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Hurricane effects on subtropical pine rocklands of the Florida Keys

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Abstract We investigate the effects of Hurricane Wilma's storm surge (23–24 October 2005) on the dominant tree *Pinus elliottii* var *densa* (South Florida slash pine) and rare plant species in subtropical pine rocklands of the Lower Florida Keys. We examine the role of elevation on species abundance in 1995 (Hurricane Betsy in 1965), 2005 (Hurricane Georges in 1998), and 2008 (Hurricane Wilma in 2005) to investigate if hurricanes influence abundance by eliminating plants at lower elevation on Big Pine Key, the largest island in the Lower Florida Keys. We compare densities before and after Hurricane Wilma over the 2005–2008 sampling period and examine the role of elevation on changes in pine and rare species densities three years after Hurricane Wilma. We use elevation to assess the impact of hurricanes because elevation determined whether a location was influenced by storm surge (maximum surge of 2 m) in the Lower Florida Keys, where pine rocklands occur

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at a maximum elevation of 3 m. In 1995 (30 years after a major storm), elevation did not explain the abundance of South Florida slash pine or *Chamaecrista lineata*, but explained significant variation in abundance of *Chamaesyce deltoidea*. The latter two species are rare herbaceous plants restricted to pine rocklands. In 2008, 3 years after Hurricane Wilma, the positive relationship between elevation and abundance was strongest for South Florida slash pine, *C. deltoidea*, and *C. lineata*. Effects of Hurricane Wilma were not significant for rare species with wider distribution, occurring in plant communities adjacent to pine rocklands and in disturbed rocklands. Our results suggest that hurricanes drive population dynamics of South Florida slash pine and rare species that occur exclusively in pine rocklands at higher elevations. Rare species restricted to pine rocklands showed dramatic declines after Hurricane Wilma and were eliminated at elevations <0.5 m. Widely distributed rare species did not show significant changes in density after Hurricane Wilma. Abundance increased with elevation for South Florida slash pine and *C. lineata* after the hurricane. In an environment influenced by sea level rise, concrete plans to conserve pine ecosystems are warranted. Results from this study will help define conservation strategies by strengthening predictive understanding of plant responses to disturbance in the backdrop of sea level rise.

1 Introduction

Hurricanes define the disturbance regime in coastal ecosystems of the southeastern US and the subtropical Caribbean (Pimm et al. 1994). A large fraction of the US mainland, all of Puerto Rico, and the US Virgin Islands are currently exposed to 4- to 35-year return periods for hurricanes, which translates to 2–16% probabilities of being in the direct path of a hurricane in any given year (Crossett et al. 2004; Neumann et al. 1987).

Hurricanes inflict mechanical and ecological damage on coastal ecosystems (Lugo 2000). The direct physical impacts of hurricanes include coastline erosion, land subidence, wind damage, and flooding and salt deposition through storm surges (Penland et al. 2005; Rosenzweig et al. 2007; Scheffer et al. 2001; Stive 2004). Ecological effects of hurricanes on coastal ecosystems range from alteration to the permanent loss of plant communities (Harcombe et al. 2009; Imbert and Portecop 2008; Middleton 2009; Smith et al. 2009; Ugarte et al. 2006). Short-term changes in communities followed by recovery among coastal ecosystems are documented as well (e.g., Bahamas: Miller et al. 2009; Morrison 2003; barrier islands off Florida's west coast: Snyder and Boss 2002) with the turnover being synchronized to the return interval of hurricane events and hurricane intensity (Scatena 1995; Scatena and Lugo 1995; Busby et al. 2009).

Even though hurricanes are a part of the natural disturbance regime in the southeastern United States (Batista and Platt 2003; Lugo 2008; Pimm et al. 1994), it is becoming evident that sea level rise compounds the effects of hurricanes on coastal ecosystems (Hopkinson et al. 2008; Smith et al. 2010; Williams et al. 2007). The effects of hurricanes on the conservation status of coastal plant communities are poorly understood (Hopkinson et al. 2008). A predictive understanding of the responses of ecosystems and associated species to hurricanes in the scenario of sea level rise is needed. Strategies for conservation and restoration can be developed to maximize the chances of survival of endemic and rare plant taxa and ecosystems that harbor them in the face of sea level rise and periodic hurricane strikes.

The subtropical pine rocklands restricted to the mainland of South Florida and the Florida Keys are an ecosystem facing periodic hurricanes. Hurricane effects are of particular interest in the Florida Keys, due to the high frequency of tropical storms and the low elevations (1–3 m) at which pine rocklands occur (Ross et al. 2009; Snyder et al. 1990). The dominant species of pine rocklands, South Florida slash pine (*Pinus elliottii* var. *densa*) and co-occurring species depend on a shallow freshwater lens, which is adversely affected (salinization) by storm surges that often accompany hurricanes (Ross et al. 2009). Due to their low elevation and coastal proximity, pine rocklands of the Keys are losing ground to the rise in sea level at the rate of 2.4 cm per decade (Ross et al. 1994). The stands of dead pine trees at the periphery of islands in the Florida Keys are testimony to the changes in soil salinity and flooding regimes resulting from sea level rise.

Here we examine the effects of Hurricane Wilma on the abundance of South Florida slash pine and rare herbaceous plants on Big Pine Key (BPK), the largest island of the Lower Florida Keys. The future of pine rocklands on South Florida's oceanic islands faces several challenges such as fragmentation resulting from agricultural and urban development and sea level rise. We examine the distribution and recovery of South Florida slash pine and rare herbaceous plants in relation to elevation because elevation determines the propensity of a location to storm surge in the Lower Florida Keys (FEMA 2006; Sah et al. 2010). We discuss the relevance of our findings for conservation and restoration of imperiled pine ecosystems in the context of continued sea level rise.

We ask questions pertaining to effects of hurricanes on abundance of pine and rare species on an island where the largest area of globally threatened pine rocklands exists outside of mainland Florida, USA. We specifically ask: (1) if the role of elevation on species abundance depends on history of hurricanes prior to sampling, and (2) whether elevation had a differential impact on species abundance after Hurricane Wilma, which generated a maximal surge of 2 m in the Lower Florida Keys.

2 Study site, methods, and analyses

2.1 Study site and species

Big Pine Key (24°41′20.70″ N and 81°22′07.30″ W) is the largest of the islands in the Lower Florida Keys, Monroe County, Florida, USA, covering approximately 4,500 ha. Pine rocklands cover approximately 582 ha of the island (Folk 1991). Geologically the islands consist of a surficial facies of oolitic Miami limestone, subtended at 4–6 m depth by the more transmissive, coralline Key Largo Limestone, which truncates separate freshwater lenses that sustain pine rocklands on the northern and southern ends of the island. The upper layer of oolitic rock is resistant to mixing of fresh and salt water so that the lens of fresh groundwater is maintained even near the edge of the sea. Skeletal, organic soils of 10 cm or less provide little rooting space in these rocklands (Ross et al. 2003), though the pine trees have some ability to access the freshwater lens through limestone bedrock (Saha et al. 2009).

Periodic fires are required to prevent succession of pine rocklands to a hardwood-dominated ecosystem (Alexander and Dickson 1972). Human settlement that started in the middle 1800s (Simpson 1982) caused modifications in fire regime (Bergh and Wisby 1996). Additional pine rocklands were lost due to sea level rise, causing a net decrease in the extent of this ecosystem. On nearby Upper Sugarloaf Key, Ross et al. (1994) found that approximately 58 ha of an initial 88 ha of pine rocklands were lost as a result of sea level rise.

Hurricane Wilma, a category 3 storm, made landfall in Florida on 24th October 2005 (FEMA 2006). A large portion of the Lower Keys was flooded because Hurricane Wilma caused two temporally distinct storm surges (23rd–24th October 2005, within hours of each other) in opposite directions generating a maximal surge of 2 m in BPK (FEMA 2006; Ross et al. 2009). Land surface elevation and drainage patterns dictated the influence of the storm surge and the duration of saltwater accumulation on BPK (Sah et al. 2010). Thus, we use elevation as an independent variable in our analysis because elevation is a proxy for inundation by storm surge. Other variables not accounted for in this study, such as distance to the coast and fine scale topography, may have played a role as well, though the high water mark data collected on the island suggests that the entire island was impacted by the surge, barring areas at highest elevations (FEMA 2006).

We focus on South Florida slash pine and four rare and/or endemic plant taxa occurring in pine rocklands and other low-lying plant communities of BPK. Three of the four study taxa were chosen because of their candidate status for listing under the U.S. Endangered Species Act. *Chamaecrista lineata* var. *keyensis* is restricted to pine understory (hence an obligate) and is endemic to the lower Florida Keys (Bradley and Gann 1999; Hodges and Bradley 2006). *C. deltoidea* (Engelm. ex Chapm.) Small subsp. *serpyllum* (Small) D.G. Burch, is an herbaceous perennial species endemic to BPK (Burch 1966; Herndon 1993; Bradley and Gann 1999; Gann et al. 2002; Small 1913, 1933) and is also a pine rocklands obligate. *Linum arenicola* (Small) H. J. P. Winkler is endemic to Monroe County in South Florida and occurs in pine rocklands and adjacent sites impacted by frequent disturbances such as mowed roadsides. Lastly, we chose the state endangered *Strumpfia maritima* (Francis 2010), a shrub occurring on the edge of low-lying pine rocklands, salt marshes, and beach strands. *S. maritima* is the most widely distributed of all species examined, and we predict it would be the most resilient to hurricanes based on its native distribution.

3 Methods

Ross and Ruiz (1996) studied rare species abundance in the pinelands of BPK by sampling 145 circular plots of 5-m radius along eight transects, except where those locations fell within small inclusions of different vegetation type within pine rocklands matrix. Precise counts of *C. lineata*, *C. deltoidea*, and *L. arenicola* were made. These data reflect conditions in the absence of storm surge in 30 years and serve as a benchmark.

In 2005, 80 sample locations were identified on a grid at points every 200 m within publicly owned pine rocklands on BPK to examine distribution and abundance of candidate and state endangered species. At each sample location, five plots of 2.5 m radius were established; a plot in the center and four additional 2.5 m radius plots

10 m from the center plot boundary in each of the four cardinal directions. We sampled to estimate population sizes and abundances of candidate species (Bradley and Saha 2009). Figure 1 depicts the distribution of plot locations from Ross and Ruiz (1996) and Bradley and Saha (2009) on BPK. Considering a hurricane timeline, data from 1995 represent the least impacted conditions due to absence of a major storm surge since 1965, while 2008 represents the most impacted scenario because of storm surges caused by Hurricane Wilma in 2005 (Fig. 2).

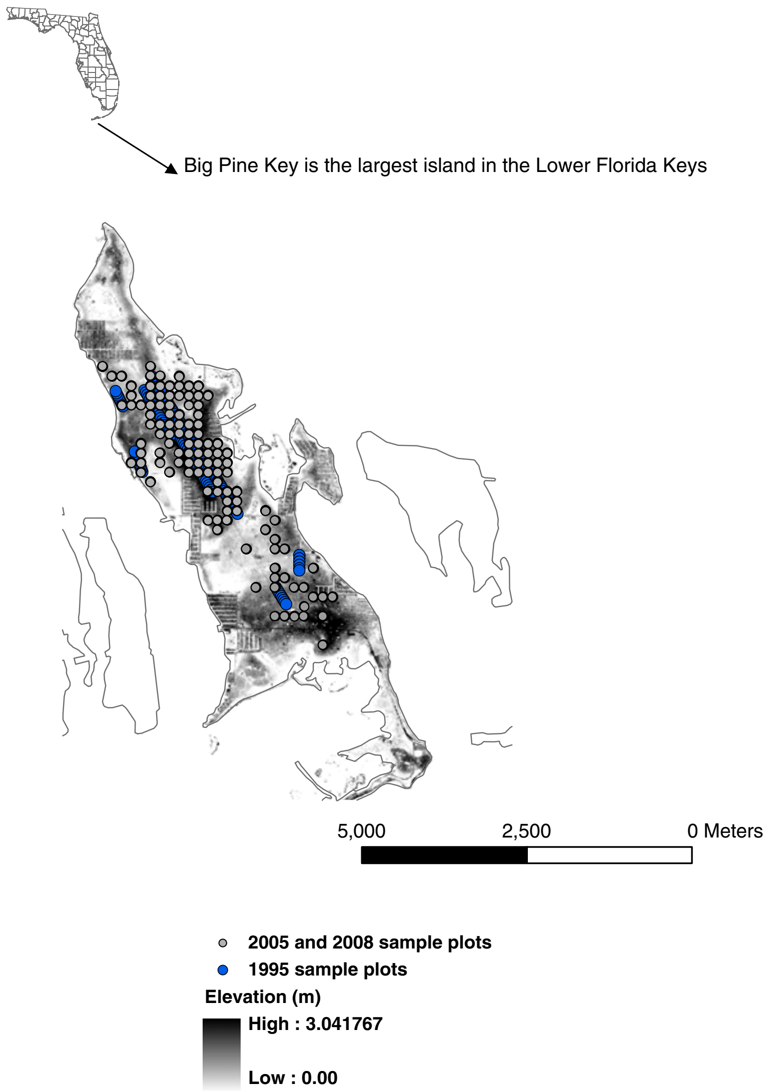

Fig. 1 Map of Big Pine Key showing the study plots. Locations are marked for plots sampled in 1995 and 2005/2008

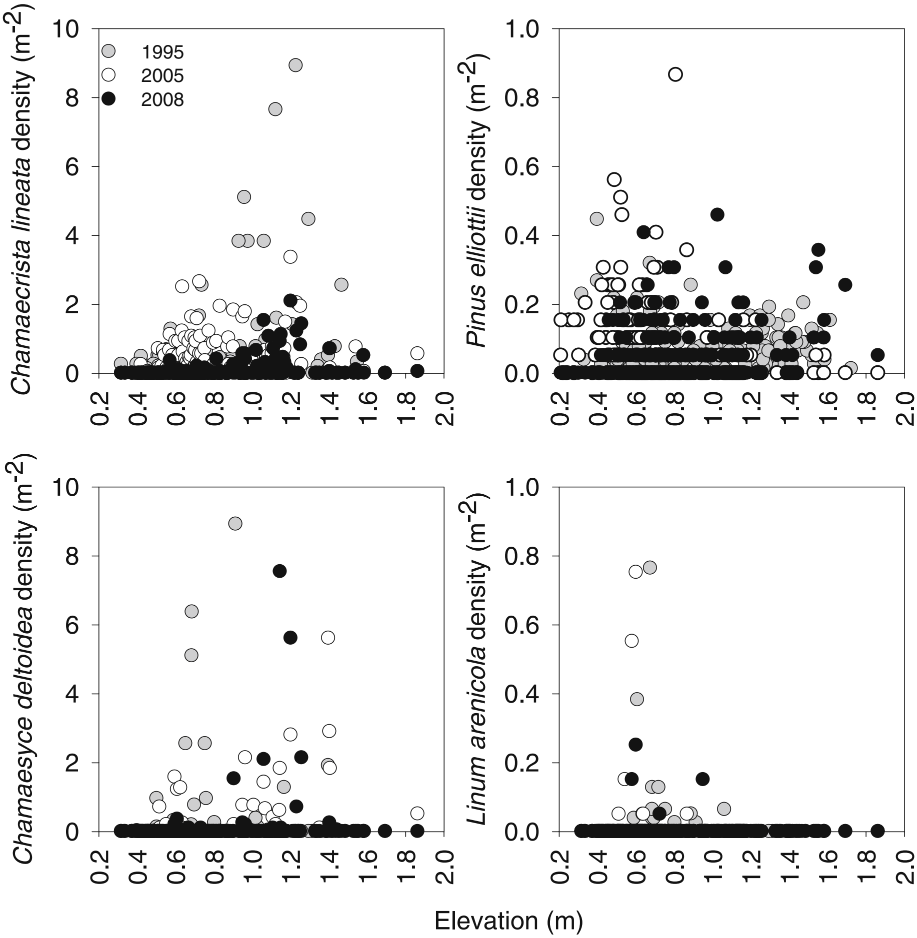

Fig. 2 Distribution of plant counts across plot locations varying in elevation. Densities of *C. lineata*, *C. deltoidea*, *L. arenicola* and South Florida slash pine (*P. elliottii* var. *densa*) are depicted because these species were consistently sampled in 1995, 2005, and 2008. We converted count data to density to make the results comparable across years, because plot size varied between 1995 and 2005/2008 sampling

A natural experiment was triggered after hurricane Wilma (October 2005) caused a maximal storm surge of 2 m in the lower Florida Keys. The plots were sampled in 2008 to test for the role of elevation (used as proxy for storm surge impact) on rare plant abundance and distribution. We discarded 92 of 400 plots because they were privately owned or occurred outside of pine rocklands. In each circular plot, total counts of individuals of *C. lineata* var. keyensis, *C. deltoidea* var. *serpyllum*, *L. arenicola*, and *S. maritima* were made irrespective of their life-history stage. Counts of South Florida slash pine include all plants >1 cm DBH.

Elevation data were obtained from The Nature Conservancy's LiDAR (Airborne Light Detection and Ranging Technology) flown in January 2007. We obtained elevation for the center of each plot. Distance between centers was greater than the error (2.5 m) associated with a LiDAR-derived elevation.

3.1 Data analyses

3.1.1 Role of elevation on species abundance over time

We performed a separate analysis for year of sampling to examine effects of elevation on plant counts and related the results to prior hurricane history. The plots sampled in 1995 were not identical to plots sampled in 2005 and 2008, but the sample sizes were large (145 and 308 plots in 1995 and 2005, respectively), and both studies documented plant counts with the objective of estimating abundance of rare species in pine rocklands of BPK. Plot elevations between 1995 and 2005 were statistically comparable as well (0.96 ± 0.001 m in 1995 and 0.87 ± 0.003 m in 2005; $t = -1.04$, $P > 0.05$).

Our count data had overabundance of zeros, exhibited overdispersion (mean < variance), and were non-normally distributed. We used counts as the dependent variable and elevation as the explanatory variable in negative binomial regression using R (R Development Core Team 2009 version R. 2.10.1). Use of a negative binomial model is recommended when count data are overpopulated with zeros because the option involving log-transformation leads to data fudging by adding a value (usually 1; O'Hara and Kotze 2010). We used MASS package (Venable and Ripley 2002) to fit the data to a negative binomial model. We used Vuong's test (Vuong 1989) to assess if the negative binomial model was adequate to fit the count data and if the zero-inflated negative binomial regression improved the likelihood of fitting the model parameters.

3.1.2 Effects of elevation on change in species abundance after Hurricane Wilma

Using pre (2005) and post hurricane data (2008) we examined change in abundance between years and asked if elevation influenced post hurricane change. We used all plots for analysis even though there was overabundance of plots with no plants. We performed Wilcoxon-Signed Rank test to compare the difference in count data between each plot pair sampled in 2005 and 2008.

We assessed the effect of elevation by regressing change in plant counts against elevation with the expectation that plots at lower elevations would show a greater decline in density than those at higher elevations. We used multinomial logistic regression with change in counts of focal species per plot as the dependent variable and elevation as the predictor variable. Multinomial logistic regression is used when the dependent variable in question is nominal (a set of categories which cannot be ordered in any meaningful way) and consists of more than two categories. The dependent variable in question here was change in plant counts, categorized as increase (2008 > 2005 counts per plot), decrease (2008 < 2005) and no change (no difference). One of the merits of using the logistic model is that the data do not need to be normally distributed. Change in plant counts was non-normally distributed and the outcome no change (2008–2005 counts = 0) was overabundant. The Wald test statistic was used to assess the significance of predictor variable (elevation) on odds of increase or decreases in plant counts versus no change in plant counts. We assume that the change in species counts result from biological processes such as colonization, extinction, and survival (Adler et al. 2007).

4 Results

4.1 Role of elevation on rare plant abundance and distribution

Of all rare species, *C. lineata* had the highest density (individuals per square meter). Median (10–90th percentile) density of *C. lineata* was 0.254 (0–1.63) in 1995, 0.05 (0–0.76) in 2005, and 0 (0–0.20) in 2008. *C. deltoidea* ranked second with densities of 0 (0–0.91) in 1995, 0 (0–0.05) in 2005, and 0 (0–0) in 2008. *L. arenicola* had density

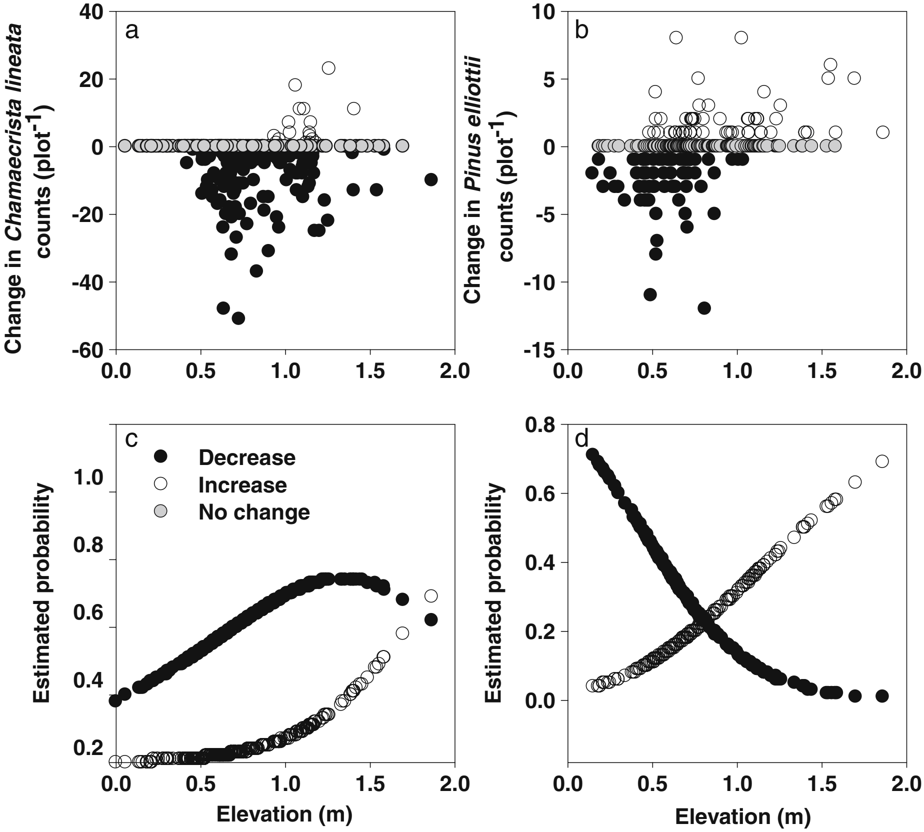

Fig. 3 **a–d** Change in plant counts between pre-and post-Hurricane Wilma sampling in relation to elevation shows that the outcome of no change in plant counts (post hurricane - pre hurricane counts = 0) dominates the response and is distributed randomly in relation to elevation. Probability of the outcome of increase in counts was positively correlated to elevation for *C. lineata* and South Florida slash pine (*P. elliottii* var *densa*). Probability of the outcome of decrease in pine counts showed a decline with elevation. Probability of decrease in *Chamaecrita lineata* counts showed a rise until a certain elevation and then declined

of 0 (0–0) across all sampling events. Density of South Florida slash pine was 0.06 (0–0.12), 0 (0–0.11), and 0 (0–0.06) in 1995, 2005, and 2008, respectively.

C. lineata occurred at elevations between 0.31 to 1.54 m in 1995, 0.42 to 1.86 in 2005 and 0.55 to 1.86 in 2008. *C. deltoidea* occurred at elevations ranging from 0.40 to 1.39 in 1995, 0.51 to 1.86 in 2005, and 0.59 to 1.44 m 2008 (Fig. 3). *L. arenicola* occurred between 0.59 to 1.06 m in 1995, 0.51 to 0.86 in 2005, and 0.60 to 0.95 in 2008. South Florida slash pine occurred at elevations from 0.31 to 1.72 m in 1995, from 0.23 to 1.64 m in 2005, and 0.40 to 1.868 m in 2008 (Fig. 3).

The results of negative binomial regression are summarized in Table 1. The sign of the regression coefficient in Table 1 indicates a positive or a negative impact of a unit increase in the predictor variable on the response variable at a constant value of other predictors in the model. The test statistic z is used to test against a two-sided alternative hypothesis that the regression coefficient is not equal to zero. Elevation did not have a significant effect on distribution of *C. lineata*, *L. arenicola*, or South Florida slash pine in 1995. Elevation explained the variation in density of *C. deltoidea* in 1995. A unit increase in elevation led to an increase in density by 3.574 ($Z = 2.571$, $P = 0.01$).

Pre-Wilma or 2005 counts of *C. lineata* were positively associated with elevation (Coefficient = 1.519, $Z = 3.995$, $P < 0.0001$). Elevation had a strong positive influence on the distribution of *C. deltoidea* in 2005 (coefficient = 4.9116, $Z = 4.916$, $P < 0.0001$). *S. maritima's* distribution was negatively influenced by elevation (coefficient = −0.9883, $Z = 4.547$, $P = 0.0012$) with plants distributed at elevation ranging from 0.05 to 0.12 m. Elevation did not explain change in South Florida slash pine density (coefficient = 2.067, $Z = 0.657$, $P = 0.361$).

Elevation had a positive influence on post-Wilma abundances of *C. lineata* and *C. deltoidea*. The sign of the regression coefficient and the P value associated with test

Table 1 Column headings provide the parameters of regression testing for the role of elevation on South Florida slash pine and rare plant density in 1995, 2005, and 2008

	1995	2005	2008
Pinus elliottii			
Coefficients	−1.853	2.067	6.48
t	−1.431	0.657	4.47
P	0.163	0.361	<0.0001
Chamaecrista lineata			
Coefficients	0.960	1.519	5.065
Z value	1.821	3.995	8.619
P (*z*)	0.068	0.0001	<0.0001
Chamaesyce deltoidea			
Coefficients	3.574	4.911	2.945
Z value	2.571	4.277	2.615
P (*z*)	0.01	0.0000	0.0089
Linum arenicola ($N < 3$)			
Coefficients	−0.004	−0.46	
Z value	−0.09	0.002	
P (*z*)	0.932	0.452	
Strumpfia maritima			
Coefficients	ND	−0.988	−0.895
Z value		−4.547	−3.776
P (*z*)		0.0012	0.077

Significant effects of predictor variables are indicated with probabilities associated with test statistic in bold. No data (ND) were collected for *Strumpfia maritima* in 1995, and *Linum arenicola* occurred in less than three plots in 2005 and 2008. Pine density was regressed against elevation using linear regression; rare species counts were regressed using negative binomial regression statistic were used to infer significance (*C. lineata*; coefficient = 5.06, $Z = 8.619$, $P <$ 0.001, *C. deltoidea*; coefficient = 2.945, $Z = 2.615$, $P = 0.008$). On the other hand, post-Wilma densities of *S. maritima* remained stable along the elevation gradient. South Florida slash pine showed a significant increase in density with elevation (coefficient = 6.48, $Z = 4.47$, $P = 0.0001$).

4.2 Effects of Hurricane Wilma on abundance

South Florida slash pine occurred in 118 plots in 2005 compared to 71 plots in 2008, with 853 and 392 trees in 2005 and 2008, respectively. Absolute counts of *C. lineata* declined from 1,540 plants in 2005 to 584 plants in 2008, and *C. deltoidea* declined from 686 plants in 2005 to 568 plants in 2008. Of 308 plots sampled, *C. lineata* occurred in 147 plots in 2005 and 60 plots in 2008. *C. deltoidea* occurred in 29 and 18 plots, respectively, in 2005 and 2008. Twenty-six plants of *L. arenicola* occurred in seven plots before Hurricane Wilma and 12 plants in nine plots were observed after Hurricane Wilma. Counts of *S. maritima* decreased from 48 plants in 2005 to 40 plants in 2008 after Hurricane Wilma in five plots.

A Wilcoxon signed-rank test showed that counts of *C. lineata* declined significantly after Hurricane Wilma ($Z = -8.29$, $P < 0.001$, $df = 308$). Counts increased in 17, decreased in 127, and remained same in 164 plots. Of 164 plots showing no change, only six plots had equal plant counts before and after Hurricane Wilma; the rest showed no change because no plants occurred there. Of 127 plots showing decline, complete loss of plants was observed in 74 plots (58%).

The decline in plant counts was marginally significant for *C. deltoidea*, ($Z = -1.96$, $P = 0.05$, $df = 308$). Plant counts declined in 24 plots, increased in 11 plots, and remained same (no change due to absence of plants before and after hurricane) in 273 plots. Of 24 plots, 15 (62%) exhibited complete loss of *C. deltoidea* plants after the hurricane. *S. maritima* did not show a significant difference in counts as result of the hurricane ($Z = -0.16$, $P = 0.87$, $df = 308$), nor did *L. arenicola* ($Z = -1.54$, $P = 0.10$, $df = 308$). Plant counts increased in seven plots, declined in two plots, and remained the same in 299 plots. Abundance of South Florida slash pine declined from 2005 to 2008, with 48 plots showing an increase, 175 plots showing a decrease, and 85 plots showing no change ($Z = -8.21$, $P < 0.0001$, $df = 308$).

4.3 Effects of elevation on change in species abundance after Hurricane Wilma

We analyzed changes in *C. lineata*, *C. deltoidea*, and South Florida slash pine, as these species showed significant hurricane-associated changes in abundance. The outcome "no change" in plant counts was evenly distributed in relation to elevation (*C. lineata* Fig. 3a; South Florida slash pine Fig. 3b).

Our analyses suggest that elevation, as a surrogate for inundation by salt water resulting from storm surge, has a significant impact on abundance after a hurricane for *C. lineata* (Table 2). Associated coefficients for increase and decrease in reference to no change in plant counts are listed in Table 2. Our data indicate that for one unit change in the elevation, the regression coefficient which is the log of the ratio of the two probabilities, [probability (increase)/probability (no change)] will rise by 3.898 ($P < 0.0001$), suggesting that the probability of increase in plant counts is positively influenced by elevation (Fig. 3c). For a unit change in elevation, the log of ratio of

Table 2 Patterns of change in plant density with respect to elevation were analyzed using multinomial logistic regression

	β	Wald Statistic	Sig.
Chamaecrista lineata			
Decrease	0.160	15.075	0.000
Increase	3.898	19.806	0.000
Chamaesyce deltoidea			
Decrease	1.509	5.404	0.052
Increase	2.072	4.358	0.051
Pinus elliottii			
Decrease	−2.841	13.682	0.000
Increase	1.61	0.914	0.003

This table summarizes the coefficients, test statistic (Wald's test), and significance (Sig.) of Wald's Statistic. A Wald test is used to test the statistical significance of each coefficient (β) in the model. Coefficients are the logs of ratio of two probabilities, probability of outcome category and reference category. Response categories are increase and decrease in plant counts relative to no change

[probability (decrease)/probability (no change)] showed a positive increase of 0.160 ($P < 0.0001$). Predicted probability of decrease against elevation is a hump-shaped relationship, suggesting that at lower elevation there was a large decline in density after Hurricane Wilma, but as the elevation increases the probability of decrease goes down (Fig. 3c). To reconcile a simultaneous rise in probabilities of increase and decrease after Hurricane Wilma, we examined coefficients that are logarithimically scaled (Harrell 2001). A visual inspection suggests that the probability of increase is almost negligible for plots located up to 1 m in elevation, while the probability of decrease rises because of greater mortality at lower elevation. However, above 1 m the probability of decrease plateaus and then declines, while the probability of increase rises almost exponentially.

Change in *C. deltoidea* counts did not exhibit a significant trend in relation to elevation. The coefficients: log [probability (increase)/probability (no change)] and log [probability (decrease)/probability (no change)] showed no significant trend.

The decrease in pine cover was influenced by elevation, with less decreases at greater elevation. Similarly, increase in pine cover was influenced by elevation; with a unit increase in elevation the log [probability (increase)/probability (decrease)] showed a rise of 1.61 U ($P < 0.003$, Fig. 3d). The log [probability (decrease)/probability (increase)] showed a decline of -2.841 U with a unit increase in elevation ($P < 0.0001$, Fig. 3d).

5 Discussion

5.1 Role of elevation on species distribution

Distribution of plant communities along elevation gradients is characteristic of coastal ecosystems (Doyle et al. 2007; Miller et al. 2009). In pine rocklands of the Lower Florida Keys we observed that the influence of elevation was more pronounced in years following a hurricane (sampling within 3 years following a storm surge) than in hurricane-free years.

Elevation did not explain distribution of the rare endemic *C. lineata* in 1995, which occurred homogeneously across pine rocklands at all elevations. The effects of elevation were stronger in 2005 and 2008 suggesting that storm surges associated with hurricanes eliminated populations at lower elevations. While this study did not include sampling after Hurricane Georges in 1998, the significant effect of elevation on *C. lineata* abundance in 2005 could have resulted from storm surges generated by Hurricane Georges (Somerfield et al. 2008). The time interval between storm surges might influence the distribution of *C. lineata* populations, allowing re-establishment of populations at lower elevations between storms.

C. deltoidea showed a strong association with higher elevations at each sampling event, although the mean elevation at which plants occurred was highest in 2008. Patterns in distribution of *L. arenicola*, a widely distributed species, were not explained by elevation across sampling years, whereas *S. maritima*, a species occurring in more saline habitats, was negatively related to elevation in 2005, with the effects disappearing in 2008, perhaps because inundation by salt water associated with storm surges killed plants at lower elevation.

South Florida slash pine was distributed homogenously across all elevations in 1995 and 2005, but showed a positive association with elevation in 2008. Our result that South Florida slash pine is declining at lower elevations is similar to findings of Ross et al. (1994) showing mortality of South Florida slash pine at lower elevations.

The benchmark data from 1995 suggests that the South Florida slash pine and rare endemics of pine forests can occur in pinelands at lower elevations in the absence of hurricanes. However, the increasing influence of elevation with shorter time since hurricanes suggest that hurricane return interval plays an important role in shaping plant distribution and community organization in coastal uplands. Beckage et al. (2006) invoked the role of hurricane frequency in shaping pine ecosystem dynamics in the southeastern United States, but we are not aware of other studies that have explicitly examined the role of hurricane return intervals on species distributions and dynamics in hurricane-prone ecosystems.

5.2 Effects of Hurricane Wilma on abundance

In contrast to studies monitoring changes in species abundances and composition of subtropical pine ecosystems after fire (Snyder et al. 2005), the effects of hurricanes were clear, although the effects were not uniform across the rare species. The obligate pineland species *C. lineata* exhibited a significant decline while *C. deltoidea* declined marginally. *L. arenicola*, a disturbance dependant species, did not show a significant decline after Hurricane Wilma. *S. maritima*, a widely distributed species considered tolerant of tidal inundation and high salinity levels did not exhibit significant declines.

Studies examining hurricane effects elsewhere suggest that coastal plant communities are resilient to storm surges. Hurricane effects documented in barrier islands of Florida where plant communities of the fore dune reverted to pre-hurricane assemblages within a period of 2 to 3 years (Miller et al. 2009; Snyder and Boss 2002) were driven by the salt tolerance of fore dune species. We observed a similar response by *S. maritima*, a species tolerant of occasional inundation. Morrison (2003) documented a decline in plant biomass and abundances in Bahamian islands after a hurricane in 1998, but did not observe population extinctions. However, when effects of two major hurricanes were monitored (Hurricane Lili in 1998 and Hurricane Michelle in 2002; Morrison and Spiller 2008) using larger sample sizes from the Bahamas archipelago, stability among salt-tolerant species and decline of species sensitive to salt was observed.

Density of South Florida slash pine showed dramatic changes between 2005 and 2008. In a study of fire and hurricane interactions, Sah et al. (2010) showed uniform declines in South Florida slash pine density at lower elevations after Hurricane Wilma irrespective of fire history. Thus, hurricanes have a major influence on South Florida slash pine, the most abundant species of pine rocklands in the Lower Florida Keys, while rare species of these ecosystems do not show such clear-cut responses.

5.3 Effects of elevation on change in abundance after Hurricane Wilma

Our analyses suggest that elevation, as a surrogate for storm surge, has a significant impact on changes in post-hurricane densities for *C. lineata* (Fig. 3). A significant increase in *C. lineata* individuals occurred in plots located at higher elevations. This result leads us to propose that *C. lineata* will show a gradual shift towards higher elevation unless no further migration is possible due to lack of suitable habitat. A negative impact on its seed banks by residual salt in the soil system will prevent recruitment at sites where reproductive individuals are present prior to hurricanes. Elevation did not have a dramatic influence on density of *C. deltoidea*. Though *C. deltoidea* showed marginal reduction in density after Hurricane Wilma, it primarily occurred in areas at higher elevations shielded from hurricane generated storm surge.

Pine density showed a larger decline at lower elevations while exhibiting significant gains along the elevation gradient. South Florida slash pine forms the canopy of pine rocklands, and its decline at lower elevations after a hurricane is alarming, especially against the backdrop of sea level rise. Because pines at lower elevation are negatively impacted by storm surge, post-hurricane colonization will be less likely with a continual rise in sea level.

5.4 Implications under a sea-level rise scenario

Our data show that in the absence of hurricane generated storm surges, South Florida slash pine and rare endemics restricted to pine rocklands have lower optimal elevation. However, if natural disturbance regimes including periodic hurricanes have shaped the dynamics of subtropical pine ecosystems, why should land managers and conservation biologists be concerned about the status of rare and endemic plants in relation to hurricanes? Studies suggest that storm surge levels will increase significantly with sea level rise (Brown et al. 2010; Smith et al. 2010), magnifying the toll sea level rise has already had on pine rocklands in the Florida Keys (Ross et al. 1994, 2009).

Pine rocklands of BPK are upland communities harboring plant species that harvest fresh water and are salt sensitive (Ross et al. 2009). Rise in sea level has stressed the pine ecosystem of the Florida Keys due to intrusion of salt water (Ross et al. 1994, 2009). Unlike pine trees, which utilize groundwater (Saha et al. 2009), we conjecture that rare herbaceous species of pine rocklands are unable to tap into groundwater because of their shallow root systems (S. Saha, personal observations on rooting depth). Thus the saltwater intrusion apparently affecting BPK's freshwater lenses and pine trees is less threatening for herbaceous species. However, the collapse of South Florida slash pine will have negative effects on rare species because pines provide canopy cover and, more importantly, provide fuel in this ecosystem shaped by fire (Snyder et al. 1990). Rare species restricted to pine rocklands may depend on pines for partial canopy cover and for fire-generated niches that might facilitate recruitment by reducing competition.

With acceleration in sea level rise, a large storm could tip the salinity balance in favor of halophytes and progressively truncate the population distribution of pine rockland obligates at higher elevations. With each storm surge the area available for recruitment will shrink until the plants have nowhere to go, such as simulated for hammock ecosystems juxtaposed next to mangrove communities (Sternberg et al. 2008; Teh et al. 2008).

Dramatic shifts in optimal altitude of plant species in response to climate change are reported across many ecosystems, especially in temperate regions (Feehan et al. 2009; Lenoir et al. 2008). In the case of species associated with subtropical pine ecosystems, we hypothesize that the availability of optimal upland habitats will become restricted with every tropical storm event in the background of sea level rise, restricting the distribution of rare species to the highest elevations. Thus, in situ conservation efforts such as maintenance of fire regimes, and a better understanding of the life history and demography of endemic plant taxa through monitoring, might delay the loss of pine rocklands and associated rare species from islands of the Lower Florida Keys under scenarios of sea level rise.

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