the next. Integral projection models differ from matrix projection models in that they model the size distribution of individuals in a population as a continuous variable instead of dividing a population into discrete size classes to model demographic transitions. Integral projection models are useful when sample sizes are relatively small because they use all available data to estimate vital rate functions (Ellner, Childs, & Rees, 2010). Therefore, the number of parameters to be estimated is much smaller than for matrix projection models (Ellner & Rees, 2006). This is especially useful in our case, where sample sizes are highly variable across sites and treatments and binning plants into size classes would have reduced our ability to confidently estimate transition probabilities. The general structure of an integral projection model takes the form of

a kernel. The kernel, $K(y,x)$ describes the probability of individuals of size x in year t surviving and transitioning to plants of size y in year $t + 1$ across all sizes from lower bound of size distribution (L) to upper bound (U):

$$n(y)_{t+1} = \int_L^U K(y,x) n(x)_t dx.$$

The kernel can be decomposed into two parts, the survival and growth kernel P , and fecundity kernel F :

$$K(y,x) = P(y,x) + F(y,x).$$

The survival and growth kernel, $P(y,x)$, describes survival of plants of size x from time = t to time = $t + 1$, $S(x)$, as well as growth of plants from size x at time = t to size y at time = $t + 1$, $G(y,x)$:

$$P(y,x) = S(x) G(y,x).$$

Our model is built as a pre-reproduction model. This means that we assume the plants censused in time t have not yet reproduced. Therefore, the fecundity kernel, $F(y,x)$, includes the probability that a plant of size x at time = t fruits, $P(x)$, given a plant fruits, how many seeds it produces, $D(x)$, the probability that a seed survives and germinates and recruits into the population at time = $t + 1$, g , and the size distribution of the new recruits at time = $t + 1$, $B(y)$.

$$F(y,x) = P(x)D(x) \times g \times B(y).$$

2.7 | Model parameterization

We fit linear functions to our data with plant height as the predictor variable for each component of the model. For both survival ($S(x)$) and growth ($G(y,x)$), we fit a distinct function for each treatment combination in each site: mechanical, control, mechanical \times Irma, and control \times Irma on Big Pine Key, and fire, no-disturbance, and fire + Irma in Everglades National Park.

To estimate the probability of fruiting ($P(x)$), we pooled data across plants regardless of sex. Although croton is a dioecious plant, there were numerous plants that could not be sexed due to lack of reproductive structures. This was especially a problem in the population on Big Pine Key. Rather than reduce our sample size by only including female plants, we assumed that growth and survival probabilities were not different by sex and included data from all plants. This means that our probability of fruiting, $P(x)$ in the model, incorporates both the probability of being female and producing fruits. Because we include male, female, and unknown plants, this parameter reaches a maximum value close to 0.5 for the largest plants in our fitted vital rate models, which describes an equal sex ratio in the population. The low number of female plants required that we pool data across all female plants at each site to estimate seed production ($D(x)$). We counted fruits prior to disturbance; therefore, pooling data were unlikely to affect our results.

Because we do not have specific data on croton seed ecology, we estimated one parameter g that describes seed survival, germination, and seedling survival to the next census. We did this by dividing the number of new seedlings that recruited into the population in year $t + 1$ by the number of seeds produced at time = t (Ellner & Rees, 2006). This gives us an estimate of recruits/seed for each treatment. Finally, for the size distribution of new recruits at time = $t + 1$, we pooled all new recruits across years and treatments and calculated the mean and standard deviation from the data. We did this separately for Big Pine Key and Everglades National Park. We used the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) in R version 3.5 for all mixed effects models (R Core Team, 2018).

2.7.1 | Big Pine Key

All vital rate models included a fixed effect of ln-transformed height at time = t , and random effects of Block and Site; control models also included a random effect of year because we sampled control plots in both 2016 and 2017. All random effects were applied to the intercept only based on results of likelihood ratio tests. For growth models in all treatments, we used linear mixed effects models with normally distributed errors. For both survival and fruiting vital rates, we fit generalized linear mixed effects models with binomially distributed errors. To model the number of fruits produced, given a plant flowers, we pooled data across units and blocks from our pre-treatment sampling in July 2015 and fit a model with Poisson error distribution. We used this function in our lambda estimates for all treatment combinations on Big Pine Key.

2.7.2 | Everglades National Park

Vital rate functions had the same general structure and error distributions as those on Big Pine Key, with ln-transformed height as the fixed effect; random effects depended on treatment. No-disturbance models included a random effect of fire unit, fire models of growth and survival included year as a random effect. We only had 1 year of pre-fire fruiting data from one fire unit so did not include random effects in that model. Fire + Irma models also had no random effects, because we only had data from one unit in 1 year before and after the storm. We did not have data on plant reproduction prior to Irma, so we used our no-disturbance fruiting model in our estimates of lambda for this treatment. We calculated the parameter g as described above, however, since we did not have data on fruits produced pre-Irma, we used our estimate of g from no-disturbance treatments in our estimates of lambda. We based this decision on evidence that the number of new recruits in time = $t + 1$ divided by the total number of plants at time = t was only slightly different between the no-disturbance treatment and the fire + Irma treatment. Like with Big Pine Key data, we pooled all pretreatment data into one model of fruit production. This model included year as a random effect. All random effects in all models were applied to the intercept estimate only. Finally, as we did on Big Pine

Key, we pooled all new recruits and calculated the mean and standard deviation from the data.

2.8 | Estimating lambda and bootstrapping confidence intervals

We calculated asymptotic estimates of lambda for each treatment combination, using the integral projection model and vital rate functions defined above (Table S1). To bootstrap confidence intervals, we resampled the data with replacement 2,000 times, refitting vital rate functions and calculating lambda each time. We then calculated 95% confidence intervals from the resulting lambda estimates.

3 | RESULTS

We found the effects of management-based disturbance interacted with hurricane impacts on pineland croton to increase post-hurricane survival and population growth rates (Figure 2). Where Hurricane Irma's wind and storm surge was most intense, Big Pine Key, the hurricane reduced survival in all plots (Figure 2a). How much survival rates declined due to the hurricane, however, depended on whether or not plots were mechanically cleared prior to the storm. Plots that were cleared had higher survival after the hurricane relative to those

that were not (Tx × Irma interaction: $\chi^2 = 14.25$; $df = 1$; $p < .001$). In the Everglades, where Hurricane Irma's winds and storm surge were less intense, its effects on survival of croton plants were less pronounced (Figure 2b). Croton survival probability in Everglades National Park was highest in no-disturbance years, and fire and fire + Irma survival rates were not different (disturbance type: $\chi^2 = 23.91$; $df = 2$; $p < .001$).

In addition to significant interactive effects of treatment and Hurricane Irma on survival, we also found a nonsignificant trend toward higher growth in mechanically cleared plots relative to controls in the year of the hurricane (Figure S2, Tx × Irma interaction: $\chi^2 = 2.93$; $p < .087$). As expected, plants effectively shrunk following fires as they were top-killed and resprouted, but their growth following the hurricane was not different from growth in no-disturbance years (disturbance type: $F_{2,457} = 132.05$; $p < .001$).

Hurricane Irma devastated populations on Big Pine Key and boosted population growth rate in the Everglades (Figure 2c,d). Prior to the hurricane, years of fire suppression have led to shrinking croton populations on Big Pine Key. With no intervention, an annual population growth rate of 0.79 will lead to extirpation of *C. linearis* in <10 years. In the year of the hurricane, however, our analysis revealed that mean lambda in mechanically cleared plots (0.388) was almost twice that in control plots (0.207).

Consistent fire management in Everglades National Park has maintained stable croton populations. We found that croton populations were increasing at a rate of 10% per year, 4 years post-fire

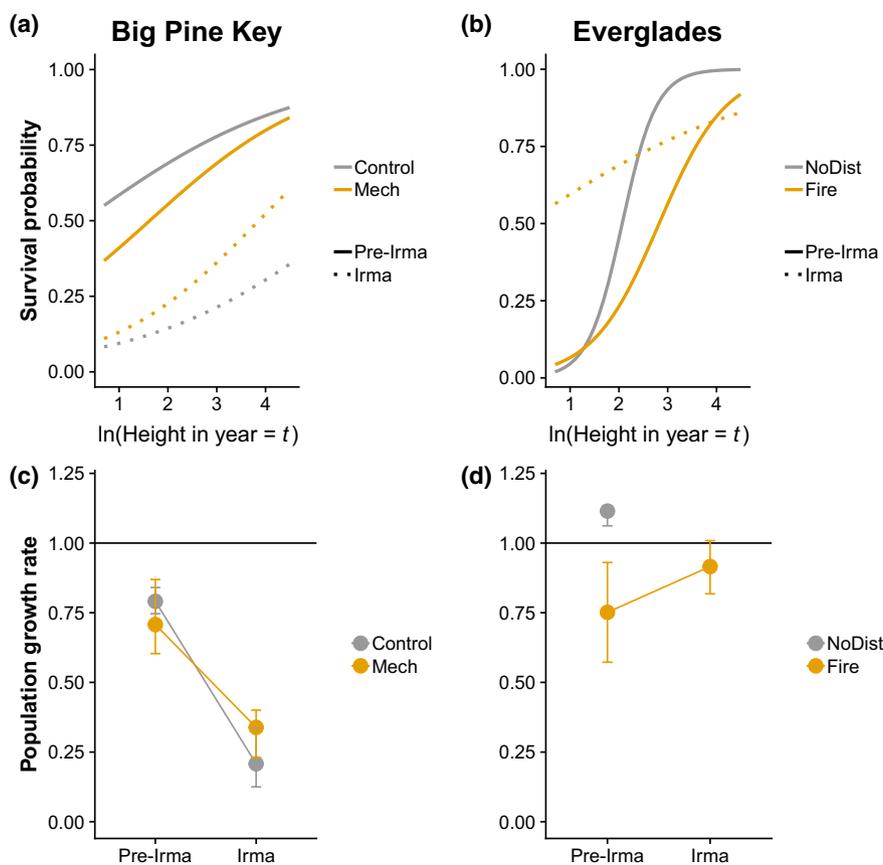


FIGURE 2 Model predictions of survival and estimated population growth rates for croton populations on Big Pine Key and Everglades National Park. In each panel, gray represents un-managed plots and orange represents managed plots. On Big Pine Key, un-managed plots are experimental controls, and the management was mechanical clearing. In Everglades, un-managed plots are years in which fire blocks had not been burned in 4 years, and the management was fire. Big Pine Key was in the eye of hurricane Irma, Everglades in the periphery of the storm. (a, b) Model predictions of survival rate as a function of size. Solid lines represent pre-Irma survival rates, dotted lines represent survival rates in the year of Irma. (c, d) estimated population growth rate projected by integral projection model. Vertical bars represent 95% confidence intervals from bootstrapping procedure

(Figure 2d). Fire initially reduced this population growth rate to one similar to both control and mechanically cleared plots on Big Pine Key. However, instead of declining further after Irma, population growth rates rebounded following the hurricane.

4 | DISCUSSION

The impact a major hurricane has on population dynamics depends on a population's position relative to the eye and the coast. The most intense effects of a hurricane, high winds and storm surge, greatly reduce populations in its path. Similar to studies that documented hurricane-driven declines (Donihue et al., 2018; Platt, Beckage, Doren, & Slater, 2002), we measured up to 70% declines in population growth rates at the center of Hurricane Irma. In the periphery of the storm, impacts were significantly less. Rather than shrinking, peripheral populations remained stable in the year of the storm, suggesting the hurricane had little effect. The marked difference in response in these two croton populations illustrates the variety of impacts a single large storm event can have on populations in its path.

Disturbances have the ability to turn growing populations into shrinking ones, or vice versa (Pulliam, 1988). Therefore, multiple, interacting disturbances can have both negative and positive consequences for populations (Paine, Tegner, & Johnson, 1998), as evidenced by the croton population at the center of the storm. Mechanical clearing prior to Hurricane Irma had initial negative effects, but increased the resilience of croton to the impacts of the hurricane such that storm-year growth rate was higher in cleared plots than controls. If these rates continue to diverge as the population recovers, it will be a strong signal that the interaction of the two disturbances is key to maintaining populations of threatened species. In our peripheral population, the effects of previous fire management on population growth rate were stronger than hurricane effects (Menges, Weekley, Clarke, & Smith, 2011; Platt et al., 2002). These results point to the importance of maintaining historic disturbance regimes to support long-term viability of threatened species. As climate change increases the probability of severe hurricanes, human management of disturbance-adapted landscapes will determine the resilience and adaptive capacity of threatened species in a storm's path.

In disturbance-adapted ecosystems, the recovery process is more important in determining a population's long-term viability than initial post-disturbance response. Although populations shrank (growth rates were <1) with mechanical clearing, prescribed fire, and Hurricane Irma, this was not unexpected. It might take 2 or more years for the positive effects of a disturbance to be realized (Liu, Menges, & Quintana-Ascencio, 2005; Warchola et al., 2018). In the periphery of the storm, post-fire growth rates began to rebound, not unlike what we might expect in the absence of a hurricane (Gross, Lockwood, Frost, & Morris, 1998; Liu et al., 2005). However, in the storm's center, post-clearing population growth rates further declined. This pattern suggests that populations might be resilient to

an increased probability of experiencing peripheral impacts of a hurricane, but not to increased probability of absorbing the impacts associated with the eye of a hurricane.

Our original interest in croton was sparked by its role as the sole host plant to two endangered butterflies. Even when storm surge decimates croton, it can regrow from roots or seeds that are protected in soil. In contrast, butterflies are exposed to the full force of a storm. For example, in the Florida Keys, hurricanes were initially thought to cause the extinction of Schaus' Swallowtail and Miami Blue butterfly (Grimshawe, 1940; USFWS, 2012). Considered in this context, it is not surprising that we have not observed a single Bartram's scrub-hairstreak on Big Pine Key, the center of Hurricane Irma's landfall, since the storm. This is despite conducting systematic adult surveys (Henry & Anderson, 2016) as well as larval surveys during croton demography data collection. Thanks to populations at the periphery of these hurricanes, none of these butterflies are extinct today.

Although extinction may occur for these butterflies and for other threatened plants and animals after a hurricane strikes, here, the cause was the interaction between hurricanes and two human-caused changes to the landscape. The first change that hastens extinction is the expansive development of the built environment and resulting fragmentation of threatened plant and animal populations (Haddad et al., 2015). Even if habitat recovers after a hurricane's direct strike, fragmentation cuts off the possibility of recolonization of extirpated populations (Spiller, Losos, & Schoener, 1998). A second cause of extirpation that is also driven by habitat loss and fragmentation is the absence of a natural disturbance, fire. Prior to Hurricane Irma, the croton population on Big Pine Key was shrinking at a rate of 20% per year due to lack of fire on the island (Figure 2). That we have not detected a Bartram's scrub-hairstreak on Big Pine Key since Irma is the logical conclusion of this prolonged loss of host plant, Irma was simply the final act (Hughes, Linares, Dakos, van de Leemput, & van Nes, 2013). The closest extant Bartram's scrub-hairstreak population is the Everglades population, 105 km from Big Pine Key. This distance makes recolonization impossible without intensive restoration and reintroduction efforts. Barring direct intervention in rare species metapopulations, projected increase in hurricanes and other major storm events as the climate continues to warm will cause the fulfillment of the extinction debt (Tilman, May, Lehman, & Nowak, 1994).

As with the majority of financial costs, the critical costs to nature associated with hurricane damage can be attributed to storm surge flooding. We observed the highest mortality rates in the croton population that was inundated by storm surge. Many of the dead plants were either buried under rafts of forest debris deposited by receding flood waters or were still standing with dead leaves, suggesting saltwater as the source of mortality. For a species that exists in a functioning metapopulation, the footprint of the storm surge may be a small proportion of a species' global distribution, thus allowing for the possibility of subpopulation recovery following a storm event. However, future global warming is projected to increase hurricane wind speeds, storm surge heights, sea levels, and the rate of coastal

erosion (Lin, Emanuel, Oppenheimer, & Vanmarcke, 2012; Patricola & Wehner, 2018). These factors all combine to predict much more extensive damage due to storm surge in the future for the built environment (Neumann et al., 2014), and our results suggest that the impacts to nature will expand as well. Following previous major storms, cities and states have implemented strict building codes to minimize damage and rebuilding costs with future storms. The same is necessary for conserving rare species and ecological systems that are vulnerable to catastrophic hurricane impacts. We have shown that appropriately managing landscapes that harbor rare species has the potential to increase species' resilience to subsequent storm events. With poor management, stronger hurricanes will accelerate extinction.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

All authors contributed to idea generation. EHH and NMH designed the experiment; EHH collected and analyzed data with advice from NMH and MBR. EHH led and MBR and NMH contributed to writing.

DATA AVAILABILITY STATEMENT

Data and code are prepared and ready to be deposited in Dryad at time of publication (<https://doi.org/10.5061/dryad.w3r2280m0>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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