Historic and Current Vegetation Communities at Chassahowitzka National Wildlife Refuge

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ABSTRACT

Accurate inventory of plant communities is fundamental to natural resource management. Coastal systems are dynamic in nature due to the ongoing disturbance processes driven by the intersection of the land and ocean and thus require more frequent monitoring. Chassahowitzka National Wildlife Refuge is located on the west coast of the Florida panhandle at the temperate-tropical climate boundary. Two of the most dramatic recent changes faced by the Refuge are mangrove encroachment and the die-off of large areas of coastal forests. The exact degree of change in plant community boundaries from historic conditions and the current composition of the flora in salt-intruded coastal "ghost" forests on the Refuge is unknown. Florida Natural Areas Inventory (FNAI) created a current (2018) and historic (1941) land cover map to compare and quantify the extent of habitat change and damage to the natural communities at the Refuge. Tidal creeks and mangrove swamps have increased by about 2,000 acres and have flooded salt marsh plant communities which have been reduced by approximately 1,950 acres, resulting in a 17% decrease since 1941. Upland forests on offshore islands have been drastically reduced. Mapping efforts using polygon delineation estimate that only 43-46 % of the total land cover of hammock forests remain. In addition, field vegetation surveys were conducted to quantify current vegetation structure, species composition, and damage levels of each natural community. It was found that ghost forests have lower richness, higher invasive plant cover, and more bare ground as compared to hammocks they are replacing. Ghost forests were found to be expanding since 1941 and could therefore have increasingly consequential impacts for species that utilize maritime hammocks, such as migratory birds. Furthermore, salt marshes replacing ghost forests are not typical of graminoid marshes historically found in the Refuge—but are instead characterized by succulent halophytic plants, low graminoid cover, mangrove species, and bare limestone. Coupled with the loss of salt marsh to open water, further investigation into secondary impacts of extensive graminoid dominated marsh loss on wildlife is warranted. In addition, these findings have potential implications for other coastal forests further north and can inform modeling attempts on the future effects of sea level rise in Florida and beyond.

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INTRODUCTION

Throughout coastal habitats, saltwater and freshwater meet and mix, creating ideal habitats for a range of plant species that fall along the spectrum of salt tolerance. However, departures from historic patterns of weather and tidal events can change the hydrology of coastal areas in ways that exceed the tolerances of current plant communities. This causes land conversion through shifts in community distribution, structure, and composition. Two visually striking examples of land conversion are the transition of coastal forest to saltmarsh, and the transition of salt marsh to mangrove. Both of these transitions are most likely driven by both push (slow rise in sea level) and pulse (storms or other extreme weather events) disturbance events. Understanding the effects of change in coastal communities is of interest due to the importance of these habitats for wildlife, water quality maintenance, and coastline protection (Barbier et al. 2011).

Tropical-temperate climate boundaries provide a unique opportunity to study the dynamics of mangrove and salt marsh communities in response to climatic change (Kelleway et al. 2016). Annual interplay between mangrove swamp and salt marsh habitat is driven by the frequency of freezes at habitat boundaries (Cavanaugh et al. 2013, Stevens et al. 2006, Stuart et al. 2006, Osland et al. 2013), where mangrove encroachment into salt marsh is pushed back during freezes. Though freezes help constrain their range expansion, a reduced frequency of freezes and rising mean low temperatures is believed to be allowing mangrove to increase in abundance (Cavanaugh et al. 2013, Alongi 2015, Giri and Long 2016). Further, permanent encroachment of mangroves into salt marsh habitat is facilitated by rising sea levels (Kelleway et al. 2016, Rogers et al. 2005). Since mangrove communities accumulate sediment faster than salt marsh communities (Rogers et al. 2005), salt marsh is increasingly vulnerable to mangrove encroachment as sea levels rise.

In addition, salt intolerant terrestrial communities, such as coastal forests and hammocks, are increasingly vulnerable to dieback and encroachment from salt marsh communities. Salt concentrations in the soil are increased by climate change-driven disturbance events such as flooding (Flynn et al. 1995), which shifts the salt and saturation levels beyond the threshold of what non-salt tolerant trees can endure (Pezeshki et al. 1990). Increased frequency and severity of storms may exacerbate the effects of salt intrusion by uprooting and blowing down trees, which creates depressions of bare soil that retain pooled saltwater, and by saturating soils for increasingly long durations. Long periods of drought can increase the salinity levels in the soil since freshwater inputs are reduced (Williams et al. 2003). Over time, continued inundation of saltwater on coastal forests leads to the creation of "ghost forests" (Kirwan and Gedan 2019), which are most obviously characterized by stumps or dead trunks in saltmarsh (formally forested) habitat.

Chassahowitzka National Wildlife Refuge (the Refuge, Figure 1), located along the western gulf coast of central Florida, is comprised of saltwater bay, estuary, brackish marsh and hardwood swamp habitat spanning approximately 31,000 acres. The Refuge is located along the tropical-temperate climate boundary and much of the Refuge lies at or near sea level. Along the gulf coast of Florida, the relative rate of sea level rise near the Refuge is 2.13 mm/year (95% CI = ± 0.18mm/year; NOAA Tides and Currents, Cedar Key monitoring station). The juxtaposition of tropical and temperate communities at the Refuge makes it an ideal location to measure the

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effects of climatic shifts on plant community structure and composition. In addition, many of the Refuge's uplands exist on outer islands with high potential exposure to saltwater from both push (slow rise in sea level) and pulse (storms or other extreme weather events) phenomena. These push and pulse events can result in loss of salt-intolerant upland species and have been documented in similar sub-tropical mesic and maritime hammocks to those found at the Refuge (Williams et al. 1999). While changes are wide-spread and evident at the Refuge due to the loss of forest cover which has long persisted on the outer islands (Florida Oceans and Coastal Council 2009; the Refuge Cooperative Conservation Plan 2012), no studies have documented the resulting vegetation composition changes as a result of increased hammock loss within the Refuge.

Changes to habitat structure and composition may have significant consequences for wildlife species that rely on habitats within the Refuge. Over the past 40 years, staff have documented a dramatic decline in overwintering waterfowl within the Refuge. A survey conducted in 1970 estimated that approximately 25,000 ducks and 30,000 coots wintered annually within the Refuge, but a repeat of the same survey in 2010 estimated that only 1,500 ducks were using the Refuge during winter months (CNWR Cooperative Conservation Plan 2012). An observed decline in species diversity accompanied the decline in species abundance. Currently, red-breasted merganser (*Mergus serrator*) is the primary species seen overwintering in the Refuge, but historically gadwall (*Mareca strepera*), American widgeon (*Mareca americana*), northern pintail (*Anas acuta*), and scaup (*Aythya affinis*) were also seen in high abundance (CNWR Cooperative Conservation Plan 2012). To make informed decisions about conservation of at-risk as well as other native resident species, land managers require accurate data on what land cover changes have occurred and may still occur within the Refuge.

Due to its geographical context, topography, and ecological importance for many species, the Refuge is particularly vulnerable to changes in climate, such as sea level rise, saltwater intrusion, and rising regional mean temperatures. Freshwater flow reversal and resultant water chemistry changes likely also impact coastal systems in the area (Williams et al. 1999, Hensley and Cohen 2016). Williams et al. (1999) demonstrated that species can shift in relation to increased flooding, but only examined shifts in halophytic species and tree species recruitment, presumably due to small sample size (n=12). Since that time, other factors such as the expansion of mangrove species and the non-native Brazilian pepper (*Schinus terebinthifolius*) have increased the magnitude of potential ecological implications. Twenty years later, we hope to build off the findings of Williams et al. (1999) by examining the current state of ghost forest conversion in west central Florida. In this study, we assess the changes in the distribution, structure, and composition of salt marsh, mangrove, invasive species, and tree island plant communities at the Refuge. Further, we implemented a permanent system for vegetation monitoring that will be used by the Refuge to monitor changes into the future.

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METHODS

Mapping

We created both historic and current natural community maps of the Refuge (Figure 2) using ArcGIS (ESRI, version 10.6). To create the historic maps, we scanned and georeferenced the earliest available aerial photographs (ca. 1940s) for the full extent of the study area (Figure 1). We chose to extend our assessment of changes back to 1941 to better capture the full extent of changes that have occurred at the Refuge, even though some periods of time may have had more rapid changes than others. Historic natural community delineations are made based on visual inspection of the historic and current photographs as well as the other resources such as digital elevation maps derived from LiDAR, aerial photographs from 1995 to present, soil maps, Florida Land Use Cover and Forms classification system (FLUCCS) shapefiles, rare species locations, and USGS 7.5 minute topographic quadrangles. Following the FNAI Natural Community Classification Guide (FNAI 2010), we created polygons to reflect these delineations as indicated by the aerial photo signatures (Figure 3). We applied a minimum mapping unit of half an acre for forest stands and one-tenth of an acre for all other features. All tidal creeks with widths greater than five meters were delineated. To create the current natural community map of the Refuge, we refined the historic map based on our field-verified observations and landscape changes that are visible on aerial imagery. In the current map, we included altered landcover types (such as roads and developed areas) and identified areas where habitat shifts have occurred (e.g. salt marsh expansion into hydric hammock).

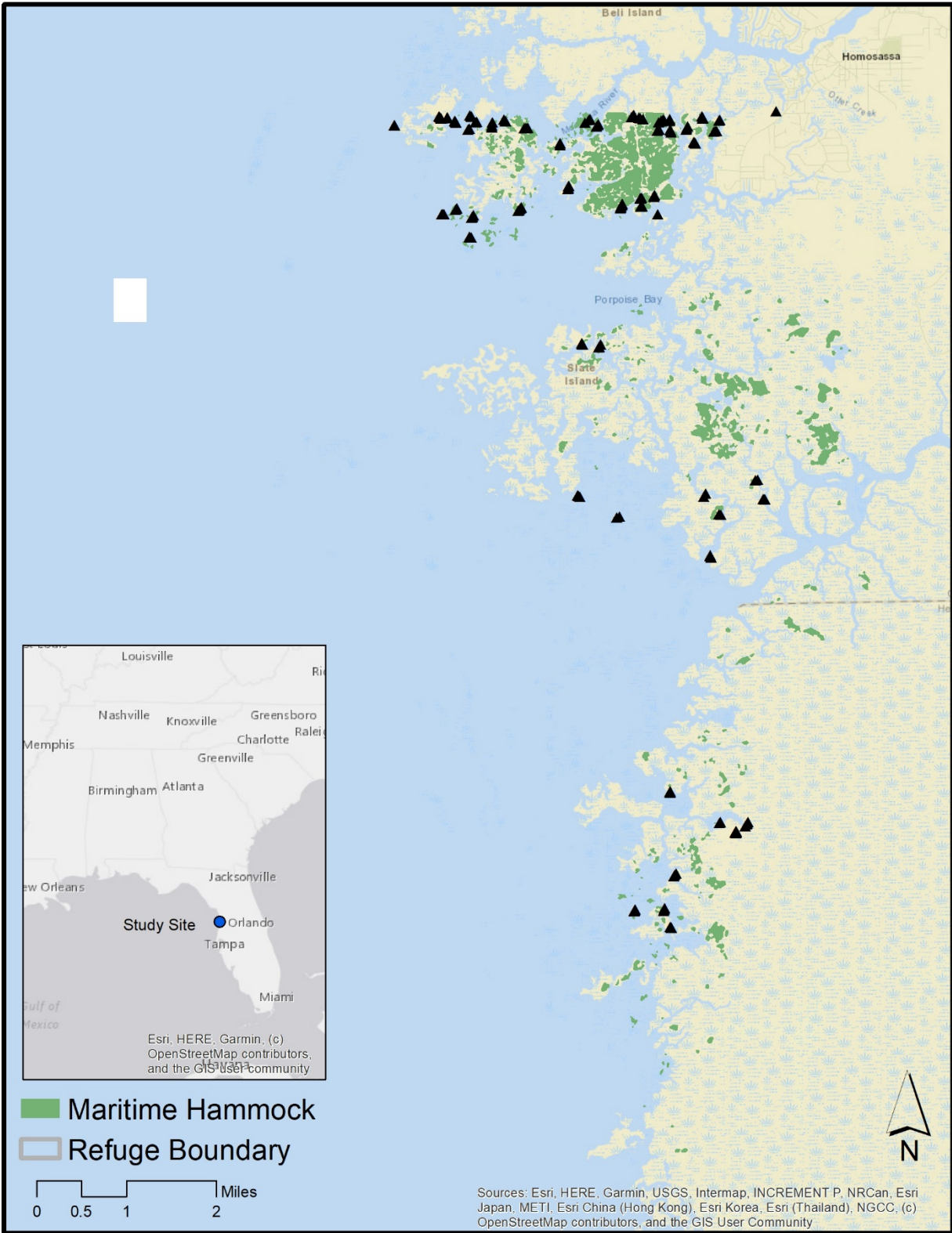*Habitat changes and current conditions at CNWR*

Figure 1. Chassahowitzka National Wildlife Refuge is located along the western coast of Florida. Triangles represent the locations of survey transects.

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In both current and historic maps, we assigned damage classes to hammock communities to quantify conversion to ghost forest. We used ocular estimates of the percent overstory damage (i.e. dead tree presence) based on aerial imagery to group all hammocks into four classes: light (0-25% cover), medium (25-75% cover), heavy (75-95%), and severe (>95%). We established these categories based on our ability to accurately classify damage from the aerial imagery. Those which were severely damaged since the 1941 imagery were reclassified to salt marsh, salt flat, or some cases, were now tidal creek in the current natural community layer. All mapping and spatial calculations were completed in ArcMap (Figure 2).

Figure 2. Example of the GIS workflow to delineate natural communities from aerial imagery. Image A shows historic imagery, B shows natural community delineation and C shows damage class assessment for hammock communities.

Vegetation Sampling and Analysis
With the goal of assessing the proportion of hammocks (each unique hammock polygon was counted as one hammock) remaining since 1941 and the species composition in all landcover types, we established 50 permanent sampling transects across the Refuge (Figure 1). To establish transects, we randomly selected 50 hammocks present in the 1941 imagery (Figure 2) and assessed their current condition. To assess the ecological gradient from sea level to upland hammock forests, we established transects from the randomly selected hammock to the nearest adjacent low marsh habitat accessible by boat. Along the habitat gradient of each transect, we established 2.5-meter radius (19.63 m^2) vegetation monitoring plots, for a total of 163 plots across all 50 transects. We permanently marked the transects with a 1-meter tall PVC stake at the first plot of the transect (in low marsh) and a 1-foot tall rebar at the conclusion of the transect (in the upland plot). The beginning and end points of each transect (which are also the center point of the beginning and ending plots) were recorded with a sub-meter accuracy GPS unit (Trimble$^©$ Geo XT).

Surveys were conducted in March and April of 2019. Along each transect, we conducted plot level sampling in each of the following land cover types: low marsh, high marsh, hammock (either mesic, hydric, or maritime), and ghost forest (any of the three hammock variants with evident damage, dead, or dying trees). Maritime hammocks were those that were present on islands, while mesic and hydric hammocks were only present on the mainland. Therefore, all of the field data from hammocks in our analysis is from maritime hammock plots, with the exception of one plot that was classified as mesic. We classified natural community types in the

field using the FNAI Natural Community Guide (2010). All of the landcover types that intersected a transect were sampled, provided the area was large enough to encompass the entire sampling plot (i.e. habitat extended beyond 2.5 meters from the center of the plot in all directions). Transects most commonly extended across four land cover types and therefore included four plots. Because it was impossible to identify community variants *a priori* using maps and aerial images, we adaptively sampled one plot per marsh variant encountered along each transect in the field (Figure 3). At each plot, we used ocular estimates of cover using modified Daubenmire classes (<1, 1-5, 6-15, 15-25, 26-35, 36-45, 56-65, 66-75, 76-85, 86-95, >95%) for bare ground, herbaceous species, invasive plants, halophyte species, shrub, tree canopy, and mangrove species. Trees (live and dead) greater than four inches diameter at breast height (DBH) were also recorded for each plot. At the center of each plot we took a 360° panoramic image, which can be compared to future photos to visually assess change over time at each site if qualitative rapid assessment is desired.
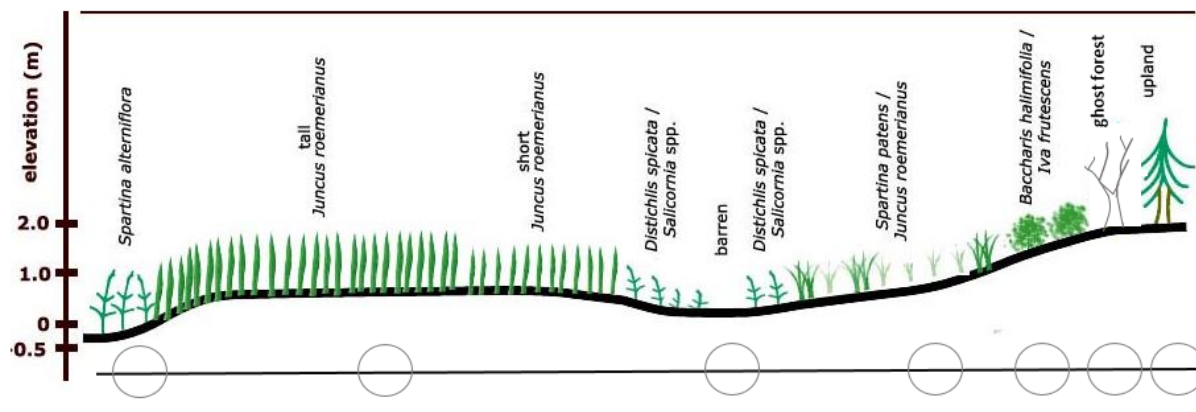

Figure 3: Adaptive transect design from low marsh to upland (hammock). One plot per transect (grey circles) was taken in each cover type and salt marsh variant (i.e. high and low marsh) encountered along the transect (black line).

We used the midpoint of cover classes as an approximation of the cover of each attribute estimated in our study. To delineate plant communities, we used k-means clustering and principal component analysis (PCA). Using the plant species data, we performed k-means clustering to determine the number of unique natural communities that were present in our data set. We tested for differences between k-means clusters using Permutational multivariate analysis of variance (perMANOVA) based on a Bray-Curtis similarity index with 9,999 permutations of N and Bonferroni-corrected p-values. We selected smaller groups until significance was achieved across all pairwise tests. We normalized the data and conducted a similarity percentage analysis (SIMPER) to summarize the differences between habitat groups by plant community. The community names were then based on plant species present in the most significant clusters. The habitat cluster delineation and testing were done in PAST (version 3, Hammer 2019). We visualized the clusters using a principal component analysis.

In our habitat structure analysis, we make comparisons between groups using 95% high density intervals, a type of credible interval (CI) used in Bayesian inference. Bayesian inference returns a

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distribution of possible effect values (the posterior), and the credible interval is the range containing a specified percentage of probable values. In this case, the CI interval is simply the central portion of the posterior distribution that contains 95% of the probable values. We compared the posterior distributions to assess the likelihood of differences between plant communities and plots with and without forest recruitment. We also use a Bayesian index of significance to describe the probability of direction (pd), which reflects the certainty associated with the most probable direction (positive or negative) of the effect for some comparisons. This is somewhat comparable to frequentist p-values where $p < 0.05 = pd > 97.5\%$, (Kruschke and Liddell 2018, Makowski et al. 2019) but allows for a continuous distribution of probability to be presented.

We developed three models to assess the effects of ghost forest formation and explore the drivers of species richness using the package 'bayestestR'. We set iterations to 40,000 and our effective sample size was many times higher than that needed for stable estimates (Bürkner 2017). The full model was composed of all variables collected aside from the species themselves (latitude, longitude, invasive plant cover, herb cover, mangrove occupancy, halophyte cover, plant community, canopy cover, red mangrove presence, black mangrove presence, white mangrove presence, and buttonwood presence). Our second model was derived using a reductive process based on probability of direction (pd) values and included parameters that had the strongest evidence (i.e. pd > 97%). We compared the effect, or significance, of the full, null, and reduced final model using Bayes factor (BF), which is a versatile index that can be used to directly compare different models. Bayes factors (BFs) are relative indices of evidence for one model over another, determined by comparing the marginal likelihoods of the two models. In this way, the BFs are a ratio informing us how much more (or less) likely the observed data are within the context of competing models (Makowski et al. 2019).

Understanding the driving factors which are governing the process of hammock loss is critical in making future predictions of hammock cover. Hammock tree species recruitment is a key indicator of future hammock loss or gain. To understand the process of forest regeneration, we compared plots that did have recruitment to those that did not. Marsh plots were excluded from this analysis, as no canopy species are expected in those communities. We then evaluated the number of plots which had young trees (< 4" DBH) across plant community types. In addition, we compared plots with recruitment to those without using all the other variables we collected (e.g. richness, proportion of dead trees, canopy cover, bare ground, and forest type).

RESULTS

Mapping
Mapping revealed dramatic changes in the spatial distribution and proportion of acreage covered by each natural community type from 1941 to 2018 (Figure 4, Table 1). In general, offshore hammocks have become largely absent from the extreme southernmost extent and the central part (north of the Chassahowitzka River and south of the Homosassa River) of the Refuge. We mapped 2,978 acres of hammock in 1941 and 2,699 acres of hammock in 2018. This represents approximately 10% total loss in hammock cover across the Refuge, with losses primarily restricted to offshore islands. As a result, maritime hammock has seen a 12% decline (-265

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acres) whereas mesic hammock and hydric hammock have both experienced a less than 1% loss in the change from historic to current land cover.

In addition to a decrease in the number of acres of hammock, damage to existing canopy trees and other upland plant species has increased. Within areas that remained classified as hammock since 1941, there has been a shift from hammocks having none to light damage, to having medium, heavy, or severe damage in modern times (Table 2). Currently, approximately 656 acres are in the < 25% damage classes and 594 acres are in the >75% damage classes, indicating a large shift in the overall condition of remaining hammock. Similarly, some hammock types have been disproportionately damaged. Maritime hammock has been the most affected, with 174 acres (38% of the total mapped acres) estimated as none-light damage in 1941 have been reclassified as medium-heavy damage in 2018. Hydric hammock has seen the second most acres reclassified from none-light damage (174 acres, 15% of the total) to medium-heavy damage. Thirty acres of mesic hammock were reclassified from none-light damage in 1941 to medium-heavy damage in 2018, which represents about 9% of the total cover of this community type.

The largest annual changes per acre were seen in salt marsh (Table 1), which declined by 9% (an average of 25 acres per year) between 1941 and 2018. In that same period, mangrove swamp has increased by 64%, which is a gain of an average of 13 acres per year on average. Additionally, tidal creek has expanded 4%, which translates to an approximately 4 acres per year gain, on average. Gains in tidal creeks and mangrove swamps (about 2,000 acres total) account for the losses of salt marsh (also about 2,000 acres). Though mangrove swamp was mapped as gaining approximately 1,000 acres, this might not fully express the expansion of mangroves, as areas with sparse mangrove cover were mapped as saltmarsh due to minimum mapping sizes. Interestingly, through comparisons of past and current aerial imagery we documented rare instances where salt marsh became hammock. However, this represented only about 12 acres in total. Across the entire refuge, we observed a general trend of increasing salt marsh loss both as a result of loss of area to mangrove swamp and tidal creek.
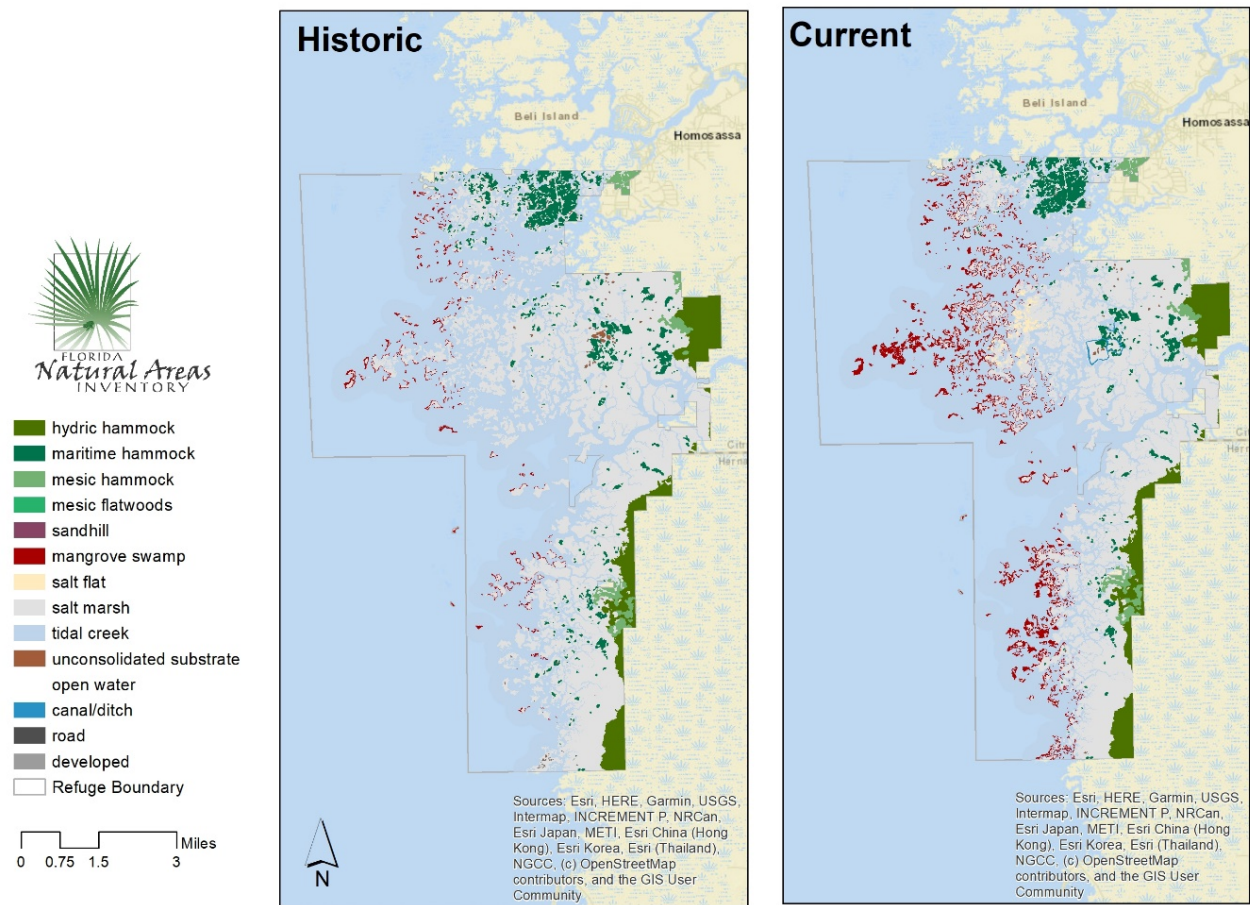
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Figure 4: Comparison of the natural community mapping based on historic (1941) and current (2018) aerial imagery. Maps can be viewed online at: https://arcg.is/1qC5Li.

Table 1. Change in acres of natural communities based on historical and current natural community mapping.

Natural Community	Historic	Current	Change	% Change	Average Acre/Year
canal/ditch	0	39	39	100	0.51
developed	0	8	8	100	0.10
hydric hammock	1392	1380	-12	-1	-0.16
mangrove swamp	291	1315	1025	353	13.31
maritime hammock	1233	968	-265	-22	-3.45
mesic flatwoods	20	17	-3	-15	-0.04
mesic hammock	352	351	-1	0	-0.02
open water	8623	8624	1	0	0.02
road	0	6	6	100	0.07
salt flat	0	137	137	100	1.78
salt marsh	11395	9436	-1959	-17	-25.44
sandhill	18	12	-7	-37	-0.09
tidal creek	13023	14114	1091	8	14.16
unconsolidated substrate	83	24	-60	-72	-0.77

Table 2. Change in acres of hammock (includes hydric, maritime, and mesic) in each damage class, as estimated by historic and current mapping.

Time	No Damage	1-25%	25-75%	75-95%	95-99%
Historic Hammock	1847	870	184	35	0
Current Hammock	1586	475	224	386	243
Change	-261	-395	40	351	243

Vegetation Sampling

We found strong support for four statistically distinct plant communities in the offshore islands of the Refuge. There was support for low marsh, high marsh, ghost forest, and hammock clusters based on our plot vegetation data (F=44.6, p=<0.0001, Figure 5). Differences between the plant communities of hammock variants (i.e. hydric, mesic, and maritime) were non-significant and therefore were not included in subsequent data analysis (F=1.24, p=0.06).
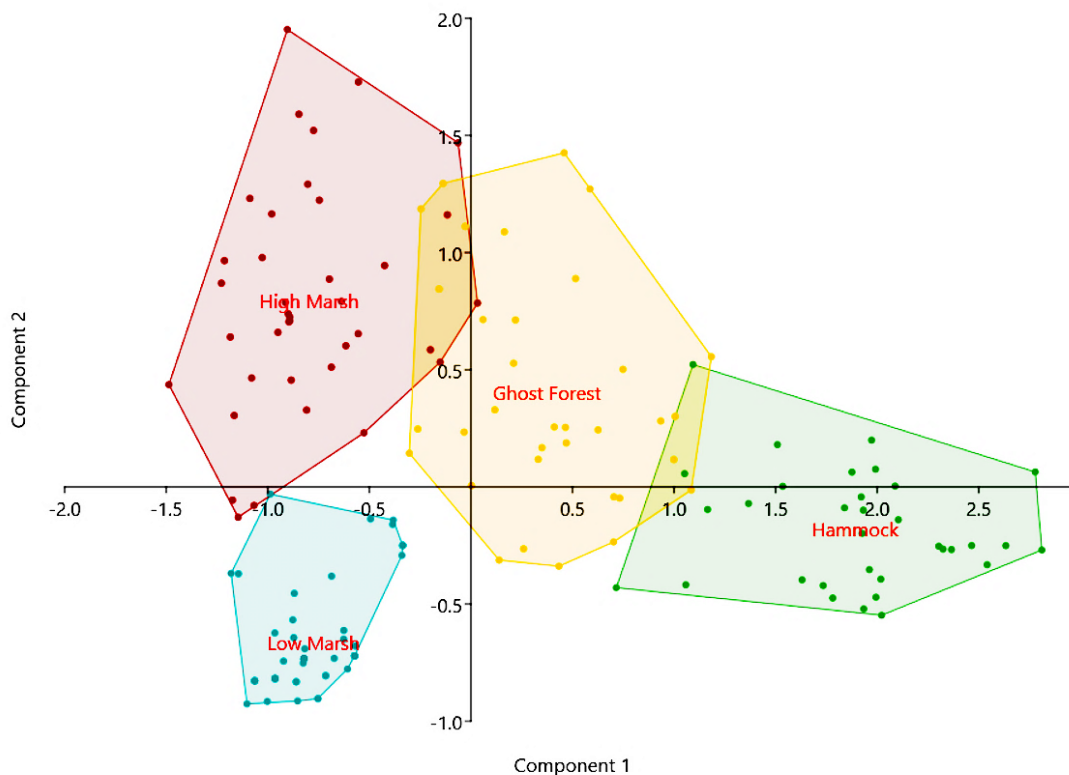
Figure 5. Principal component analysis (PCA) used to visualize the four natural community clusters determined by k-means clustering using vegetation species data.

Using the frequency of species occurrences (i.e. the percentage of plots in which the species was present), we characterized the dominant plants in each community type. Low marsh (58/163 plots) was characterized by black needle rush (*Juncus roemerianus*), red mangrove (*Rhizophora mangle)*, black mangrove (*Avicennia germinans*), giant leather fern (*Acrostichum danaeifolium*), white mangrove (*Laguncularia racemosa*), sawgrass (*Cladium jamaicense*) and saltmarsh cordgrass (*Spartina alterniflora)*; these plants had frequencies of 31, 20, 13, 7, 6, 6, and 6%, respectively. The total plant richness found in low marsh was 16 species. All other species found in low marsh plots had less than 5% frequency.

High marsh (38/163 plots) was characterized by woody ox-eye daisy (*Borrichia arborescens*), Christmas berry (*Lycium carolinianum*), red mangrove, marsh elder (*Iva frutescens*), glasswort (*Salicornia ambigua*), buttonwood (*Conocarpus erectus*), perennial saltmarsh aster (*Symphyotrichum tenuifolium*), white mangrove, salt grass (*Distichlis spicata*), and black mangrove; these plants occurred with 20, 19, 17, 11, 9, 8, 7, 6, 6, and 6% frequency in high marsh plots, respectively. The total plant species richness for high marsh was 26. All other species recorded in high marsh occurred with less than 5% frequency in plots.

Ghost forest (34/163 plots) was primarily composed of Brazilian pepper overstory, with a mix of hammock and salt marsh species in the understory, including cabbage palm (*Sabal palmetto*),

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saltwater falsewillow (*Baccharis angustifolia*), red cedar (*Juniperus virginiana*), giant leather fern, sawgrass, and marsh elder; these plants occurred with 20, 11, 9, 9, 8, 5, and 5% frequency. All other species recorded in ghost forest plots occurred with less than 5% frequency. We found a total of 37 species in ghost forest plots.

Hammock (33/163 plots) was the most floristically rich community. Hammock was primarily composed of cabbage palm, red cedar, Brazilian pepper, live oak (*Quercus virginiana*), Myrsine (*Myrsine cubana*), yaupon holly (*Ilex vomitoria*), snowberry (*Chiococca alba*), white indigoberry (*Randia aculeata*), and woodoats (*Chasmanthium* sp.); the percent frequency of these plants was 35, 21, 17, 16, 11, 9, 7, 6, and 5% in plots, respectively. A total of 56 species were recorded in hammock plots.

The SIMPER analysis, using both percent cover and species frequency metrics, identified five variables that are the primary drivers of the difference between the four community types. Most influential was the proportion of dead trees, followed by the percent frequency of cabbage palm, Brazilian pepper, red cedar, and Christmas berry. Cumulatively, these variables accounted for 77% of the difference between the groups. Other species explained only minor differences in the groups (<1% contribution).

Plant Species Richness
Mean plant richness was different between the four communities (Figure 6). Hammocks had the highest average number of species per plot (mean=9.2, CI=8.1-10.1). High marsh had slightly fewer species per plot than hammock (mean=7.32, CI=6.5-8.1), followed by ghost forest (mean=5.7, CI= 4.9-6.5). Low marsh had the lowest average richness per plot (mean=2.83, CI=2.51-3.18).
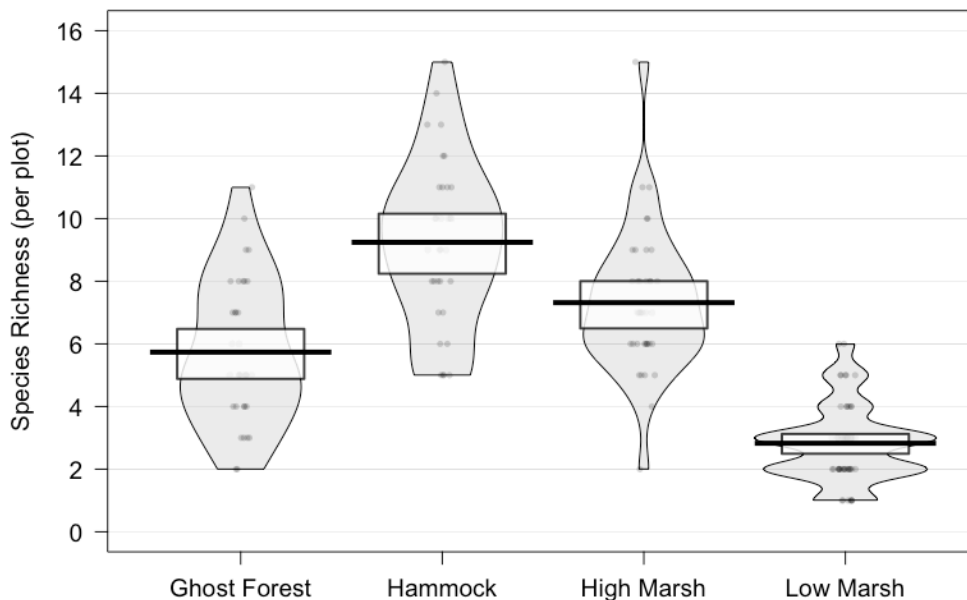

Figure 6. Species richness in each of the four natural communities found at Chassahowitzka Natural Wildlife Refuge. Boxes represent the 95% high density intervals (HDI) and the black line represents mean richness.

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In addition to differences in overall richness, we observed differences in average herb, shrub, and tree richness across community types. Herb richness was highest in high marsh (mean=3.3, CI= 2.8-3.7) and lower on average in all other communities (low marsh: mean=1.6, CI=1.4-1.9, hammock: mean=1.6, CI= 1.0-2.1, ghost forest: mean=2.1, CI=1.4-2.3). Shrub richness was highest in hammock communities (mean=5.4, CI=4.7-6). Average shrub richness in ghost forests (mean=2.6, CI=2-3) and high marsh (mean=3.0, CI=2.5-3.5) were similar. As one would expect, shrub diversity was poor in low marsh (mean=1.2, CI=0.9-1.4), except where mangroves were present. Tree diversity was higher on average in hammocks (mean=2.24, CI=1.9-2.5) than in ghost forests (mean=0.97, HDI=0.72-1.8). High marsh and low marsh had decreasing amounts of trees per plot, nearing zero trees per plot on average.

Structural Differences between Plant Communities
Several structural differences were found in ground cover variables between community clusters. Bare ground was highest in ghost forest (mean=29.8%, CI=21.6-36.8%) followed by high marsh (mean=22.1%, CI=17.3-26.2%), and low marsh (mean=14.7%, HDI=10.8-18.4%, Figure 7). Hammock communities had almost no bare ground cover (mean=2.3%, CI=0.3-4.2%). Herb cover was highest in low marsh (mean=66.7%, HDI=56.9-74.4%), followed by high marsh (mean=45.18%, CI=35.5-52.2%, Figure 8). Ghost forest had sparse herb cover (mean=20.1%, CI= 10.4-27.7%) and in hammock herb cover was virtually absent (mean=0.95%, CI=0.24-1.50%). Halophyte cover was highest in high marsh, as would be expected (mean=35.3%, CI=25.8-42.3%). Halophyte cover was similar in ghost forest (mean=3.7%, CI=0.4-6.5%) and low marsh (mean=1.3%, CI=0.0-2.8%). Not surprisingly, halophytes were virtually absent in hammock communities (mean=0.0%, CI=0.0-0.1%).

Differences were also found in woody cover variables. Shrub cover (<4' DBH woody vegetation) was highest in hammock (mean=45.8%, CI=36.4-55.38%) though CIs were overlapping with ghost forest (mean=40.5, CI=26.8-49.8, Figure 9). High marsh had the second highest shrub cover (mean=25.9%, CI=17.3-33.4%) though the lower end of the credible range was overlapping with low marsh (mean=15.8%, CI=8.7-22.3%). Brazilian pepper was the only invasive plant observed in plots and cover was highest on average in ghost forest (mean=15.9%, CI=4.0-24.5%). The variability of Brazilian pepper cover was high (ranging from 0-100% cover) resulting in uncertainty in the estimates. The CIs of Brazilian pepper cover were overlapping for hammock and ghost forest clusters (Figure 10). A probability of direction test resulted in a 94.4% chance that Brazilian pepper cover was higher in ghost forest than hammock. Hammock had low to moderate amounts of Brazilian pepper cover depending on distance to forest edge (mean=8.9%, CI=1.6-15.8%). High marsh and low marsh both had negligible amounts of Brazilian pepper cover (high marsh: mean=1.2%, CI=0.0-3.1%; low marsh: mean=0.0%, CI=0.0-0.1%). Canopy cover (cover of trees with a DBH >4') was much higher in hammock (mean=46.0%, CI=36.5-54-3%) than ghost forest (mean=13.5%, CI=6.8-19.6%), and was negligible in both high marsh and low marsh.

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Figure 7. Percent cover of bare soil ghost forest (n= 34), hammock (n= 33), high marsh (n= 38), and low marsh (n= 58). Boxes represent the 95% high density intervals (HDI) and the black line represents the mean.
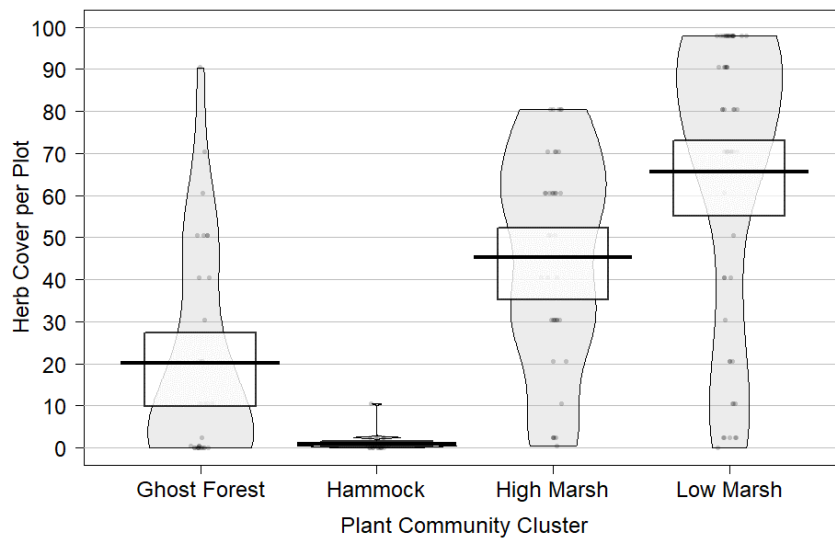
Figure 8. Percent cover of herbs in ghost forest (n= 34), hammock (n= 33), high marsh (n= 38), and low marsh (n= 58). Boxes represent the 95% high density intervals (HDI) and the black line represents the mean.

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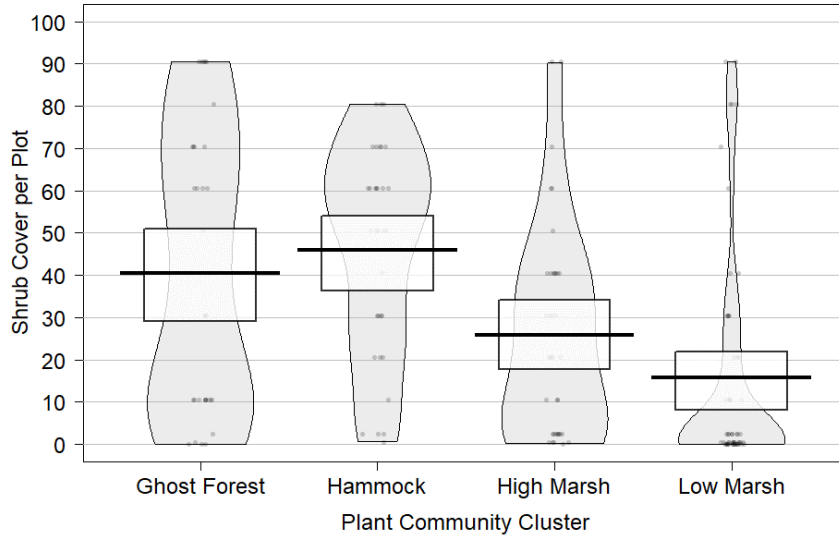
Figure 9. Percent cover of shrub in ghost forest (n= 34), hammock (n= 33), high marsh (n= 38), and low marsh (n= 58). Boxes represent the 95% high density intervals (HDI) and the black line represents the mean.
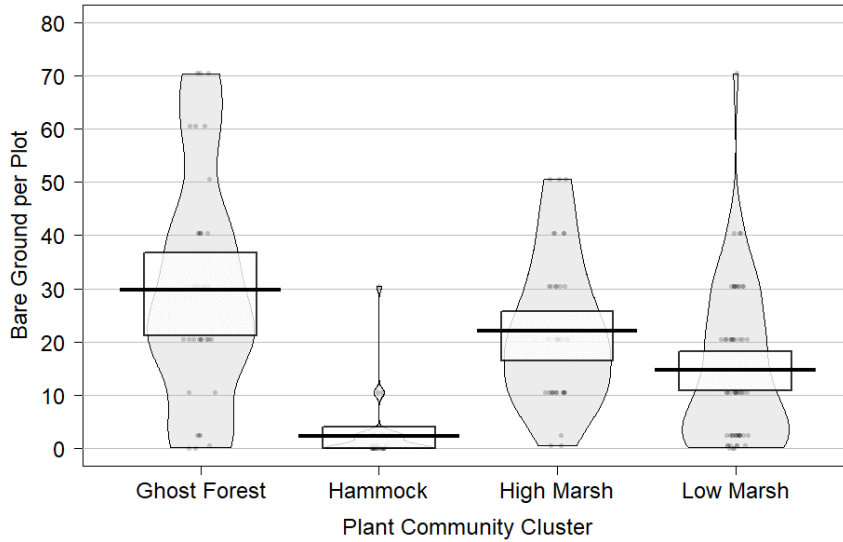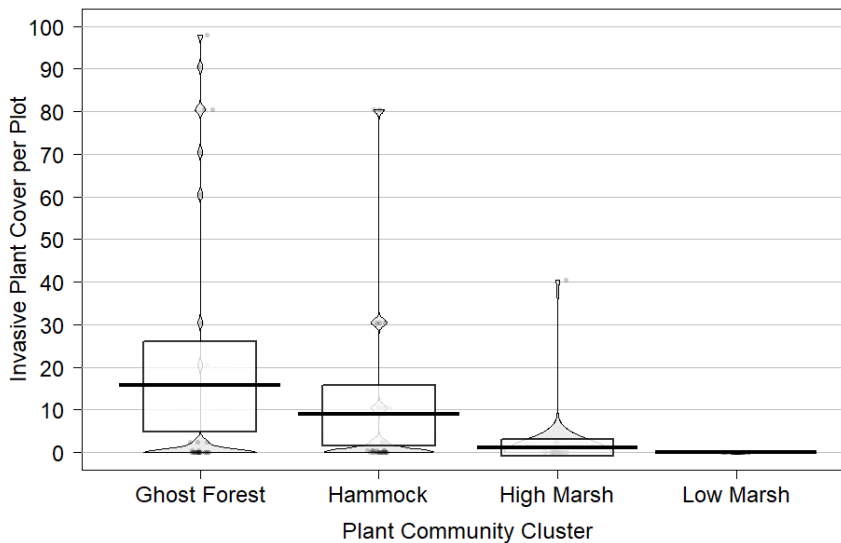

Figure 10. Percent cover of Invasive Plants in ghost forest (n= 34), hammock (n= 33), high marsh (n= 38), and low marsh (n= 58). Boxes represent the 95% high density intervals (HDI) and the black line represents the mean.

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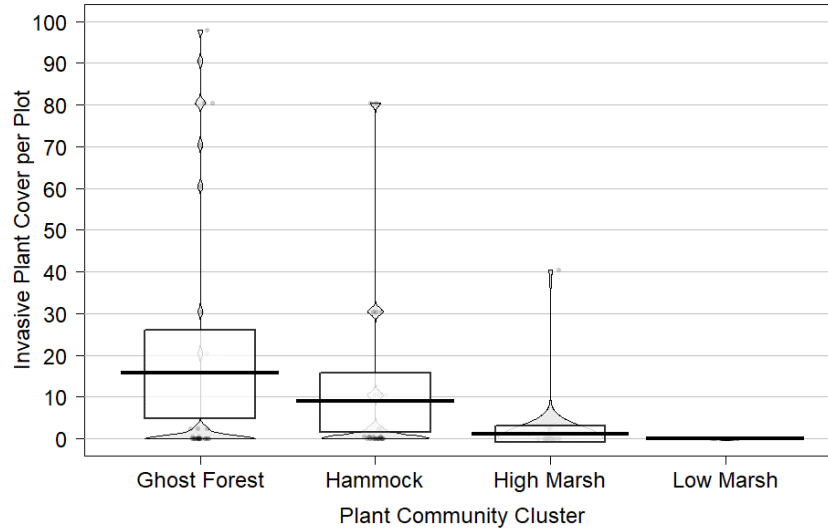
Figure 11. Proportion of snags (dead trees) in ghost forest (n= 34), hammock (n= 33), high marsh (n= 38), and low marsh (n= 58). Boxes represent the 95% high density intervals (HDI) and the black line represents the mean.

*Mangrove Cover and Occupancy*

Average mangrove frequency (all species) was 65.5% (CI=52.6-76.5) in low marsh, 76.3% (CI=60.6-86.7) in high marsh, 23.6% (CI=12.5-40.1) in ghost forest, and almost absent in hammocks (<1%, Figure 12). Red mangrove cover was highest in low marsh with an average cover of 9.2% (CI=3.2-14.0%) followed by high marsh, which had an average cover of 3.6% (CI=0.9-5.7%). However, the credible intervals of red mangrove cover in high marsh and low marsh overlapped, indicating the differences observed between these groups might be negligible. Ghost forest and hammock were similar in that they had nearly no red mangrove cover (<1%). Black mangrove was slightly less common with a similar trend of having higher cover in low marsh (mean=4.2%, CI=1.3-6.6%) than in high marsh (mean=1.8%, CI=0.3-3.1%), but these credible intervals were somewhat overlapping. Black mangrove was also largely absent from ghost forest and hammock. White mangrove was uncommon in all community types but had the highest cover in high marsh (mean=1.7%, CI=0.0-3.5%). Cover of white mangrove was less than 1% for all other communities. Buttonwood, the mangrove relative which is a high marsh specialist, was most common in high marsh (mean=9.0%, CI=1.4-15.8%) but had overlapping credible intervals with ghost forest (mean=3.0%, CI=0.0-7.9%).

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Figure 12. Proportion of mangroves in in ghost forest (n= 34), hammock (n= 33), high marsh (n= 38), and low marsh (n= 58). Boxes represent the 95% high density intervals (HDI) and the black line represents mean proportion.

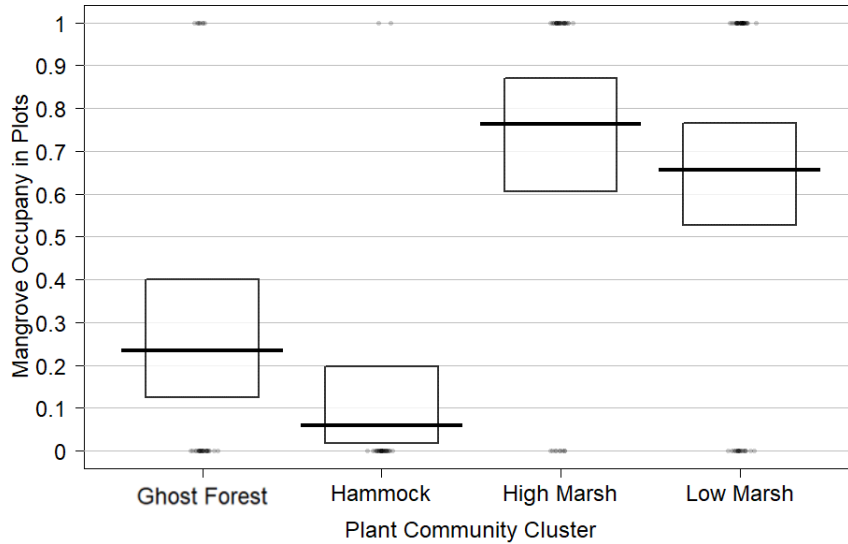*The Effects of Ghost Forest and Other Drivers of Plant Species Richness*
We found that low marsh had a strong negative effect on richness, accounting for a loss of 3.3 species per plot (pd=100%), when compared to ghost forest (Table 3). Presence of forest recruitment had the strongest positive effect on richness with an expected 2.3 additional species (pd=99.8%). Presence of hammock also had a strong positive effect on richness when compared to ghost forest, with 1.9 additional species expected (pd=90%). We also found strong evidence (pd=98%) that herb cover has a positive effect on species richness, with about 2 additional species per plot when herb cover was high. Mangrove occupancy also resulted in a gain of species 0.8 per plot (98% pd) when compared to ghost forest. We observed mature mangrove species in all plant community clusters, and even observed seedlings and hammock areas among wrack line debris, which presumably comes in at extreme tides. Invasive cover had a negative effect on species richness (pd=97.2%); about 2 species were lost on average when invasive cover was at 100%. High marsh had about one more species per plot than ghost forest (pd=95%). We modeled location using longitude to explore north-south effects. We found a marginal positive effect (pd=93%) of richness being higher in northern areas of the Refuge. Credible interval values widely overlapped zero (effect could be negative or positive) demonstrating uncertainty about the likelihood of effect (Table 3). We created a model based off those variables with a greater than 97% pd (Table 4, Figure 13).

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Table 3. Probability of direction (pd) in full model used for final variable section

Parameter	pd
Intercept	75.99%
White Mangrove	84.30%
Red Mangrove	77.78%
Buttonwood	94.20%
Latitude	63.81%
Herb Cover	95.05%
Halophyte Cover	68.00%
Cluster:Hammock	98.72%
Cluster:HighMarsh	98.75%
Cluster:LowMarsh	100.00%
Proportion of Snags	55.14%
Longitude	97.70%
Bare Ground Cover	92.94%
Shrub Cover	97.33%
Invasive Cover	99.27%
Canopy Cover	85.85%
Recruitment:Yes	99.80%

The final model reduced the estimate error and therefore increased the significance index (pd) of the final model (Table 4). Comparing the models using Bayes Factor, we found strong evidence in favor of the reduced final model over the full model (BF=$1.82e^{-13}$ less likely) and very strong evidence against the null model (BF=$1.52e^{-30}$ less likely).

Table 4. Model output for the final model predicting species richness.

	Estimate	Est.Error	Lower 95% CI	Upper 95% CI	Bulk ESS	Tail ESS	pd
Intercept	5.99	0.38	5.24	6.73	51738	53475	100.00%
Cluster:Hammock	1.78	0.72	0.36	3.19	50964	52524	99.31%
Cluster:HighMarsh	1.35	0.5	0.38	2.33	57396	58531	99.65%
Cluster:LowMarsh	-3.16	0.46	-4.06	-2.26	55472	57216	100.00%
Invasive cvr	-0.02	0.01	-0.04	0	70802	60712	98.30%
Recruitment:Yes	2.28	0.74	0.82	3.73	55589	54442	99.88%
Sigma (σ)	2.02	0.12	1.81	2.26	73923	59146	NA

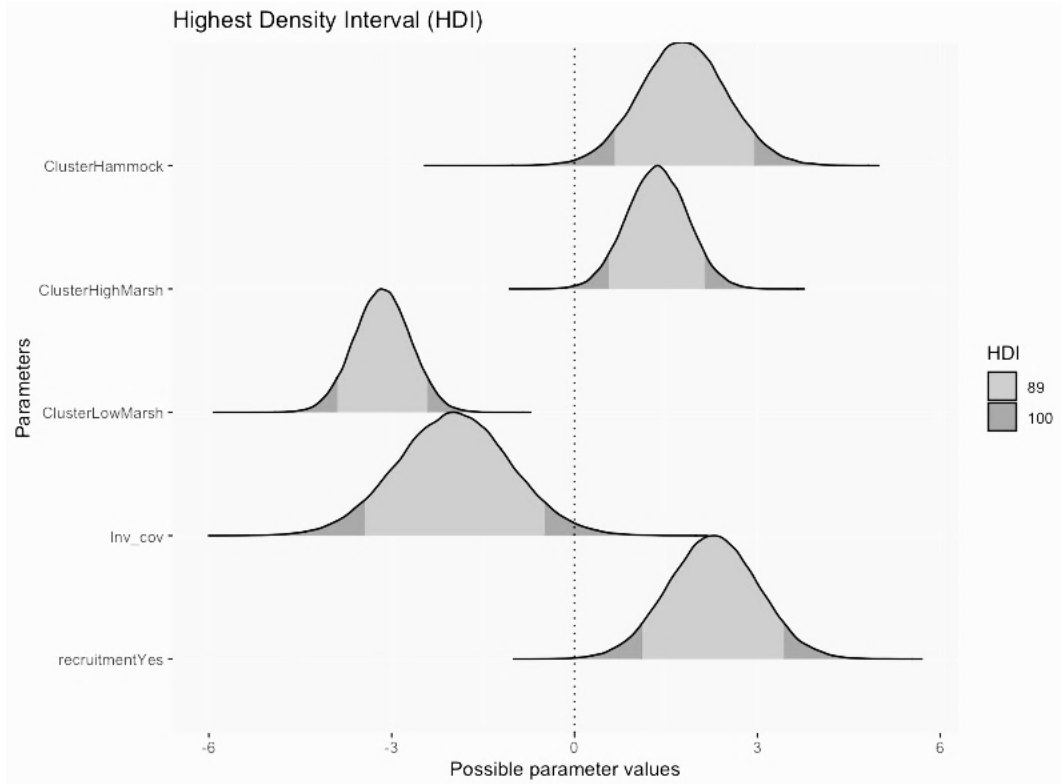*Habitat changes and current conditions at CNWR*

Highest Density Interval (HDI)

Figure 13. Final model parameter values.

Tree Recruitment
We found multiple differences between plots that had recruitment of hammock canopy tree species (oak species, red cedar, and cabbage palms were included) and those which did not. Where recruitment was absent, 65.8% of trees in plots were dead (CI=56.0-73.3). In contrast, where recruitment was present, only 27.4% of trees in plots were dead (CI=14.7-37.0). Plant richness was higher in plots where recruitment was present. Plots with recruitment had a plant richness of 9.8 species (CI=0.6-10.8), as compared to plots without recruitment, which had 5.1 species (CI=4.6-5.5). In addition, we found structural differences between plots with recruitment and those without. Plots with recruitment had a canopy cover of 40.1% (CI=31.8-47.6%) whereas those which did not have recruitment had a canopy cover of 23.2% (CI=14.6-28.5%). Bare ground was 24.7% (CI=17.31.8%) in plots without recruitment and 2.1% (CI=0.1-3.4%) in those with recruitment. Shrub cover was similar (approximately 30-50%) in forest plots with and without recruitment. Recruitment was unlikely when halophyte cover exceeded 1% and halophyte cover was virtually absent in forest plots with recruitment. Brazilian pepper cover was similar in sites with and without recruitment.

Comparing Estimates from Mapping and Plot-based Methods
Plot-based sampling methods indicated that the frequency of hammocks on transects was 36% (CI=24.13-49.93%). Because all samples were drawn from sites which were hammock in 1941, we interpreted this as a 50-75% of reduction in the proportion of hammocks remaining. Our plot data shows conversion to ghost forest occurs sometime within two damage classes delineated from the aerial imagery. For this reason, we estimate ghost forest acreage from mapping efforts

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at both the >50% damage and the >75% classes to address this uncertainty. Including hammocks with greater than 75% damage (dead tree cover) as ghost forests, mapping based estimates show a decline from 1,581 acres (including both maritime and mesic hammock) to 690 acres, indicating only 43.6% of the total land cover of hammocks still remain from 1941. Using 50-75% damage threshold for conversion to ghost forest, the estimate of remaining hammock is 46.14% (about a 54% loss). Collectively, both methods illustrate a clear pattern of continued hammock loss before and since 1941.

DISCUSSION

Our results suggest that saltwater damage is drastically affecting the distribution and composition of natural communities present at the Refuge. Our findings are consistent with what is currently known about the process of hammock die off and the transition to ghost forest (Liu et al. 2017, Kirwan and Gedan 2019), and mangrove expansion (Cavanaugh et al. 2013). However, because of the proximity of the Refuge to sub-tropical climate zones, new species are arriving which further compound changes from altered climate and sea level. Over twenty years ago, Williams et al. (1999) documented vegetation successional shifts occurring as a result of salt intrusion that was causing a cessation of recruitment of tree species at Waccasassa Bay State Preserve, FL, USA.

Structural and species differences between marsh and hammock communities were as expected, but observations of ghost forests provide new insight into the structural differences and species composition of this novel community at the Refuge. Some projections of the effect of sea level rise on coastal communities have assumed that rising tide lines would result in communities shifting inland, while species composition remains constant (Borcher et al. 2018, Enwright et al. 2016). However, our data suggest that some ghost forests may represent a novel, divergent pathway with unique features that may persist for a long period before salt marsh forms, and that salt marsh, once established, may be dissimilar from those which currently exist.

We found that ghost forest structure differed from other communities in ways that suggested it was not simply a midpoint between high marsh and hammock communities. Species richness in ghost forest was lower than both hammock and high marsh, adding some evidence that ghost forest may not be a simple midpoint between the two communities. In addition, there was more bare ground in ghost forest than in either hammock or high marsh communities. The differences in richness and bare ground deviate from the linear trend expected if ghost forest was simply a midpoint in a transition from hammock to salt marsh as communities migrated inward. In addition to describing the unique structure of ghost forest, we also characterized the ghost forest community using ordination of the species level data. We found that the presence of exotic species, namely Brazilian pepper, made this community distinct in its species composition. It appears that the ghost forest community observed at the Refuge is more of an analog to the rock barren communities found in South Florida than to salt marsh habitat at the Refuge. This could be because the hammocks at the Refuge are on limestone caps, which would have historically been an elevation barrier against the migration to salt marsh. The position of the ghost forest on these caps may be one of the reasons this community has a unique structure and species composition, rather than converting to salt marsh as historically observed in the area.

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Mangroves are now a prominent feature defining the structure of salt marsh at the Refuge. Mangroves have been present, though at a much lower cover, since before the earliest aerial imagery we were able to obtain. What is known from the 1941 aerial imagery is that mangroves were generally only present on the most seaward islands. By using mapping techniques to quantify change, we offer the first estimates of the rate and degree of coastal community shifts since 1941. These results show that mangrove expansion has increased over time. This increase in mangrove extent is most likely due to the decrease in frequency and intensity of freezes along their northern boundary (Cavanaugh et al. 2013, Giri and Long 2016, Alongi 2015). Multiple years with no significant freezes would allow mangrove islands to become established and likely explain their expansion. As mangrove cover increases, large canopies presumably create microclimates where the effects of freezing temperatures are mitigated. This "microclimate anchoring" further aids expansion by increasing the survival rate of those seedlings which have a canopy shelter. Mangrove habitats are considered as highly valued areas of biodiversity; however, the effects of increasing mangrove cover in an area typically characterized by graminoid-dominated salt marsh is unknown. Further monitoring of the permanent transects established during this study, and perhaps the addition of wildlife, invertebrate, or other surveys could add additional insight that will help quantify the effects of the loss of open salt marsh to mangrove communities.

Based on our data, we believe that changes occurring at the Refuge are most likely due to both pulse (storms) and push events (sea level rise, rising minimum temperature). We observed a lack of recruitment across all species and tree death that occurred along a gradient, with variable proportions of tree death ranging from none to abundant within hammocks. Tree species recruitment in damaged hammocks is lacking after 50-75% percent of canopy species are dead, indicating that these forests will not regenerate. The patterns of hammock loss at the Refuge were not patchy, but rather showed a trend of increased proportional tree death as distance from the mainland increased. Further, the encroachment of mangrove species into salt marsh habitat likely results from climate change over time, as reduced frequency of winter freezes is the most plausible mechanism to explain mangrove range expansion since 1941. Though it's likely that the effects of climate change on these communities have been exacerbated by a few pulse events, the changes observed in both the field data and mapping project indicate push processes are the important drivers of these changes over time.

We did not include LiDAR derived elevation in our model as a potential predictor of natural community structure and species composition changes. The currently available LiDAR data on the Refuge is incomplete due to the remote nature of much of the Refuge. Further, much of our study area is over salt marsh, which is notorious for being difficult to accurately measure using LiDAR as the returns do not penetrate the vegetation but instead reflect and overestimate elevation (Chassereau et al. 2011). This problem is compounded if adjacent plants have different height classes (called "the *Spartina* problem"), as the error becomes less uniform and harder to correct (reviewed in Hladki et al. 2013). Despite not having an elevation variable in our models, the natural communities themselves are informative of the relationship between elevation and the effects of sea level rise. The presence of a given habitat is dependent on its elevation, as that creates the conditions necessary for the characteristic vegetation species to survive. In this way, habitat type and elevation are direct correlates (e.g. hammock must be at a higher elevation than

salt marsh). Therefore, even though we do not explicitly test elevation in our model, we are still able to understand the relationship between sea level rise and habitat changes.

Relationships between the spring hydrology of the landscape and climate change could be an additional factor that influences these communities' response to shifting climates. The degree to which fluctuations in freshwater discharge from the mainland has affected coastal plant communities, and the interaction between these hydrologic changes and climate change events is unknown. Climate change induced drought can exacerbate damage in freshwater dependent systems, which could amplify any effects of observed sea level rise or the impacts of single storm event (Williams et al. 2003). Due to the limitations of this study, we did not explore a model that included the impacts of alterations of freshwater inputs. However, we recommend that further investigations include some method to model how changes in salinity may influence mangrove succession and the creation of ghost forests. Secondary ecological impacts, such as effects to wildlife, of these differences are unknown and also warrant further investigation.

ACKNOWLEDGMENTS

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DATA APPENDIX

Species table noting the presence (1) or absence (0) of each species in the study in each of the four community types.

Species	Damaged Hammock	Hammock	Low Marsh	High Marsh
Andropogon sp.	0	1	0	0
Andropogon virginicus	0	1	0	0
Ardisia escallonioides	0	1	0	0
Avicennia germinans	1	0	1	1
Baccharis angustifolia	1	1	0	1
Blutaparon vermiculare	0	0	0	1
Bolboschoenus robustus	1	0	1	0
Borrichia arborescens	1	0	1	1
Borrichia frutescens	1	0	0	1
Callicarpa americana	0	1	0	0
Chasmanthium sp.	0	1	0	0
Chiococca alba	1	1	0	0
Citrus sp.	0	1	0	0
Citrus x aurantium	0	1	0	0
Cladium jamaicense	1	0	1	0
Conocarpus erectus	1	0	1	1
Dichanthelium sp.	0	1	0	0
Distichlis spicata	1	0	1	1
Encyclia tampensis	1	1	0	0
Epidendrum conopseum	1	1	0	0
Erythrina herbacea	0	1	0	0
Eugenia axillaris	0	1	0	0
Eugenia foetida	1	1	0	0
Eustachys sp.	0	1	0	0
Eustoma exaltatum	0	0	0	1
Fimbristylis sp.	1	0	0	0
Heliotropium curassavicum	1	0	0	0
Ilex vomitoria	0	1	0	0
Iva frutescens	1	0	0	1
Juncus roemerianus	1	0	1	1
Juniperus virginiana	1	1	0	1
Laguncularia racemosa	0	0	1	1
Limonium carolinianum	1	0	0	1
Lycium carolinianum	1	1	1	1
Maytenus phyllanthoides	1	1	0	0
Morella cerifera	0	1	0	0
Myrsine cubana	0	1	0	0
Oplismenus sp.	0	1	0	0
Opuntia humifusa	0	1	0	0

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Opuntia stricta	0	1	0	0
Panicum sp.	0	1	0	0
Passiflora suberosa	0	1	0	0
Pleopeltis michauxiana	0	1	0	0
Poaceae	1	0	0	0
Psychotria nervosa	0	1	0	0
Pteridium aquilinum	0	1	0	0
Quercus geminata	0	1	0	0
Quercus virginiana	0	1	0	0
Randia aculeata	1	1	0	0
Rhizophora mangle	1	1	1	1
Sabal palmetto	1	1	0	1
Salicornia ambigua	0	0	0	1
Salicornia bigelovii	0	0	1	1
Salvia coccinea	0	1	0	0
Schinus terebinthifolia	1	1	0	1
Serenoa repens	0	1	0	0
Sesuvium portulacastrum	1	0	0	0
Sida elliottii	1	0	0	0
Smilax laurifolia	0	1	0	0
Smilax tamnoides	0	1	0	0
Solidago arguta var. caroliniana	1	1	0	1
Solidago stricta	1	0	0	0
Spartina alterniflora	0	0	1	0
Spartina bakeri	1	0	0	1
Spartina patens	1	1	1	1
Sphagnum affine	0	1	0	0
Sporobolus virginicus	0	1	0	0
Stenotaphrum secundatum	0	1	0	0
Suaeda linearis	1	0	0	0
Suaeda linearis	1	0	1	1
Symphyotrichum tenuifolium	0	0	0	1
Symphyotrichum tenuifolium	1	0	1	1
Tillandsia sp.	1	1	0	0
Tillandsia usneoides	1	1	0	0
Toxicodendron radicans	0	1	0	0
Vittaria lineata	0	1	0	0
Ximenia americana	0	1	0	0
Yucca aloifolia	0	1	0	0
Zamia integrifolia	0	1	0	0
Zanthoxylum fagara	0	1	0	0
Zanthoxylum flavum	0	1	0	0

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