Shifting baselines in coastal forests: Rising seas transform plant communities from the 'ground' up

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A B S T R A C T

Increases in the rate of sea level rise are likely to result in changes to disturbance-adapted coastal forests and associated freshwater resources over the next several decades. In this study, we investigated how the press disturbance of two decades of sea level rise altered island hydrology and interacted with pulse disturbances (frequent hurricane impacts) to alter coastal forest composition and structure. The research was conducted on two low-elevation islands located within the lower Florida Keys: Big Pine and Upper Sugarloaf Keys. Groundwater salinity and vegetation structure and composition were sampled in the early 1990s prior to impact from two hurricanes – Hurricanes Georges (1998) and Wilma (2005) – and again in 2012/2013 in permanent plots inside and outside the boundaries of the islands' freshwater lenses. Using linear mixed effects modeling, we examined whether groundwater salinity varied over time among locations, and investigated whether this variation was reflected in changes in forest structure and composition in three height strata. The results of this analysis revealed that groundwater salinity underlying plots outside the freshwater lens increased over the two decades, while salinity of groundwater at plots inside the freshwater lens remained stable. The greatest shift in composition occurred in the understory strata along a gradient of increasing salinity, and plots located outside the freshwater lens gained species typical of tidally-influenced buttonwood forest and lost glycophytic species. Viewed against the background of recurring hurricane impacts, these findings suggest that sea level rise is currently altering both groundwater resources and the composition of coastal forests in the Florida Keys. Similar dynamics should be observed in low-lying coastal forests within ocean basins subject to increased tropical cyclone activity. Management of these island coastal forests must now consider the continually shifting nature of the resource in light of acceleration in sea level rise.

1. Introduction

Coastal plant communities are of scientific and conservation concern owing to sustained as well as projected increases in sea level (Rahmstorf, 2007) that may dramatically change their structure and composition. Over the last few decades, forest retreat and compositional changes related to rising seas have been documented in a variety of coastal forest types, from mangrove forests (Ellison, 2015) to hydric hammocks (Saha et al., 2011, Williams et al., 1999a,b). In general, disturbance regimes of varying spatial and temporal scale characterize all biological systems, altering both abundance of individuals and resource availability (White and Pickett, 1985). In low elevation terrestrial coastal forests, increasing sea level operates as a press or ramp

disturbance (Glasby and Underwood, 1996; Lake, 2000), leading to higher water tables (Rotzoll and Fletcher, 2012) and increasing groundwater salinity as the salt water intrudes into freshwater aquifers (Guha and Panday, 2012). The result is the eventual replacement of glycophytes by halophytic plant communities (Saha et al., 2011). Additionally, in many parts of the world, coastal forests are impacted frequently by tropical cyclones, large infrequent disturbances (Turner et al., 1998) that are typically accompanied by strong winds and storm surge flooding. These cyclones are classified as "pulse" disturbances (Glasby and Underwood, 1996). Disturbance from tropical cyclones influences both forest structure (Van Bloem et al., 2006, 2007) and composition (Vandermeer, 2000). Strong winds snap stems and uproot trees, while storm surge may inundate interior forest not adapted to
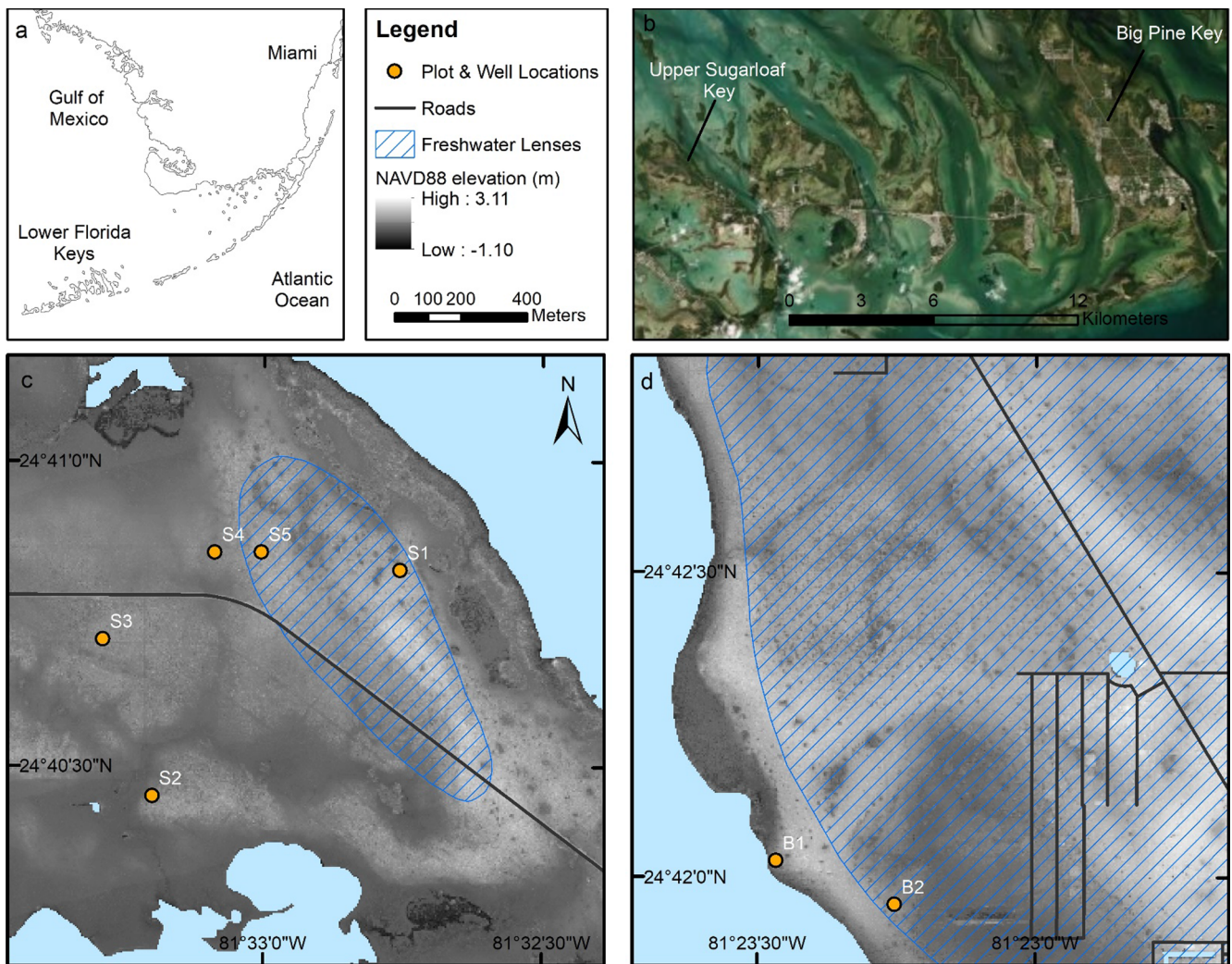
Fig. 1. Location of seven permanent plots and associated groundwater monitoring wells in (a) south Florida's, (b) lower Florida Keys on, (c) Upper Sugarloaf (SLK) and (d) Big Pine Keys. Boundaries of the freshwater lens(es) for each island, as determined by Wightman (1990) and Caballero (1993), respectively, are displayed.

flooding by saline waters. Furthermore, not only do storm-induced mortality rates differ among species, but post-storm community development may take alternative trajectories as a result of ecological legacies (Buma, 2015). In combination, pulse and press disturbances may lead to different successional trajectories than either disturbance type individually (Glasby and Underwood, 1996; Ross et al., 2009).

The combined effects of rising sea level and hurricanes on coastal vegetation communities are especially pressing in south Florida, where large stretches of forest exist a few meters or less above sea level. The coastal forests of south Florida, especially pine rockland and dry tropical broadleaf forest (hardwood hammock), host a unique assemblage of species, many of them endemic (Snyder et al., 1990). On the low-lying islands of the Florida Keys, where maximum elevation is often less than 2 m, declines in the extent of glycophytic coastal forests have been well-documented in the 20th century (Alexander, 1974; Ross et al., 1994). The extent of pine forests and adjacent patches of hammock in the Keys has been decreasing since the end of the last ice age (18,000 years BP), as sea level rose first rapidly (until ~5500 year BP) and then ever more gradually to present day (Wanless et al., 1994), dissecting the island chain, and isolating it from the once-contiguous landmass of south Florida (Lidz and Shinn, 1991). However, it is likely that the rate of structural and compositional change in these insular forests has increased since sea level rise began an acceleration in the late-twentieth century (Church and White, 2006). To date, an analysis of the impacts of rising seas on well-drained Keys' forests, including

both fresh water resources and vegetation structure, has not been completed.

On limestone islands such as the Florida Keys, available fresh water occurs in lenses that are recharged by precipitation. These freshwater lenses 'float' on the underlying salt water and their lateral extent is determined by the island's geomorphology combined with the seasonal distribution of precipitation. Surveys employing electrical resistivity tomography (ERT) and electromagnetic (EM) techniques in the lower Keys have identified central lenses of fresh groundwater surrounded by increasingly brackish groundwater approaching the coast (Vacher et al., 1992; Meadows et al., 2004; Ogurcak, 2015). Coastal forests in the lower Florida Keys occur at locations both inside and outside the central lenses of freshwater, which suggests that the species in these forests tolerate a range of groundwater salinities. And although more salt-tolerant species are often found in closer proximity to the coast and at lower elevations (Ross et al., 1994; Saha et al., 2011), the karstic nature of the islands results in interior depressions and coastal highs, making these two variables potentially less useful in prediction of salinity-stress experienced by a plant community. Designation of forest as either occurring inside or outside the freshwater lens thus serves as a useful template for study of change across scales of space and time.

In 2012, we revisited pine and hammock forest plots established in 1990 (Ross et al., 1992) on two islands in the Lower Florida Keys with the objective of documenting changes in ground water salinity and vegetation at locations inside and outside the islands' freshwater lenses.

We hypothesized that sites located outside the lens would display larger increases in groundwater salinity than sites within it. After accounting for variation in precipitation between the sampling periods, we attributed any changes in groundwater salinity between the first and second sampling periods to increasing sea level. We then investigated whether these sea level-driven changes in salinity could explain any observed shifts in plant community structure and composition. A complicating factor in the analysis was the occurrence of two storms, Hurricane Georges (1998) and Hurricane Wilma (2005), which struck the lower Keys during the study period. These hurricanes brought a combination of damaging winds and storm surges to the study location accompanied by average to below average rainfall amounts (Pasch et al., 2001, Beven et al., 2008). We hypothesized that although direct disturbance impacts from the two hurricanes, including stem breakage and salt-water induced mortality, should be present across all sites, such changes in plant composition and structure should be greater at locations in which groundwater salinity had also increased in response to the press disturbance of sea level rise. If sea level rise is in fact currently affecting these forests, changes in the structure and composition of forests located outside of the freshwater lens should be of greater magnitude and changes should favor salt-tolerant species, with potential colonization of species from nearby mangrove or buttonwood forest.

2. Methods

2.1. Study area

Big Pine and Upper Sugarloaf Keys (N 24.67°, W 81.36°, and N 24.66°, W 81.53°, respectively) are islands in the lower (southwestern) Florida Keys (Fig. 1 inset) separated by a distance of 17 km. On these islands, study sites are located within the U.S. Fish and Wildlife Service National Key Deer Refuge (NKDR) within 0.8 km of the coast of the Gulf of Mexico and at elevations less than 1 m above local mean sea level (LMSL). Both Hurricane Georges, a category 2 storm at the time of landfall in Key West on 25 Sep 1998, and Hurricane Wilma, a category 3 storm at time of landfall near the Cape of Florida on 24 Oct 2005, flooded the islands with salt water and brought winds ranging in speed from 30 to 40 m/s (Kasper, 2007; Zehr and Knaff, 2007). A combination of field evidence (Sah et al., 2010) and remotely-sensed data (Ogurcak, 2015) confirm that all island locations below 1 m in elevation received storm surge flooding from Hurricane Wilma, while Hurricane Georges resulted in only minor coastal flooding. The low-moderate amounts of precipitation that accompanied both storms — 21.4 cm total recorded in Tavernier, FL for Georges (Pasch et al., 2001) and 5.13 cm total recorded in Key West, FL for Wilma, (Beven et al., 2008) — combined with extended periods of very little rainfall in the ensuing months (Hurricane Wilma), certainly exacerbated the effects of salt water flooding on plants (Ross et al., 2009).

Bedrock on the two islands consists of high permeability Key Largo Limestone (Hoffmeister and Multer, 1968), overlain by several meters of less permeable Miami Limestone (Hoffmeister et al., 1967), both of Late Pleistocene age (Perkins, 1977). Freshwater lenses (Fig. 1) exist on both islands as a result of lower secondary permeability of the Miami Limestone (Coniglio and Harrison, 1983), with the depth of the lenses truncated near the contact between the formations (Vacher et al., 1992). Recharged by seasonal precipitation, these lenses provide a source of fresh groundwater to the coastal forest plants (Ross et al., 1994, Ogurcak, 2015). While residential development on these island has certainly affected groundwater recharge and discharge (Langevin et al., 1998), water for consumption has been transported via an aqueduct from mainland Florida since the 1940s. Additionally, the greatest density of housing is located along the Overseas Highway and along the coasts, outside the boundaries of the freshwater lenses studied here. The Florida Keys encompasses a climatic gradient, becoming drier and warmer as one moves away from mainland south Florida. Throughout the Keys, the climate is typified by a dry season that stretches from November through May, and a wet season from June through October, during which approximately two-thirds of the year's precipitation falls (102.2 cm yearly average for years 1984–2013 at Key West International Airport, http://www.ncdc.noaa.gov).

Pine rockland and hardwood hammock forest communities are rarely flooded, and thus serve as "upland" habitat in the low elevation Keys landscape. They are composed of species that share a requirement for access to the limited freshwater resources yet have some level of tolerance to periodic seasonal drought and salt stress. Limestone is exposed at the ground surface in many places (Snyder et al., 1990), and soils, if present, are < 10 cm in depth (Ross et al., 2003) with little organic matter. These forests are dominated by a single canopy tree species, *Pinus elliottii* var. *densa* (slash pine), with a shrub layer consisting of West Indian hardwood species and palms and a diverse herbaceous layer of approximately 150 species (Snyder et al., 1990). In the absence of fire, pine rocklands lose their herbaceous flora and succeed toward hardwood hammock as the growth of woody species shade the understory and change microclimatic conditions necessary for carrying fire (Snyder et al., 1990). Hardwood hammocks are generally found coastward of the pine rocklands, and are characterized by species that display a range of salt tolerances. Hardwood hammocks of the lower Florida Keys have a diverse assemblage of woody species of West Indian origin with several palm species, but few non-epiphytic herbaceous plants (Ross et al., 1992). Soils are organic and are typically less than 0.3 m in depth (Ross et al., 2003). Invasive exotic plant species are abundant within the lower Keys, but they are infrequent within more remote areas NDKR away from private development (Kruer et al., 1999). More recently (2008–2013), treatment and removal of invasive exotics has been conducted on private lands in the Keys to decrease the potential spread of exotics (https://www.regionalconservation.org/ircs/aboutus/projects.asp).

2.2. Vegetation sampling

We relocated seven permanent plots established in 1990 (Ross et al., 1992) in pine rockland (three plots) and hardwood hammock habitats

Table 1
Permanent plot environmental variables and average groundwater salinity (PPT) ± SE for each sample period.

Plot	Island	Habitat	Lens Location	Sub Plots	DIST (m)	ELEV (m above LMSL)	1990s Groundwater Salinity (PPT)	2010s GroundwaterSalinity (PPT)	1990s # of Sample Events	2010s # of Sample Events
B1	BPK	HH	Outside	6	46	0.91	4.29 ± 0.34	7.67 ± 0.30	34	6
B2	BPK	PR	Inside	6	189	0.69	2.26 ± 0.09	1.13 ± 0.26	24	6
S1	SLK	HH	Inside	6	308	0.88	2.77 ± 0.36	2.57 ± 0.48	35	6
S2	SLK	HH	Outside	6	282	0.66	9.76 ± 0.27	10.48 ± 0.15	34	6
S3	SLK	PR	Outside	6	758	0.59	9.29 ± 0.37	12.68 ± 1.08	35	6
S4	SLK	HH	Outside	5	633	0.52	10.51 ± 0.67	28.57 ± 3.47	35	6
S5	SLK	PR	Inside	6	535	0.91	1.74 ± 0.25	0.67 ± 0.03	34	6

Island codes: BPK = Big Pine Key, SLK = Sugarloaf Key. Habitat codes: PR = pine rockland; HH = hardwood hammock. DIST = Distance to coast; ELEV = elevations above local mean sea level as of 2012.

(four plots) on Big Pine and Upper Sugarloaf Keys (Table 1, Fig. 1). Five plots were located on Upper Sugarloaf Key and two on Big Pine Key at varying elevations and coastal proximity. Plots on Big Pine Key are separated from each other by less than 0.5 km and the five plots on Upper Sugarloaf Key are located within 1 km of each other. Each plot was 600 m², consisting of six 10 m × 10 m subplots, except for one hardwood hammock plot of 500 m² where patch size was limited. The corner of each subplot was marked with a metal rebar and GPS co-ordinates were obtained with a Garmin GPSmap76Cx having horizontal accuracy of 5 m. Sampling procedures were identical during our 1990 and 2012 surveys. Basal area was calculated from diameter at breast height (DBH) for all tree species greater than 3 cm DBH and taller than 2 m. Percent cover of herbaceous vegetation, seedlings, and low shrubs (0–1 m height), hereafter 'ground layer', and saplings and high shrubs (> 1 m height and < 3 cm DBH), hereafter 'shrub layer', was estimated for each species present in a 5 × 5 m quadrat located at the center point of each subplot. Cover was estimated using the following cover classes: 1 = < 1%, 2 = 1–4%, 3 = > 4–16%, 4 = > 16–32%, 5 = > 32–66%, and 6 = > 66–100%. The midpoint of each cover class was used as the percent cover for each species in subsequent analyses.

2.3. Groundwater sampling

Salinity data were collected at regular intervals at each plot to capture the yearly range in salinity for both the 1990 and 2012 sampling periods (Table 1). Wells constructed of PVC pipe with outer diameter 3.2 cm were installed through bedrock to an approximate depth of 1 m. At site B2, the 1 m deep well of 1990 could not be relocated in 2012, and instead a nearby 5 cm diameter well installed by the U.S. Geologic Survey in 1989 was used. This well was 3 m deep and screened along its entirety.

Beginning in January 1991, all 1 m deep wells were sampled at bi-monthly intervals. The sampling interval became monthly in December 1991 and continued through 1992; this sampling is hereafter referred to as 1990s sampling. Prior to obtaining the sample, wells were evacuated using a syringe and tube to remove standing water and the well was allowed to refill with surrounding groundwater. The 3 m deep well was sampled approximately every two weeks beginning August 1989 to June 1990, was not evacuated prior to sampling, and is hereafter referred to as part of the 1990s sampling. Salinity of each groundwater sample was measured using a handheld refractometer with a resolution of 1 PPT and accuracy of ± 1 PPT. Twenty years later, the wells were sampled every two months beginning May 2012 and ending May 2013; this sampling is hereafter referred to as 2010s sampling. Wells were evacuated using a peristaltic pump before each sample was obtained. Salinity was measured with a YSI model 30 handheld probe with a resolution of 0.1 PPT and accuracy of ± 0.1 PPT.

2.4. GIS data processing

Using ArcMap 10.2, we extracted average elevation in NAVD88 (m) for each permanent plot from the lower Keys LiDAR-derived Digital Terrain Model (5 m horizontal resolution) (Zhang et al., 2010). For each well and plot, we calculated the distance to the nearest coastline. The vertical datum was then converted to meters above local mean sea level (LMSL) using NOAAs Vertical Datum Transformation program, VDatum v.3.4 (http://vdatum.noaa.gov/). Tidal transformations in VDatum extend only slightly inland from the mean high water shoreline (~1 km), resulting in three of the permanent plot centroids and wells falling just beyond the VDatum model grid. For these locations, the difference between the two datums for the nearest plot falling within the model grid was used to convert from NAVD88. The difference between datums at each plot centroid (averaging 20 cm) was added to the plot average elevation (NAVD88) to obtain meters above LMSL for each plot.

Permanent plots were located either within the freshwater lens (inside lens) or outside the boundary of the freshwater lens (outside lens) on both islands (Fig. 1). Lens boundaries were obtained for Big Pine Key from the lens' wet season extent as modeled by Wightman (1990) using Depuit-Ghyben-Herzberg analysis (Vacher, 1988) and for Upper Sugarloaf Key from modeled terrain conductivities (Caballero, 1993). Both maps were georeferenced into the NAD83 horizontal datum and UTM 17 projection. While it is expected that the extent of the freshwater lenses varies over time, it is not expected that any shifts would be large enough to result in changes in plot assignment over the time period as all plots were located more than 40 m from the lens boundary. This assumption is supported by results of groundwater sampling in each time period and resurvey of the lens on Big Pine Key in 2009–2010 (Wightman, 2010).

2.5. Sea level and meteorological data

Annual mean sea level data were obtained from the Permanent Service for Mean Sea Level (http://www.psmsl.org/data/obtaining/stations/188.php, accessed 10 May 2014) for the Key West Tide Gauge (N 24.56°, W 81.81°) (Holgate et al., 2013). The mean sea level trend for the last 100 years (1914–2013) was calculated and the rate of increase of sea level over 100 years was multiplied by the time span of the study (22 years) to adjust for the difference in sea level at well and plot locations in 1990 compared to current day (2012–2013) elevation.

Daily climate data were downloaded from the National Climate Data Center (http://www.ncdc.noaa.gov/) for Key West International Airport from 1984 to 2013. Deviations from the 30-year average (1984–2013) annual rainfall were plotted to qualitatively examine whether sample years received less or more precipitation than the average. The total amount of rain that fell in the 30 days prior to each groundwater sampling event, hereafter referred to as 30-day precipitation, was calculated and included in subsequent modeling to determine if any relationship existed between sampled groundwater salinity and recent precipitation.

2.6. Data analysis

Linear mixed effects modeling with repeated measures (Zuur et al., 2009) was used to determine the effects of geographic location (LENS: inside and outside), sampling period (PERIOD: 1990s and 2010s), and 30-day precipitation (PRECIP) on groundwater salinity (SAL). Random effects for the intercepts of sampling well (WELL) (n = 7) and sampling day (DAY) (n = 65) addressed non-independence related to repeated measures and accounted for differences in initial salinity at each sampling location and any effect related to day in which a sample was taken. The model included a random slope which allowed salinity to vary independently at each well during each period. An investigation of residuals showed that groundwater salinity was heteroscedastic; therefore, salinity data were log transformed after adding an integer of 1 to each salinity value ($LOG_{10}SAL$). Models were run in R v.3.1.2 (R Core Development Team, 2014) using the *lmer* function in the 'lme4' package and p-values were obtained for each effect using the Satterthwaite approximations to degrees of freedom (*merModLmerTest*; Bates et al., 2015). Restricted maximum likelihood (REML) was used to obtain unbiased estimates of variance for the model. Competing models were evaluated by comparing the full-model to a nested model without the effect in question using the *krmodcomp* function in the 'pbkrtest' package with the Kenward-Roger approximation for F-test (Halekoh and Højsgaard, 2014). Salinity means (± SE) for each factor level of the pairwise interaction between PERIOD and LENS were obtained using the 'lsmeans' package (Lenth, 2016). P-values were obtained for pairwise contrasts using Bonferonni 2-sided tests. To assess any differences in climatic conditions between sampling periods, we compared average 30-day precipitation in each period using a student's *t*-test.

Changes in abundance and species richness between sites inside and

outside the lenses between the two sampling periods were assessed using paired *t*-tests. Levene's test was used to check for homogeneity of variances prior to conducting all *t*-tests. For the tree stratum, two measures of abundance were calculated: basal area ha^{-1} and stem density ha^{-1}. Whereas for the shrub and ground layers, total percent cover was used as the abundance measure. In each stratum, species richness was calculated as the total number of species occurring within all subplots in each plot at each time period. Disappearance of species characteristic of hammock and pine communities was noted, while appearance of exotic invasive species and salt-tolerant species typical of nearby buttonwood-dominated communities were noted.

Composition data were analyzed for tree, shrub, and ground layer strata using Non-Metric Multidimensional Scaling (NMDS). Ten random starts were selected, and a solution scaling option based on half-changes was used. Abundance data were standardized to the species maximum across all plots, i.e. abundance values for each species in a plot was divided by the maximum abundance attained by that species in all plots, to reduce excessive influence of any dominant species in the calculation of dissimilarities (Faith et al., 1987). Fourteen samples (seven permanent plots and two sampling periods) were chosen for the ordination and all species with at least one occurrence in a plot were used in each stratum. Bray-Curtis distance was chosen to calculate the dissimilarity matrix (Bray and Curtis, 1957). Vector fitting was used to find the best fit of environmental variables to the composition data (Kantvilas and Minchin, 1989). Environmental variables selected were the average groundwater salinity in PPT (SAL), distance to nearest coastline from each well location (DIST), and plot elevation as meters above LMSL (ELEV). The 2-D result of the ordination was rotated to align with the groundwater salinity vector on the primary axis, so that changes in the NMDS axis 1 score of a plot re-sampled over time is equivalent to the response of the vegetation composition to the groundwater salinity between the two time periods. Therefore, this score was used to assess change in composition attributable to salinity along that vector between the 1990s and 2010s sampling events for inside-lens and outside-lens locations using paired *t*-tests. Ordination and vector fitting, as well as calculation of species richness, were done in the program DECODA (version 3.01, Anutech Pty. Ltd., Canberra, AU).

3. Results

3.1. Changes in climate and sea level

Total mean increase in sea level over the 22-year period (1990 to 2012) was 5 cm, derived from a linear regression of the 100-year record, equating to an annual increase of 2.3 mm yr^{-1} (Fig. 2). While the local rate of SLR has increased in the past two decades to 3.6 mm yr^{-1} (1994–2013), coinciding with observed increases in global mean sea level (~3 mm yr^{-1} Nerem et al., 2018), we use the rate based on the longer dataset for subsequent analysis of environmental variables. The average annual precipitation (± SE) over the 30-year time period (1984–2013) was 102.2 ± 2.67 cm $year^{-1}$. Departures from the precipitation average were observed during both periods of groundwater sampling. In the 2010s sampling, the years 2012 and 2013 received above average precipitation, approximately 17 cm more than the annual average (Fig. 3). In contrast, three of the four years during the 1990s sampling were below average rainfall years, and 1989 was especially dry, receiving only 79.2 cm.

3.2. Changes in groundwater salinity

Average groundwater salinity at sites inside the lens ranged from < 1 to 3 PPT in both sampling periods, whereas sites outside the lens had higher average groundwater salinities (4–11 PPT in 1990s; 7–29 PPT in 2010s), as well as a much wider range in salinities (Table 1). Increases in groundwater salinity between the two time
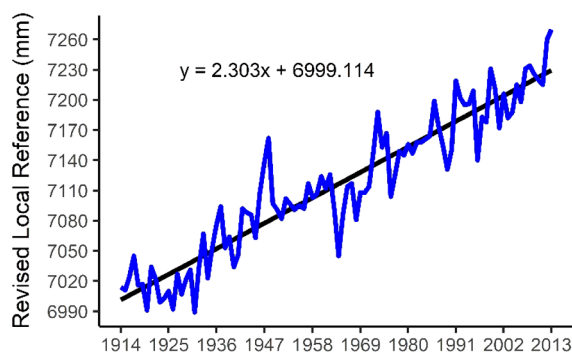

Fig. 2. Annual mean sea level (mm) at Key West Tide Gauge (1914–2013) with linear regression equation displaying annual increase over 100-year period of 2.3 mm yr^{-1}. Data obtained from the Permanent Service for Mean Sea Level (PSMSL) (http://www.psmsl.org/data/obtaining/stations/188.php). The Revised Local Reference (RLR) is the common datum of tide stations within the global PSMSL network, with the datum of each station defined to be approximately 7000 mm below mean sea level.
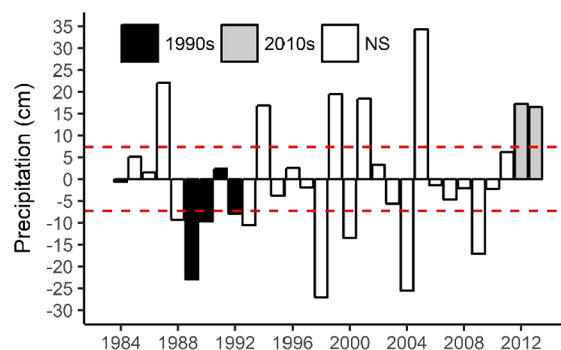

Fig. 3. Deviation from the 30-year average annual precipitation received at Key West International Airport from 1984 to 2013 (http://www.ncdc.noaa.gov). Horizontal dashed lines denote 95% confidence interval. SD of mean = 14.57 cm. NS = non-sample year.

Table 2
Estimates and standard error for each fixed effect from linear mixed effects modeling of $\log_{10}$ salinity at 7 wells with 65 sampling events from 1990s to 2010s. Estimates and SE are reported as salinity (PPT), n = 237. Intercept represents the outside-lens location for the 1990s sampling.

Fixed Effects	Estimate	Std. Error	df	P value
Intercept	9.77	1.19	6.8	< 0.001
Lens Location (Inside)	−2.83	1.28	5.4	< 0.01
Period (2010s)	1.67	1.23	9.5	0.032
30-day precipitation	−1.01	1.01	80.2	0.034
Lens Location (Inside): Period (2010s)	−1.87	1.31	5.1	0.065
Lens Location (Inside): 30-day precipitation	−1.01	1.01	223.8	0.017

periods were observed only for sites outside the freshwater lens. Including interactions between LENS and PERIOD and LENS and PRECIP resulted in greater explanatory power than the model that included only the three main effects (Table 2). The preferred model included five fixed effects and the two random effects (WELL and DAY):

$$LOG_{10}SAL \sim LENS + PERIOD + PRECIP + LENS{:}PERIOD$$
$$+ LENS{:}PRECIP + (1+PERIOD|WELL) + (1|DAY)$$

All fixed effects were significant at p < 0.05, with the largest estimated effect related to lens location (Table 2); specifically, sites inside the freshwater lens had groundwater salinities 2.83 PPT less on average than those located outside the lens (p < 0.01). The estimated effect of PERIOD in the model was an increase in groundwater salinity of 1.67

Table 3
Mean ± SE groundwater salinity (ppt) for inside versus outside-lens locations in each period (1990s and 2010s). P-values for each pairwise comparison with Bonferroni method are reported.

	Inside	Outside	p-Value
1990s	2.77 ± 1.21	8.71 ± 1.18	0.001
2010s	2.41 ± 1.33	14.85 ± 1.29	< 0.001
p-Value	0.542	0.020	

PPT from the 1990s to 2010s (p = 0.032). As expected, PRECIP had a negative effect on the groundwater salinity (p = 0.034). The significant interactions in the model exist between lens location and the two other fixed variables. The interaction between LENS and PRECIP indicated that the effects of precipitation were not the same inside and outside the freshwater lens, with rainfall primarily decreasing groundwater salinity at locations inside the lens. The interaction between LENS and PERIOD indicated that the change in groundwater salinity over the two decades differed depending on lens location. Regardless of sampling period, groundwater salinity differed between the inside and outside-lens locations (p < 0.001) (Table 3). However, this difference was much higher in the 2010s than in 1990s, as mean salinity increased only at the outside-lens sites over the 22-year time period (p = 0.02). The slightly (and non-significant) lower mean salinities observed in the inside-lens sites in 2010s compared with the 1990s (Table 3) were attributable to the greater amount of 30-day precipitation in the 2010s (1990s mean: 8.49 cm, 2010s mean: 12.42 cm, p = 0.001).

3.3. Changes in vegetation

Across all sites, tree basal area decreased significantly between 1990 and 2012 (paired *t*-test; p < 0.01), with five of the seven plots decreasing by amounts greater than 40% of their 1990 values (Fig. 4). However, when taken separately, decreases in basal area at interior lens plots were not statistically significant (p = 0.12), nor at outside plots (p = 0.06), likely as a result of low n, but perhaps also suggesting that changes in groundwater salinity did not drive the observed declines. Regardless of lens location, slash pine all but disappeared from the tree strata, while hardwoods slightly decreased in basal area and changes in palm and buttonwood basal area varied by plot (Fig. 4).

Losses in tree density were significant between 1990s and 2010s samplings but were restricted to plots located outside the lens (paired *t*-test; p < 0.01) (Fig. 5), with an average decrease of approximately 1900 stems ha^{-1} (~50%) in outside-lens plots over the time period. The wide variation in tree density among plots located inside the lens is a function of the structural differences between a more open pine forest (B2 and S5) and dense hardwood hammock (S1).

Changes in total percent cover in the shrub stratum did not differ statistically from zero in either lens location. However, in the ground

layer, increases in percent cover were observed in plots located outside the lens boundary but they were not statistically significant between the two sampling events (p = 0.08). In contrast, ground layer plots located inside the lens decreased significantly (p = 0.04), by almost 40%. Changes in total species richness were not statistically significant in any strata inside or outside the lens. No trend was observed toward either increasing or decreasing diversity. However, in the outside-lens locations, species characteristic of coastal buttonwood scrub forest, such as *Spartina spartinae*, *Borrichia arborescens*, and *B. frutescens* colonized the ground layer and coverage of the mangrove-associate, buttonwood, *C. erectus*, increased. Additionally, the only invasive exotic species observed in any plot was *Schinus terebinthifolia*, brazilian pepper, which appeared in the ground layer in the 2010s sampling within a single plot located outside the lens boundary.

3.4. Relationship between community composition and environmental variables

Ordination and vector fitting across all sites and survey periods demonstrated strong fits between vegetation composition and average groundwater salinity, height above LMSL, and distance to coast (Fig. 6). The composition of the ground layer was significantly correlated with all three environmental variables, but its relationship with groundwater salinity (SAL) was strongest (r = 0.88; p < 0.001) (Fig. 6c). Although compositions of the other two strata were also correlated with the groundwater salinity vector, correlations with distance to coast (DIST) and height above LMSL (ELEV) were not significant for the tree stratum and shrub stratum, respectively (Fig. 6a and b).

Little directional consistency existed among sites in how tree composition changed between the 1990s and 2010s (Fig. 6a). Accordingly, for this stratum, the mean positions (centroids) of both the inside and outside-lens sites did not differ significantly along the salinity vector between sampling periods. In contrast, for both the shrub and ground layer strata, the general shift in position of sites in ordination space was in the direction of increasing salinity (Fig. 6b and c). For the shrub stratum, the mean site score along axis-1 for sites outside-lens was significantly greater in 2010s than for the 1990s (p < 0.05). However, the shift was not significant for plots located inside the lens (p = 0.10). The results were similar for the ground layer stratum, with plant compositions of outside-lens (p = 0.03), but not inside-lens sites moving along the salinity vector over the time period (p = 0.16).

4. Discussion

4.1. Climate change impacts on groundwater resources alter coastal forests

In the lower Keys, the effect of sea level rise is visible through the relationship between increasing groundwater salinity and associated changes in forest composition and structure, beyond the effects of
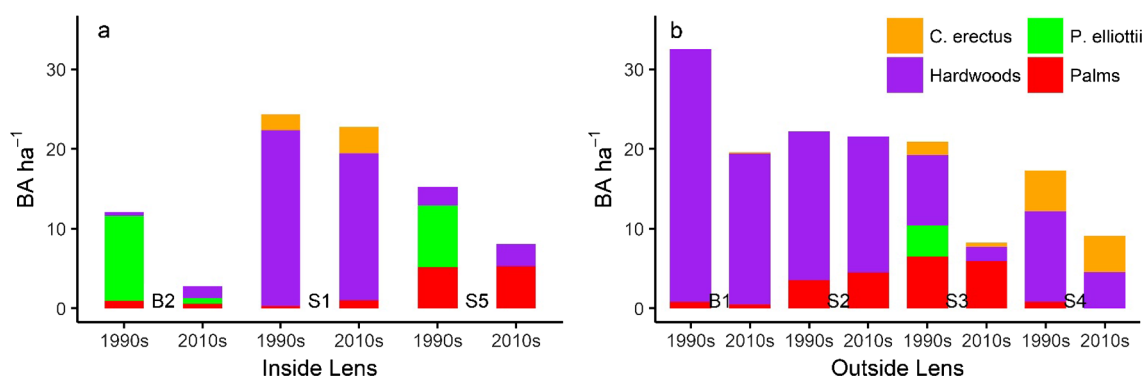
Fig. 4. Average basal area (BA ha^{-1}) of hardwood species, palms, *P. elliottii* and *Conocarpus erectus* (buttonwood) for 1990s and 2010s samplings of permanent plots located (a) inside (n = 3) and (b) outside the lens (n = 4).
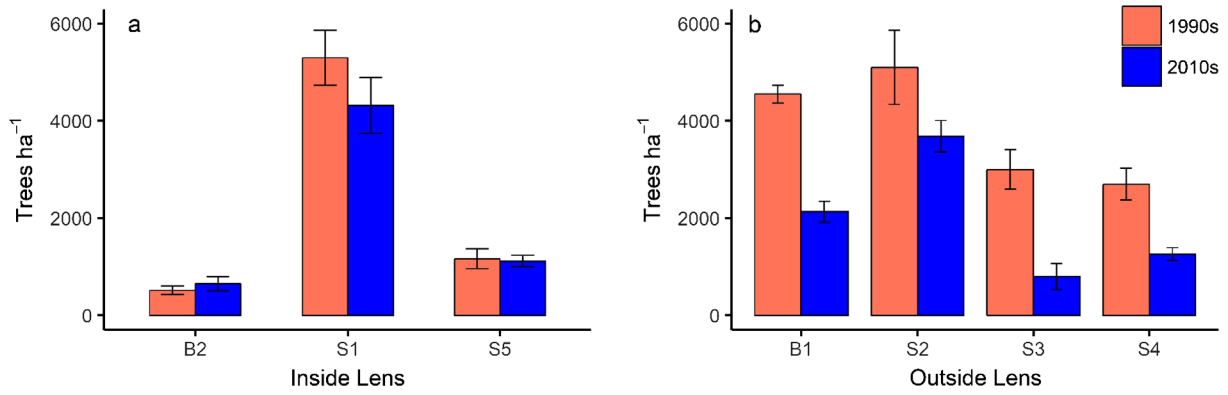
Fig. 5. Average tree density (trees ha^{-1}) for 1990s and 2010s samplings in (a) inside-lens and (b) outside-lens plots. Minimum stem dbh ≥ 3 cm.

hurricane impacts, including storm surge flooding. The rise in sea level during last few decades resulted in large, spatially variable increases in groundwater salinity outside the boundary of the freshwater lens, i.e., in the mixing zone between salt and fresh water, that were not observed inside the freshwater lens of the interior. Additionally, the high tidal efficiencies of the aquifer, i.e. the change in groundwater level with that of the semi-diurnal tides, lead to a wide zone of fresh-salt water mixing, and increasingly brackish conditions as one moves away from the
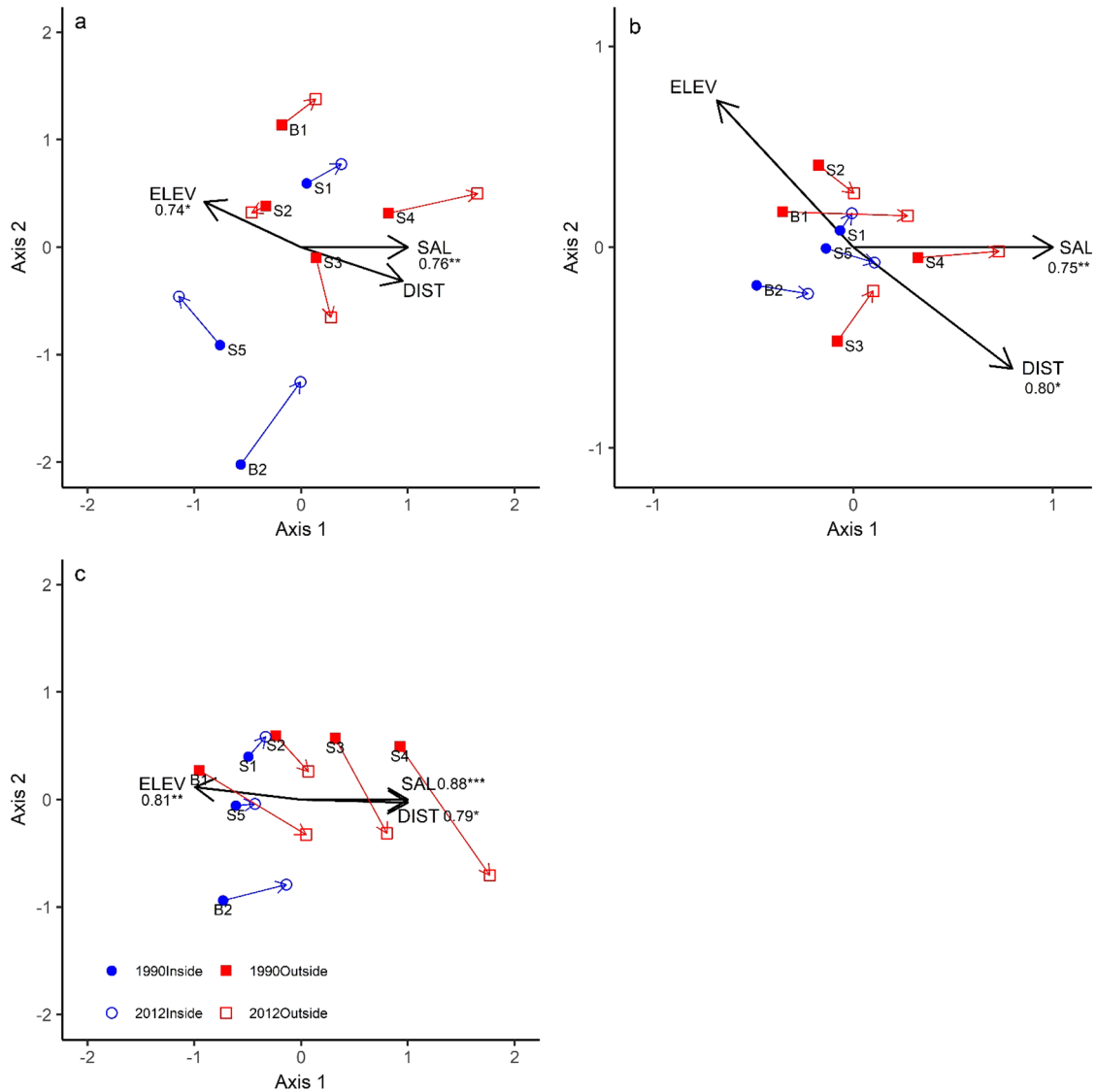

Fig. 6. NMDS ordination of (a) tree stratum, (b) shrub stratum, and (c) ground layer stratum at seven sites in the 1990s and 2010s. Sites are grouped by lens location. Arrows between symbols indicate change in vegetation composition from 1990s to 2010s for each plot. Arrows corresponding to the three environmental variables – groundwater salinity in PPT (SAL), distance to coast in m (DIST), and height above LMSL in m (ELEV) – originate at location 0.0 on both Axis 1 and Axis 2. Correlations between fitted vectors and ordinations are indicated where significant at p < 0.05 (*), p < 0.01 (**), and p < 0.001 (***).

center of the freshwater lens (Meadows et al., 2004). The combination of increasingly saline freshwater resources and the dynamic nature of the resource itself outside the lens interior has likely translated into altered species composition in the understory strata.

The importance of aquifer recharge from precipitation is illustrated both by the significant interaction of lens location and precipitation in the model and by the lower groundwater salinity recorded at sites inside the freshwater lens during the most recent sampling period, during which sites received greater than average rainfall. The decrease in salinity at these sites, despite 5 cm of sea level rise, indicates that interior lens locations are still primarily influenced by seasonal and inter-annual variation in precipitation. This has important ramifications for freshwater-requiring coastal forests that rely on a combination of precipitation and groundwater resources, especially for forests reliant on aquifers recharged solely by rainfall. Predicted summer drying trends in the Central American-Caribbean region for the late 21st century (Neelin et al., 2006) would lead to more frequent droughts and would simultaneously decrease aquifer recharge, exacerbating the impact of the press disturbance of sea level rise. South Florida is especially vulnerable since the majority of annual rainfall occurs during the summer and fall months. In combination with groundwater salinization, drought conditions will likely lead to decreased primary productivity and species turnover in these forests, as has been observed at other locations in Florida (Williams et al., 2003; Desantis et al., 2007). The stress of drought conditions and increasingly brackish groundwater will likely hasten the change in species composition from glycophytic to halophytic even within the currently buffered interior lens forests.

As observed after Hurricanes Hugo (1989), Wilma (2005), and most recently Hurricane Irma (2017), changes in coastal forest structure and composition can result from direct mortality of salt-sensitive canopy trees (Conner and Inabinette, 2003; Gardner et al., 1991; Ross et al., 2009, 2019). In south Florida, Category 4 storms occur at a 15-year interval (Keim et al., 2007). Given the regular occurrence of strong hurricanes, the persistence of freshwater-requiring coastal forests in the region suggests ecosystems that are adapted to both high winds and occasional flooding by salt water, as is evidenced by the relatively low canopies and high stem density in hardwood hammocks (Gillespie et al., 2006, Van Bloem 2006, 2007) and open forest structure in pine lands, where the largest trees are the most vulnerable to windthrow (Platt et al., 2000; Ross et al., 2019; Sah et al., 2010). Yet in low-lying coastal environments, the conditions and resources available for recovery are now being influenced by the press of sea-level rise. In this study, although hurricane impacts resulted in tree mortality and decreased basal area throughout the plots (Figs. 4 and 5), the greatest changes in composition were observed in the shrub and ground layer strata (Fig. 6b and c). The compositional change in these ordinations along the groundwater salinity vector was only significant for outside-lens plots, suggesting that increasing sea level and likely its interaction with storm surge are driving changes in these strata, not yet observed in the canopy. Indeed, the presence of relict stands has long been identified in the literature as a pattern of coastal forest retreat associated with rising seas (Williams et al., 1999b), as regeneration ceases prior to canopy mortality, with regeneration failure related to salt exposure in limestone karst settings (Williams et al., 1999a). Tolerance to salinity has been found to increase as trees mature to adulthood, whereas germinating seeds and emerging seedlings, enumerated in our study in the ground layer, are more sensitive to increasing salinity (Kozlowski, 1997). Additionally, mortality of seedlings of tree species rarely subjected to high tides has been observed at salinities as low as ~4 PPT (Williams et al., 1998) and decreases in stomatal conductance and photosynthesis observed in some species at salinities of 2 PPT (McLeod et al., 1996).

Though the decrease in basal area across all plots suggests mortality from storm surge affected the entire island, the decrease in tree density restricted to outside-lens locations could be indicative of conditions unfavorable to subsequent post-hurricane re-establishment.

Specifically, differences in stem density could be the result of recruitment into the tree canopy inside the lens boundary that is inhibited at outside-lens sites (Fig. 4). Alternatively, inside-lens plots could have been less severely affected by the storms, perhaps as a function of the buffering capacity of underlying fresh groundwater and lower likelihood of saline water pooling at the surface at interior locations having larger vadose zones (Ogurcak and Price, 2019). Regardless, recruitment into the tree layer did not occur in outside-lens plots.

4.2. Combined disturbances in the pine rockland

In pine rockland plots (B2, S3, S5), the greatest change in structure in the tree stratum was attributable to the loss of *P. elliottii* var. *densa*. All plots, located both inside and outside the lens, were burned in prescribed fires in the late 1990s or early 2000s. This disturbance most certainly had an impact on decreasing tree density and basal area in these plots, as some trees would have succumbed to the fire and species composition would have been altered (Sah et al., 2010). The presence of fire as an additional disturbance could help explain the lack of agreement in plot movement along environmental vectors in the tree ordination (Fig. 6a). However, changes in composition in the shrub ordinations do not appear to be driven by fire over the 2 decades, as both hammock (which received no fire) and pine plots move in the same direction.

Slash pine was absent from the low shrub/herbaceous layer in most of the sites in 2010s sampling despite being present in those plots in the 1990s. The absence of pine regeneration results from a combination of factors. First, the reduction in adult trees due to storm surge decreases the availability of seed sources. Second, the environmental conditions necessary for germination may cease to exist once more halophytic shrubby plants invade the understory as soil salinity increases. A lack of recruitment of new individuals limited by salt-saturated soils was observed for *Pinus taeda* in Maryland, and it was predicted that, combined with a loss of adults from storm surge events, recruitment failure would lead to stepwise retreat of these forests (Kirwan et al., 2007). Third, storm surge can alter the fire regime necessary to maintain the open nature of the pine rockland, eventually resulting in a closed canopy forest dominated by woody hardwood species (Ross et al., 2009). Mortality of large diameter individuals due to Hurricane Wilma (Sah et al., 2010), and the associated loss of pine needle litter which carries fire, resulted in a positive feedback loop where woody shrubs encroached and changed the microclimate and fuel moisture (Sah et al., 2006).

4.3. Species turnover: Succession to salt-tolerant scrub

While anthropogenic changes in environment are predicted to lead to species turnover and loss of species diversity (Tilman and Lehman, 2001), this pattern was not observed at our sites in the Florida Keys. Although we did observe species turnover, species losses in the shrub and ground layer strata were balanced by gains in new species and subsequently, species richness did not significantly decline over the time period. Specifically, the loss of existing woody species in the ground layer was eclipsed by an increase in the number of new woody trees and shrubs, grasses, vines, and herbaceous species. Several species with relatively high salt but low shade tolerance colonized these sites over the sampling period. These included shrubs *Conocarpus erectus*, *Borrichia arborescens* and *B. frutescens*, grasses (*Spartina spartinae* and *Sporobolus virginicus*) and sedges (*Fimbristylis spadicea*). In the Florida Keys, these species are abundant adjacent to the mangrove forest, in the buttonwood-dominated supratidal scrub and cordgrass salt marsh communities found coastward of both pine rockland and hardwood hammock forests (Ross et al., 1992). Storm surges likely brought propagules of these halophytes inland, where they established in the presence of altered resource conditions and the absence of competing glycophytes. Propagules of red mangroves, *Rhizophora mangle*, have

been found in the interior of islands after recent storm surge from Hurricane Irma (2017), but this species has not yet been observed to establish at those locations (D. E. Ogurcak, pers. obs.). The appearance of seedlings of the invasive exotic *S. terebinthifolia* in the most recent sampling event could also be mediated by storm surge waters. However, as the species is also animal-dispersed, the species could be gaining a new foothold within the interior of the refuge as a result of disturbance and changing resource conditions.

The increase in the percent cover of the *C. erectus*, a common back-mangal constituent, but one that only typically receives flooding with the highest tides, is consistent with succession to a more salt-tolerant flora. The widespread increase of this species seems to provide early evidence of a succession of hardwood hammocks to mangrove from a combination of press and pulse disturbance as proposed by both numerical modeling (Sternberg et al., 2007; Teh et al., 2015, 2008) and a conceptual model for south Florida coastal forests (Ross et al., 2009). The increase of *C. erectus* across communities and strata, combined with the loss of *P. elliottii* in pine forests, supports the hypothesis that change from freshwater-requiring coastal forests to salinity-tolerant forests is underway (Ross et al., 1994; Saha et al., 2011; Williams et al., 1999a,b).

4.4. Challenges for management of coastal forest communities

Coastal forest management is presented with new challenges in the current era of shifting baselines resulting from climate change. Sea level rise will substantially alter the freshwater resource these forests depend upon within the next several decades, likely resulting in novel assemblages of species as environmental gradients shift (Williams and Jackson, 2007). Salinization will not only change the conditions available during recovery from episodic pulse disturbances, but will likely alter ecosystem response to necessary management interventions, such as prescribed burning in coastal pine rocklands. Consideration of future climate conditions on fire and associated ecosystems in the southeastern U.S. has focused largely on interactions with temperature and precipitation (Mitchell et al., 2014). Slash pine, the foundation species of the pine rockland on the islands of the lower Florida Keys, has been retreating to an interior core (Ross et al., 1994, 2009) coincident with a shrinking freshwater lens. The capacity of this ecosystem to carry fire once it lacks the fine fuels supplied by live pines is uncertain, as is the flora that will establish in post-fire conditions from a modified seedbank. Threatened endemic species pose another great concern for managers, especially those of island flora that may require facilitated migration outside of historic ranges (Maschinski et al., 2011). Additionally, the role of non-native species as colonizers of novel communities with open niches is an important management issue, as introduced species can have deleterious impacts to forests, including exclusion of endemic species and alteration of ecosystem function ((Simberloff, 2000), but see Schlaepper et al. (2010) and Hill and Hadley (2018)). This study adds to a body of work that has found that changes to coastal forests in the eastern U.S. have been first observed in the understory of vulnerable stands years before they are reflected in the canopy (Clark, 1986; Conner and Day, 1988; Kirwan et al., 2007; Williams et al., 1999). Long-term monitoring in both interior and exterior locations of coastal forests is critical to inform management decisions.

5. Conclusion: Future of coastal forests on small islands

This study has provided preliminary evidence of sea level rise-induced changes to structure and community composition in both hardwood hammock and pine rockland communities, focused especially in compositional changes to the shrub and ground layer strata at locations outside the boundary of the fresh groundwater resource. Despite the limited sampling design – relatively few plot replicates for each lens location and lack of non-hurricane-impact control sites – we detected shifts in species composition among sites differentially affected by sea-

level rise (press event) and hurricane storm surge (pulse events). The forests on these islands persist today as refugia for biodiversity, where they serve as indicators of the effects of climate-change on disturbance regimes and fresh water resources (Ross et al., 2009).

Rising seas increase the likelihood of surface inundation by salt water during a storm surge (pulse event) as the elevation of coastal surfaces above mean sea level decreases (Tebaldi et al., 2012). Given that the frequency of severe hurricanes in the western Atlantic is predicted to increase in the 21st century (Bender et al., 2010), hurricanes will alter forest composition and structure as species slow to recover from storm surge impacts are eliminated and those with rapid post-storm recovery are favored. The result of interacting pulse and press disturbances will perhaps increasingly favor halophytic assemblages by causing direct mortality of salt-sensitive species, inhibiting the recruitment of glycophytes, and decreasing freshwater resource availability.

Beyond some threshold, rising seas will result in the replacement of an interior freshwater lens by an aquifer having a zone of fresh-salt mixing that extends to the center of the lens, as has been observed in Pacific atolls (Oberdorfer et al., 1990). While this hasn't yet occurred on our study islands, this has occurred on other islands in the lower Florida Keys and we should expect coastal forests on small islands to change more rapidly to halophytic vegetation like mangrove and buttonwood as a result of the interacting effect of rising seas and storm surges. Small islands are especially vulnerable and face threats to biodiversity separate from coastal forests located on the continents as species do not have the prospect of migrating further inland (Mimura et al., 2007) and are in much the same situation as montane flora (Bell et al., 2014). Land managers could best use limited resources for management of endemic and rare species and habitat by focusing on the core of larger islands (Ross et al., 2009) and in the lower Florida Keys this means prioritizing management actions in forests located within the boundaries of the freshwater lenses of these islands.

Acknowledgments

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