50 Years of Vegetation Change in a Holly Maritime Forest

THESIS

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Abstract

The Sunken Forest, located on Fire Island National Seashore, is a critically imperiled habitat and is one of only two known old-growth maritime holly forests in the world. Analysis of a dataset that dates back to nearly half a century has helped to identify major drivers influencing changes within the forest. These major drivers include; white-tailed deer herbivory, erosion, sea level rise, increased storm events, and canopy-gap dynamics. As of 2013, the Sunken Forest canopy is still analogues of 1967, but over the last 35 years vegetation recruitment within the forest has become limited due to white-tailed deer (*Odocoileus virginianus*) herbivory. The bayside of the Sunken Forest has also been eroding. Erosion with added pressure from sea-level rise is causing mortality of trees/understory vegetation, limiting seedling and herb recruitment, and shifting vegetation toward the bayside and low elevation areas within the interior of the forest.

Chapter 1: Vegetation Changes in the Sunken Forest from 1967-2012

Introduction

Fire Island National Seashore (Seashore) is located on a barrier island known as Fire Island. Fire Island is located to the south of the south shore of Long Island, NY and is separated by the Great South Bay (Figure 1). The Seashore was established as a National Park by US Congress in 1964. While portions of Fire Island are developed, there are many natural areas interspersed throughout the island within Seashore boundaries. The Seashore also has the only federally designated wilderness area in the State of New York within its boundaries, known as the Otis Pike Fire Island High Dune Wilderness Area. The natural areas that encompass the Seashore are very unique and diverse ecosystems which include, but are not limited to: maritime forests, extensive saltmarshes, fresh and brackish wetlands, and open maritime swale habitats. Among all of these natural areas within the Seashore, the area known as Sailors Haven is a prime example of barrier island ecosystems because it encompasses all of the unique habitats listed above. One of the most well-known ecosystems on Fire Island located in Sailors Haven is the Sunken Forest (40°39' N, 73°07' W). The Sunken Forest is a critically imperiled (G1 status) habitat and is one of only two known old-growth maritime holly forests in the world (Forrester, 2004; NatureServe, 2004).

Figure 1. Location of Fire Island National Seashore.

Barrier island vegetation and the habitats that exist within are unique unto themselves. The formations of these habitats are heavily influenced by disturbances such as erosion, accretion, storm surge, overwashes, heavy winds, and salt spray. Typically there is a steep gradient in vegetation when moving from the ocean toward the bay. Dunes and elevation can also influence the vegetation community and diversity within the interior habitats of a barrier island (Ehrenfeld, 1990). There is a typical continuum of plant communities and zones along a barrier island from ocean to bay (Figure 2). Starting from the ocean beach to the bay, the typical "zones" of plant communities are: 1) Beach colonizing plants, located at the toe of a primary dune; 2) Dune building grasses and forbs, usually found at the primary dune; 3) On the leeward side of a primary dune, dwarf shrubs start to replace herbs; 4) The swale, which has a variety of plant communities (e.g. herbs and dwarf shrubs) 5) Shrub thickets and some grasses start again on either side of the secondary dune; 6) Maritime forest on the leeward side of a secondary dune; and 7) Saltmarsh (Murphy, 1933; Art, 1976; Ehrenfeld,1990; Forrester, 2004).

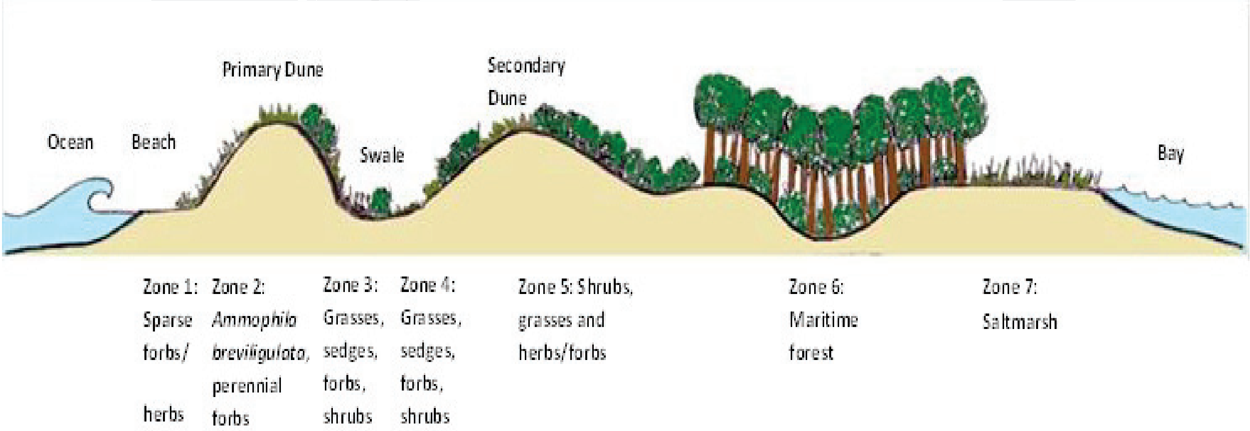

Figure 2. Typical continuum of plant communities and zones along a barrier island (adapted from Ehrenfeld, 1990)

Fire Island, similar to many barrier islands, is post-glacial and was formed by wave and tidal action (Throne, 1953; Art, 1976). The area in which the Sunken Forest is located is estimated to be several thousands of years old (Thorn, 1953; Sirkin, 1972). The evolution of this area is fascinating and demonstrates how barrier island ecosystems are dynamic. Currently, Sailors Haven is located in the core of the island but at one time numerous inlets were located within this area (Figure 3). Today, Sailors Haven has a well-established secondary dune, which is the driving factor to the presence of the Sunken Forest. The secondary dune in Sailors Haven was most likely a primary dune in the past but over time a new seaward dune formed. Vegetation, such as, *Ammophila breviligulata* (American beach grass) helped in the formation of the primary dune that exists there now. Beach grass thrives in sand located seaward of a primary dune and its growth is stimulated when buried by sand (Ehrenfeld, 1990). When the process of being buried and growing is repeated over time it helps in the formation of dunes (Olson, 1958a; Olson, 1958b; Art, 1976). Vegetation does not only build dunes but it also helps to stabilize them (Travis, 1977). The roots, rhizomes, and exposed parts of a plant help to trap sand and prevent the particles from moving. When a dune is stable, it allows other plant species to grow there i.e. other herbaceous and woody species. Once this new primary dune was formed at Sailors Haven, additional vegetation zones seen in Figure 2 started to develop. It is the secondary dune, in which the Sunken Forest grows behind, that has allowed this old-growth forest to mature into what we see today.

Before today's primary dune developed, the area where the Sunken Forest lies was probably, at one time, very similar to what we see in the open swale now. These swales are dominated by low growing species, such as, *Hudsonia tomentosa* **(**beach heather)*,* *Arctostaphylos uva-ursi* (bearberry)*,* and dwarf-shrubs (Art, 1976; Klopfer et al., 2002). Once the primary dune started to develop, the swale shifted to a salt pruned shrubland. As the primary dune grew this salt pruned shrubland converted into a forest dominated by *Pinus rigida* (pitch pine), *Juniperus virginiana* (red cedar), and *Quercus* spp. (oaks) (Thorne, 1953; Schulte, 1965). The primary dune continued to develop adding adequate protection for forest development. By the late 1700's through 1800's, *Ilex opaca* (American Holly) became established in the forest. Peak releases of *I. opaca* seemed to coincide with Hurricanes dating back to 1804 and 1869 in which Fire Island was impacted (Forrester et al., 2007). Once *I. opaca* became established they gradually shaded out many of the *P. rigida* and *J. virginiana* trees. Evidence of this can be seen to this day, with remains of dead and a few living *P. rigida* and *J. virginiana* trees still present in the forest. As *I. opaca* became established, other associates started to emerge in the forest (Thorne, 1953; Art, 1976; Stalter, 1979; Forrester, 2004). *Nyssa sylvatica* (black gum) seemed to have low but steady recruitment in the forest from the 1820's to the 1960's (Forrester et al., 2007). *Sassafras albidum* (sassafras) started to grow in the forest toward the late 1800's and *Amelanchier canadensis* (Shadblow) toward the early 1900's. Both *S. albidum* and *A. canadensis* seemed to go through peak recruitment from the 1940's-1960's (Forrester et al., 2007).

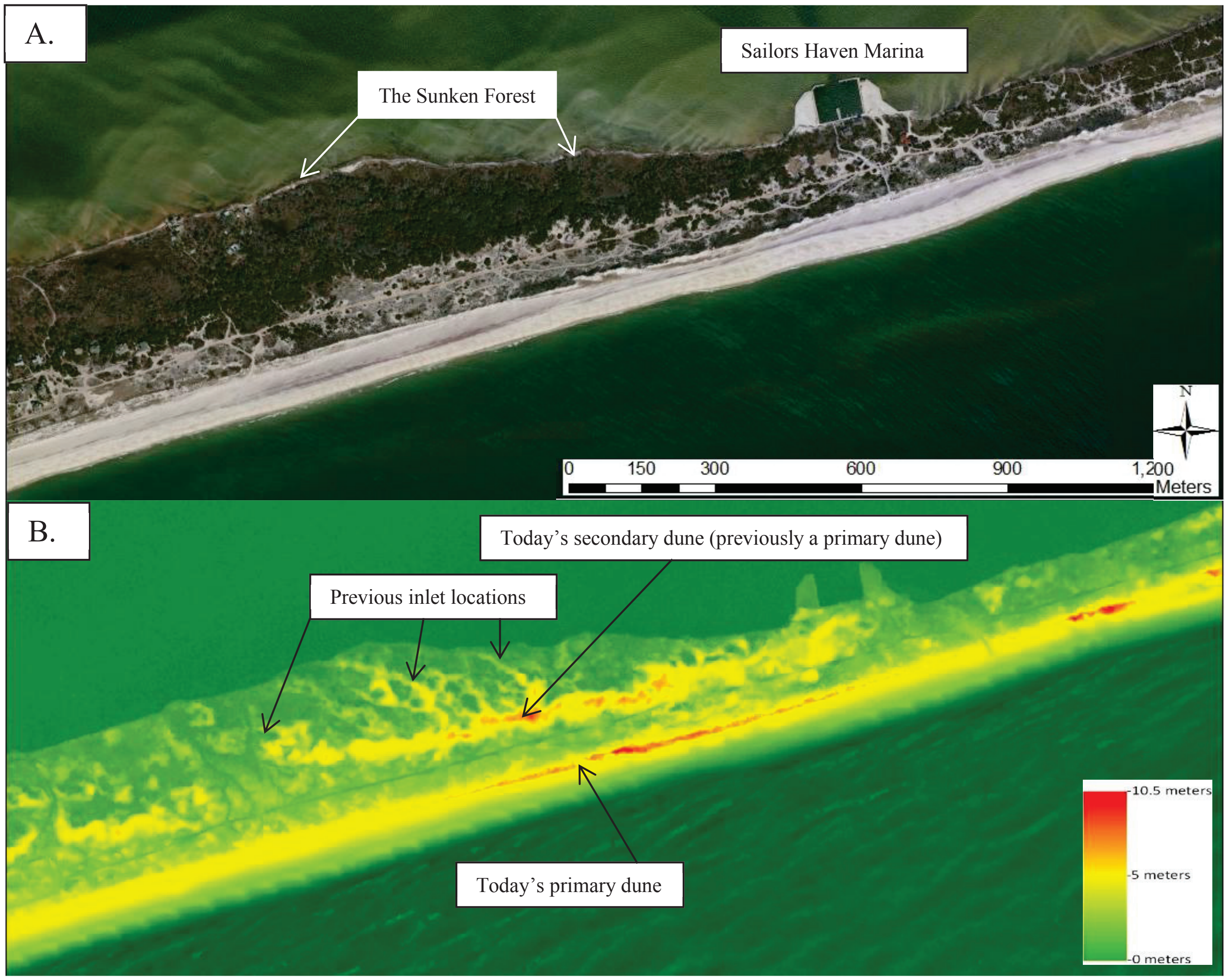

Figure 3. A.) Aerial image and B.) LiDAR map of the Sailors Haven/Sunken Forest area showing locations of old inlets, primary dunes, and secondary dunes

When the Seashore was established in 1964, the importance of the Sunken Forest was recognized in its enabling legislation, stating that the "area known as the Sunken Forest Preserve shall be preserved from bay to ocean in as nearly its present state as possible" (PL 88-587). The Sunken Forest is small at less than 40 acres in size, and the old growth forest is about 300-350 year-old. The canopy is dominated by *I. opaca*, *S. albidum*, *A. canadensis*, and *N. sylvatica* respectively (Thorne, 1953; Schulte, 1965; Art, 1976; Forrester, 2004). Around the time the Seashore was established and before, the sapling and shrub layer of the Sunken Forest was described as being dominated by *A. canadensis*, *Gaylussacia baccata* (Black huckleberry), *Aronia arbutifolia* (red chokeberry), *Ilex glabra* (inkberry), and *Vaccinium corymbosum* (highbush blueberry). The herb layer was described as being dominated by *Aralia nudicaulis* (Wild Sarsaparilla), *Maianthemum stellatum* (little false Solomon's seal)*,* and *Maianthemum canadense* (Canada Mayflower) (Murphy, 1933; Thorne, 1953; Schulte, 1965; Art, 1976). Currently, the canopy layer is similar to what was described in its first official documentation in 1932 (Murphy, 1933). Today, this is not the case for the sapling/shrub and herb layers. These two vegetation layers have drastically decreased in density and percent cover since the Seashore was established.

The Sunken Forests has been well studied over the years and these studies give descriptions of the habitat and vegetative communities (Murphy, 1933; Thorne, 1953; Schulte, 1965; Art, 1976; Stalter, 1979; Art, 1987; Forrester, 2004; Forrester et al., 2007). They have also been used to help the Seashore in making science based management decisions for the preservation of this rare habitat (Forrester et al., 2008). In this chapter, I will describe the changes that have occurred in this forest since the Seashore was established in 1964 by using a historical data set spanning almost half a century and recent data I collected from 2011-2012. In

1967, a number of permanent vegetation plots were randomly established in the forest (Art, 1976) and these plots have been surveyed several times since then (Art, 1976; Art, 1987; Forrester, 2004). This chapter will focus on the vegetation changes that have occurred in the forest and in Chapter 2, I will explore drivers of these changes. Understanding the changes in the forest over the last half century and the drivers of these changes is important to explore. Continued research is needed to be able to make informative management decisions in the face of climate change and sea level rise.

Methods

Sunken Forest Permanent Plot Vegetation Surveys

Surveys were conducted in 2011-2012 in the 100m^2 permanent vegetation plots established by Hank Art in 1967 to evaluate changes in the Sunken Forest vegetation. Permanent plots were surveyed using a modified method from Art (1976): Woody stems ≥ 3.0 cm diameter breast height (DBH), at 1.5 meters, were recorded by species in the entire 100 m^2 plot. Shrub/sapling individuals > 1.0 m tall and < 3.0 cm DBH were recorded within a 25 m^2 (5 m x 5 m) subplot. The percent cover of all vascular plants < 1.0 m tall were recorded using a modified version Domin-Krajina cover class (Elzinga et al., 1998) (Table 1) within four 1 m^2 subplots located at the corners of the 100 m^2 plot. *Smilax* spp. (brier), *Phragmites australis* (common reed), and woody species densities were also recorded within 1 m^2 subplots. Each woody seedling was recorded as either a yearling or ≥ 2 years old.

Table 1: A revised version of Domin-Krajina cover class

Class	Domin-Krajina
1	<1%
2	1%
3	2-5%
4	6-10%
5	11-25%
6	26-33%
7	34-50%
8	51-75%
9	76-95%
10	96-100%

Vegetation layers were (adapted by Art 1976):

1.) Canopy Layer: stems ≥ 3.0 cm DBH.

2.) Sapling/Shrub Layer: individuals ≥ 1.0 meter in height and < 3.0 cm DBH. Saplings refer to species that will grow in to the canopy.

3.) Ground Layer: any vascular plant <1.0 meter in height.

Sunken Forest Permanent Plot Vegetation Analysis

In 2011, there were only 20 open plots to survey from the original 34 plots established in 1967 (Figure 4). The other plots within the Sunken Forest were lost either from the construction of the boardwalk, finished in the mid-1980's, or erosion on the bay side. Deer exclosures were established around three plots following the surveys completed in 1986 to examine the impacts of white-tailed deer and other herbivores (Art, 1987; Forrester, 2004; Forrester et al., 2006). I analyzed long term trends using the raw data from 1967, (Art, 1976), 1986 (Art, 1987), 2002 (Forrester, 2004), and the most recent surveys I finished in 2011-2012 from the 20 open plots still present in the forest.

For the canopy layer, I analyzed the fluctuations in the importance values, density, and basal area between different sampling years using paired t-tests with Bonferroni corrections. I also analyzed changes between two different sampling years using paired t-tests (e.g. 1967-2011). Importance values were calculated as follows: Relative Density + Relative Basal Area / 2. Previous studies in the Sunken Forest have calculated mortality and recruitment rates for canopy layer stems ≥10.0 cm DBH (Forrester, 2004; Forrester et al., 2007) and this analysis was continued with the data from 2012. For this analysis, recruitment referred to trees growing into the larger size class of ≥10.0 cm DBH. These rates focused specifically on the four most dominant species within the canopy, which include: *I. opaca, S. albidum, A. canadensis,* and *N. sylvatica,* respectively. Mortality (M) and recruitment (R) rates were calculated as follows:

$$M = \{1 - [(NO - m)/NO]^{1/Dt}\} \times 100$$

NO = stems at the beginning of the measurement interval, m = number stems that died since the initial measurement, Dt = measurement interval between measurements (tl – t0) and:

$$R = \{[(NO + r)/NO]^{1/Dt} - 1\} \text{ x } 100$$

r = number of stems recruited, between the measurements (Sheil and May, 1996).

I also calculated percent change in stem densities by survey year based on the difference between mortality and recruitment rates, R – M = Rate of Change (Nepstad et al., 2007). Positive values show that recruitment is at a high enough rate to offset the mortality occurring in the canopy layer. Negative values show the mortality rate is higher than what is recruiting or growing into the ≥10.0 cm DBH size class.

For the sapling/shrub layer, I analyzed the fluctuations in density between different sampling years using paired t-tests with Bonferroni correction. I also analyzed changes between two different samplings years using paired t-tests (e.g. 1967-2011). Lastly, for the ground layer analyses I converted all visual percent cover estimates from the different survey years to a modified version Domin-Krajina cover class (Elzinga et al., 1998) (Table 1). I compared the changes in the ground cover of all years using Tukey-Kramer HSD.

JMP 9 (statistical package) was utilized for most of the statistical analysis. R statistical package was also used for the correspondence analyses seen throughout the chapter. All vascular plant nomenclature throughout this chapter follows (USDA, NRCS. 2014. The PLANTS Database (http://plants.usda.gov, 6 December 2014).

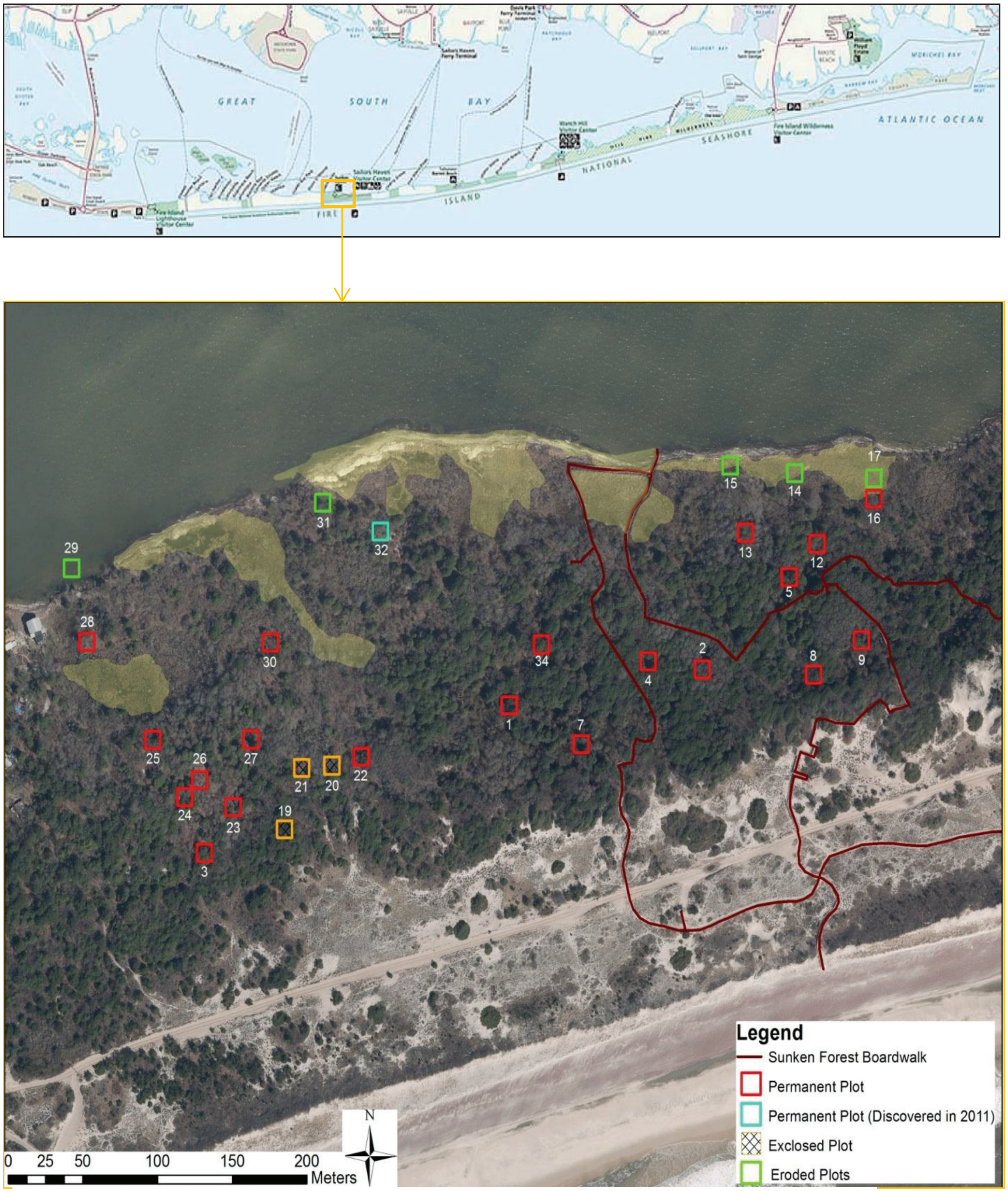

Figure 4. Map Fire Island National Seashore and the Sunken Forest Permanent Vegetation Plots. (Established by Art, 1976)

Results

Canopy Layer

The canopy layer of the Sunken Forest in 2011-2012 was, for the most part, representative of what was seen in 1967 (Figure 5). The 2012 canopy was dominated by *I. opaca, S. albidum, A. canadensis,* and *N. sylvatica,* respectively (Figure 5). Within the last decade *S. albidum* and *A. canadensis* have switched places in dominance and *I. opaca* had become more dominant. While there was a decrease in *A. canadensis* and an increase in *I. opaca,* the differences are not statistically significant. *S. albidum, N. sylvatica, Quercus velutina,* and *P. rigida* did not change in importance over the last 45 years. *Rhus copallinum* (shining sumac), *Quercus stellata* (post oak), and *Quercus coccinea* (scarlet oak) are no longer present in any of the permanent plots.

The densities and basal areas of the canopy layer stems (≥3.0 cm DBH) were calculated for each of the canopy species from the year they were surveyed (Table 2). The total density from 1967 to 2012 and 1986-2012 showed statistically significant declines (t = -2.58, p = 0.0145 and t = -2.71, p = 0.0106, respectively). While there are significant declines in stem density there were significant increases in basal area. The total basal area from 1967 to 2002 and1967 to 2012 showed statistically significant increases (t = 2.53, p = 0.0159 and t = 2.47, p = 0.0185, respectively).

The densities and basal areas of the larger shrubs stems (≥3.0 cm DBH) were calculated for each of the species from the year they were surveyed (Table 3). Most species within this layer have maintained their densities with *V. corymbosum* dominating this layer over the last 45 years. *A. arbutifolia* and *I. glabra* has declined continuously through the years while *Parthenocissus* *quinquefolia* (Virginia creeper) has increased (Table 3).

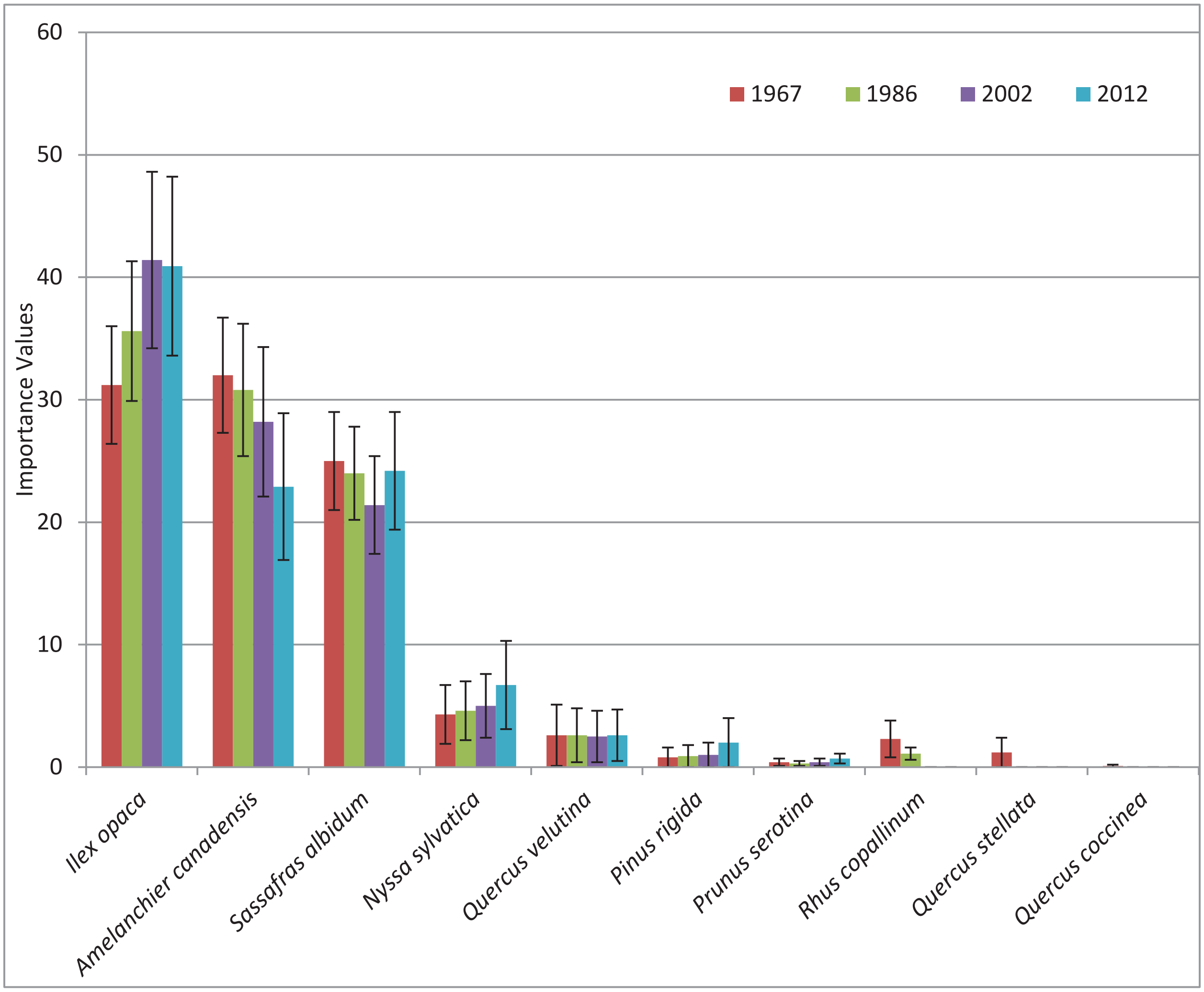

Figure 5. Overall Importance Values of Canopy Layer Stems. Error bars show standard error. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)).

Table 2. Basal area and density of canopy layer stems (≥3cm DBH). Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)). Values are means ± standard errors. ** shows a significant change from 1967 to 2012. * shows a moderate change

Species	BASAL AREA m^2 ha^{-1}				DENSITY Stems ha^{-1}			
	1967	1986	2002	2012	1967	1986	2002	2012
Ilex opaca	8.9±1.6*	11.7±2.2	14.6±2.9	14.8±3.0*	670±136	645±115	620±114	545±114
Amelanchier canadensis	5.1±1.0	6.3±1.1	5.7±1.2	4.1±1.1	895±160*	940±211	755±192	475±139*
Sassafras albidum	6.5±1.4	8.0±1.7	8.3±1.7	9.2±1.9	345±49	370±85	275±77	250±69
Nyssa sylvatica	1.5±1.0	1.8±1.1	2.5±1.4	2.8±1.6	80±43	85±44	85±44	75±40
Quercus velutina	1.2±1.2	1.3±1.2	1.5±1.3	1.7±1.4	10±7	20±12	15±8	10±7
Pinus rigida	0.2±0.2	0.3±0.3	0.5±0.5	0.7±0.7	10±10	10±10	15±15	15±15
Prunus serotina	0.02±0.02	0.04±0.03	0.1±0.1	0.1±0.1	15±11	10±7	10±7	20±12
Rhus copallinum	0.2±0.1	0.1±0.1	0	0	50±27*	25±12	0	0*
Quercus stellata	0.6±0.6	0	0	0	10±10	0	0	0
Quercus coccinea	0.01±0.01	0	0	0	5±5	0	0	0
Total	24.3±2.2**	29.6±2.5	33.2±2.8	33.3±2.8**	2090±228**	2105±219	1775±199	1390±147**

Table 3. Basal area and density of liana and shrub stems (≥3cm DBH). Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)). Values are means ± standard errors. ** shows a significant change from 1967 to 2012. *

Species	BASAL AREA m^2 ha^{-1}				DENSITY Stems ha^{-1}			
	1967	1986	2002	2011/2012	1967	1986	2002	2011/2012
Vaccinium corymbosum	0.5±0.2	0.8±0.3	0.8±0.3	0.6±0.2	420±132	550±194	585±201	420±169
Aronia arbutifolia	0.05±0.02	0.05±0.05	<0.01	<0.01	40±21	60±39	15±15	5±5
Ilex glabra	0.01±0.01	0.02±0.01	0	0	15±15	20±16	0	0
Rhododendron viscosum	0.02±0.02	0.1±0.1	0.02±0.02	0.05±0.05	25±16	90±53	15±15	45±45
Myrica pensylvanica	0	0	0	<0.01	0	0	0	5±5
Baccharis halimifolia	0	0	0	0.06±0.02	0	0	0	45±45
Toxicodendron radicans	0.02±0.02	0	0.04±0.03	<0.01	10±7	0	20±12	5±5
Parthenocissus quinquefolia	0	0	0.06±0.01	0.1±0.1	0*	0	45±23	45±20*
Total	0.6±0.2	1.0±0.3	1.0±0.3	0.08±0.03	510±152	720±273	680±220	570±196

Mortality and recruitment rates of canopy trees (≥ 10 cm DBH)

From 1967 to 2002, there was no difference in recruitment or mortality rates for *I. opaca,* but from 2002-2012 mortality in *I. opaca* increased with only a few recruits growing into this canopy size class. *A. canadensis* showed steady mortality rates that were not being offset by recruitment from 1967 to 2002 with a dramatic mortality rate from 2002-2012. *S. albidum* also showed a steady decline from 1967-2002 but maintained well from 2002-2012. Lastly, *N. sylvatica* has maintained its densities over the last 45 years (1967 to 2012) (Table 4).

The percent change in canopy layer stems ≥10 cm DBH show that *I. opaca* has been positive from 1967 to 2002 but shows a negative value from 2002 to 2012 (Figure 6). *A. canadensis* has had negative values over the last half a century and that has been exponential after each survey. *S. albidum* has also had negative values over the last half a century with no change from 2002 to 2012. *N. sylvatica* seems to be the only species that has increased since 1986 with little change from 2002 to 2012 (Figure 6). Overall the rate of change analysis indicates that mortality rates seem to be increasing while recruitment rates decreasing in the larger trees (≥10.0 cm DBH) of the Sunken Forest.

Table 4. Mortality and recruitment rates of the four most common canopy layer stems (≥10cm DBH). Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)).

Species	**Mortality Rate $\%yr^{-1}$**			**Recruitment Rate $\%yr^{-1}$**		
	1967 -1986	**1986-2002**	**2002-2012**	**1967 -1986**	**1986-2002**	**2002-2012**
Ilex opaca	0.8	0.4	1.1	1.0	0.8	0.1
Amelanchier canadensis	2.6	2.8	6.9	2.1	1.7	2.0
Sassafras albidum	3.2	2.2	1.4	2.7	1.4	1.4
Nyssa sylvatica	1.7	0	1.0	1.3	1.1	0.9

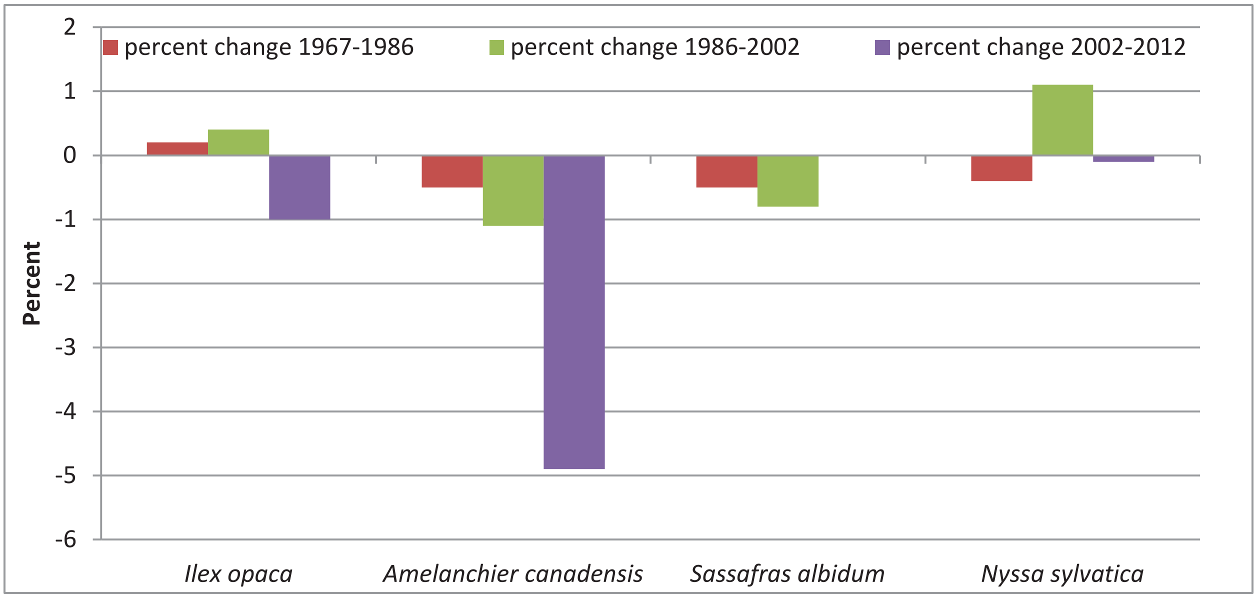

Figure 6. Percent rate of change of the four most dominate canopy species in the forest (≥10cm DBH). Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)).

Sapling/Shrub Layer

There were some significant changes when comparing the densities of the four major canopy constituents in the sapling layer over the last 45 years. The total densities of *I. opaca*, *A. canadensis, S. albidum*, *and N. sylvatica* stems added together by year were: (mean=720, SE= ±102 per ha^{-1} in1967), (440±71 per ha^{-1} in 1986), (200±37 per ha^{-1} in 2002), and (320±47 per ha^{-1} in 2011) (Table 5). The total density of the four major canopy constituents from 1967 to 2002 showed a decline (t = -1.84, p = 0.0735) (Table 5). There was no significant decline in this total density from 1967 to 2011, most likely due to the increase in *S. albidum* from 2002 to 2011 (t=1.84, p = 0.0794) (Table 5). However, *I. opaca*, *A. canadensis* and *N. sylvatica* saplings have continuously declined over the last 45 years (Table 5). The total density of these three species (*I. opaca*, *A. canadensis* and *N. sylvatica*) added together showed a statistically significant decline from 1967 (660±233 per ha^{-1}) to 2011 (140±88 per ha^{-1}) (t = -2.09, p = 0.0473).

There has also been a decrease in *A. arbutifolia* and *I. glabra* over the last 45 years (Table 5). *A. arbutifolia* significantly decreased from 1967 to 2011 (t= -2.40, p =0.0266) (Table 5). Another species worth noting is *Toxicodendron radicans* (poison ivy); it was once very abundant within this layer during the first survey in 1967 but has significantly decreased to zero in all the years following (t= -2.21, p =0.0392) (Table 5). The total density of *A. arbutifolia*, *I. glabra* and *T. radicans* added together showed a statistically significant decline from 1967 (1540±531 per ha^{-1}) to 2011 (20±20 per ha^{-1}) (t= -2.86, p=0.0100).

While there have been decreases amongst some of the major canopy species in the sapling/shrub layer, there has been an increase in species which are not important components of the canopy. For example, there has been an increase in *Prunus serotina* (black cherry) density within the sapling/shrub layer since 1967. *P. serotina* increased from (20±20) in 1967 to (480±324) in 2011 (Table 5).

A correspondence analysis shows *I. opaca* and *N. sylvatica* were mostly associated within the sapling layer in 1967. *A. canadensis* was also an important component in the sapling layer in 1967 but was still important in 1986 as well. *S. albidum* was an important component of the sapling layer during the 1986 and 2011 surveys. Finally, *P. serotina* seemed to be a dominant component of the sapling layer during the 2002 and 2011 surveys (Figure 7).

Table 5. The density of stems in the sapling/shrub layer (≥1 meter in height and < 3 cm DBH). Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004). Values are means ± standard errors.

Species	**Density** Stems ha^{-1} 1967	1986	2002	2011
Saplings				
Ilex opaca	40±28	20±20	0	0
Amelanchier canadensis	480±213	320±115	160±160	140±88
Nyssa sylvatica	140±106	20±20	20±20	0
Total: *I. opaca, A. canadensis, N. sylvatica*	660±233**	360±123	180±160	140±88**
Sassafras albidum	60±44	80±62	20±20	180±84
Prunus serotina	20±20	0	100±100	480±324
Total: *S. albidum, P. serotina*	80±47*	80±62	120±101	660±356*
Shrubs/Lianas				
Aronia arbutifolia	540±216**	220±182	20±20	20±20**
Ilex glabra	420±284	80±62	0	0
Toxicodendron radicans	580±262**	0	0	0**
Total: *A.arbutifolia, I. glabra, T. radicans*	1540±531**	300±531	20±20	20±20**
Vaccinium corymbosum	1800±550	980±302	2260±881	2060±1034
Rhododendron viscosum	0	0	20±20	0
Myrica pensylvanica	0	60±44	100±81	140±106
Gaylussacia baccata	720±372	200±149	240±175	320±300
Baccharis halimifolia	0	0	2020±2020	800±652
Parthenocissus quinquefolia	0	0	20±20	40±28
Rubus spp.	20±20	0	0	80±80

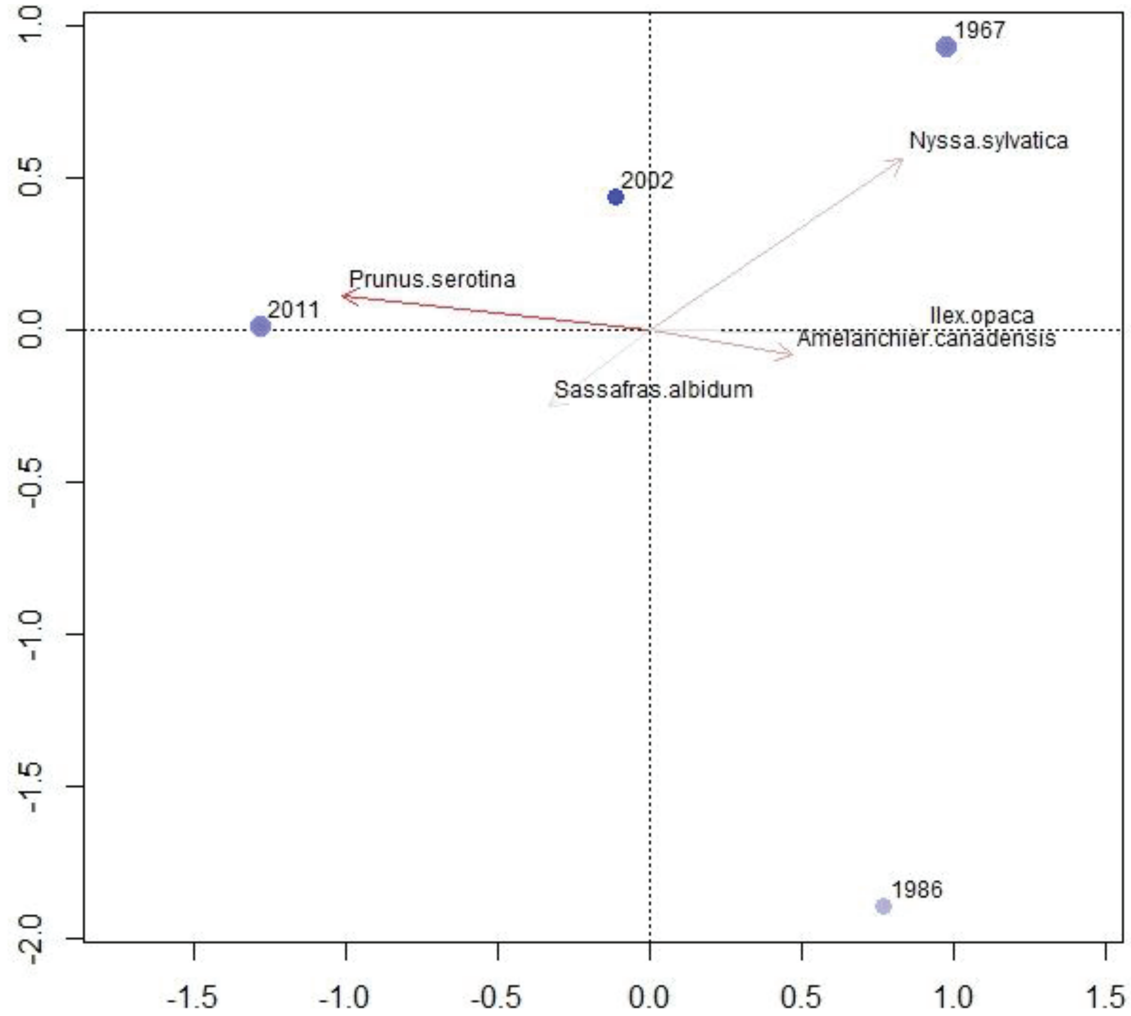

Figure 7. Correspondence analysis showing which species of sapling is most associated with the year the plots were surveyed.

<u>Ground Layer</u>

Percent Cover of Herb, Liana, and Woody Species

The total percent cover ground layer vegetation decreased dramatically from 1967 to 1986, 2002, and 2011 (mean = 41.7, SE=±4.6%, 13.7±2.1%, 8.3±1.8%, and 15.6±1.9% respectively). The difference in percent cover from 1967 to all other time periods is statistically significant (*p* <0.0001).

Some species that were once abundant in 1967 dropped to 0% in 2011. *A. nudicaulis* was the most abundant herb in the ground layer in 1967 at 8.1±1.0%; it dramatically decreased in the follow years to 0.1±0.1% in 1986 and 0% in both 2002 and 2011 (p <0.0001). *M. canadense* had a percent cover of 1.7±0.6% in 1967, and decreased in the following years to 0.2±0.1% in 1986 and 0.1±0.1% in both 2002 and 2011 (p = 0.0049 and 0.0019 respectively). *M. stellatum* had a percent cover of 1.4±0.5% in 1967 then also decreased to <0.1% in 1986 and 0% in both 2002 and 2011 (p = 0.0013 and 0.0009, respectively).

T. radicans was also very common in the ground layer at 7.9±1.8% cover in 1967 then falling to 0.9±0.3% (1986), 0.4±0.1% (2002), 1.0±0.3(2011) (p <0.0001). Other species that show significant decreases (p <0.05) from 1967 to all of the other years were: *Pteridium aquilinum* (common bracken), *V. corymbosum* and *P. quinquefolia* (Figure 8; Figure 9)

While many species within the Sunken Forest decreased there were a number of species that increased in the ground cover. Most notable is *P. serotina*, which was very minimal in the forest in 1967 at 0.1±0.1%, it then steady increased in 1986, 2002, and 2011 at 0.9±0.2%, 1.3±0.3%, and 2.6±0.7% respectively (p <0.0001(from 1967-2011)). Grasses/sedges (*Carex* spp. and *Panicum* spp.) and *Polygonum hydropiperoides* (swamp smartweed) have also increased over the last 45 years (Figure 8; Figure 9).

A correspondence analysis shows how diverse the ground layer vegetation was in1967 compared to all other years. This analysis also displays how dominant *P. serotina* and Grasses/sedges (*Carex* spp. and *Panicum* spp.) were during the 2011 survey (Figure 10)

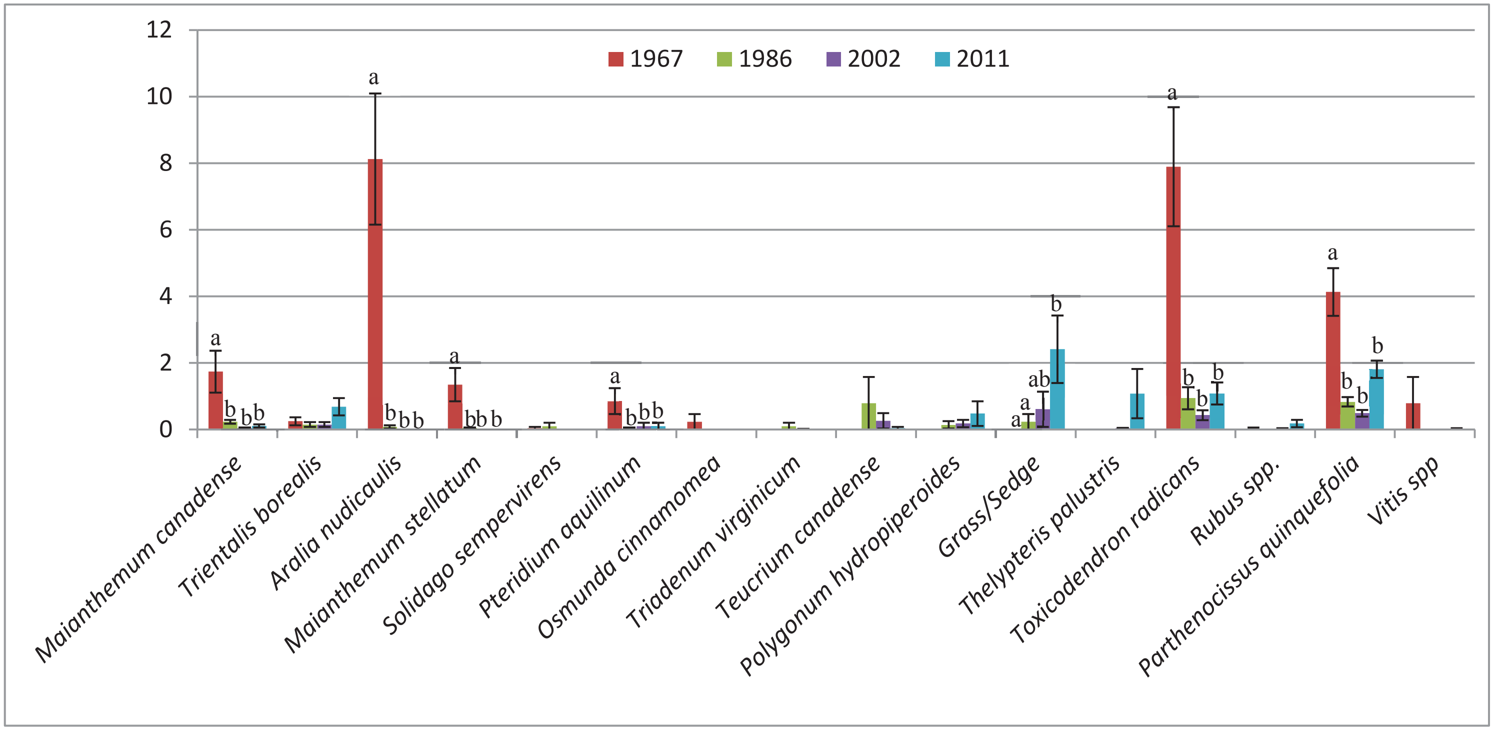

Figure 8. Percent cover of herbs and lianas (<1.0 meter in height) (using revised form of Domin-Krajina cover class). Error bars show standard error. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)). Levels within species not connected by same letter are significantly different.

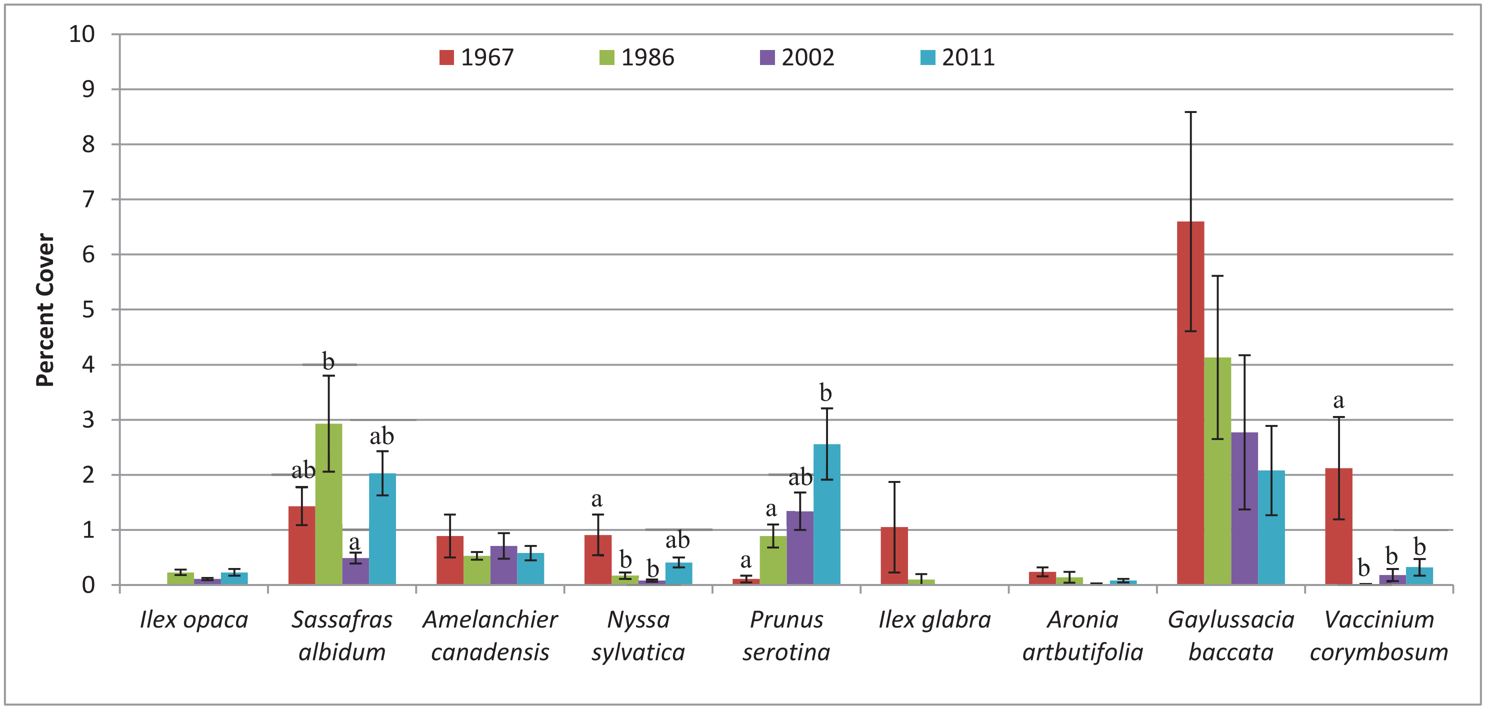

Figure 9. Percent cover of woody species (<1meter in height) (using revised form of Domin-Krajina cover class). Error bars show standard error. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)). Levels within species not connected by same letter are significantly different.

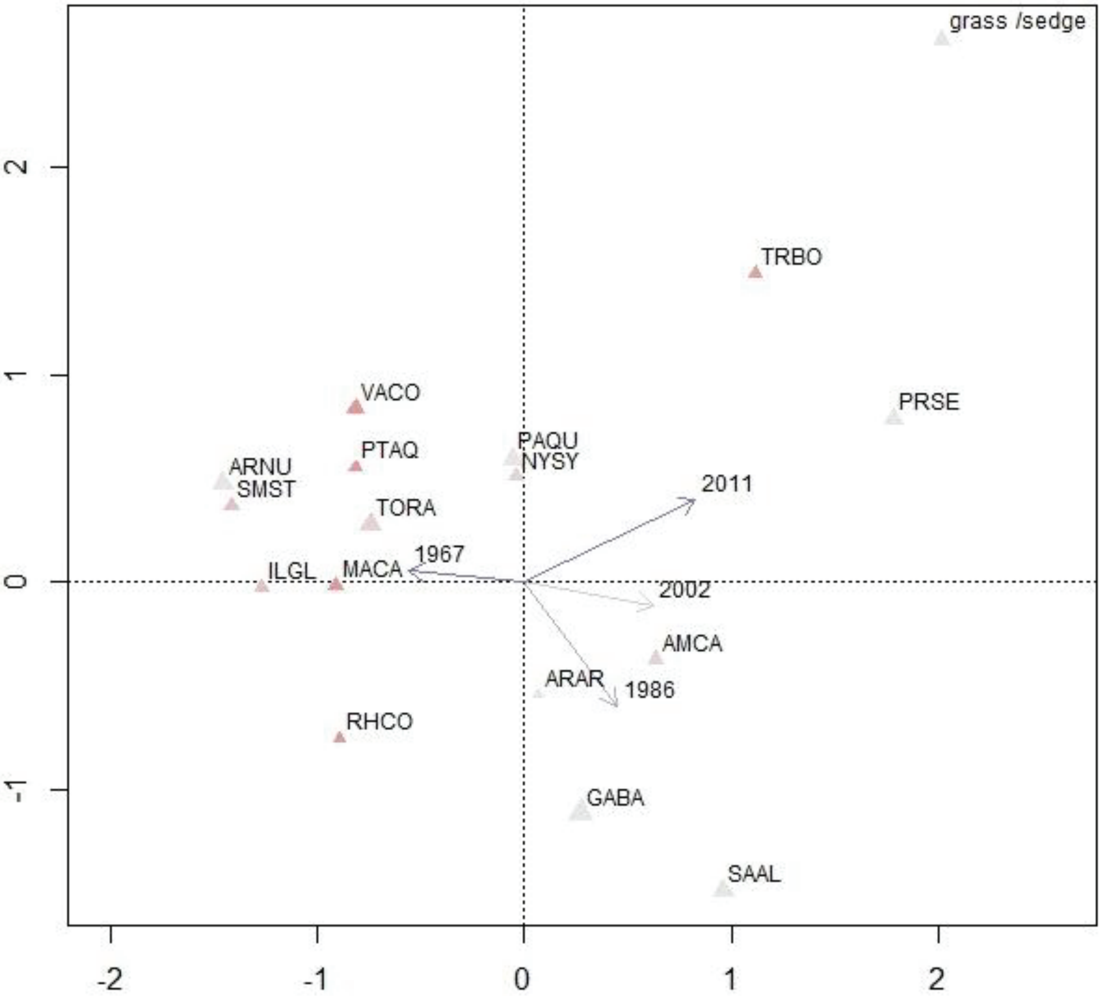

Figure 10. Correspondence analysis showing which species within the ground layer is most associated with the year the plots were surveyed.

Smilax densities

Smilax rotundifolia (common greenbrier) *and Smilax glauca* (sawbrier), are both found in the Sunken Forest ground layer (Table 6). *S. rotundifolia* is most common and the density of stems seems to fluctuate over the last 45 years with no noticeable significant trends.

Table 6. Densities of *Smilax rotundifolia and Smilax glauca.* Values are means ± standard errors. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)). Levels within species not connected by same letter are significantly different.

Species	DENSITY Stems m^{-2}			
	1967	1986	2002	2011
Smilax rotundifolia	3.5±0.4^{b}	1.1±0.1^{c}	6.8±0.7^{a}	3.1±0.4^{b}
Smilax glauca	0.2±0.1^{ab}	0.3±0.1^{a}	0^{c}	0.1±0.1^{bc}

Discussion

The major patterns of vegetation change in the Sunken Forest over the last 45 years has been the mortality of large canopy trees, shifts in sapling/shrub layer and seedling layer, including the dominance of *P. serotina*, and the loss of common herbaceous species. For the canopy and sapling/shrub layers, mortality has been higher than recruitment for many of the most common species. In the ground vegetation, the loss of common herbaceous species is substantial.

The 2012 canopy layer survey was similar to what was observed in the 2002 survey (Forrester, 2004), although the morality of canopy layer stems (≥10.0 cm DBH) increased dramatically, specifically with *I. opaca* and *A. canadensis*. The cause of this mortality and limited recruitment needs to be further explored. Trees in this size class (≥10.0 cm DBH) could eventually be impacted from the limited recruitment occurring in the sapling layer. Although, in an old growth forest like the Sunken Forest, it should take longer for this size class to be effected by limited recruitment (Stalter, 1979). The *I. opaca* trees that are currently in the canopy went through peak recruitment through the 1800's (Forrester, 2004). Therefore, 30 years of limited recruitment in the sapling layer should not affect *I. opaca* within this size class. Although, this could possibly impact *A. canadensis*, which is an early successional species (DeGraaf and Yamasaki, 2003). The *A. canadensis* trees currently in the canopy went through peak recruitment between 1950-1990 (Forrester, 2004). This along with other added pressures could be the cause of the dramatic decrease observed.

There has also been a major shift in the sapling/shrub layer. Most of these changes occurred by the 1980's. The most striking was the extreme decrease in *I. opaca* to 0 stems per ha^{-1} in 2002 and 2011. *I. opaca* is a slow growing species that is extremely shade tolerant

(Forrester et al., 2006), which can allow it to compete with some of the faster growing species. Even in the 1950-1960's, *I. opaca* was never a dominant component of the sapling layer (Thorne, 1953; Schulte, 1965; Art, 1976) but for the species there was enough to maintain its dominance within the canopy (Stalter, 1979). Also, the declines in both *A. canadensis* and *N. sylvatica* saplings suggest that recruitment in this forest is very limited. *S. albidum* is the only species out of the four most common canopy constituents that is currently recruiting in the forest. The increase of *P. serotina* in this size class is also hard to ignore, especially because of it low importance within the canopy layer. Forrester (2004), documented *P. serotina* as a dominant in the ground cover within the permanent plots in 2002 and almost a decade later it has dominated the sapling layer as well. Recruitment at this level is very important because these are the species that will become the canopy layer; with different species now dominating the sapling layer the future canopy will be different to what is currently there (Horn, 1975; Denslow, 1987; Runkle, 1998).

Other species that were once very important within the shrub layer were *A. arbutifolia, I. glabra,* and *T. radicans* (Art, 1976). These species have been seldom found in the forest since 1986 (Art, 1987; Forrester, 2004). This trend can also be seen within the next size class (≥3.0 cm DBH) for these species, starting in 2002. Recruitment is much lower than the mortality occurring in the forest within this layer, particularly for *I. opaca*, *A. canadensis* and *S. albidum*. Other species such as *Myrica pensylvanica* (Northern bayberry) and *Baccharis halimifolia* (Groundsel) shrubs started to appear in the permanent vegetation plots toward the late 1980's and can now be found in the next size class (≥3.0 cm DBH) as well (Table 3; Table 5).

Common species found in the ground/herb layer between the early 1930's into the 1970's were *M. canadense*, *A. nudicaulis*, *M. stellatum*, *T. radicans,* and *P. aquilinum* (Murphy, 1933;

Thorne, 1953; Schulte, 1965; Art, 1976) but these species have significantly declined since the mid- 1980's as well (Art, 1987; Forrester, 2004; Forrester et al., 2007). Currently, *A. nudicaulis* and *M. stellatum* are on the brink of extirpation in the Sunken Forest, but on rare occasions can be found in other areas of the island (Forrester, 2004; Raphael personal observation). In my four years of surveying the Sunken Forest, I have only seen *A. nudicaulis* toward the western section of the Sunken Forest toward the community of Point O Woods. The only other place I have seen it growing on Fire Island is near the camp grounds at Watch Hill and under smilax mats in the Wilderness Area. The only time I found *M. stellatum* was in 2011, growing in a stand of cherry saplings, but I have seen it elsewhere on the island (Bluepoint, Talisman, and Wilderness). Many other herbs, lianas, and woody species have declined over the last 45 years while others have increased, again most notably *P. serotina*, grasses/sedges (*Carex* spp. and *Panicum* spp.), and *P. hydropiperoides.*

While some of the changes in the Sunken Forest can be attributed to natural disturbances, most of the observations and research conducted in the Sunken Forest point to indirect anthropogenic influences. Since the park was established there has been an irruption in white tailed deer (O'Connell, 1989; Underwood, 2005). This has added browsing pressures and has impacted the shrub, sapling, and herb layers (Art, 1987; Forrester, 2004). The level of herbivory occurring in the sapling, shrub, and ground layer is most likely the cause to the decline observed within these vegetation layers. There has also been a significant amount of erosion that has occurred since the marina was constructed in Sailors Haven in the 1950's. Erosion has changed the structure of the Sunken Forest, particularly on the north side of the forest. Depressions within the interior of the forest are also changing at an alarming rate. Drivers that may cause these changes in the Sunken Forest will be explored more in Chapter 2. In chapter 2, I will also analyze other impacts that have not been fully explored in past research within the Sunken Forest.

Chapter 2

Ecological Drivers Influencing Long-term Vegetation Changes in the Sunken Forest

Introduction

The Sunken Forest is one of only two known old-growth holly maritime forest left in the world. This rare habitat is located within the boundaries of Fire Island National Seashore (Seashore). The dominance of *Ilex opaca* (American Holly) within the canopy is one of the aspects of the forest that makes it unique. This 300-350 year old forest is also very small at less than 40 acres in size. An historical dataset spanning nearly half a century indicates that this climax community is changing (Chapter 1).

Understanding the ecological drivers that influence change within an ecosystem is important. This is especially important when trying to manage a critically imperiled ecosystem, such as the Sunken Forest. Many factors can come into play and the forest cannot be conserved in its current form unless these impacts can be managed. There are different ecological drivers, both biotic and abiotic, that could cause changes within a forest. These drivers include but are not limited to: herbivory (from both small and large mammals), insect pests, non-native invasive plant species, habitat destruction, and climate change (Rooney and Dress, 1997; Dale et al., 2001; Gan, 2004; Pimentel et al., 2005; Poland and McCullough, 2006; Stinson et al., 2006; Aronson et al., 2007; Eschtruth and Battles, 2008). Erosion and sea level rise are also important drivers of change for maritime forests in particular (Nordstrom and Jackson, 2005; Masterson et al., 2014).

White-tailed deer browsing impacts have been documented in the Sunken Forest for close to 30 years (Art, 1987; Forrester, 2004). These impacts coincide with the irruption of the white-tailed deer population on Fire Island, which started in the mid-1980's. The white-tailed deer population continued to increase up into the early 2000's (O'Connell, 1989; Underwood, 2005).

While deer over-abundance is a major impact to the forest, deer herbivory can sometimes overshadow other impacts occurring throughout the island and the Sunken Forest. Both erosion and sea level rise seem to be affecting the forest quite rapidly. These impacts are hard to ignore but this is a much broader issue, when compared to herbivory, and most likely much more difficult to manage. Pressures to this rare old-growth maritime holly forest do not stop at white tailed deer, sea level rise, and erosion. An increase in storm events, such as hurricanes or nor-easters, could also be a major role in the future. Hurricane Sandy hit Fire Island on October 29, 2012 and following Sandy a number of nor'easters also blew through the area. These storms made 2012/2013 a higher than average stormy winter (Hapke et al., 2013). The timing of these storms gave me an opportunity to look at how major storm events may impact this forest in the future.

There are other pressures and drivers that can play a role in the dynamics of the forest. Some are not significant enough to contribute to the major changes seen while others are just products of some of the larger pressures mentioned above. In Chapter 2, I will explore a few of these drivers to determine the disturbance regime causing the various changes in the vegetation that has been documented in the Sunken Forest over the last half a century. The particular drivers I will focus on will be: white-tailed deer *(Odocoileus virginianus)* herbivory, bayside erosion, sea level rise, canopy gap dynamics, temperature/precipitation, storms events (i.e. hurricanes and nor'easters), and propagule availability. While not all of these drivers play large roles in the changes seen in the forest it is important to analyze each one. When analyzing all possible drivers it will help to further isolate and identify the drivers most important for management.

Methods

In order to examine the drivers of vegetation change, I examined three vegetation strata as defined in Chapter 1 (adapted from Art, 1976):

1.) Canopy Layer: stems ≥ 3.0 cm DBH.
2.) Sapling/Shrub Layer: individuals ≥ 1.0 meter in height and < 3.0 cm DBH. Saplings refer to species that can grow in to the canopy.
3.) Ground Layer: any vascular plant <1.0 meter in height.

Isolating the disturbance caused by white-tailed deer (Odocoileus virginianus)

I will first examine the disturbance caused by white-tailed deer herbivory using the long-term dataset (from 1967 to 2013) and deer exclosures. Long-term dataset results were described in Chapter 1. In 1967, a number of permanent vegetation plots were randomly established and surveyed in the forest (Art, 1976). These plots have been surveyed a several times from the mid-1960's through the early 2000's (Art, 1976; Art, 1987; Forrester, 2004). I re-located these plots in 2011 and surveyed them again from 2011-2013 using the vegetation survey methods described in Chapter 1 (Art, 1976).

Following the surveys completed 1986, deer exclosures were constructed around three of the permanent vegetation plots that were first established in 1967 (Art, 1987; Forrester, 2004). In 2013, I surveyed the exclosed plots and paired each of these 3 plots to another 3 unexclosed (open) plots. These open plots represented similar habitat and were closest to the exclosed plots. In these six plots, I surveyed all woody stems ≥ 3.0 cm diameter breast height (DBH) (1.5m height) and shrub/saplings ≥ 1 m tall and < 3.0 cm DBH were recorded by species in the entire $100m^2$ plot. The percent cover of all vascular plants < 1.0 m tall were recorded using a revised form of Domin-Krajina cover class within ten 1 m^2 subplots located at randomly within the

$100m^2$ plot. *Smilax* spp. (brier), *Phragmites australis* (common reed), and woody species densities were also recorded within 1 m^2 subplots. Each woody seedling was recorded as either a yearling or ≥ 2 years old. In my analysis, I focused on both the sapling/shrub layer and ground layer because this is where most of the impacts from deer herbivory occur. I analyzed the differences in the density of saplings, density of shrubs, importance values of saplings, density of seedlings, and percent cover of ground layer vegetation between exclosed and open plots using paired t-tests. Importance values for saplings were calculated as: relative density + relative frequency/2.

In late-August/early September of 2013, I also resurveyed all 1 m^2 subplots in the permanent vegetation plots throughout the Sunken Forest. During this survey, I noted whether the plot was protected by a brier tangle or branches from down trees. I did this to further isolate browsing impacts in the Sunken Forest; these natural exclosures do not allow deer to access the plants. All 1 m^2 subplots that were >50% protected were paired with the closest 1 m^2 subplot that was <25% protected. The differences in percent cover of all plots >50% protected and <25% protected were tested using paired t-test.

Isolating the disturbance caused by bayside erosion and sea level rise

Using the 45 year data set I also analyzed the impacts bayside erosion and sea level rise had on all three vegetation layers. I delineated how much habitat has been lost due to erosion using ArcGIS and historic geo-referenced imagery from 1938, 1969, 1986, 2002, 2012, and 2013. I used the aerial images close to or on the year the permanent plots were surveyed (except for 1938). Using LiDAR (**LI**ght **D**etection **A**nd **R**anging) and ortho-imagery I identified 5 out of the 20 open permanent vegetation plots most impacted by erosion and sea level rise using vegetation as an indicator. To focus on the impacts, I analyzed how vegetation changed in these

5 plots compared to the other 15 plots over the last 45 years. I examined the changes in mortality and recruitment of the most important canopy species, *I. opaca, S. albidum, A. canadensis,* and *N. sylvatica* trees, ≥ 10.0 cm DBH over the last half a century. The change in the density of trees (≥ 3.0 cm DBH), density of saplings/shrubs (> 1.0 meter in height and < 3.0 cm DBH), and the changes in the ground layer were also analyzed. The 5 plots that represented impacted sections of the forest were 2, 5, 13, 16, and 28 (Figure 11). Plots 2, 5, and 13 represented areas within the interior of the forest at a lower elevation (Figure 11). Plots 16 and 28 are in close proximity to the current bayside shoreline. These two plots (16 and 28) represent habitat that has been significantly changed within areas adjacent or closer to the bay, which has increased due to the bayside erosion. These 5 plots will be referred to as the "impacted plots" and the other 15 plots will be referred to as the "forested plots" throughout this chapter. Changes within the vegetation in the 5 "impacted plots" over time were analyzed using paired t-tests. Also, correspondence analyses were used to show how vegetation in the 5 "impacted plots" differs from the 15 "forested plots".

Isolating the disturbance caused by storms

To examine how the forest could be impacted from major storms all permanent vegetation plots were resurveyed the summer following Hurricane Sandy (2013) and subsequent winter storms using the 2011/2012 data as a baseline. I analyzed the differences in the density of canopy layer stems, basal area of canopy layer stems, density of saplings, density of shrubs, and percent cover of ground layer vegetation from 2011/2012 to 2013 using paired t-tests.

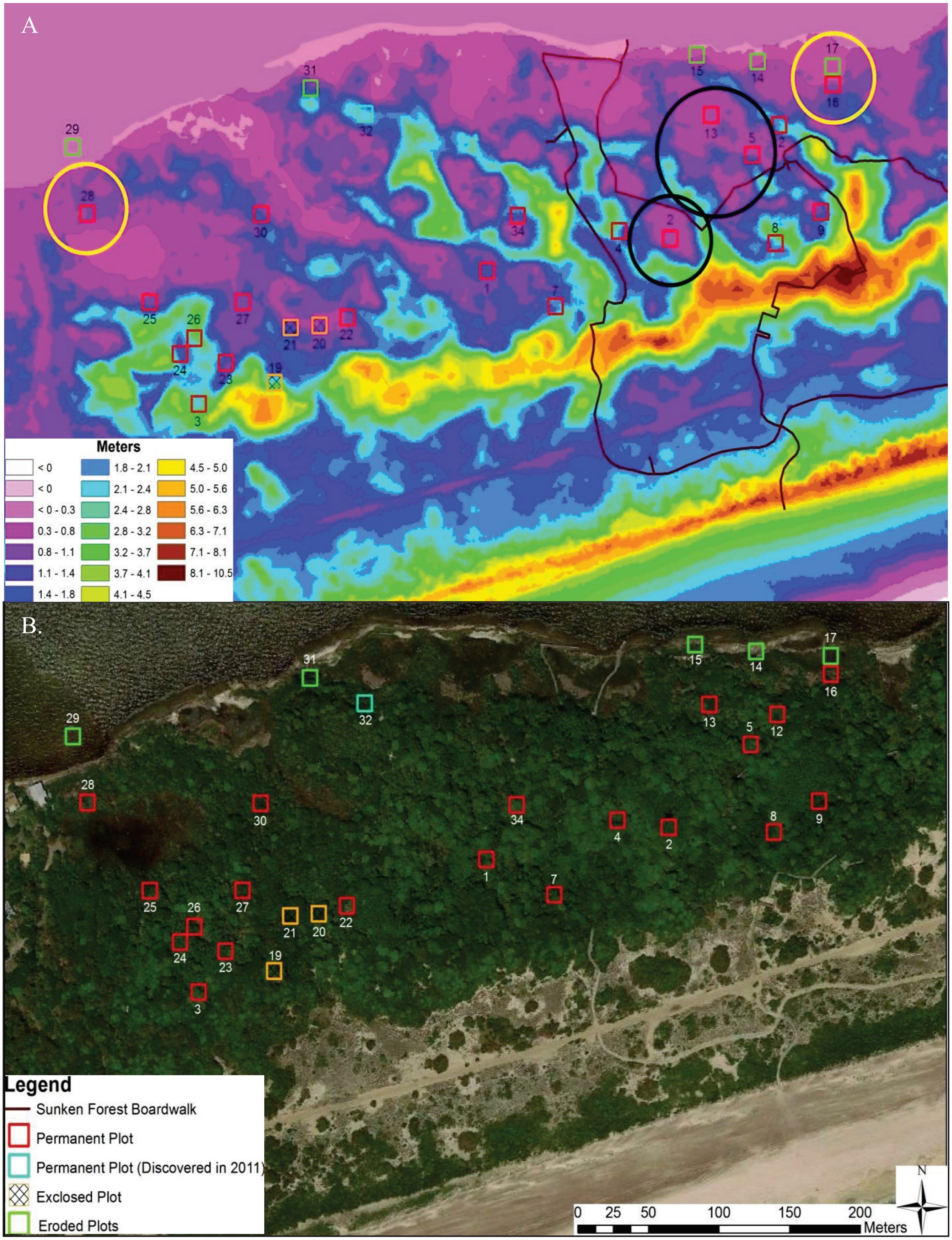

Figure 11. A. 2010 LiDAR image of the Sunken Forest B. Same area shown in 2014 aerial imagery. In image A yellow circles identify plots 16 and 28, these plots represent areas of the forest that were impacted by erosion. Black circles (in image A) identify plots 2, 5, and 13 represents lower elevated areas of the forest impacted by the thinning of the vadose zone.

Canopy gap dynamics

Similar to Forrester (2004), I examined canopy gap dynamics using plots along a number of transects. Twelve south/north transects were established within the Sunken Forest. To determine the location of the transects, a starting point was randomized along Burma Road. Burma Road is located outside the Sunken Forest, seaward of the secondary dune. Once a starting point was established, each south to north transect was laid out 50 m apart from one another (Forrester, 2004; Forrester and Leopold, 2005). Once on the transect, another starting point was randomized which signified the first 100 m^2 plot. Each plot following that random point was laid out 40 m apart from one another. Woody stems ≥ 3.0 cm diameter breast height (DBH) (1.5m height) were recorded by species in the entire 100 m^2 plot, shrub/saplings ≥ 1.0 m tall and < 3.0 cm DBH were be recorded within 5 random 1m x 10m quadrats. The percent cover, using Daubenmire cover class (Table 7), of all vascular plants < 1 m tall were recorded in 5 random 2 m x 1 m quadrats. If a canopy gap was encountered while walking the transect, a 100 m^2 plot was laid out within the gap and vegetation was surveyed using the same methods above (Runkle, 1990; Forester, 2004). Canopy gaps, were identified by a canopy gap maker, which was a down tree. In some cases the plots were shifted so that the plot was located under the gap. Typically every random point along the transect represented the southeast corner of the plot. This point along the transect was never moved but instead the corner was changed which in turn shifted the plot to a more representative sample. Out of the 30 plots in the 12 transects, 19 of them were within the closed canopy and 11 of them were in canopy gaps. I analyzed the difference in the density of canopy layer stems, density of saplings, density of shrubs, and

Table 7. Daubenmire cover class

Daubenmire cover class
0%
5-25%
26-50%
51-75%
76-95%
96-100%

percent cover of ground layer vegetation (only species that had a total percent cover >0.1%) using student t-tests.

Temperature/precipitation

Lastly, I examined differences in climate from when the plots were surveyed over the last half a century. This historic climate dataset was from the New York Division 4 Area (Coastal/Long Island), provided by National Oceanic and Atmospheric Administration (NOAA). Temperature, precipitation, and Palmers Drought Severity Index (PDSI) from 1950-2013 were used for this analysis.

Statistical software

JMP 9 (statistical package) was utilized for most of the statistical analysis; $\alpha < 0.05$ represents statistical significance and $\alpha < 0.1$ represents moderate significance. R statistical package was also used for the correspondence analyses seen throughout the chapter. All vascular plant nomenclature throughout this chapter follows (USDA, NRCS. 2014. The PLANTS Database (http://plants.usda.gov, 6 December 2014).

Results

Deer Exclosures

The amount of sapling and shrub recruitment within the exclosures was much greater than unexclosed (open) areas (Figure 12). The difference between the exclosed and open plots was apparent even with only 3 exclosed plots compared to the 20 open plots throughout the Sunken Forest (Table 8). Density was higher in exclosed plots for almost every species except *Prunus serotina* (black cherry). Additionally, *Baccharis halimifolia* (Groundsel) and *Myrica pensylvanica* (Northern bayberry) were only found outside the exclosures (Table 8).

Figure 12. Looking into an exclosure from the outside. Notice the bare forest ground outside the exclosure compared to the lush green forest understory within the exclosure.

Table 8. The density of stems in the sapling/shrub layer (≥ 1.0 meter in height and <3.0 cm DBH) in 3 exclosed plots vs. 20 open plots. Values are means ± standard errors. Data from permanent plots in the Sunken Forest in 2013.

Species	**Density (mean ± standard error) Individuals per plot**	
	Exclosed	**Open**
Amelanchier canadensis	70.0±37.64	0.35±0.21
Pinus rigida	1.0±1.0	0
Nyssa sylvatica	11.67±7.62	0.25±0.16
Vaccinium corymbosum	17.0±7.64	5.7±2.77
Ilex opaca	3.66±2.19	0
Aronia artbutifolia	27.33±19.06	0.05±0.05
Ilex glabra	18.33±18.33	0
Toxicodendron radicans (sapling)	0.67±0.67	0
Prunus serotina	4.0±3.06	8.7±4.6
Sassafras albidum	21.0±8.19	4.3±1.58
Gaylussacia baccata	15.0±8.39	12.6±8.43
Baccharis halimifolia	0	1.55 ±1.27
Myrica pensylvanica	0	8.0±4.4

While there were also vast differences in the density of saplings and shrubs in the exclosed plots vs the open paired plots there is no statistical significance (Figure 13). The lack of statistical significance was most likely due to the small sample size, but it may still be valid to accept that the differences are ecologically significant. Out of all of the plots in the forest, *I. opaca, Ilex glabra* (inkberry)*, Toxicodendron radicans* (poison ivy), and *Pinus rigida* (pitch pine) saplings/shrubs were only found in plots that were exclosed. One *Aronia arbutifolia* (red chokeberry), was found in an open plot, none of them present in any of the open paired plots. *Amelanchier canadensis* (shadblow) could be found in open plots but was minimal when compared to what was recruiting within the exclosures. *Sassafras albidum* (sassafras)*, Nyssa sylvatica* (black gum)*,* and *Vaccinium corymbosum* (highbush blueberry) also had higher densities within the exclosures then in the open paired plots. There was no difference in density between the open plots and exclosed paired plots for *P. serotina.* Lastly, *Gaylussacia baccata* (Black huckleberry) was the only species that was higher in the open plots vs exclosed paired plots (Figure 13).

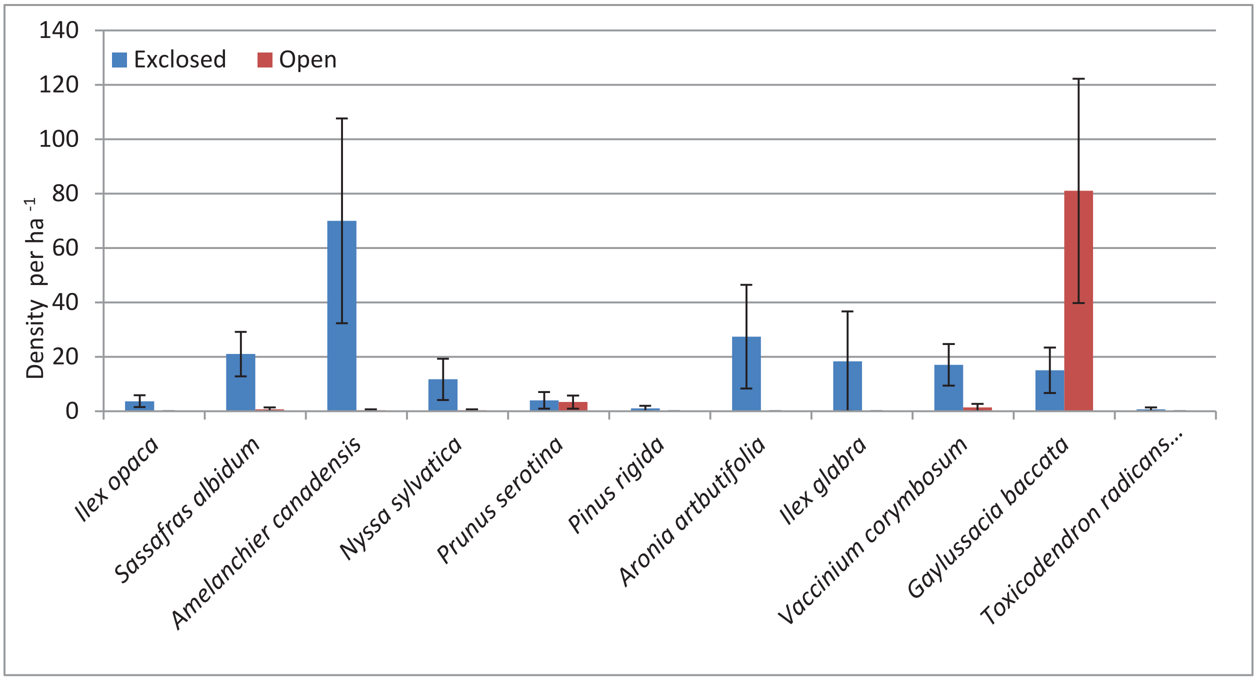

Figure 13. The density of individuals in the sapling/shrub layer (≥ 1.0 meter in height and<3.0 cm DBH) in the 3 exclosed plots vs. 3 open plots. Error bars show standard error. Levels not connected by same letter are significantly different. Data from permanent plots in the Sunken Forest in 2013.

When examining importance values of saplings (Figure 14), *I. opaca*, the most important component within the canopy of the Sunken Forest, was significantly higher within the exclosed plots compared to the open paired plots (*t* = -2.83, *p* = 0.0527). While it is not statistically significant, importance value data also shows that *P. serotina* was thriving outside the exclosures (*t* = 1.58, *p* = 0.2472) (Figure 14).

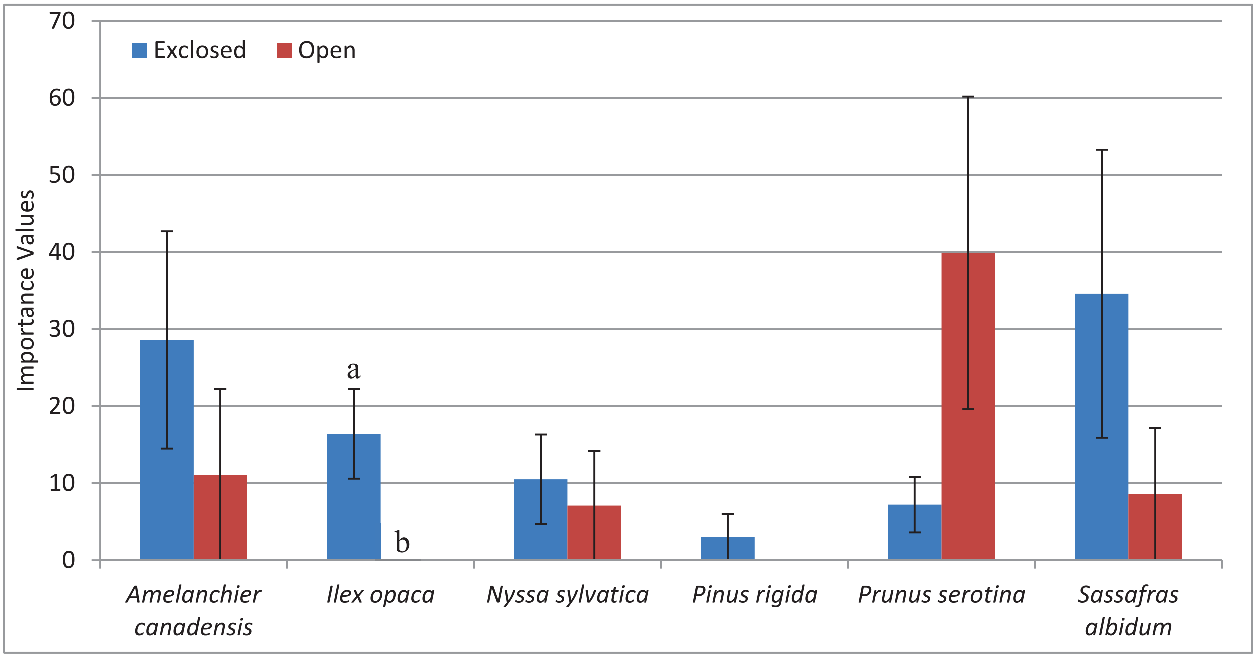

Figure 14. Importance values for saplings (species that growing into the canopy) (≥ 1.0 meter in height and<3.0 cm DBH) in the 3 exclosed plots vs. 3 open plots. Error bars show standard error. Levels not connected by same letter are significantly different. Data from permanent plots in the Sunken Forest in 2013.

The total percent cover of ground layer vegetation was higher in the exclosed plots (Mean = 22.9%, SE = ±2.4%) than in the open paired plots (17.4±2.4%) (*t* = -4.53, *p*=0.1096). *Trientalis borealis* (star flower) and *A. arbutifolia* had significantly higher percent cover in the exclosed plots than in the open plots (*t* = -4.53, *p*<0.0001 and *t* = -3.81, *p*=0.0006*,* respectively) (Figure 15). While it was not statistically significant it is worth noting that both *M. canadense* and *Polygonatum biflorum* (Solomon's seal) were only found in the exclosed plots. In fact, the exclosures were the only place *P. biflorum* was found in the entire forest. *N. sylvatica* and *G.*

baccata were the only species that was significantly lower in the exclosed plots compared to the open plots (t = 2.28, p = 0.0272 and t = 2.78, p = 0.0089, respectively) (Figure 15).

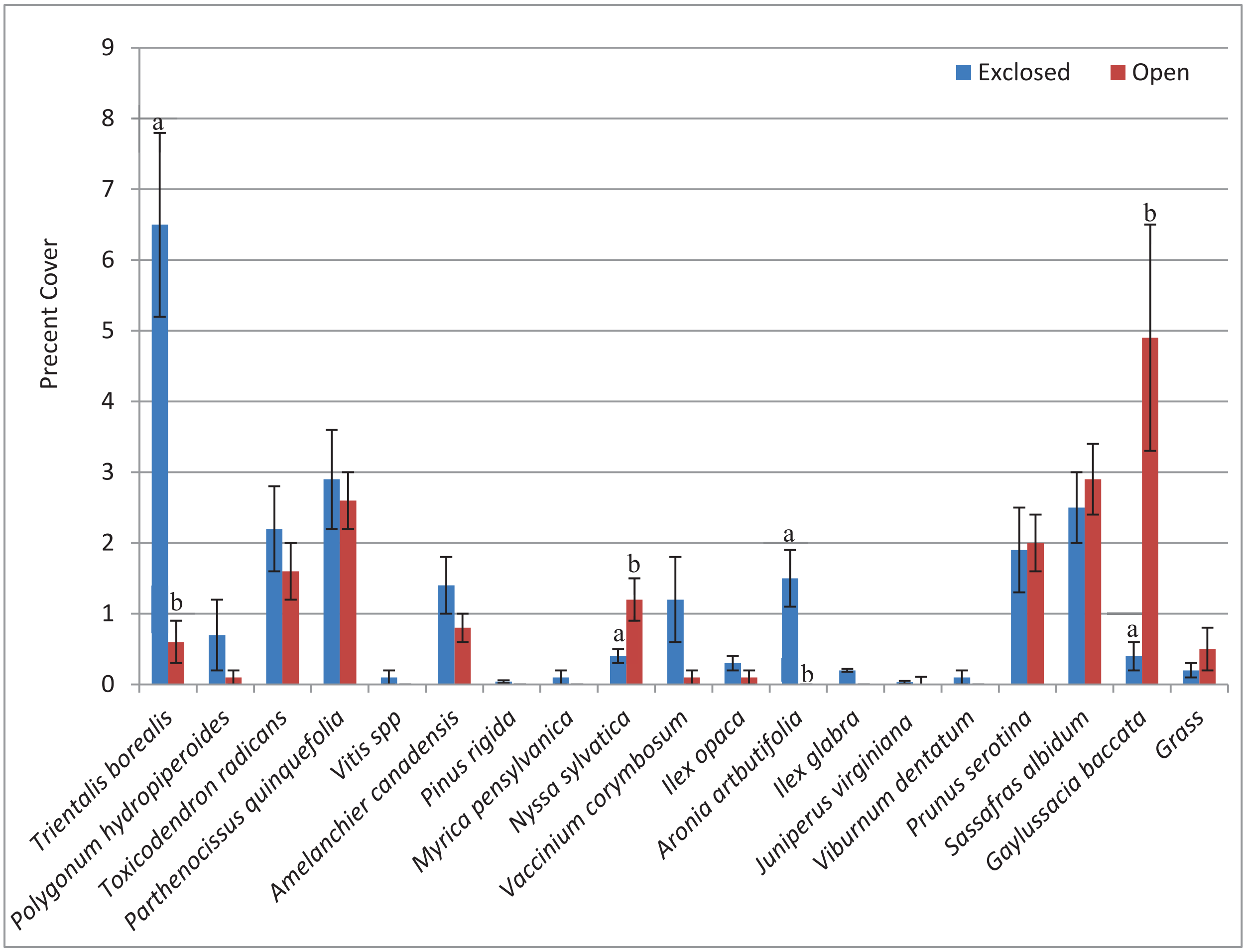

Figure 15. Percent cover of herbs, lianas, and woody species in the ground layer (<1.0 meter in height) in the 3 exclosed plots vs. 3 open plots. Error bars show standard error. Levels not connected by same letter are significantly different. Data from permanent plots in the Sunken Forest in 2013.

The total woody species density in the ground layer was higher in the exclosed plots (10.2±3.0m^2) vs open plots (7.7±2.9m^2) (t = 0.59, p=0.5573). *A. arbutifolia* was the only species that was significantly higher (t=-3.42, p=0.0046) in the exclosed plots, while *N sylvatica* was significantly higher in open plots (t =2.26, p = 0.0298) (Figure 16). For seedlings that were ≥2 years old, there were no significant differences in density between exclosed plots (7.8±1.4) and open plots (7.9±1.1) (t = 0.03, p = 0.9736). While total density did not differ, species composition did differ. *A. arbutifolia* and *I. opaca* showed significantly higher densities (t = -

3.19, $p = 0.0032$ and $t = -2.33$, $p = 0.0260$, respectively) in the exclosed plots than in the open plots (Figure 17). While, *S. albidum* and *N. sylvatica* had significantly higher densities ($t = 2.71$, $p = 0.0097$ and $t = 2.47$, $p = 0.0184$, respectively) in the open plots than the exclosed plots (Figure 17). Lastly, there was a significant difference in percent cover within plots covered in brier tangles and/or branches from down trees compared to being open at (11.7±2.4%) and (6.0±1.3%), respectively ($t = -2.09$, $p = 0.0501$).

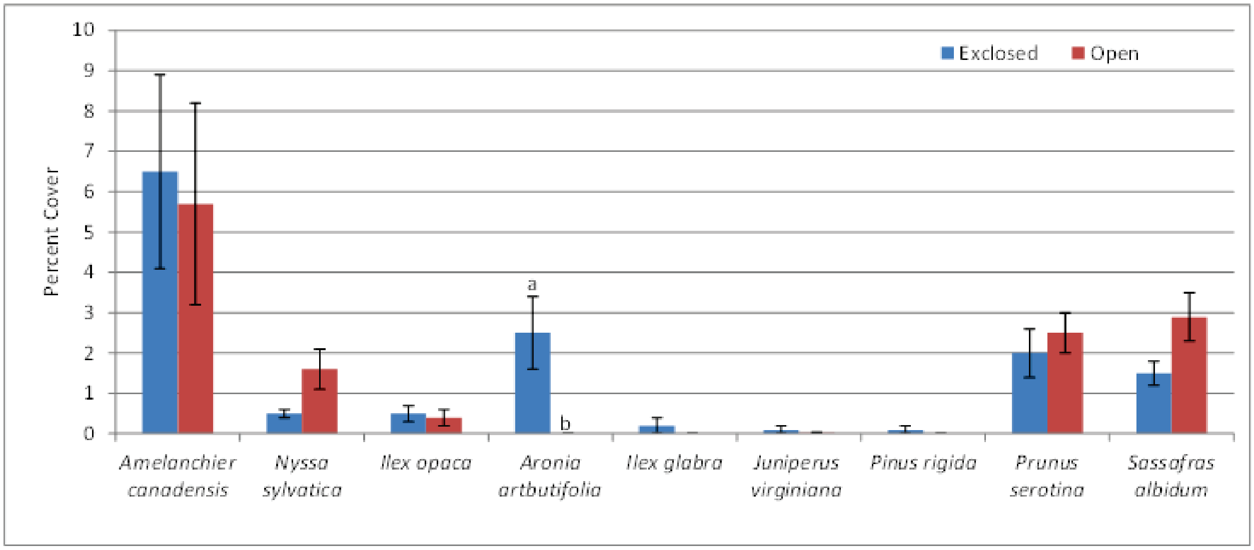

Figure 16. Woody species density in the ground layer (<1.0 meter in height) in the 3exclosed plots vs. 3 open plots.
Error bars show standard error. Levels not connected by same letter are significantly different. Data from permanent plots in the Sunken Forest in 2013.

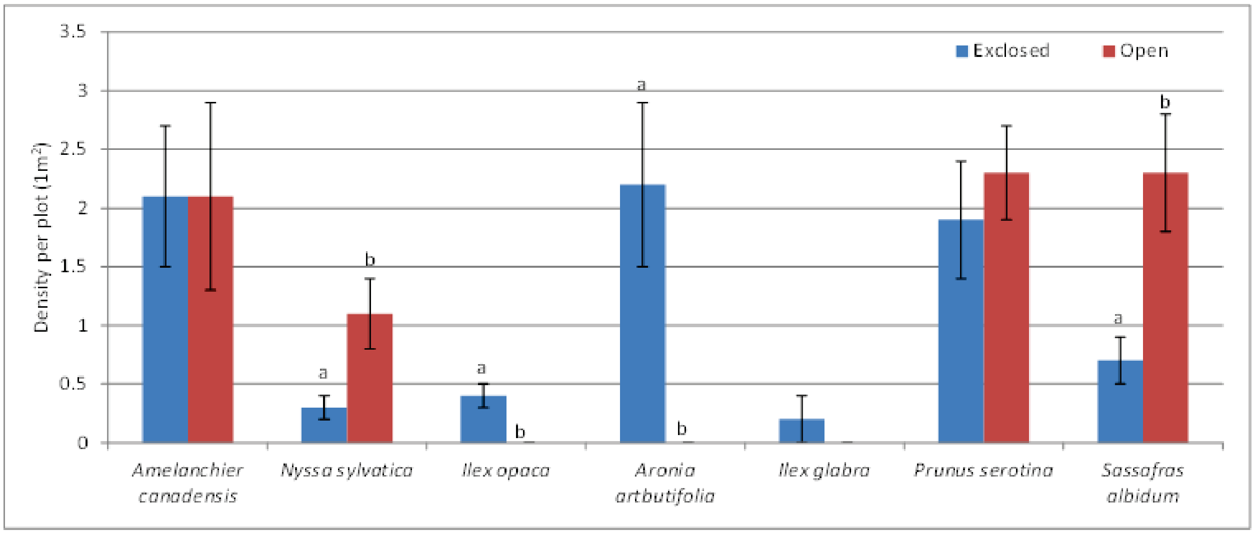

Figure 17. Woody species density ≥2 years that are in the ground layer (<1.0 meter in height) in the 3 exclosed plots vs. 3 open plots.
Error bars show standard error. Levels not connected by same letter are significantly different. Data from permanent plots in the Sunken Forest in 2013.

Erosion/Sea Level Rise

The original area of research in the Sunken Forest, established in 1967 by Dr. Art, was approximately 39.5 acres. Since then, ≈ 4.5 acres has been lost due to erosion, with ≈ 2 acres lost in the last 10-15 years. Separate from the 5 “impacted plots”, another 5 of the original permanent vegetation plots from 1967 have been lost due to bayside erosion. The loss of these plots can give another perspective of how much the Sunken Forest has eroded. Plots 14, 15, 17, and 31 are all located on the edge of the bay shoreline which are now monocultures of *Phragmites* and plot 29 is now located in the Great South Bay. These 10 plots, both the 5 “impacted plots” and the 5 plots already lost, once represented old-growth holly maritime forest (Art, 1976). Approximately, 5 acres of the old-growth holly maritime forest has been lost over the last half a century due to: 1.) The sheer loss of habitat from erosion and sea level rise; 2.) Areas adjacent to the bay changing from what was once old-growth holly forest to stands of *Phragmites*; 3.) The lower elevated areas within the interior of the forest converting to wetlands due to the rise in sea level and/or other shifts in the environment.

Trees ≥ 10 cm DBH:

I. opaca, *A. canadensis*, and *S. albidum* experienced a negative rate of change in the plots located at both low elevations and adjacent to the bay (plots 2, 5, 13, 16, and 28; Figure 18). This shows that the recruitment of larger trees within the canopy were not high enough to offset the mortality occurring in these areas. For all the other plots (15 “forested plots”), *I. opaca* and *S. albidum* did not have high (either positive or negative) rates of change while *A. canadensis* still seemed to have a high negative rate of change (Figure 19). The recruitment of larger *I. opaca* and *S. albidum* trees within the canopy are just high enough to offset mortality in these areas. *A. canadensis* continues to have high mortality rates with little to no recruitment throughout the study site. Finally, *N. sylvatica* did not have high (either positive or negative) rates of change for either the "impacted plots" or "forested plots".

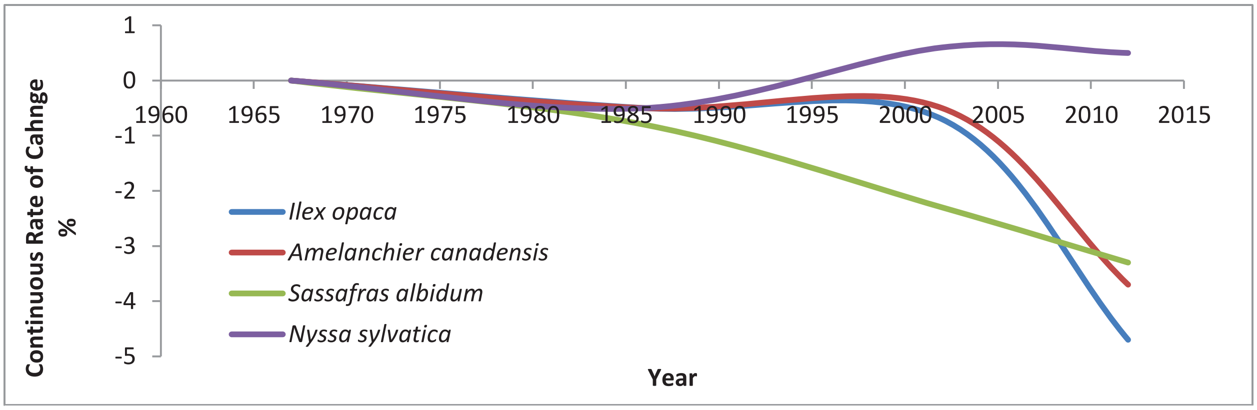

Figure 18. Rate of change in the 4 most common canopy trees species that are ≥ 10.0 cm DBH in the 5 "impacted plots" (plots 2, 5, 13, 16, and 28). Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)).

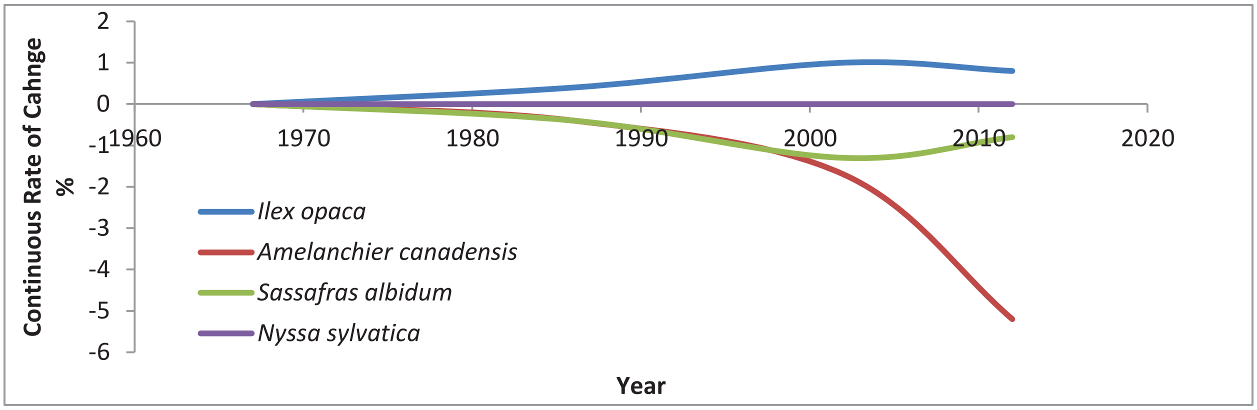

Figure 19. Rate of change in the 4 most common canopy trees species that are ≥ 10.0 cm DBH in the other 15 plots "forest plots". Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)).

Trees ≥ 3 cm DBH:

Out of the 4 most common canopy constituents, *I. opaca*, *A. canadensis*, and *S. albidum* all showed declines in density within the 5 "impacted plots" over the last half a century. *N. sylvatica* is the only species that has not changed, within the impacted plots. When looking at the data from the 15 "forested plots", *I. opaca*, *S. albidum,* and *N. sylvatica* all showed consistent densities over the last 45 years, while *A. canadensis* still shows a decline (Figure 20; Figure 21).

Overall, the five impacted plots also show how much they contribute to the decline in the density of canopy species (≥3.0 cm DBH) over the last 45 years (Table 9).

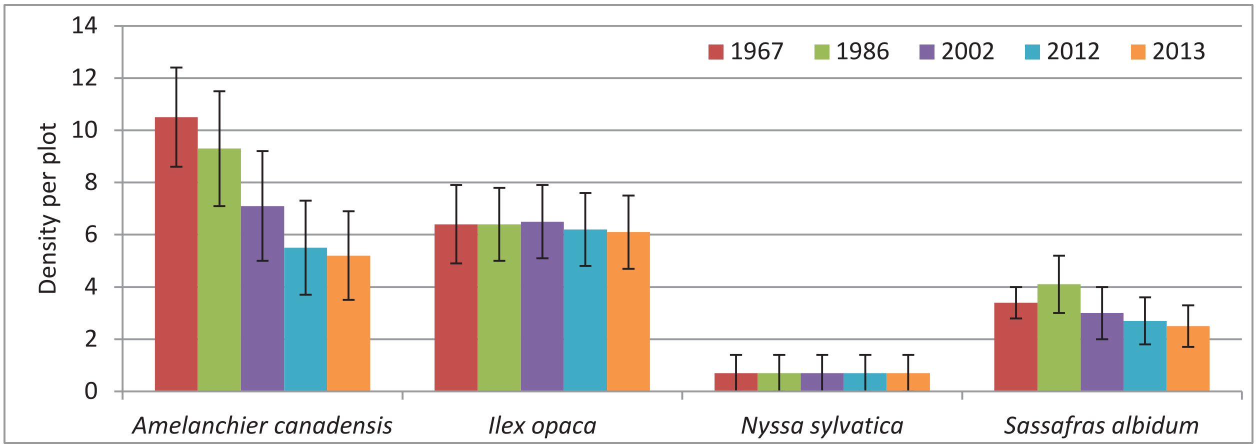

Figure 20. Density of canopy stems (>3.0 cm DBH) in the maritime forest plots. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)). Error bars show standard error.

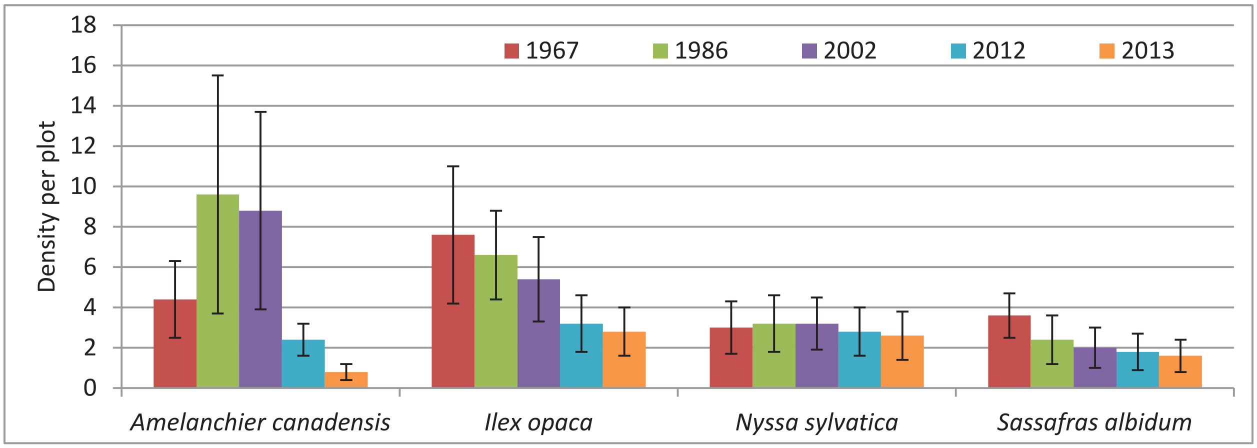

Figure 21. Density of canopy stems (>3.0 cm DBH) in the impacted plots. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)). Error bars show standard error.

Table 9. Density of the 4 most common canopy species canopy stems (>3.0 cm DBH) in the impacted plots. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)). Levels not connected by same letter are significantly different. (Pre Hurricane Sandy*, Post Hurricane Sandy**)

Total of the *Ilex opaca, Sassafras albidum, Amelanchier canadensis,* and *Nyssa sylvatica*	DENSITY Stems per plot 1967	1986	2002	2012*	2013**
Maritime forest plots	20.3±3.1	19.9±2.5	16.7±2.2	14.5±1.8	13.9±1.8
Impacted plots	18.6±2.4^{ab}	21.8±4.2^{a}	19.4±3.5^{a}	10.2±1.2^{bc}	7.8±1.6^{c}

Sapling/Shrub Layer:

Erosion and sea level rise are also impacting the sapling/shrub layer. Data from the most recent surveys show that sapling densities were extremely low within the 5 "impacted plots" (Figure 22). The 5 "impacted plots" had a presence of *I. opaca, A. canadensis,* and *N. sylvatica* in 1967. In 1986, there was no presence of *I. opaca* but *A. canadensis* and *N. sylvatica* were still present. By 2002, there was very minimal recruitment overall within these plots (Figure 22). The long term data shows that in the other 15 "forested plots", there is a decrease of *I. opaca* and *A. canadensis* with an increase in *P. serotina* and *S. albidum*. It is worth noting that *N. sylvatica* was never an important component within these higher elevated areas ("forested plots").

Currently, there is no recruitment of saplings in the 3 plots that represent low elevation (plots 2, 5, and 13). When these three plots were paired with the closet plots at a higher elevation there was a significant differences with (0 sapling per ha^{-1}) in low elevated plots and (mean = 20, SE = ±7 sapling per ha^{-1}) in the higher elevated paired plots ($t = 2.89$ $p = 0.0501$). It should be noted that the saplings in the elevated plots were mostly comprised of *P. serotina* and *S. albidum*, respectively.

Data from the most recent surveys also showed that shrub densities were extremely low within the 5 impacted plots (Figure 23 and 24). Species that were once abundant in the forest, i.e. *A. arbutifolia*, *G. baccata*, and *I. glabra* have drastically declined in these impacted sites in the lower elevated plots, while *V. corymbosum* did not change. Other species, such as, *M. pensylvanica* and *B. halimifolia* are increasing in plots closer to the bay. A correspondence analysis shows that the presence *B. halimifolia* (BAHA) and *M. pensylvanica* (MYPE) were most associated with the change in habitat in areas adjacent to the bay, represented by plots 16 and 28 (Figure 25).

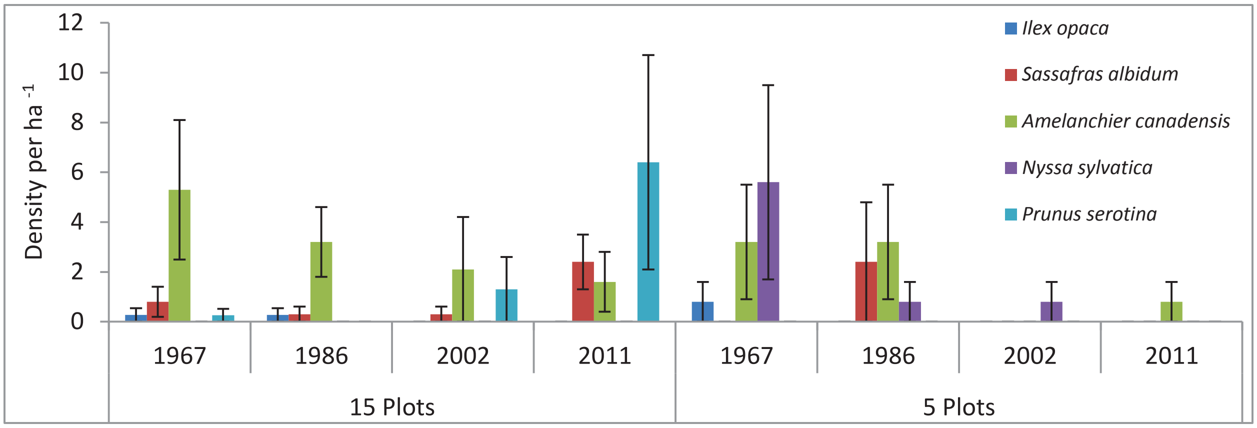

Figure 22. The density of individuals in saplings (species that growing into the canopy) (≥ 1.0 meter in height and<3.0 cm DBH). Data is separated between the 15 maritime forest plots vs. 5 "impacted" plots. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004). Error bars show standard error. Levels not connected by same letter are significantly different (by species).

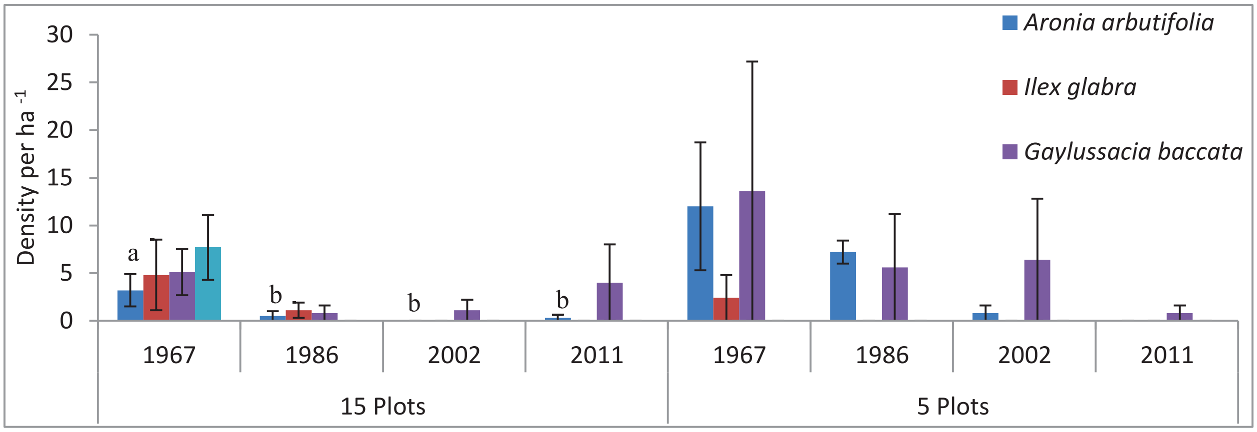

Figure 23. Density of individuals in the shrub layer (≥ 1.0 meter in height and<3.0 cm DBH). Data is separated between the 15 maritime forest plots vs. 5 "impacted" plots. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004). Error bars show standard error. Levels not connected by same letter are significantly different (by species).

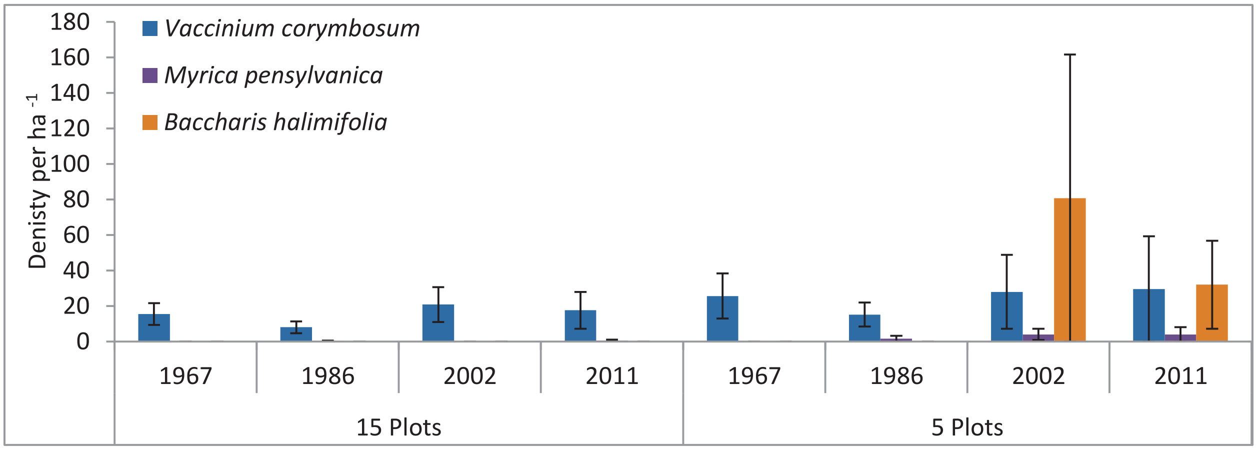

Figure 24. Density of individuals in the shrub layer (≥ 1.0 meter in height and<3.0 cm DBH). Data is separated between the 15 maritime forest plots vs. 5 "impacted" plots. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004). Error bars show standard error.

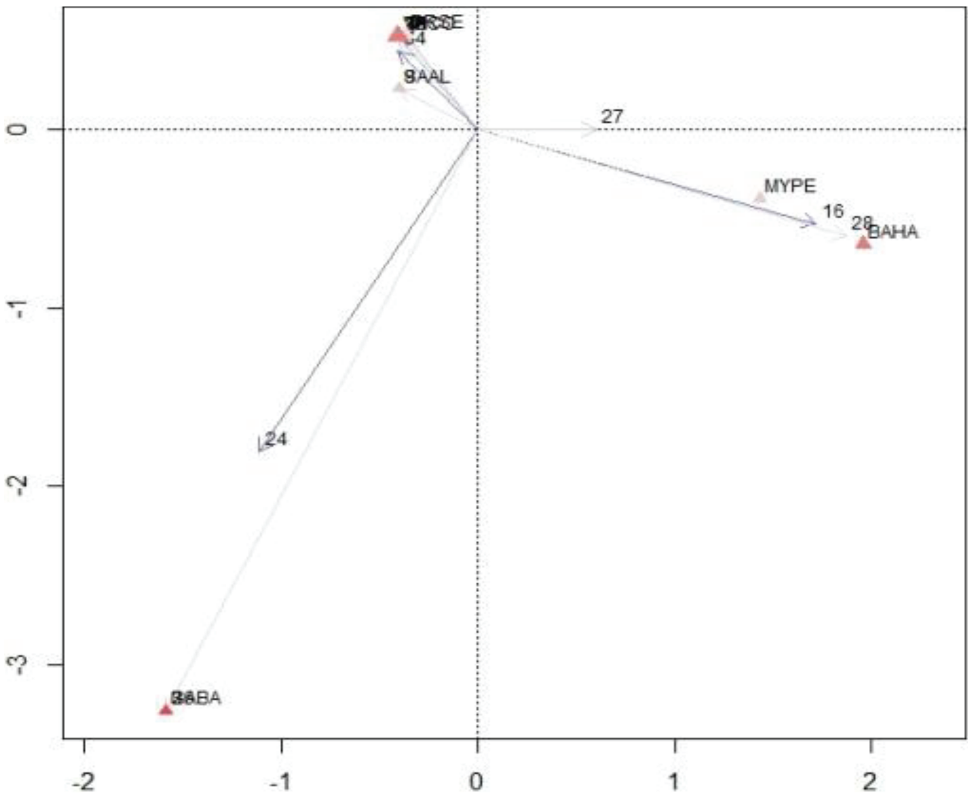

Figure 25. Plots 16 and 28 are the two “impacted” plots that are most associated with changes in the forest areas adjacent to the bay. BAHA=*Baccharis halimifolia*, MYPE= *Myrica pensylvanica*. Data from permanent plots in the Sunken Forest in 2013.

Ground Layer:

Using ground layer vegetation as a primary indicator, a correspondence analysis also shows how the Sunken Forest has changed as a result of this erosion and sea level rise (Figure 26). Plot 16 and 28 were most associated with *P. australis* (Phrag) and plots 2, 5, and 13 were most associated with *Polygonum hydropiperoides* (swamp smartweed) (POHY) (Figure 26). *P. australis* was not present in plots 16 and 28 in 1967 but started to appear in these plots by 1986 and has significantly increase from 1967 to 2013 (t = 2.65, p = 0.0331) (Figure 27). *P. hydropiperoides* was not present in plots 2, 5, and 13 in 1967 or 1986 (Figure 28). It appeared in these plot in 2002 and significantly increased in 2013 (1967 and 1986 to 2013; t = 2.03, p = 0.0010) (2002 to 2013; t = 2.03 p = 0.0069).

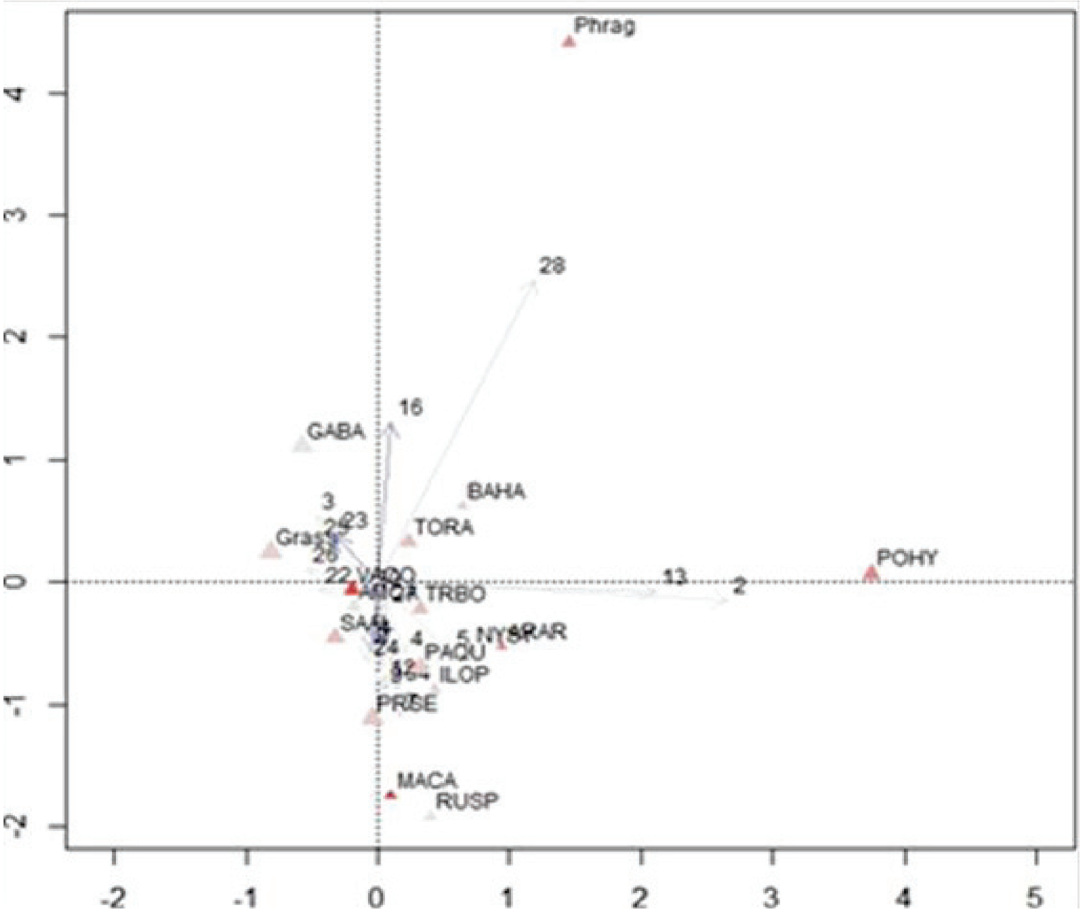

Figure 26. Plots 16 and 28 are the two “impacted” plots that are most associated with changes in the forest areas adjacent to the bay. plots 2, 5, and 13. The three “impacted” plots that are most associated with changes in the low depressions within the forest. Phrag =*Phragmites*, POHY= *Polygonum hydropiperoides.* Data from permanent plots in the Sunken Forest in 2013.

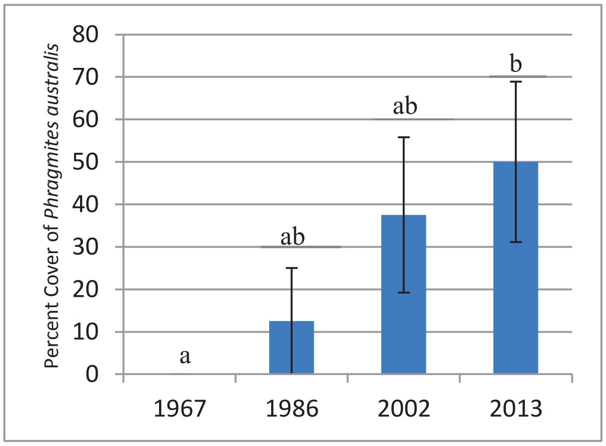

Figure 27. Percent cover of *Phragmites australis* in plots 16 and 28. The two “impacted” plots that are most associated with changes in the forest areas adjacent to the bay. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004). Error bars show standard error. Levels not connected by same letter are significantly different.

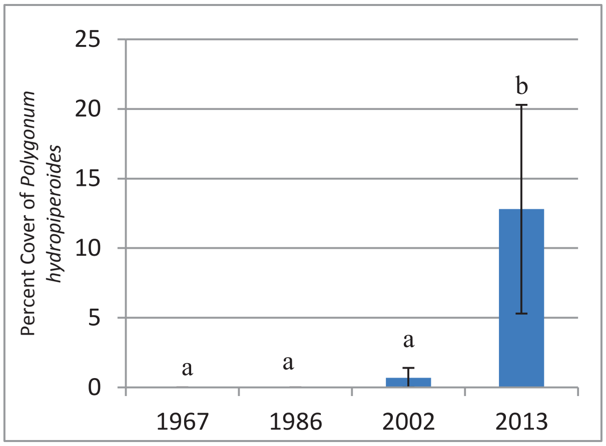

Figure 28. Percent cover of *Polygonum hydropiperoides* in plots 2, 5, and 13. The three “impacted” plots that are most associated with changes in the low depressions within the forest Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004). Error bars show standard error. Levels not connected by same letter are significantly different.

Storms

Canopy Layer:

There was a slight decline in the basal area and densities of canopy layer stems (≥ 3.0 cm DBH) in the Sunken Forest the summer following Hurricane Sandy and subsequent winter storms. Overall basal area fell from (Mean = 33.3 m^2 ha^{-1}, SE = ±2.8 m^2 ha^{-1}) to (31.8±2.9 m^2 ha^{-1}) (Figure 29) and densities of canopy layer stems from (1390±147 ha^{-1}) to (1275±151 ha^{-1}) (Figure 30). However, these declines were not significantly significant. Twenty-one canopy layer stems died in the permanent vegetation plots, which accounted for 7.6% of the canopy stems overall (Table 10).

Table 10. Number and percent of canopy layer stems (≥3.0 cm DBH) that died from Hurricane Sandy and subsequent winter storms. Data from permanent vegetation plots in the Sunken Forest from 2012 (pre-Sandy) vs. 2013 (post-Sandy).

SPECIES	No. STEMS 2012-2013 ≥3 cm DBH	MORTALITY (%)
Amelanchier canadensis	94-83	11.7
Ilex opaca	109-106	2.8
Nyssa sylvatica	15-14	6.7
Pinus rigida	3-3	0
Prunus serotina	4-3	25
Quercus spp.	2-2	0
Sassafras albidum	50-45	10

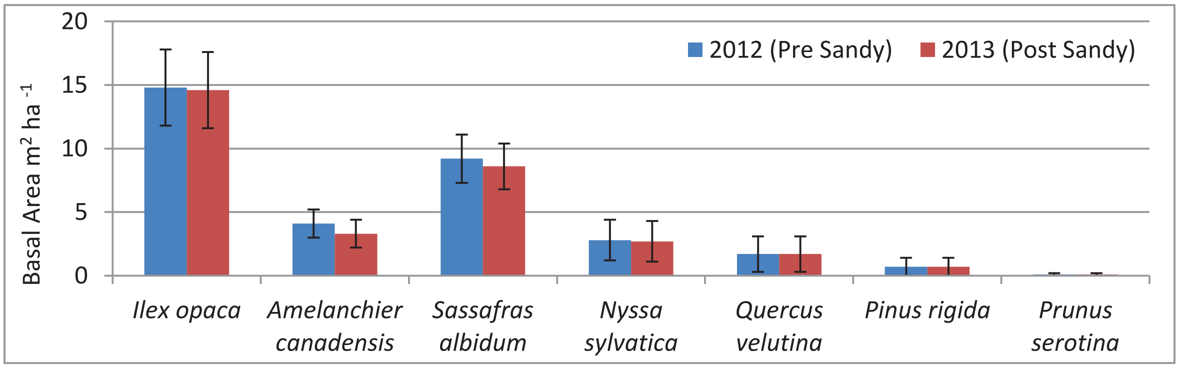

Figure 29. Basal area of canopy layer stems (≥3.0 cm DBH). Data from permanent vegetation plots in the Sunken Forest from 2012 (pre-Sandy) vs. 2013 (post-Sandy). Error bars show standard error.

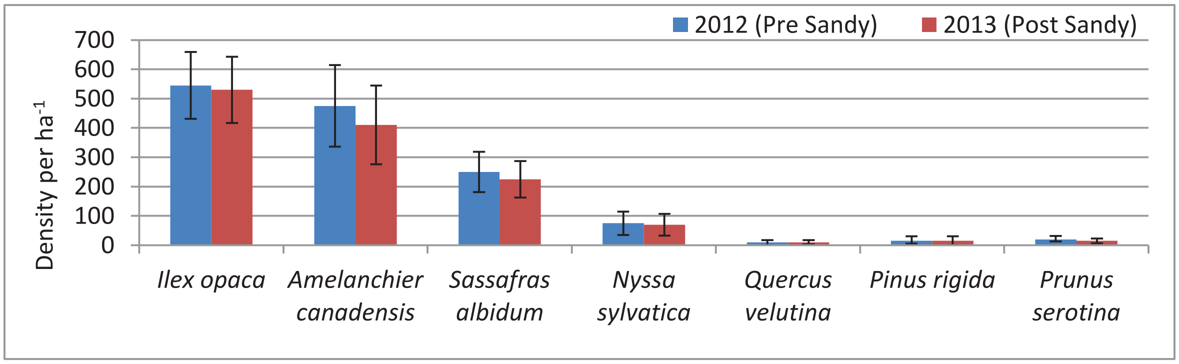

Figure 30. Density of canopy layer stems (≥3.0 cm DBH). Data from permanent vegetation plots in the Sunken Forest from 2012 (pre-Sandy) vs. 2013 (post-Sandy). Error bars show standard error.

Sapling/Shrub Layer:

There was not a large difference in the sapling layer the summer following Hurricane Sandy and subsequent winter storms. *A. canadensis* declined while there was an increase in both *S. albidum* and *P. serotina* (Figure 31).

There also was not a large difference in the shrub layer following Hurricane Sandy and subsequent winter storms. *B. halimifolia* slightly declined and *M. pensylvanica* slightly increased (Figure 32).

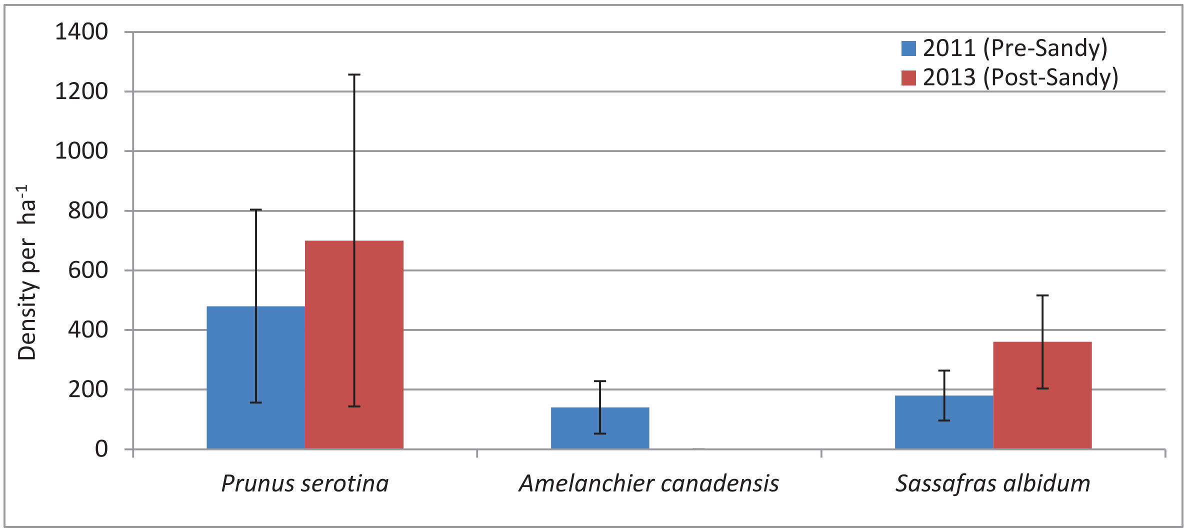

Figure 31. The density of individuals in saplings (species that growing into the canopy) (≥ 1.0 meter in height and<3.0 cm DBH). Data from permanent vegetation plots in the Sunken Forest from 2012 (pre-Sandy) vs. 2013 (post-Sandy). Error bars show standard error.

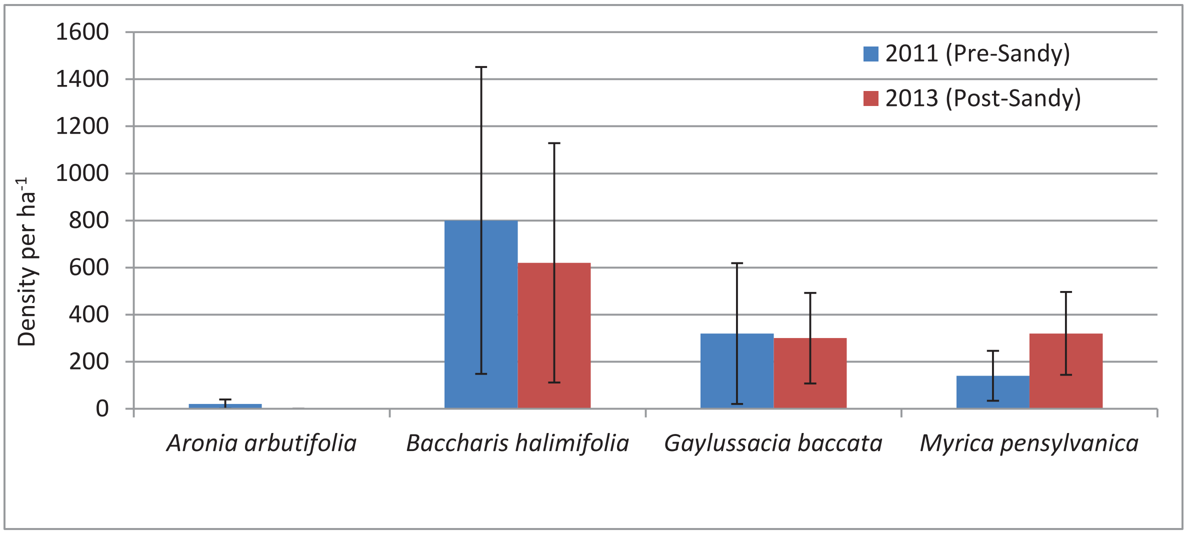

Figure 32. The density of individuals of shrubs (≥ 1.0 meter in height and<3.0 cm DBH). Data from permanent vegetation plots in the Sunken Forest from 2012 (pre-Sandy) vs. 2013 (post-Sandy). Error bars show standard error.

Canopy Gap Dynamics

Canopy Layer:

When looking at the 30 plots (both open and closed canopy) together the densities, basal areas, and importance values are similar to what was seen in the permanent plots from the 2011-2012 dataset. There were differences in species composition once the data were split between the closed and open canopy plots (Figure 33). *I. opaca, A. canadensis*, and *N. sylvatica* were all higher in the closed canopy compared to the open. The opposite trend occurred with *P. serotina* and *S. albidum*, both slightly increased in canopy gaps (Figure 33).

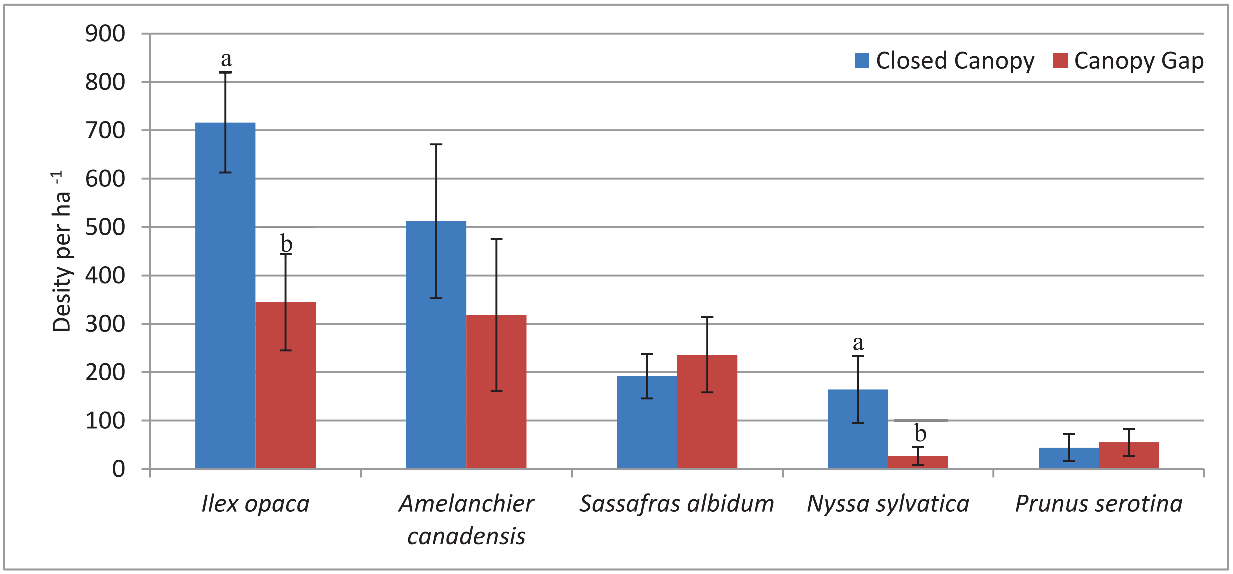

Figure 33. Density of canopy layer stems (≥3.0 cm DBH) in closed canopy plots vs. plots in canopy gaps. Data from transect plots collected in 2011. Error bars show standard error. Levels not connected by same letter within the same species are significantly different ($p < 0.05$).

Sapling Layer:

P. serotina, *S. albidum*, *A. canadensis*, and *N. sylvatica* saplings were all present within the transect plots. *I. opaca* remained to be absent from the transect plots as well. *P. serotina* was by far the most dominant sapling in both the closed and open canopy plots followed by *S. albidum*. *P. serotina*, *S. albidum*, and *A. canadensis* were all higher in canopy gaps vs closed canopy while *N. sylvatica* was only found in closed canopy plots (Figure 34).

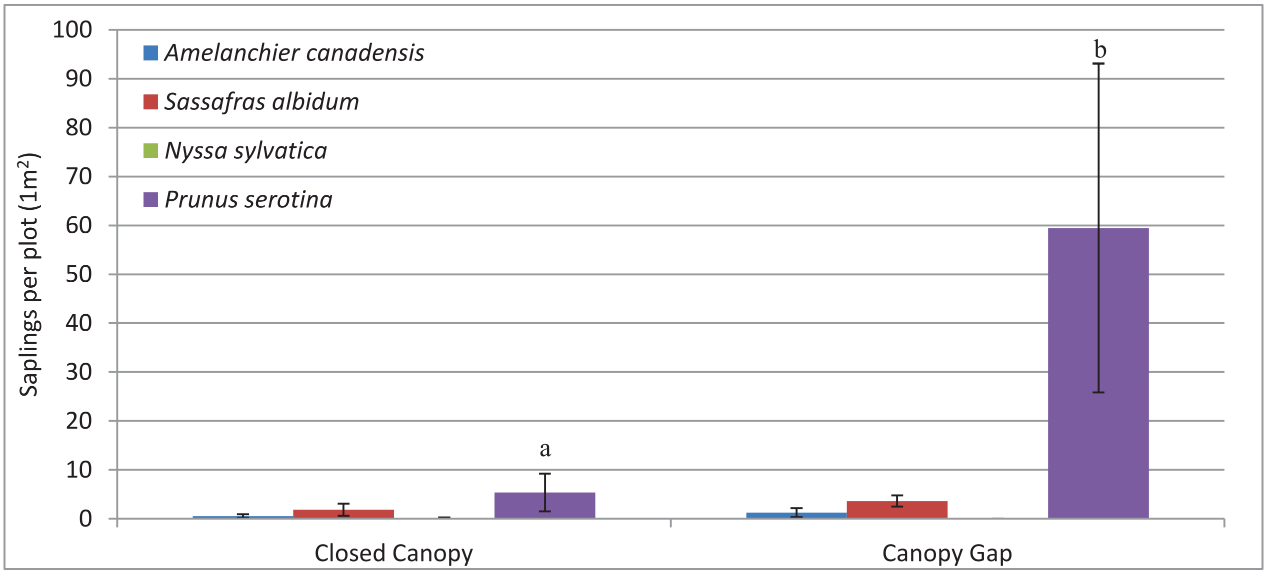

Figure 34. Density of (species that growing into the canopy) (≥ 1.0 meter in height and<3.0 cm DBH) in closed canopy plots vs. plots in canopy gaps. Data from transect plots collected in 2011. Error bars show standard error. Levels not connected by same letter within the same species are significantly different ($p < 0.05$).

Ground Layer:

The ground layer was also higher in canopy gaps compared to closed canopy at (Mean = 25.6%, SE = ±2.4%) and (20.8±1.2%), respectively. Although, some species had slightly greater percent cover within the canopy gaps, the only species that were noticeably more abundant in the canopy gap than in closed canopy were *P. serotina, S. albidum,* and sedge/grass (Figures 35; Figure 36).

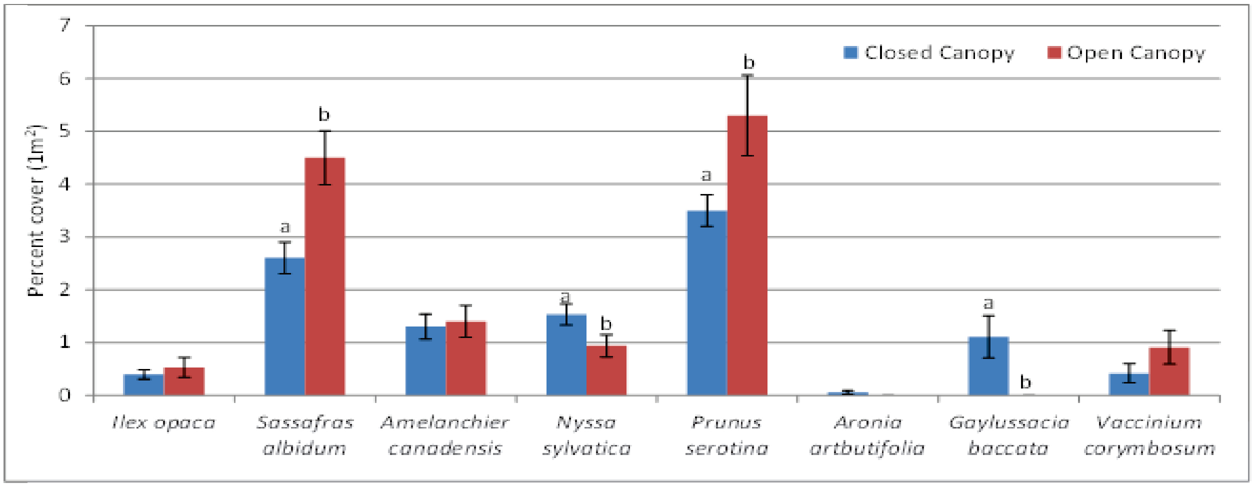

Figure 35. Percent cover of woody species in the ground layer (<1.0 meter in height) in closed canopy plots vs. plots in canopy gaps. Data from transect plots collected in 2011. Error bars show standard error. Levels not connected by same letter within the same species are significantly different ($p < 0.05$).

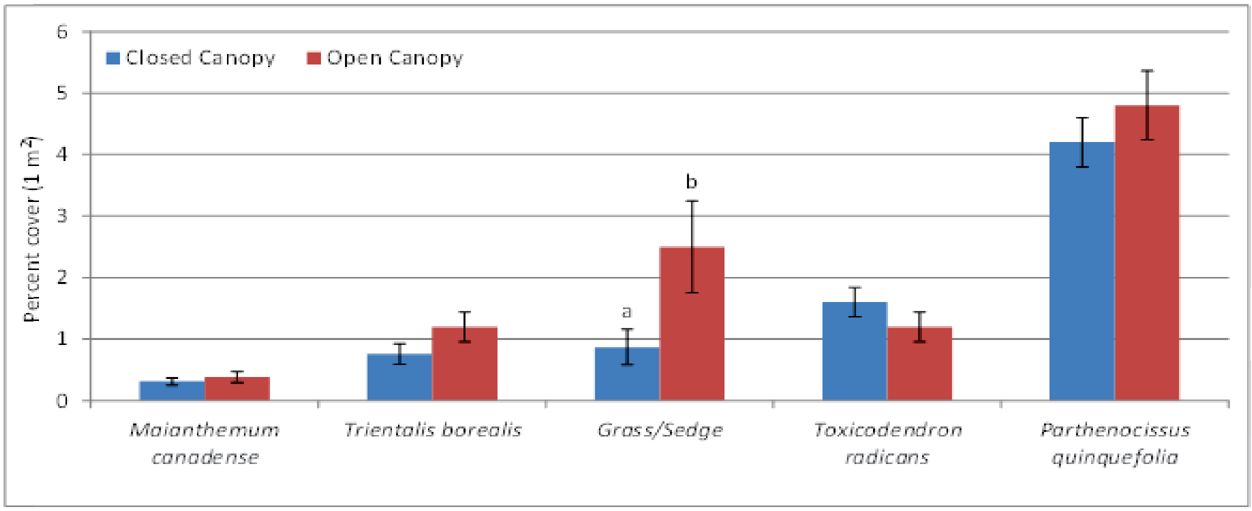

Figure 36. . Percent cover of herbs and lianas in the ground layer (<1.0 meter in height) in closed canopy plots vs. plots in canopy gaps. Data from transect plots collected in 2011. Error bars show standard error. Levels not connected by same letter within the same species are significantly different ($p < 0.05$).

Climate:

Climate data shows that the temperature has been slightly increasing since the first survey in 1967 but 2013 seemed to be a cooler year compared to temperatures over the last decade but was still warmer than the 1967 and 1986 survey years. The Palmer Drought Severity Index and precipitation data shows that 2011 was the wettest year followed by 1967. The drier years: 1986, 2002, 2012, and 2013 were all similar, ranking as mild drought year.

Discussion

The changes in the vegetation observed over the last 50 years have been due to a mixture of different ecological pressures and cannot be rooted to one factor alone. Changes within a forest are expected but the trajectories of these changes are a product of new ecological drivers introduced to the forest within the last half a century. In this discussion, I will describe each of the major pressure that are driving the changes observed over the last 50 years.

The Role of White-tailed Deer Herbivory

The impacts of white-tailed deer on vegetation has been well documented across the Midwest and eastern North America (Whitney, 1984; Tilghman, 1989; Trumbull et al., 1989; Healy, 1997; Russell et al., 2001; Rooney, 2001; Horsley, 2003; Rooney and Gross, 2003; Côté, et al., 2004; Baiser et al., 2008; Martin et al., 2010; Abrams et al., 2012; McShea, 2012)

Even the famous book, A Sand County Almanac, Aldo Leopold documented browsing impacts in areas where wolves were being extirpated from the land. “I have watched the face of many a newly wolfless mountain, and seen the south-facing slopes wrinkle with a maze of new deer trails. I have seen every edible bush and seedling browsed, first to anaemic desuetude, and then to death. I have seen every edible tree defoliated to the height of a saddlehorn.” (Leopold, 1949).

The Sunken Forest first started to experience issues with white-tailed deer herbivory in the early to mid-1980’s following the rapid increase in the population (Art, 1987; Forrester, 2004; Underwood, 2005). O’Connell (1989), reported that white-tailed deer densities increased from 12 deer/km^2 in 1983 to 25 deer/km^2 in 1988. By the mid-1990’s, deer population estimates reached 80 deer/km^2 (Underwood, 2005). This was also around the time a deer immunocontraceptive research project began in 1993. This research focused on how effective immunocontraceptives, specifically porcine zona pellucida (PZP), were in managing the population. This project continued until 2009 and data showed that it was effective in reducing the population by 58% in the western communities of Fire Island, specifically Kismet to Lonleyville (Underwood, 2005; Rutberg and Naugle, 2008; Underwood et al., 2011 (unpublished)). Nonetheless, the impacts of white-tailed deer on vegetation in the Sunken Forest and elsewhere on Fire Island are still apparent and the population is still thought to be too high (per communication Seashore staff). Once the PZP research ended the park started to develop a white-tailed deer management plan in 2010. This management plan specially focuses on vegetation impacts in the Sunken Forest and other rare-maritime habitats on the island. This clearly shows how valuable this resource is to the Seashore.

The irruption of white-tailed deer on Fire Island has led to declines in herbs, seedlings, and saplings in the Sunken Forest. Data collected from the exclosures supports many of the trends seen in the long term analysis. Data collected in 2011-2013 seems to support previous studies in the Sunken Forest, with data analysis indicating herbivory impacts in the Sunken Forest are still occurring. The 1967 dataset gave a good indication of what the Sunken Forest was like when the Seashore was established in 1964 and before white-tailed deer herbivory became an issue on Fire Island. This has been identified as the desired condition of the forest per Fire Island National Seashores enabling legislation which states that the “area known as the Sunken Forest Preserve shall be preserved from bay to ocean in as nearly its present state as possible” (PL 88-587). Management of the white-tailed deer population could benefit the Sunken Forest by reducing the herbivory impacts. Many studies have shown that forest vegetation in the United States have recovered and benefited from deer management. Most of this deer management was a reaction to the initial impacts observed from herbivory by an overpopulation of deer (Anderson and Katz, 1993; Jenkins, 2011; Bush et al., 2012). Jenkins et al., 2014; Other studies in forests throughout the North America have also used exclosures and have shown significant differences within exclosed areas versus areas exposed to deer (Abrams and Johnson, 2012; Bressette et al., 2012; DiTommaso et al., 2014).

Canopy Layer:

The long-term dataset suggest that the white-tailed deer have not impacted most of the canopy. Although, it seems that the forest is at a tipping point and some of the early successional species are starting to decline. This decline could be a result of the 30 plus years of chronic herbivory that has occurred in the forest. There have been significant declines in the early successional species such as *Rhus copallinum* (shinning sumac) and *A. canadensis*. Even impacts on the larger *A. canadensis* (≥10.0 cm DBH) trees can be seen in the mortality and recruitment analysis. Many of the *A. canadensis* trees (≥3.0 cm DBH) found in the Sunken Forest now are recruits from 1950-1990, with peak recruitment occurring in the 1970's (Forrester, 2004). It is clear that herbivory will impact early successional and/or short lived species like *A. canadensis* sooner than others like *I. opaca*. Many of the *I. opaca* trees (≥3.0 cm DBH) found in the Sunken Forest now are recruits from the late 1700's to 1970's, with peak recruitment occurring through 1800's (Forrester, 2004). *I. opaca* within the canopy layer, as it relates to herbivory, would probably take a number of decades or possibly another century under current conditions before its impacted.

S. albidum, one of the three most dominant species in the canopy, seems to have adequate recruitment within the sapling layer. *S. albidum* trees currently in the canopy (≥3.0 cm DBH) went through peak recruitment from the 1900's up until the 1990's. The decline in *S. albidum* and *I. opaca* detected in the canopy layer as of recent seems to be associated with other impacts and not white-tailed deer herbivory.

Sapling/Shrub Layer:

Much of the long-term changes seen in this layer can be attributed to deer browsing that has occurred in the forest since the mid-1980's. The exclosure experiment helped confirm and isolate the browsing impacts observed in the long-term dataset. The most important species among the canopy are *I. opaca, S. albidum*, *A. canadensis*, and *N. sylvatica* (respectively). *I. opaca* saplings have not been observed in the forest since the late 1980's (Art, 1987). Currently, *I. opaca* saplings can only be found in the exclosures or in a few isolated areas protected by tangles of brier, which make natural deer exclosures (Forrester et al., 2006). There are a few *I. opaca* trees that are at sapling height (1-1.5 meters) within the forest, but these seem to be hollies that were saplings when the deer irruption first began and never grew higher. The basal diameters of these shorter trees are larger than the saplings found in the deer exclosures, which indicates that they are much older. In 2012, I cored several *I. opaca* "saplings" in the maritime forests, to the east of the Sunken Forest referred to as Blue Point, and they were aged between 20-35 years old. Observations in the field indicate that the new growth of *I. opaca* is soft and palatable to the white-tailed deer. Once a holly sprouts new growth in the spring it is usually nipped off by the middle of the summer (Figure 37; Figure 38). This seems to happen to the majority of new growth on *I. opaca* stems and nothing has seemed to recruit above the browse line since the late 1980's (Forrester, 2004).

Figure 37. *Ilex opaca* sprout in early-May 2012 with spring new growth

Figure 38. Same *Ilex opaca* sprout in July 2012 with all new growth browsed off.

The density of *A. canadensis* saplings has also declined over the last 45 years and is also significantly higher in the exclosures than in open areas. This suggests that herbivory from white-tailed deer has been a major contributor to this decline. *A. canadensis* has been documented as a species that is often browsed by deer (Forrester et al., 2006; Jordan and Scheibel, 2014). The decline of *A. canadensis* saplings will continue with the current deer browsing pressures. The dataset suggests that the recruitment of both *A. canadensis* and *I. opaca* are too low to sustain their dominance within the forest. As mentioned before, these impacts are already happening within the canopy layer for *A. canadensis*. While, under current conditions, these impacts will take longer to see for *I. opaca* in the canopy.

The role of herbivory on *S. albidum* and *N. sylvatica* saplings are a bit more difficult to understand. The density of *S. albidum* has fluctuated over the last 45 years; it increased slightly from 1967-1986 but then dramatically decreased in 2002. It has then increased significantly, showing its highest densities in 2011 and 2013 at (Mean=180, SE= ±84) and (360±156) individuals per ha, respectively. *S. albidum* saplings are also significantly higher in exclosed plots than in open plots. In 2012 and 2013 vegetation surveys, *S. albidum* has been shown to be dominant in this layer in other forests within the boundaries of Seashore that seem to be experiences comparable browsing pressures (Raphael, 2014 (unpublished); Raphael et al., 2014 (unpublished)). *S. albidum* has also been documented as being deer tolerant (Halls et al.,1970; Fargione et al.,1991). While the exclosure data indicate that deer can impact *S. albidum* the recent data collected in the Sunken Forest and other maritime forest on Fire Island seem to indicate that *S. albidum* can be deer tolerant compared to other species in the forest. Abrams et al. (2012), reported that *S. albidum* recruited within both deer exclosures and outside deer exclosures in a mixed-oak forest in Pennsylvania with high deer densities.

While the *S. albidum* sapling data in the exclosed and open paired plots are less clear, some of the seedling data can help to display this species tolerance to deer a little better. *S. albidum* seedlings that are ≥ 2 years old and < 1.0 meter in height are significantly higher outside exclosures compared to inside ($t = 2.71$, $p = 0.0097$). Both *I. opaca* and *A. canadensis*, deer intolerant species, are significantly higher in exclosured plots vs the open paired plots within this size class ($t = -3.19$, $p = 0.0032$ and $t = -2.33$, $p = 0.0260$, respectively). *P. serotina*, a documented deer tolerant species, shows no differences in this size class between exclosed and open paired plots. This size class, ≥ 2 years old and < 1.0 meter in height, for woody species is a good stage to assess browsing impacts. One year seedlings are sometimes difficult to use because they can have high mortality rates and/or could even be more abundant due to browsing pressures not allowing them to grow into the next year. This is seen in the Sunken Forest with first year seedlings of *A. canadensis*. As an early successional species it has a high surge of recruitment in the spring and early summer and is observed at high densities. In June of 2013, there was a density of (mean = 6.8, SE = ± 2.5) first year seedlings in the permanent plots. By September of 2013, the permanent plots had a density (0.5±0.2) first year seedlings. The difference in first year seedlings densities between the two surveys were statistically significant at (t = -2.54, p = 0.0131). This can sometime give people the wrong impression when this is observed in the forest. Many deer management plans that have seedling recruitment targets use height thresholds for this reason (McWilliams et al., 2005; Shirer and Zimmerman, 2010). Seedlings that are ≥ 2 years old and < 1.0 meter in height show they are surviving despite browsing pressures. While saplings (<3.0 cm DHB and ≥ 1.0 meter in height) are ideal for assessing browsing impacts, seedlings that are ≥ 2 years old and < 1.0 meter are also good to focus on simply because there is a larger sample size.

N. sylvatica saplings have also been declining in the Sunken Forest over the last 45 years and are higher in the deer exclosed plots vs open plots. Although, *N. sylvatica* saplings has also been documented as being dominant, along with *P. serotina,* in forests with high deer densities (Diefenbach et al., 2008, Abrams et al., 2012, Raphael et al 2014 (unpublished)). *N. sylvatica* has also been documented as being deer tolerant (Abrams, 2007). Abrams et al. (2012) also reported that *N. sylvatica* recruited both within deer exclosures and outside deer exclosure in a mixed-oak forest in Pennsylvania with high deer densities. Similar to *S. albidum, N. sylvatica* seedlings that are ≥ 2 years old and < 1.0 meter in height are also statistically higher outside exclosures compared to inside (t = 2.28, p = 0.0272). While, the role of deer herbivory on the decline of *N. sylvatica* saplings is also difficult to understand, data indicates herbviory is not the major cause to the decline detected in the Sunken Forest. The decline over the last 45 years could be due to other habitat changes, such as; sea-level rise and bayside erosion. This can be seen by looking at the decline in *N. sylvatica* saplings within the 5 “impacted plots” described above (Figure 19).

While many of the saplings have been declining in the Sunken Forest, *P. serotina* has been increasing over the last 45 years. There was no difference in density within the exclosed plots vs open paired plots. *P. serotina* was also seen thriving outside the exclosures at (mean =8.7, SE = ±4.6) saplings per plot in the 20 open plots and (4.0±3.0) saplings per plot in the 3 exclosures. Many forests in the Northeastern United Sates with high deer browsing pressures show similar trends, with low densities of saplings overall but high densities of *P. serotina* (Whitney, 1984; Trumbull et al., 1989; Healy, 1997; Horsley, 2003; Long et al., 2007; Diefenbach et al., 2008). This species is considered to be extremely deer resistant and is most likely the reason it's been increasing in the Sunken Forest over the last 45 years.

Other shrub species, such as; *I. glabra, T. radicans* and *A. arbutifolia* have significantly declined over the last 45 years in the forest. The deer exclosures is one of the few places you can even find these species in this layer. These species have also been found to be highly preferred by deer (McCullough, 1985; Stalter and Lamont, 2000; Asnani et al., 2006). Evidence suggests that the decline in these three species within this layer is a result of the increase in deer herbivory. *G. baccata* has also declined over the last 45 years but seems to do well in both exclosed and open plots. This decline does not seem to be due to white-tailed deer because it is commonly found in the shrub layer and most declines are associated with habitat changes within the 5 "impacted plots". *G. baccata* is also found to do well in other forests in Northeastern United States with high deer browsing pressures and is thought to be deer tolerant (Parkhurst and O'Connor, 1991; Matlack et al., 1993; Forrester et al., 2006; Rawinski and Square, 2008). It is also abundant in other areas in Fire Island National Seashore with high deer densities (Raphael, 2014 (unpublished); Raphael et al., 2014 (unpublished)). *V. corymbosum* also seems to be avoided by deer (Parkhurst and O'Connor, 1991; Diefenbach and Fritsky, 2007) and its densities have not changed within the Sunken Forest since the first survey in 1967.

Ground Layer:

When the park was established in 1964, common herbaceous species, such as *Maianthemum canadense* (Canada Mayflower), *Aralia nudicaulis* (Wild Sarsaparilla), *Pteridium aquilinum* (common bracken), and *Maianthemum stellatum* (little false Solomon's seal) blanketed the forest floor (Schulte, 1965; Art, 1976). Since that time, these species have significantly declined and in some cases are close to being locally extirpated (Figure 39; Figure 40).

Figure 39. (left) *Aralia nudicaulis* with other herbs and saplings in the understory of the Sunken Forest in 1968. Photo credit: Henry Art.

Figure 40. (below) Barren understory in the same area of the Sunken Forest in 2012.

Many other herbs, lianas, and woody species have declined since the park was established. There are many species that have increased since the irruption of white-tailed deer i.e. *P. serotina*, grass/sedge (*Carex* spp. and *Panicum* spp.), and *P. hydropiperoides.* It has been found that species that are avoided by deer or resilient to deer browsing such as *P. serotina* and grasses/sedges can increase with increasing deer density (Horsley, 2003). The declines in most species within this layer but increase in *P. serotina* and grass/sedge (*Carex* spp. and *Panicum* spp.) seem to be a result of an exorbitant amount of deer browsing pressure.

Again, the deer exclosures in the forest can help to verify that much of the decline in the ground cover is related to white-tailed deer herbivory. There are other herbivores in the Sunken Forest, such as cotton tailed rabbits (*Sylvilagus floridanus*) and voles (*Microtus spp*) but these populations do not impact the vegetation when compared to white-tailed deer (Forrester, 2004). Visually, the difference in vegetation cover inside the exclosures compared to outside is staggering. The total percent cover in the ground layer was higher in the exclosed plots vs open at (mean= 22.9 SE= ± 2.4%) and (17.4±2.4%), respectively. This difference is not statistically significant and in this case is not due to a lack of sample size. The lack of statistical significance is because these totals have both deer resistant and tolerant species within them. Once these species are taken out (which include: *G. baccata*, *S. albidum*, *P. serotina*, and grass/sedge) the total percent cover in the ground layer is significantly higher in exclosed plots vs open plots ($t = -5.20$, $p < 0.0001$) at (17.9±1.9%) and (7.1±0.8%), respectively. Looking at the data in another way, the percent cover of *G. baccata*, *S. albidum*, *P. serotina*, and grass/sedge within the ground layer is significantly lower ($t = 2.33$ $p = 0.0239$) in exclosed plots vs open plots at (5.0±1.0%) and (10.3±2.0%), respectively.

The exclosures in the Sunken Forest have been up for almost 30 years. While it is only a small sample of the forest overall both *A. nudicaulis* and *M. stellatum* are still not found within the exclosures. Both of these species were two of the most abundant herbaceous species within the understory before the white-tailed population exploded (Murphy, 1933; Thorne, 1953; Schulte, 1965; Art, 1976). These two species were also on the brink of extirpation before the exclosures were erected in the late 1980's and both *A. nudicaulis* and *M. stellatum* are highly preferred by deer (Balgooyen and Waller, 1995; Augustine, 1997; Rooney, 1997; Waller and Alverson, 1997; Augustine and Frelich, 1998; Wiegmann and Waller, 2005). While the recovery within the exclosures are apparent it is possible more intervention may be necessary to bring some of the browse sensitive herbs back to the forest, other than deer population control. The Great Smokey Mountains National Park constructed exclosures following a rapid increase in the deer population and subsequent vegetation impacts via browsing (Webster et al., 2005). Webster et al. (2005) found that once the deer exclosures were constructed only species that were able to persist during the deer irruption recovered. The more browse sensitive species had yet to recover and recolonize the exclosed sites. Nuttle et al. (2014) reported that browsing impacts can last over 20 years and vegetation cannot fully recover after deer population is controlled. This suggests that deer management is not the only answer when trying to manage a recovery in the vegetation (Royo et al., 2010). It has been documented that deer browsing can impact seed bank dynamics (DiTommaso et al., 2014, Aronson and Handel, 2011). DiTommaso et al. (2014) found that native and deer preferred species were less abundant in the seed bank in areas with high deer browsing pressure. Native and deer preferred herbaceous species seemed to be impacted the most. This could be happening in the Sunken Forest because many of the herbaceous species that were dramatically reduced after the deer irruption were at browsing height. It would most likely take longer for deer herbivory to impact many of the longer lived woody species that were higher than browsing height. These species can still produce seeds that can eventually make it in to the seed bank regardless of deer browsing pressures.

The smilax exclosure study helped to verify deer browsing pressures and the theory that brier tangles can act as refugia for plants in areas with a high population of white-tailed deer. Forrester et al. (2006) also found that tangles of catbrier (*S. rotundifolia and S. glauca*) acted as a natural barrier to deer within the Sunken Forest. These natural exclosures provided spatial refugia for many regenerating plants. Other studies have identified fallen trees can also work as a barrier and boulders in which deer cannot transverse provide refugia for regenerating plants (Rooney and Dress 1997; Long et al., 1998; Banta et al., 2005; Moore and Crawley, 2014).

While the impacts from the deer are apparent there seems to be some recent changes that suggest the Sunken Forest could be recovering in some areas on a small scale due to lower deer densities in the area as of recently. Even with the significant declines in percent cover from 1967 to 2011, there seems to be a little bit of an increase in ground layer vegetation within the last decade. Ground cover showed consistent declines through 1986 and 2002 with a small increase in 2011. Paired t-test comparing total ground cover in 2002 to 2011 shows a statistically significant increase from (8.28±1.78%) to (15.59±1.87%) ($t = 2.82$, $p = 0.0053$). This increase of vegetation coincides with a recent decline in the white-tailed deer *(Odocoileus virginianus)* population in the Sailors Haven/Sunken Forest area. This data suggests that the ground layer vegetation can recover once the pressures of white-tailed deer herbivory decreases. Deer densities seemed to be at its highest during the vegetation surveys in 2002 which is when the vegetation layer was at its lowest (Underwood et al., 2011 (unpublished), Forester, 2004) (Figure 41). Densities in the early 2000's were estimated to be ~ 75-140 deer/km^2 (Underwood, 2005). The white tailed deer populations in 2011 also seem to be closer to the population in the mid-1980's. The total percent cover of ground layer vegetation in 2011 was also closer to what the 1986 cover was at (15.59±1.87%) and (13.74±2.07%), respectively ($t = 1.96$, $p = 0.6034$). The recent decline in the white-tailed deer population in the area could be due to 4-posters (deer baiting stations) located toward the western end of the island. It is possible for the deer to be moving out of the Sunken Forest because of supplemental food in the communities. Another more plausible explanation of the decline could be due to the hunting that has occurred in Point O' Woods, the community adjacent to the Sunken Forest, which started in the mid-2000's. An estimated 50-60 deer were harvested from Point O' Woods since the mid-2000's to the early 2010's (per commination Justin McCarthy, General Manager at Point O'Woods Association). This number is quite significant for the area and due to its close proximity to the forest this scenario is most likely the result of the small scale recovery detected.

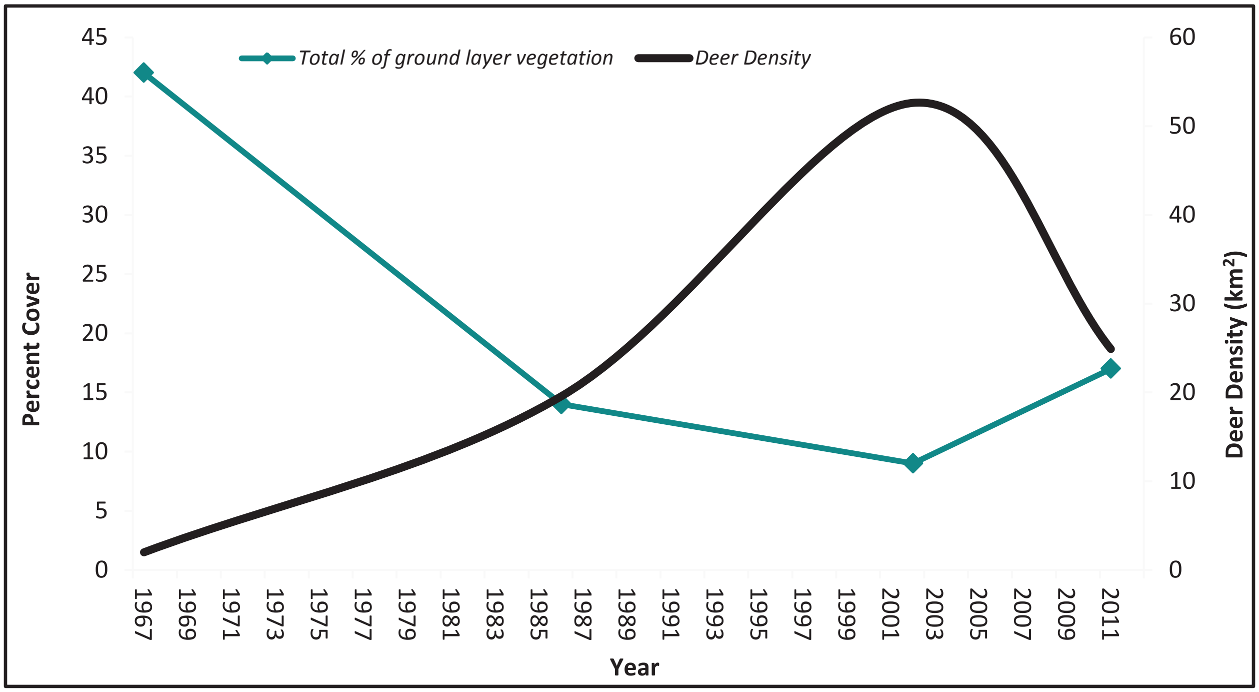

Figure 41. Deer population irruption in the Sunken Forest over the last 50 years and vegetation responses. (Adapted from Underwood et al 2011).

Role of Erosion and Sea Level Rise

Erosion and accretion are natural processes that occur on a dynamic barrier island like Fire Island National Seashore (Rampino and Sanders, 1981; Leatherman, 1985; Nordstrom and

Jackson, 2005). Past and present aerial images show that the north side (bayside) section of the Sunken Forest has been dramatically eroding (Figure 42). The 1938 imagery shows the island before major development occurred and before the marina was built at Sailors Haven. The cause of the erosion occurring on the bayside of the Sunken Forest is somewhat a subject of debate. Nordstrom and Jackson (2005) reported that the erosion along the bayside of the Sunken Forest area seems to be accelerated by the marina in Sailors Haven. The marina blocks much of the sediment longshore transport. This leaves the Sunken Forest starved of sand and when sediment transports from the bayside of the Sunken Forest it is not replenished, thus erosion occurs. Hard structures along the bayside are known to cause erosion in many other areas of Fire Island. Therefore, the marina in Sailors Haven is most likely the primary cause of the erosion. Other pressures that could cause bayside erosion include: sea level rise, ferry wakes, nor'easters, and suppression of overwashes (Nordstrom et al., 2009; personal comm. Seashore staff)

As the bayside erodes sections of the forest are exposed to the elements and these areas experience mortality in the canopy and sub-canopy (Figure 43). The sapling and shrub layer in these areas are changing from maritime forest species to species commonly seen in the edge habitat, when forest meets saltmarsh, such as *M. pensylvanica* and *B. halimifolia*. As the shoreline erodes further, these areas eventually become monocultures of *Phragmites* (Figure 44), and then open water habitats. As mentioned before, this process has already happened to five of the original plots, with four of them currently monocultures of *Phragmites* and one now located in the Great South Bay. More old growth holly maritime forest will be lost if erosion continues at the rate it is currently experiencing.

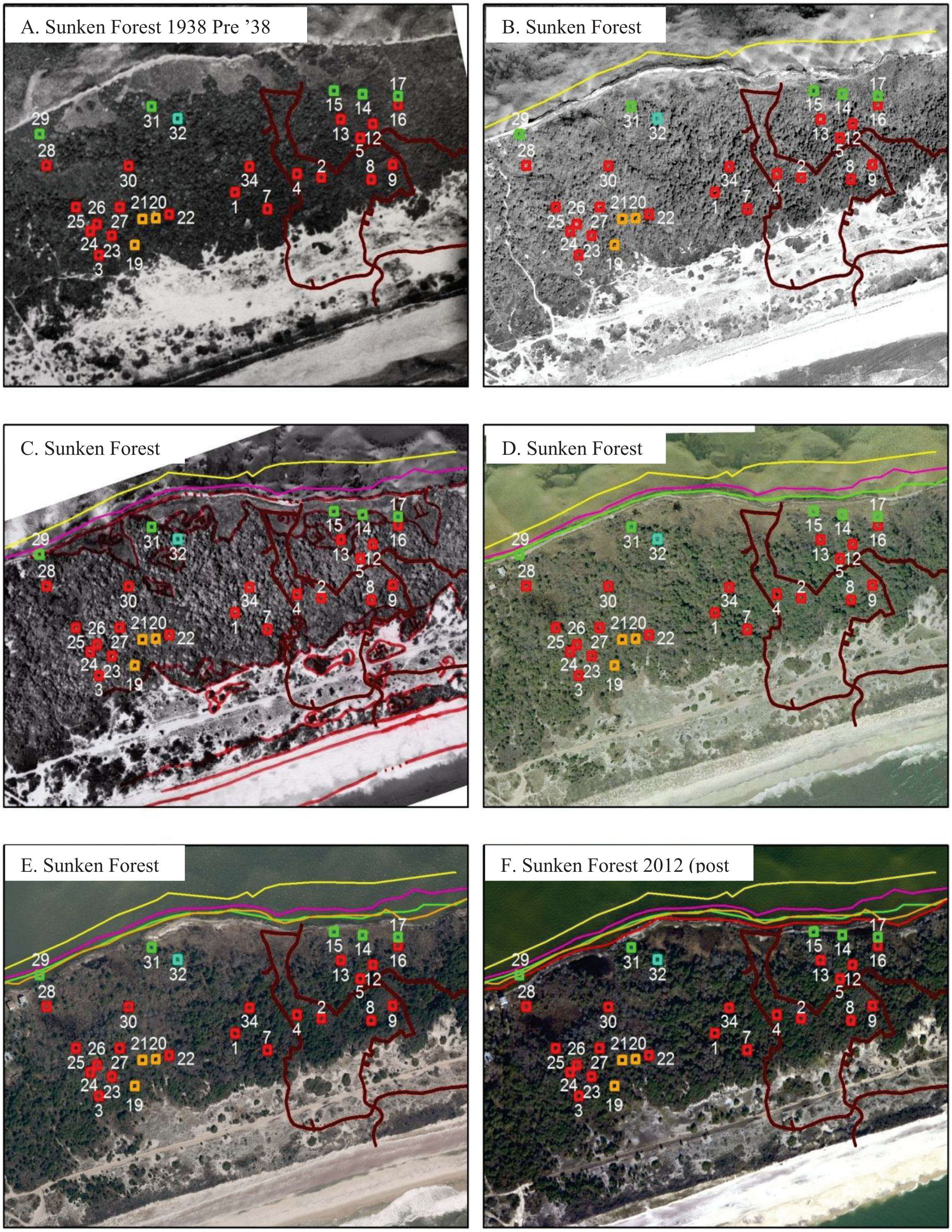

Figure 42. Aerial image of the Sunken Forest from 1938-2012. Yellow line represent 1938 bay shoreline, Purple = 1969 bay shoreline, Green=1986 bay shoreline, Orange = 2001 bay shoreline, Red = 2010 bay shoreline. NOTE: Permanent plots were not in the forest until 1967 and the boardwalk was not built until the mid-1980’s, they were left in all images for scale.

Figure 43. Erosion along the bayside of the Sunken Forest.

Another more noticeable change occurring is within the interior of the forest in lower elevations (depressions). The data from plots 2, 5, and 13 display this process. Schulte (1965) described the Sunken Forest as irregular with high areas and depressions that were only a few feet above sea level. These depressions were also described as being poorly drained but still dominated by maritime forest vegetation (Schulte, 1965; Art, 1976). These depressions within the forest are now becoming saturated throughout the growing season, which has changed the vegetation community within them. Wetland herbaceous species that were never an important component of the Sunken Forest are now invading these areas, such as *P. hydropiperoides, Decodon verticillatus* (swamp loosestrife), and others (Figure 45). *P. hydropiperoides* was rarely seen in the forest, present in one depression within the Sunken Forest in the 1960's (Schulte, 1965). *P. hydropiperoides* can now be found in most depression areas in the forest and has increased within these depressions since the 1960's.

There is also a great amount of mortality in the canopy layer and limited seedling/sapling recruitment occurring within these depressions (Figure 46). The mortality of vegetation, limited seedling/sapling recruitment, and vegetation shifts in the lower elevations of the forest is most likely due to thinning of the vadose zone, caused by sea level rise. The vadose zone is the unsaturated portion of earth between the land surface and the underlying groundwater system. There are many examples of coastal habitats experiencing vadose zone thinning caused by sea-level rise (Ross et al., 1994; Hayden et al., 1995; Kirwan et al., 2007; Saha et al., 2011; Masterson et al., 2014). Vadose zone thinning essentially brings the underlying ground water system closer to the ground surface. The vadose zone thickness is dependent on ground water elevation and surface elevation. Therefore, the lower elevated portions of the Sunken Forest are expected to have a thinner vadose zone. If these depressions already have a thin vadose zone, these areas should be the first to experience impacts with increased thinning. Vadose thinning has been documented on other barrier island similar to Fire Island, such as, Assateague Island (Masterson et al., 2014).

In the mid 1960's, *I. opaca* and *N. sylvatica* dominated the canopy in these lower elevated areas (Schulte, 1965; Art, 1976). Currently, *I. opaca*, the defining canopy species in this forest, is dying within these depression areas and shows no signs of recruitment. *S. albidum*, the second most dominant species in the forest overall, also showed high mortality rates in the same areas. *N. sylvatica* which is almost exclusively found within these depressions is also dying off but seems to tolerate this disturbance a little better than the other species.

The five impacted plots also show how much they contribute to the decline in the density of canopy species (≥3.0 cm DBH) over the last 45 years as well. While *I. opaca* and *S. albidum* are mostly impacted from the thinning of the vadose zone; it seems that *A. canadensis* is being impacted by the erosion within these disturbed plots. Forrester (2004), also found that *A. canadensis* mortality, in the Sunken Forest, was higher toward the bay. *A. canadensis* within the canopy seems to be the most at risk species among the four most common canopy species in the forest. This species seems to be most impacted by both white-tailed deer and erosion.

The rate of change analysis for trees ≥ 10.0 cm DBH shows that the recruitment of the larger trees within the canopy is not offsetting the mortality in these impacted areas. This is most likely a product of both erosion and vadose zone thinning. Maritime forest viability is dependent on vadose zone thickness and saturation of the low areas can limit the growth of canopy trees and cause an increase in mortality (Clark, 1986; Johnson and Young, 1993; Masterson et al., 2014) (Figure 47). Sea-level rise has also increased salinity within the ground water while thinning the vadose zone in many coastal habitats. This has changed the structure of the habitat and results in patterns of vegetation die off (Hayden et al., 1995). This change has also resulted in mortality of slash pine (*Pinus ellioti*) on Sugarloaf Key, Florida and coastal hardwood hemlocks-buttonwood forests of Everglades National Park (Ross et al.,1994; Saha et al., 2011). This has also impacted vegetation in coastal areas of Virginia (Hayden et al., 1995).

While the thinning of the vadose zone can result in saltwater intrusion within the fresh water table, it also seems to push more freshwater toward the surface (Werner and Simmons, 2009; Terry and Chui, 2012; Holding and Allen, 2014; Masterson et al., 2014). This could be why freshwater wetland herbaceous species (i.e. *P. hydropiperoides*) are starting to colonize these depression sites in the Sunken Forest. Deeper in the water table, saltwater can mix with the freshwater (Saha et al., 2011). While this interface is closer to the surface at lower elevations it seems to be at a level in which fresh water herbaceous species can thrive. The trees, which have a deeper root system, could be reaching this brackish water causing the mortality observed. Erosion could also be playing a role in this by causing these depressions to be closer to the bay. The closer these depressions are to the bay, the ground water below is more susceptible to saltwater intrusion by bring the saltwater/freshwater interface closer to the surface (Ataie-Ashtiani, 1999; Werner and Simmons, 2009).

The changes in the sapling/shrub layer can also be detected in these impacted plots. When the five impacted plots are taken out of the long-term analysis data indicates that *N. sylvatica* sapling declines are more associated with disturbances from sea-level rise and erosion compared to deer herbivory. When examining *I. opaca*, it seems to be impacted by deer, erosion, and sea-level rise. Schulte (1965) described the depression areas being mostly dominated by *N. sylvatica* saplings with the presence *I. opaca* and others. Currently there are no *N. sylvatica* or any saplings recruiting in these areas. On other barrier islands, it has been found that coastal loblolly pine forests require sufficient vadose zone thickness for saplings to efficiently recruit (Kirwan et al., 2007; Masterson et al., 2013) and this is almost certainly what is occurring within the sapling layer in the Sunken Forest as well. Other woody species, such as, *G.baccata* has been on the decline over the last 45 years. The decline in this species seems to be mostly associated with these habitat changes. While, *A. arbutifolia* and *I. glabra* also seem to be impacted from these changes the data suggests that deer herbivory has played a larger role in the decline of these species.

There have been some recent restoration efforts to slow down the erosion along the bayside of the Sunken Forest. In 2011, the Seashore dredged the channel of the Sailors Haven Marina. The sediment from the dredging was placed along the bay beach shoreline toward the northeast section of the Sunken Forest, this was referred to as a feeder beach (Nordstrom et al., 2009). It is thought that much of the sediment moving along the shoreline of the bay via longshore transportation deposits into the channel. Along with the marina blocking longshore sediment transport this could be another site where sediment settles while not replenishing the bay shoreline of the Sunken Forest (per comm. Seashore staff). Research continues at this site and shows that the feeder beach is moving sediment along the shoreline toward the Sunken Forest. I surveyed the forest the three summers following this restoration project. The feeder beach seemed to transport sand along the bayside shoreline but inundated the section of the forest just to the south of it with sand. It seems that the benefits outweigh the costs and that this could be a good a good way to slowdown erosion but most likely not solve the problem.

Figure 44. Picture (to the left) taken from a elevated area of the Sunken Forest looking down slope to a depression that in being invaded with *Polygonum hydropiperoides*

Figure 45. Picture (below) shows the eroded bayshoreline of the Sunken Forest with a monoculture *Phragmites australis* where old growth forest used to be located.

Figure 46. Depression in the forest that has become completely saturated causing mortality in the canopy, limited recruitment of understory vegetation, and invasion of *Polygonum hydropiperoides*.

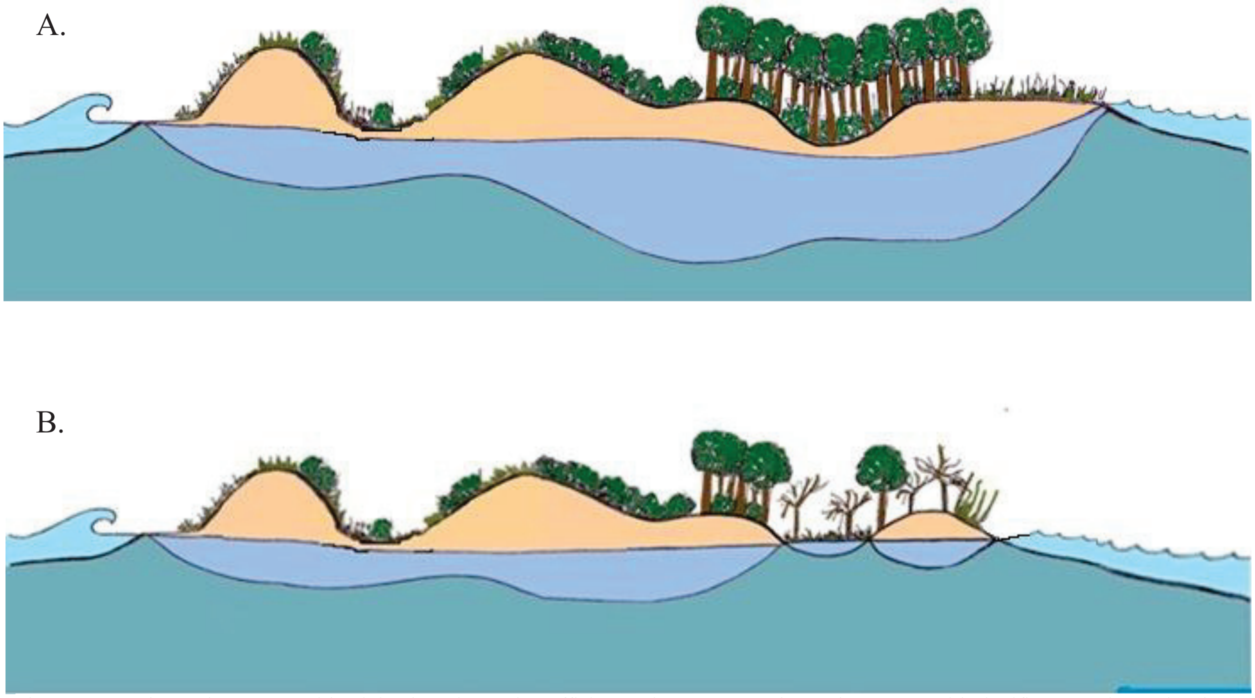

Figure 47. A. The Sunken Forest with minimal erosion and a sufficient vadose zone. B. The Sunken Forest with significant erosion and vadose zone thinning. Notice the mortality in the understory and canopy with a shift in vegetation within the depressions of the forest and toward the bays shoreline. In both images: light blue = fresh water lens, turquoise = saltwater (adapted from Masterson et al., 2014)

Role of Storms

It is thought that, due to climate change, there will be an increase in major storm events (IPCC, 2001; Bromirski et al., 2003; Harley et al., 2006) which could directly impact forests in the future (Dale et al., 2001). If there will be an increase in hurricanes and/or storms of high magnitude, then how will this impact the forest in the long-term? Hurricane Sandy and subsequent winter storms gave an opportunity to see how the Sunken Forest can be impacted by a hurricane and a higher than normal storm season.

While the forest did experience mortality in the canopy, data indicates it was not significant. Evidence suggests it was mostly wind-blown mortality in the canopy. While other sections of Fire Island overwashed, many of the maritime forests were not affected. The understory (sapling/shrub and ground layers) was also not significantly impacted by Hurricane Sandy. However, there were slight increases in some deer resistant and/or tolerant plant species, *P. serotina* and *S. albidum,* which could have been a response to the increase in sunlight created by new canopy gaps, thinnings, and openings. While several canopy gaps were formed by tree blow-downs much of the increased sunlight was from the living trees still standing after Sandy. Many living trees lost branches/limbs and many of the *I. opaca* trees, which are evergreen, lost all of their leaves due to salt spray, and it took until May/ June of 2013 for them to fully leaf out again. It also took other deciduous trees a little more time to fully leaf out in the spring following Sandy (personal observation 2013). All of these combined created more sunlight reaching the floor of the Sunken Forest and could have aided in the increase of the deer tolerant species in the understory. Art (1987) noted similar responses in the Sunken Forest the spring/summer following Hurricane Gloria. For the most part Hurricane Sandy and Hurricane Gloria both had minimal impacts to the Sunken Forest.

The more important question, as it relates to hurricanes and storms, is how the forest will respond or recover following these events. It took one growing season after Hurricane Sandy for many of the deer tolerant species take advantage of the increase in sunlight. The other vulnerable areas of the forest may have trouble recovering to what they were before the storm. 52% of the mortality within the canopy layer from Hurricane Sandy was in the five impacted plots, where there are many other changes occurring. While one hurricane event and several winter storms seems to have slight impacts to the forest an increase in storms could potentially have greater impacts to the forest if left at current conditions. Barrier islands rely on storm events such as Hurricane Sandy. Storms are very healthy for dynamic ecosystems and would be beneficial to the Sunken Forest before the added pressures of deer and sea level rise were overwhelming.

Role of Canopy Gap Dynamics

Canopy gap dynamics is an important component to forest regeneration and succession (Runkle, 1981; Lertzman, 1992). The sapling layer is important to examine because they are the next recruits to grow into the canopy. Forrester et al. (2005) reported that in 2002 about 11% of the Sunken Forest canopy was comprised of gaps. In 2002, the Sunken Forest also had a high number of *P. serotina* seedling and sapling in canopy gaps (Figure 48). *P. serotina* seedlings were also found growing under the closed canopy in 2002 and a decade later they were found at sapling height in closed canopy sites. The big difference, between the two surveys, was the increase in *S. albidum* saplings within canopy gaps since 2002, although, *S. albidum* seedling were detected at that time. *A. canadensis* saplings were also found in 2011 but at much lower densities then in 2002 (Forrester, 2004).

Currently, only deer tolerant or resistant plants seem to be recruiting in the seedling and sapling level. This seemed to be occurring more at the ground layer in 2002 and in the sapling layer by 2011. This change from ground to sapling/shrub layer is most likely due to a recruitment lag from the high amounts of deer hebivory occurring in the Sunken Forest during the early 2000's (Kuijper et al., 2010).


Figure 48. *Prunus serotina* saplings beginning to fill in a canopy gap.

In a natural forest ecosystem, gaps allow saplings to recruit into trees and for herbs regenerate. With browsing pressure so high in the Sunken Forest only deer tolerant species seem to be able to take advantage of the increased light levels in the gaps. Forrester et al. (2014), documented that in forests of Wisconsin deer resistant or tolerant tree species are better in filling in canopy gaps then other species in forests with high deer densities. It's thought that with different species dominating the sapling layer, due to deer herbivory, the dominance in canopy species could eventually shift (Kitterage et al., 1995; Rossow et al., 1997; Sendak, 2002; Martin et al., 2010). It would take some time but under current conditions the canopy layer of the forest could shift from an *I. opaca- S. albidum- A canadensis* forest to a *P. serotina- S. albidum* forest via canopy gap replacement, among other pressures. While it's not significant *P. serotina* and *S. albidum* are also the only two species with higher densities, within the canopy layer, in canopy gaps compared to the closed canopy. This serves as more evidence to suggest that the forest is already starting to shift within the canopy layer and not just within the ground and sapling/shrub layer. The dataset of 2011 and 2002 also suggests that this is happening at a much faster rate than previously expected (personal communication with Seashore staff)

Other Biotic and Abiotic Pressures

Propagule availability:

Forest regeneration is highly dependent on propagule availability (Peterson and Carson, 1996). Fortunately, Forrester 2004, was able to examine propagule availability in the Sunken Forest. The data collected suggested that, *R. copallinum* has the highest propagule availability compared to all other woody species. *I. opaca* was a far second but still significantly higher than all other woody species. There is not much of a difference in propagule availability between *P. serotina, A. canadensis,* and *S. albidum*. This dataset suggested that the limited recruitment of *I. opaca* and *A. canadensis* is not due to the lack of propagule availability. Instead the lack of recruitment in the Sunken Forest is most likely due to the other pressures discussed above.

Climate:

Based off the weather data collected by NOAA for coastal New York, it doesn't seem that the climate itself has changed to significantly. Both temperature and precipitation data suggests that the changes observed in the forest are not a result of direct changes in the climate.

Conclusion

The Sunken Forest is a unique ecosystem; it is a place that people should be able to see and experience for generations to come, but unfortunately it is at risk. This forest is experiencing a number of different pressures and the Sunken Forest will not be able to persist, in its current state, much longer under current conditions. Its global status of a G1 habitat is not the only reason it is important but the preservation of the forest is also explicitly stated in the Seashore's enabling legislation (PL 88-587). Based off the data and the current state of the Sunken Forest, the Seashore is arguably not meeting their own goals stipulated within the enabling legislation.

As of 2014, the Sunken Forest is not "in nearly its present state as possible" (PL 88-587) from when the Seashore was established in 1964. The Seashore can try to meet the enabling legislation through management but unfortunately some of these changes could be out of the Seashore's control.

The forest has limited recruitment occurring in the herb layer. Saplings of the important species that make the forest so unique are unable to grow and replace canopy trees that die. The major threat to the forest seems to be the impacts from browsing as a result of the high deer population on the island. Although, this is not the only pressure, as of recent the impacts from both erosion and sea-level rise are too hard to ignore. The thinning of the vadose zone, as a result of sea-level rise, is causing the depressions with the forest to become completely saturated. There is massive mortality within the canopy, zero recruitment, and a complete shift in habitat occurring with these depressions. The mortality of *I. opaca* and *S. albidum* trees, the lack *N sylvatica* and *I. opaca* sapling recruitment, little to no recruitment of forest ground layer species (both woody and herbaceous), and the invasion *P. hydropiperoides* all seem to be mostly associated with this thinning of the vadose zone occurring within the depressions.

If an area has sufficient vadose zone thickness, then the impact seems to be mostly associated with the white-tailed deer herbivory. The herbaceous species most impacted by white-tailed herbivory seem to be *M. canadense, T. radicans, and P. aquilinum.* White- tailed deer have also brought *A. nudicaulis* and *M. stellatum* to the brink of local extirpation. These species could require additional management, other than deer population control, to become reestablished within the forest. Saplings that are most impacted by white tailed deer herbovory seem to be *I. opaca* and *A. canadensis*. Evidence also suggests that the once common shrubs of the forest, which include *A. arbutifolia*, *I. glabra* and *T. radicans,* have been on the decline since the deer population has increased. The only species recruiting in areas with sufficient vadose zone thickness are deer resistant or tolerant plants species. The most deer resident plant being *P. serotina,* which has never been an important component of the forest in the past. Other species that seem to be resistant to white-tailed deer in the Sunken Forest include: *S. albidum*, *G. baccata*, and grass/sedge. Many of these deer resistant saplings also seem to be taking advantage of canopy gaps and are filling them in quite rapidly. This could eventually change the structure of the forest canopy if not managed. This process could be accelerated with the increase of major storm events. Lastly, after 30 years of chronic herbvory, *A. canadensis* seems to be the first species to be impacted with in the canopy layer.

All this is happening while the forest is shrinking as a result of bayside erosion. As the bayside erodes more canopy trees die with *A. canadensis* being the most impacted species. The shrub layer in these areas are converting to maritime forest species to species commonly seen in the edge habitat, when forest meets saltmarsh, such as *M. pensylvanica* and *B. halimifolia*. As the shoreline erodes further, these areas eventually become monocultures of *Phragmites*, and then open water habitats.

Vegetation and deer management could be one way to aid in conserving the Sunken Forest but these other impacts should not be ignored. More research is needed to investigate the true impacts to sea-level rise and erosion to help the park determine if this is something they should or can even manage in the hopes to maintain the forest to be here for future generations to enjoy.

Sunken Forest Management and Monitoring Recommendations:

In the Sunken Forest's current state, active management seems to be the best course of action in meeting the objects stated in the Seashore's enabling legislation (PL 88-587) and White-tailed Deer Management Plan. It seems that the population of white-tailed deer would need to be reduced to promote the regeneration of the herbs, seedlings, shrubs, and saplings. Additional management, other than just deer reduction, may be necessary to restore many of the browse sensitive herbaceous species. It also may be useful to manage some of the *P. serotina* saplings within canopy gaps to allow other species a chance to fill in these sites once deer herbivory is appeased. Once management is implemented Art (1976) permanent vegetation plots should continue to be surveyed on a 3-5 year basis to monitor how the vegetation will respond to deer and vegetation management.

Unfortunately, the management of deer and vegetation alone will not solve the impacts occurring in the forest. Research on the rate of erosion occurring in the Sunken Forest should continue. Further recommendations on how this could be managed should be a priority for the Seashore and these recommendations should be implemented as soon as possible.

Additional research is also needed to gain a better understanding the vadose zone thinning occurring and its impacts to the Sunken Forest. Some of this has already begun and we've replaced Art (1976) monitoring wells in the forest with new equipment. The change in the water table elevation can be assessed by using the 1967 well data as a baseline. This can give the Seashore a better perspective of how much the vadose zone is thinning in these areas and the vegetation impacts associated with the change. This impact is most likely much more difficult to manage but this shouldn't stop the Seashore from investigating this problem.

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Appendix A

Table A- 1. Percent cover of woody species (<1.0 meter in height) (using revised form of Domin-Krajina cover class) . Error bars show standard error. Data available from permanent plots in the Sunken Forest (Art (1976), Art (1987), Forrester (2004)). Levels not connected by same letter with in species are significantly different. Tukey-Kramer HSD was used for statistical analysis.

Species	Form	Percent cover (mean ± standard error)					
		1967	1986	2002	2011	2013 Early Summer	2013 Late Summer
Maianthemum canadense	Herb	1.74±0.63^{a}	0.23±0.06^{b}	0.04±0.02^{b}	0.11±0.05^{b}	0.04±0.02^{b}	0.04±0.02^{b}
Trientalis borealis	Herb	0.25±0.12^{ab}	0.15±0.07^{ab}	0.15±0.07^{ab}	0.68±0.26^{a}	0.50±0.15^{ab}	0.09±0.05^{b}
Aralia nudicaulis	Herb	8.12±1.97^{a}	0.08±0.05^{b}	0^{b}	0^{b}	0^{b}	0^{b}
Maianthemum stellatum	Herb	1.35±0.5^{a}	0.04±0.02^{b}	0^{b}	0^{b}	0^{b}	0^{b}
Solidago sempervirens	Herb	0.04±0.04	0.1±0.1	0	0	0	0
Pteridium aquilinum	Herb	0.85±0.39^{a}	0.03±0.02^{b}	0.1±0.1^{b}	0.1±0.1^{b}	0^{b}	0^{b}
Osmunda cinnamomea	Herb	0.23±0.23	0	0	0	0	0
Dryopteris carthusiana	Herb	0.04±0.04	0	0	0	0	0
Triadenum virginicum	Herb	0	0.1±0.1	0.01±0.01	0	0.01±0.01	0
Teucrium canadense	Herb	0	0.79±0.79	0.26±0.23	0.04±0.04	0.01±0.01	0.1±0.1
Polygonum hydropiperoides	Herb	0^{b}	0.14±0.11^{ab}	0.18±0.11^{ab}	0.48±0.37^{ab}	0.61±0.32^{ab}	2.33±1.25^{b}
Grass/Sedge	Herb	0	0.23±0.23	0.61±0.53	2.41±1.01	2.65±1.22	1.60±1.08
Impatens capensis	Herb	0	0	0.02±0.01	0.01±0.01	0.01±0.01	0
Thelypteris palustris	Herb	0	0	0.04±0.01	1.08±0.74	0	0
Spartina patens	Herb	0	0	0	0.23±0.23	0	0
Lactuca canadensis	Herb	0	0	0	0	0	0.18±0.11
Toxicodendron radicans	Herb/ Liana/Woody	7.89±1.79^{a}	0.94±0.33^{b}	0.43±0.15^{b}	1.08±0.33^{b}	0.61±0.31^{b}	0.87±0.20^{b}
Rubus spp.	Liana	0.03±0.03	0	0.02±0.02	0.18±0.11	0.23±0.10	0.39±0.25
Parthenocissus quinquefolia	Liana	4.13±0.72^{a}	0.83±0.14^{b}	0.49±0.1^{b}	1.81±0.26^{b}	1.41±0.16^{b}	1.40±0.19^{b}
Vitis spp	Liana	0.79±0.79	0	0	0.02±0.02	0	0
Amelanchier canadensis	Woody	0.89±0.39	0.53±0.07	0.71±0.23	0.58±0.13	0.63±0.15	0.29±0.07
Baccharis halimifolia	Woody	0.11±0.11	0.04±0.04	0.27±0.23	0.01±0.01	0.08±0.02	0.06±0.04
Gaylussacia baccata	Woody	6.6±1.99^{a}	4.13±1.48^{ab}	2.77±1.4^{ab}	2.08±0.81^{ab}	1.78±0.59^{ab}	0.73±0.29^{b}
Myrica pensylvanica	Woody	0.23±0.23	0.15±0.11	0.05±0.04	0.01±0.01	0.04±0.04	0.1±0.1
Nyssa sylvatica	Woody	0.91±0.37^{a}	0.17±0.06^{b}	0.08±0.02^{b}	0.41±0.09^{ab}	0.12±0.03^{b}	0.3±0.08^{ab}
Prunus serotina	Woody	0.11±0.06^{a}	0.89±0.21^{a}	1.34±0.34^{ab}	2.56±0.65^{b}	1.49±0.32^{ab}	1.31±0.24^{ab}
Rhododendron viscosum	Woody	0.04±0.04	0.39±0.37	0.04±0.04	0.23±0.23	0	0
Sassafras albidum	Woody	1.43±0.34^{ab}	2.93±0.87^{a}	0.49±0.1^{b}	2.03±0.4^{ab}	1.05±0.2^{ab}	1.98±0.32^{b}
Vaccinium corymbosum	Woody	2.12±0.93^{a}	0.01±0.01^{b}	0.18±0.11^{b}	0.32±0.15^{b}	0.34±0.15^{b}	0.96±0.37^{ab}
Ilex opaca	Woody	0^{a}	0.23±0.05^{b}	0.11±0.02^{ab}	0.23±0.06^{b}	0.19±0.05^{b}	0.18±0.05^{b}
Aronia artbutifolia	Woody	0.24±0.08	0.14±0.1	0.02±0.01	0.08±0.03	0.03±0.01	0.12±0.06
Ilex glabra	Woody	1.05±0.82	0.1±0.1	0	0	0.01±0.01	0.01±0.01
Rosa Carolina	Woody	1.35±0.77^{a}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}
Vaccinium oxycoccus	Woody	0.79±0.79	0	0	0	0	0
Vaccinium macrocarpon	Woody	0	0.23±0.23	0	0	0	0
Quercus velutina	Woody	0.13±0.13	0	0	0	0	0
Rhus copallinum	Woody	0.39±0.24	0.1±0.05	0	0.01±0.01	0.01±0.01	0
Juniperus virginiana	Woody	0^{b}	0.01±0.01^{b}	0^{b}	0.01±0.01^{b}	0.07±0.02^{ab}	0.03±0.01^{a}
Viburnum dentatum	Woody	0	0.04±0.04	0	0.01±0.01	0	0
Total	ALL	41.67±4.58^{a}	13.74±2.07^{b}	8.28±1.78^{b}	15.59±1.87^{b}	11.89±1.62^{b}	13.06±1.79^{b}

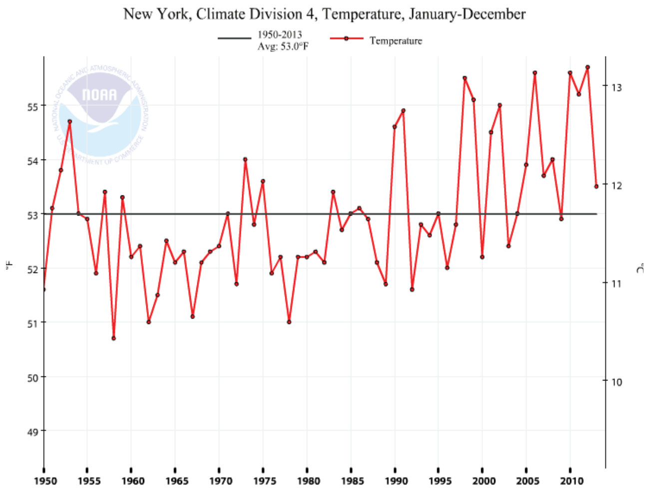

Figure A - 1. Temperature data for coastal New York from 1950-2013).

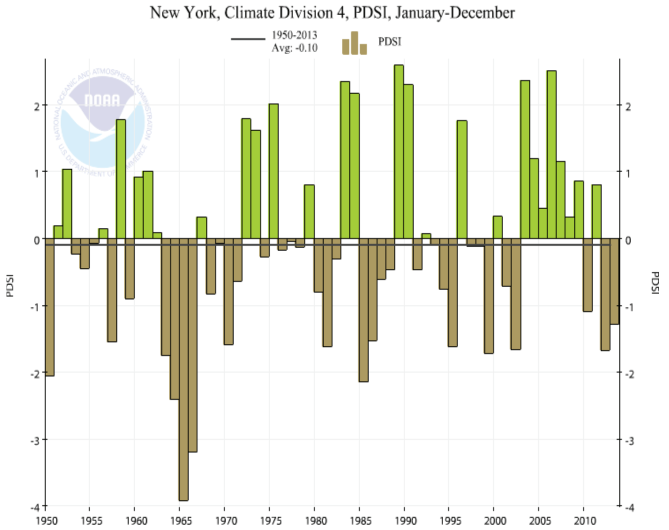

Figure A - 2. Precipitation from 1950-2013 for coastal New York (Data from NOAA) Data available from NOAA

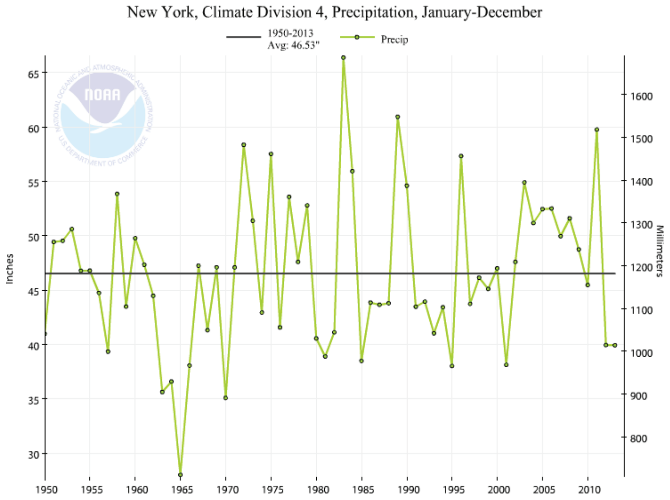

Figure A - 3. PDSI from 1950-2013 for coastal New York (Data from NOAA)