



Dune Slack Wetland Vegetation Monitoring, Cape Cod National Seashore

Floristic Changes Between 2004 and 2019

Natural Resource Report NPS/CACO/NRR—2021/2312



ON THE COVER

Dune slack wetland in the Province Lands, 2009

NPS / Jesse Wheeler

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Executive Summary

In 2019, the vegetation in 28 dune slack wetlands were surveyed along permanent transects, fifteen of which were originally surveyed in 2004 and subsequently in 2009 and 2014. An additional 38 sites were assessed in a more general way as was done in previous surveys as well. Significant findings are described below.

- Significant floristic changes between 2004 and 2019 were detected at most sites
- The process of succession from open, graminoid and forb-dominated systems to shrubby, more wooded communities continues
- In general, the floristic changes were largely the result of declines in *Juncus greenei* (Greene's rush), *Cladium mariscoides* (smooth sawgrass), and *Vaccinium macrocarpon* (cranberry) concurrent with increasing abundances of *Pinus rigida* (pitch pine) and *Vaccinium corymbosum* (highbush blueberry)
- Continued succession will result in the disappearance of early successional, open habitat taxa (grasses, rushes, forbs) and the proliferation of woody shrubs and trees
- Opportunities for new wetlands to form in this region of CACO are increasingly limited by dune stabilization through increasing vegetation cover. Over the long term, however, sea level rise is expected to push the fresh groundwater lens upwards – which could eventually flood topographic depressions that are currently dry
- *Phragmites australis* (common reed), *Salix cinerea* (gray willow), *Typha angustifolia* (cattail), *Rosa rugosa* (salt spray rose) were four exotic species found in the surveys
- The exotic, invasive *Phragmites australis* (common reed) increased at three sites where it was present in 2004, particularly at one site (RPA) where sea water from an adjacent salt marsh is now periodically flooding this wetland during large storms and extreme high tide events

Introduction

At the northern tip of Cape Cod, spanning approximately 1,800 hectares (ha) within the Cape Cod National Seashore (CACO), lies a vast system of dunes and interdunal wetlands known as the Province Lands. This part of the Cape Cod peninsula began forming roughly 6,000 years ago as longshore currents transported eroded materials from Atlantic-side beaches in a northward direction. Concurrently, wind carried sand grains inland and the landform gradually assumed its characteristic shape.

Once covered by mature forest, European settlers engaged in clear cutting and grazing practices that by the early 1800s had eliminated much of this community and destabilized the ground surface. The legacy of these activities is a sparsely vegetated landscape of shifting dunes and interdunal depressions. The latter are formed by the scouring action of wind, which can lower ground elevations to the point that they intersect the groundwater table for part of the year. These seasonally flooded wetlands, also known as dune slacks, develop distinctive hydrophytic plant communities in an otherwise desert-like environment. Dune slacks are one of the last refuges on the outer Cape for species such as the insectivorous sundews (*Drosera* spp.) and orchids (*Calapogon tuberosus*, *Pogonia ophioglossoides*). From a wildlife perspective, they are critical habitat for the reproduction and survival of numerous invertebrates and amphibians such as the spadefoot (*Scaphiopus holbrookii*) and Fowler's toad (*Bufo fowleri*). For larger mammals and birds, dune slacks are an important source of drinking water, succulent forage, and prey. Finally, these areas are very popular with visitors, as they possess aesthetic qualities that are a valued component of the Province Lands scenery.

To date, a total of 524 dune slack wetlands have been mapped and inventoried within CACO. The wetlands occur throughout the entire extent of the Provincetown and Truro dunes region (Figure 1). This report summarizes floristic changes that have occurred between 2004 and 2019 based on repeated vegetation monitoring that has been conducted every five years at a subset of fifteen wetlands that were established in 2004. This subset was increased to 28 wetlands in 2009. Another subset of 40 randomly chosen wetlands, in which vegetation is assessed in a coarser manner, was also analyzed to detect floristic changes between the initial (2004) and most recent (2019) surveys.

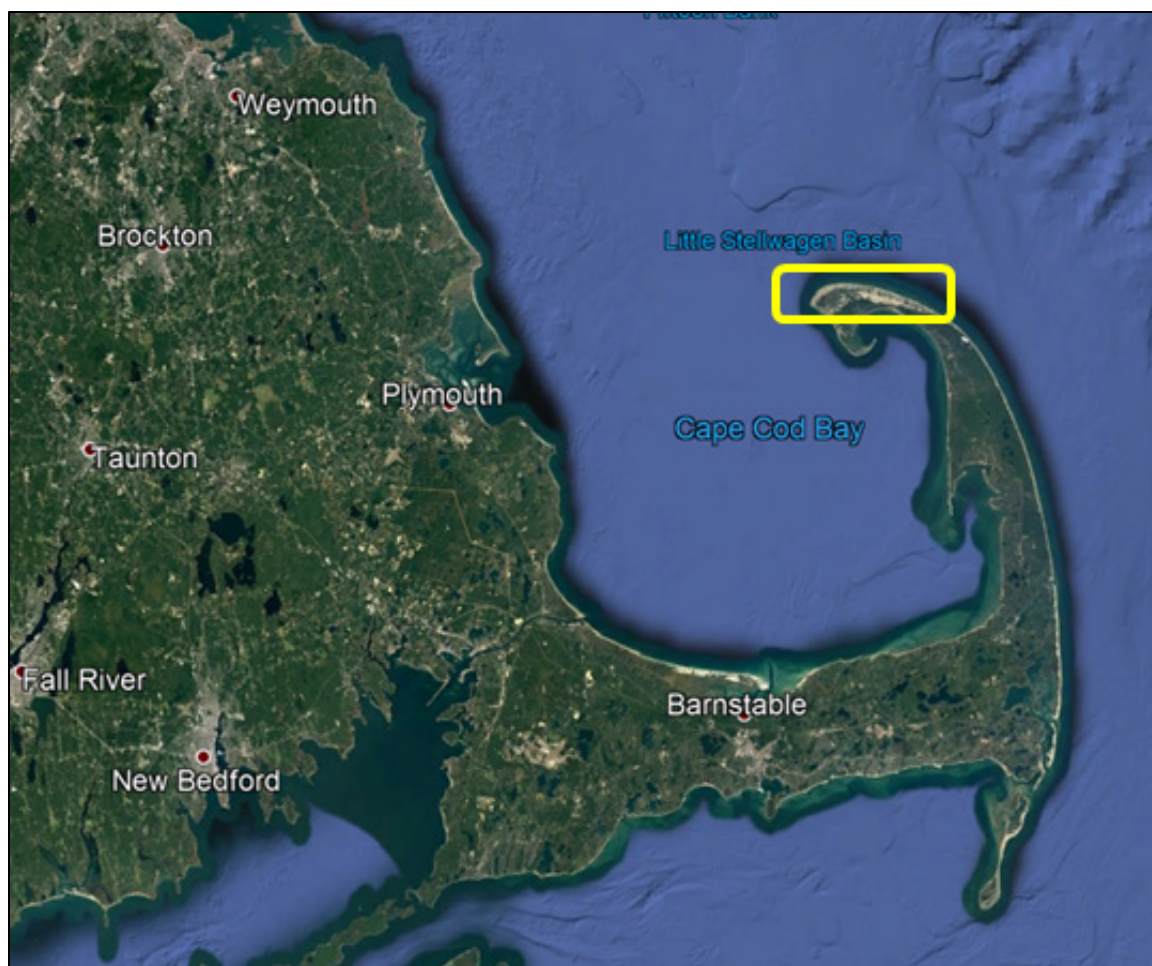


Figure 1. Map of southeastern Massachusetts and the Cape Cod peninsula with the Province Lands dune area of CACO enclosed in the polygon.

Methods

Potential dune slack wetlands were originally identified using 2000/2001 georeferenced images of Provincetown and Truro. Coordinates and general information for 66 previously known dune slacks were provided by Dr. Robert Cook (Wildlife Biologist, CACO). Using ArcGIS, each potential wetland was identified, and the coordinates of these points were then exported and uploaded into a GPS unit. The characterization of sites as wetlands was based on the presence of hydrophytic taxa with wetland indicator designations (USACOE 1987) of facultative (FAC), facultative-wet (FACW), or obligate (OBL). An additional criterion was the exclusion of upland taxa (FACU, UPL) as a ubiquitous member of the community. Field crews have subsequently visited subsets of these wetlands for more intensive monitoring in 2009, 2014, and 2019 as described below.

Vegetation

Intensive sites (IS)

The 15 original IS wetlands that were surveyed in 2004 were re-surveyed in 2019 by the same methods described in Smith et al. (2008) (Figure 2).

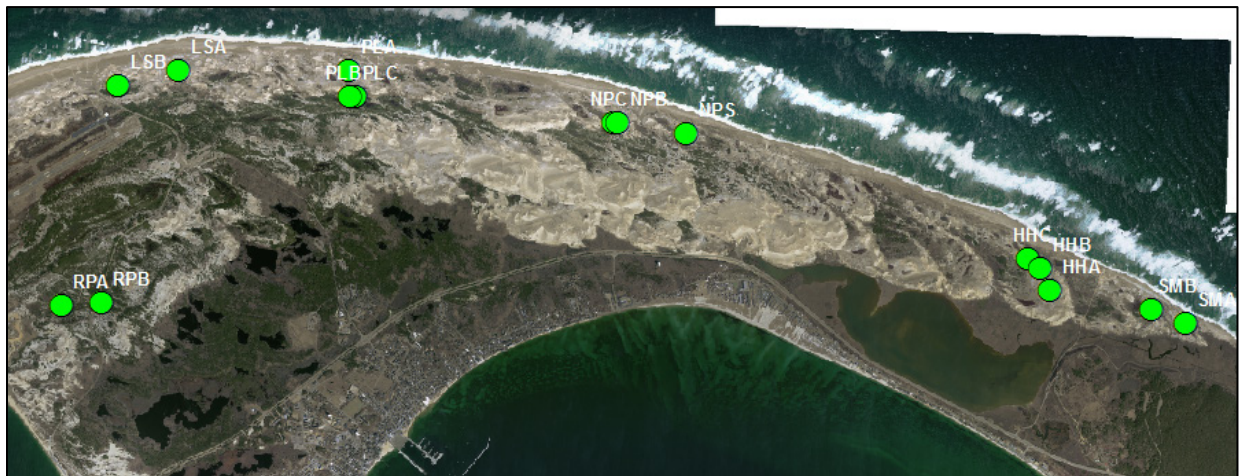


Figure 2. Map of original 15 monitoring sites (IS sites) located on the northern tip of the Cape Cod Peninsula. For reference, Provincetown, MA is shown.

In addition, in 2009 thirteen more IS sites were added to the original 2004 sites to bring the total number of IS sites to 28 (Figure 3).

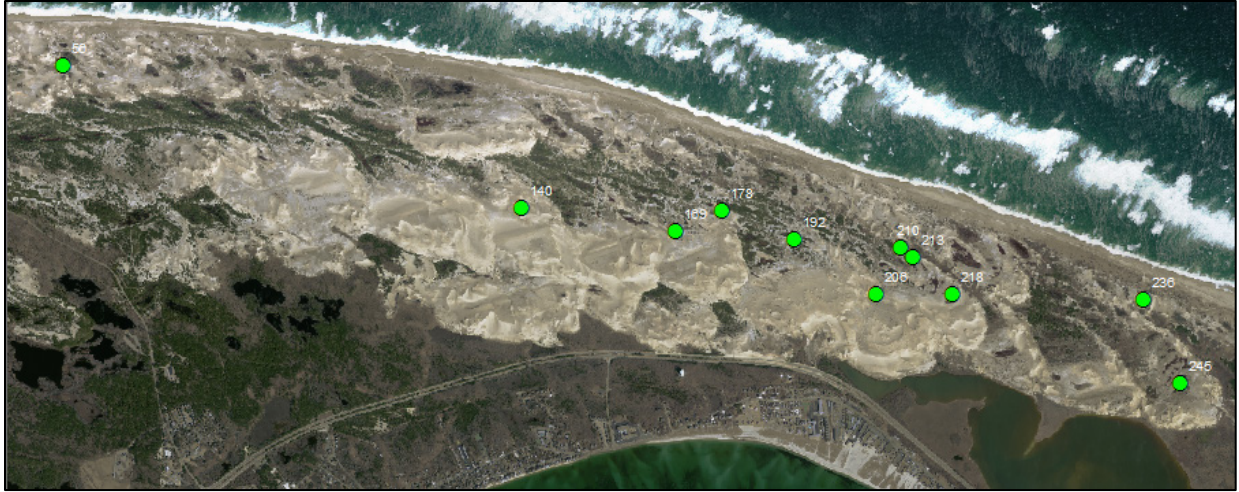


Figure 3. Map of IS sites added in 2009.

Monitoring of the IS sites consisted of collecting point intercept data every 0.5 m along 5 randomly placed, permanent transects within each wetland (Figure 4). To do this, a field tape was stretched out between the two transect end points, which are demarcated with PVC pipes. Vegetation was recorded at 0.5 m intervals along the line by point intercept (the rod was placed 0.5 m to one side of the line to avoid trampled vegetation caused by running out the field tape). All plants that make contact with a vertical rod placed at each point were recorded by species and percent abundances were then estimated from the number of “hits”. Transects were surveyed in August. This method provides percent cover data along each transect. In addition, species abundances across the entire wetland (hereafter referred to as “whole-wetland” surveys) were recorded as cover class ranks based on a modified Braun-Blanquet scale (0=0%, 1=<1%, 2=1–5%, 3=6–25%, 4=26–50%, 5=51–75%, 6=76–100%).

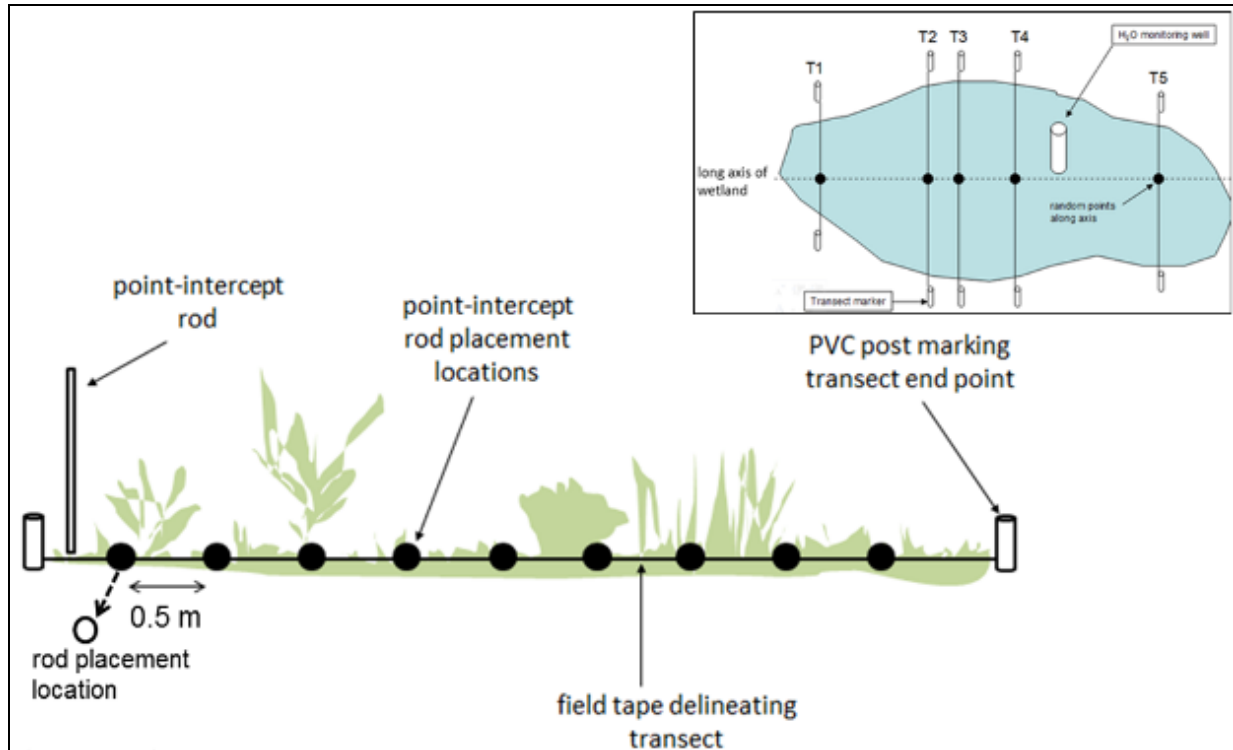


Figure 4. Diagram of an intensively monitored site with transect layout. Transect markers are PVC pipes with GPS coordinates.

Non-IS sites

Forty wetlands randomly selected in 2004 for a coarser type of vegetation assessment (based on ranked abundance throughout the entirety of each wetland (i.e., no transects) (Figure 5) were re-surveyed. For this subset, the three most dominant species are recorded and ranked (1, 2, or 3) depending on visual estimates of abundance, as was done in the initial (2004) dune slack wetland floral inventory (Smith et al. 2005). This was included in all subsequent monitoring efforts.

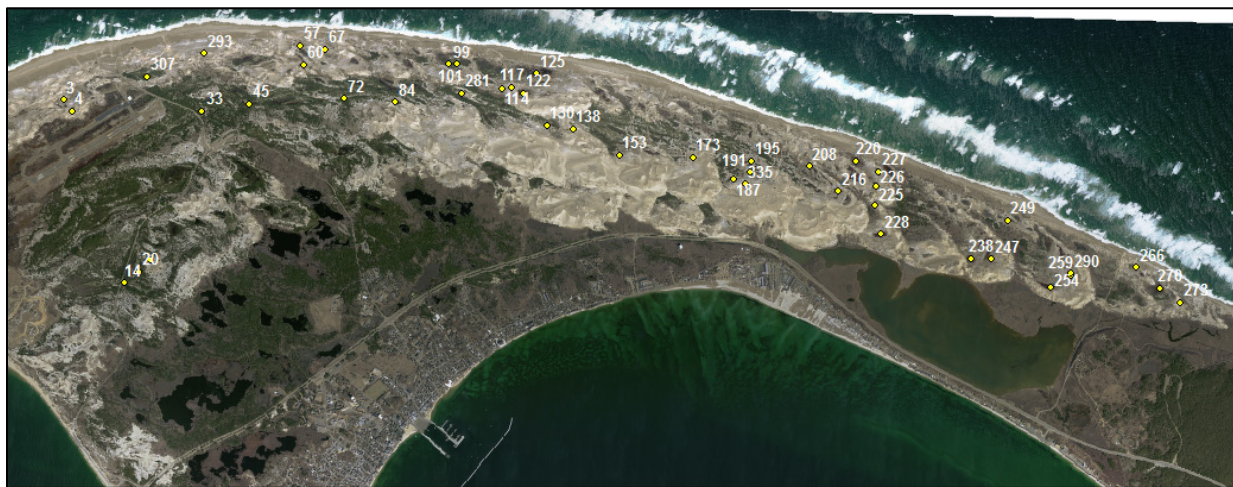


Figure 5. Subset of non-IS dune slack wetlands (n=40) for whole-wetland vegetation surveys.

Environmental variables

Porewater quality

Porewater was collected from IS sites in the month of July from the mid-points of the three middle vegetation transects (i.e., three samples per wetland in both original and new IS sites). Samples were obtained by inserting a stainless-steel probe into the sediment to a depth of 10 cm and then drawing 30 ml of pore-water into a syringe fitted over top of the probe. Samples were then tested for pH, conductivity, and salinity using a pre-calibrated portable field unit (Oakton Multi-Parameter PCSTestrTM35).

Soil properties

Three soil cores were extracted using a 4-cm diameter butyrate coring tube inserted to a 20-cm depth from the three middle transects in each IS wetland. After extraction, the thickness of the organic matter layer (quite distinguishable from the subjacent inorganic sand layer) was measured to the nearest cm. Organic matter as a percentage of the total core was determined using loss on ignition techniques (Smith 2014).

Data analysis

Statistical analyses were conducted using Primer-7 (Plymouth Laboratories, UK) and JMP ver. 10 software. Non-Metric Multidimensional Scaling (nMDS) and Similarities Percentages (SIMPER) analysis were used to illustrate variability in community composition and the key species contributing to similarity/dissimilarity among sites. Analysis of Similarities (ANOSIM) was run on community composition between the 2004 and 2019 surveys of the original IS wetlands (n=15) (Clarke and Warwick 2001). T-tests were used to test for differences in mean % cover and species richness between 2004 and 2019 and for comparisons of species grouped by growth form – i.e., tree, shrub, subshrub, forb, graminoid (USDA, NRCS 2015). Regression analysis was used to evaluate temporal trends in specific variables (including climate conditions).

Results

Plant communities in 2019

A list of plant taxa found in the 28 IS wetlands in 2019, ranked by cumulative abundance (sums of midpoint cover class values) is presented below (Table 1). In calculating cumulative percent cover using these values, it becomes apparent that roughly 12 taxa contribute to 80% cover of these wetlands (Table 1, Figure 6).

Table 1. Species observed in all IS wetlands (n=35) in 2019 ranked by average midpoint percentage values.

Species	Common name	means	cum means
<i>Vaccinium macrocarpon</i> ¹	American cranberry	33.50%	21.30%
<i>Pinus rigida</i> ¹	pitch pine	16.10%	31.50%
<i>Morella pensylvanica</i> ¹	northern bayberry	15.70%	41.50%
<i>Toxicodendron radicans</i> ¹	poison ivy	10.80%	48.30%
<i>Vaccinium corymbosum</i> ¹	highbush blueberry	8.20%	53.50%
<i>Kalmia angustifolia</i> ¹	sheep laurel	8.20%	58.70%
<i>Ammophila breviligulata</i> ¹	beachgrass	8.00%	63.80%
<i>Phragmites australis</i> ¹	common reed	6.40%	67.80%
<i>Deschampsia flexuosa</i> ¹	common hairgrass	5.70%	71.50%
<i>Cladium mariscoides</i> ¹	twig-rush	5.60%	75.00%
<i>Gaylussacia baccata</i> ¹	black huckleberry	5.10%	78.30%
<i>Ilex verticillata</i> ¹	winterberry	5.00%	81.50%
<i>Scirpus cyperinus</i>	woolgrass	3.60%	83.70%
<i>Photinia</i> spp.	chokeberry	2.60%	85.40%
<i>Schoenoplectus pungens</i>	common threesquare	1.90%	86.60%
<i>Juncus greenei</i>	rush	1.60%	87.60%
<i>Osmunda regalis</i>	royal fern	1.60%	88.70%
<i>Spiraea alba</i>	meadowsweet	1.50%	89.60%
<i>Juncus effusus</i>	common rush	1.50%	90.50%
<i>Salix cinerea</i>	gray willow	1.20%	91.30%

¹ Taxa contributing to ~80% pf the cumulative mean cover values, also shown shaded gray.

Table 1 (continued). Species observed in all IS wetlands (n=35) in 2019 ranked by average midpoint percentage values.

Species	Common name	means	cum means
<i>Rubus hispidus</i>	swamp dewberry	1.20%	92.00%
<i>Parthenocissus quinquefolia</i>	Virginia creeper	1.10%	92.70%
<i>Quercus ilicifolia</i>	scrub oak	1.00%	93.40%
<i>Lechea maritima</i>	beach pinweed	0.90%	93.90%
<i>Smilax rotundifolia</i>	common catbrier	0.90%	94.50%
<i>Acer rubrum</i>	red maple	0.70%	95.00%
<i>Agrostis hyemalis</i>	southern ticklegrass	0.60%	95.40%
<i>Juncus canadensis</i>	Canada rush	0.60%	95.70%
<i>Quercus velutina</i>	black oak	0.50%	96.10%
<i>Euthamia tenuifolia</i>	slender goldenrod	0.50%	96.40%
<i>Amelanchier canadensis</i>	juneberry	0.40%	96.70%
<i>Triadenum virginicum</i>	marsh St. John's-wort	0.40%	96.90%
<i>Rhododendron viscosum</i>	swamp azalea	0.40%	97.10%
<i>Rosa carolina</i>	pasture rose	0.30%	97.40%
<i>Dichanthelium acuminatum</i>	panic-grass	0.30%	97.60%
<i>Rosa rugosa</i>	salt spray rose	0.30%	97.80%
<i>Calamagrostis canadensis</i>	bluejoint	0.30%	98.00%
<i>Typha angustifolia</i>	narrow-leaved cattail	0.30%	98.20%
<i>Trientalis borealis</i>	starflower	0.30%	98.40%
<i>Carex</i> sp.	Carex sedge	0.30%	98.50%
<i>Rosa palustris</i>	swamp rose	0.20%	98.70%
<i>Solidago sempervirens</i>	seaside goldenrod	0.20%	98.80%
<i>Carex scoparia</i>	broom-sedge	0.20%	98.90%
<i>Rubus flagellaris</i>	northern dewberry	0.20%	99.10%
<i>Clethra alnifolia</i>	coast white alder	0.20%	99.20%
<i>Thelypteris palustris</i>	marsh fern	0.20%	99.20%
<i>Viola lanceolata</i>	lance-leaved violet	0.10%	99.30%

¹ Taxa contributing to ~80% pf the cumulative mean cover values, also shown shaded gray.

Table 1 (continued). Species observed in all IS wetlands (n=35) in 2019 ranked by average midpoint percentage values.

Species	Common name	means	cum means
<i>Betula populifolia</i>	gray birch	0.10%	99.40%
<i>Spiraea tomentosa</i>	steeplesbush	0.10%	99.50%
<i>Lythrum salicaria</i>	purple loosestrife	0.10%	99.60%
<i>Rosa virginiana</i>	Virginia rose	0.10%	99.60%
<i>Hudsonia tomentosa</i>	beach heather	0.10%	99.70%
<i>Viburnum dentatum</i>	southern arrow-wood	0.10%	99.80%
<i>Prunus serotina</i>	black cherry	0.10%	99.80%
<i>Acorus americanus</i>	sweet flag	0.10%	99.90%
<i>Osmunda cinnamomea</i>	cinnamon fern	0.10%	99.90%
<i>Prunus maritima</i>	beach plum	0.10%	99.90%
<i>Populus tremuloides</i>	quacking aspen	0.10%	100.00%
<i>Decodon verticillatus</i>	water-willow	0.10%	100.00%

¹ Taxa contributing to ~80% pf the cumulative mean cover values, also shown shaded gray.

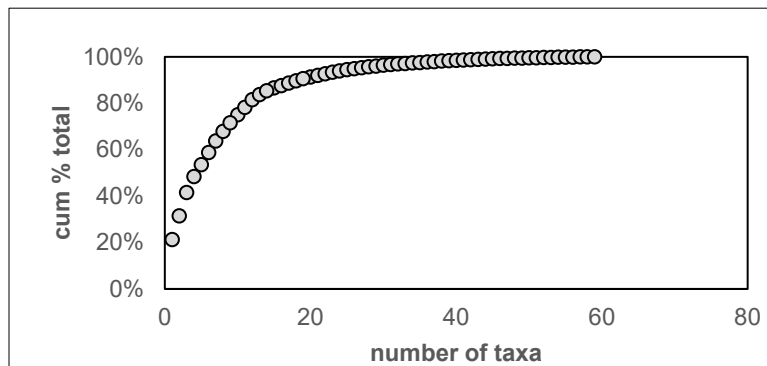


Figure 6. Cumulative percent of ranked mean cover values of individual taxa.

Among the IS sites, species richness in 2019 varied widely, ranging between 9 at SMA and 44 at HHC, with an average of 22 taxa per wetland (Figure 7).

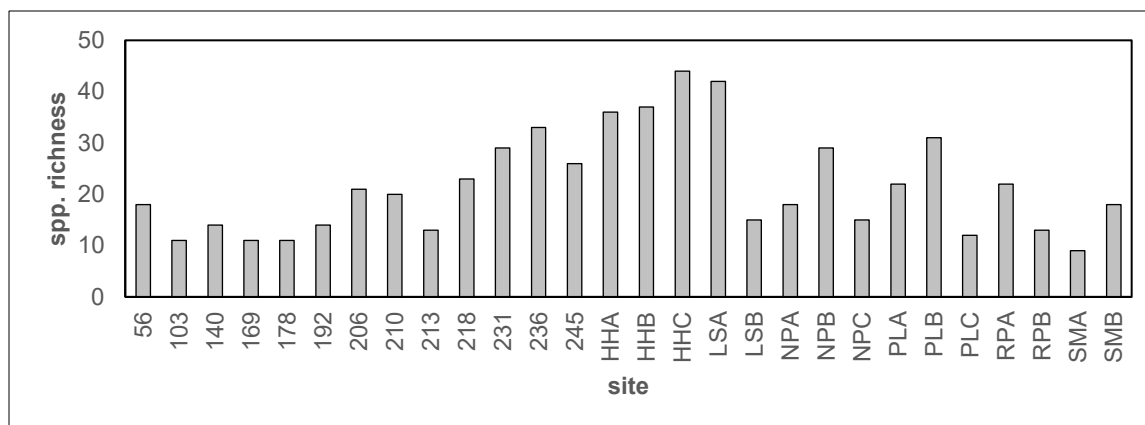


Figure 7. Species richness by site in 2019.

A nMDS of species composition by percent cover illustrates similarities/dissimilarities among the IS sites as depicted in ordinal space (Figure 8). The high abundance of *Phragmites australis* at RPA distances this site from the rest. The figure shows a central cluster of ~17 sites that have a fair amount of taxonomic overlap. About 10 sites are somewhat removed from the rest, revealing the extent to which their plant communities are dissimilar to this main group of sites.

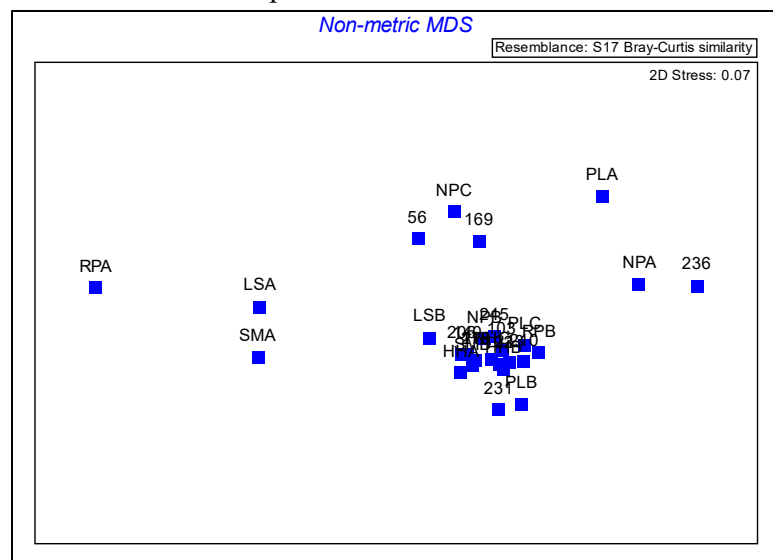


Figure 8. nMDS of floristic composition at the IS sites in 2019.

A total of 74 species of vascular plants were recorded within the IS sites in 2019. *Vaccinium macrocarpon* (cranberry), *Pinus rigida* (pitch pine), *Morella pensylvanica* (northern bayberry), *Kalmia angustifolia* (sheep laurel), and *Toxicodendron radicans* (poison ivy), were the most abundant taxa. *Phragmites australis* (common reed), *Salix cinerea* (gray willow), *Typha angustifolia* (cattail), *Rosa rugosa* (salt spray rose) were four exotic species found in the surveys.

Changes in floristic composition among the fifteen original IS sites between 2004 and 2019

Significant changes in the floristic composition of the IS sites as a group (i.e., all sites pooled) has occurred since 2004 (ANOSIM $R=0.25$, $p<0.01$) (Figure 9). This was mainly due to large reductions in the abundance and spatial distribution of *V. macrocarpon*, *C. mariscoides* (smooth sawgrass), and *J. greenei* (Greene's rush) (Table 2).

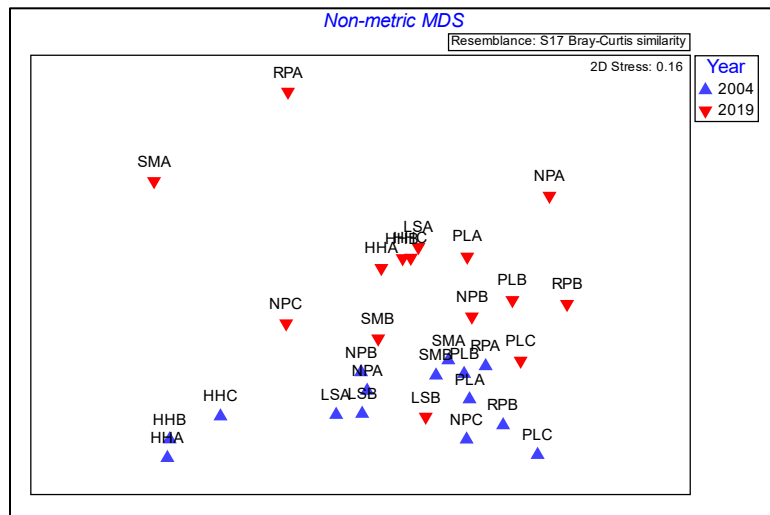


Figure 9. nMDS of species composition by percent cover along transects at the IS sites in 2004 and 2019.

Table 2. SIMPER results from analysis of species composition change along transects between 2004 and 2019 in the 15 original IS sites (SS=sub-shrub, GR=graminoid, SH=shrub, TR=tree).

Species	Growth form	2004	2019	%Cum Var
<i>Vaccinium macrocarpon</i>	SS	0.73	0.33	17.9
<i>Cladium mariscoides</i>	GR	0.36	0.06	28.5
<i>Juncus greenei</i>	GR	0.20	0.02	37.9
<i>Ammophila breviligulata</i>	GR	0.10	0.08	43.9
<i>Pinus rigida</i>	TR	0.03	0.16	49.6
<i>Morella pensylvanica</i>	SH	0.18	0.16	54.8
<i>Toxicodendron radicans</i>	SH	0.04	0.11	58.7
<i>Kalmia angustifolia</i>	SH	0.04	0.08	61.9
<i>Deschampsia flexuosa</i>	GR	0.10	0.06	64.8
<i>Vaccinium corymbosum</i>	SH	0.01	0.08	67.8
<i>Photinia</i> sp.	SH	0.09	0.03	70.7

In terms of species richness, there were no temporal trends in the mean value for all IS sites collectively (Figure 10). However, there were some large changes (both positive and negative) in certain wetlands from survey to survey. For example, SMA and SMB lost 10 and 8 species, respectively, compared to the initial values in 2004, whereas other sites such as HHA, NPB, NPC, and PLA gained four species (Table 3). Possible reasons for this are explored in the discussion section of this report.

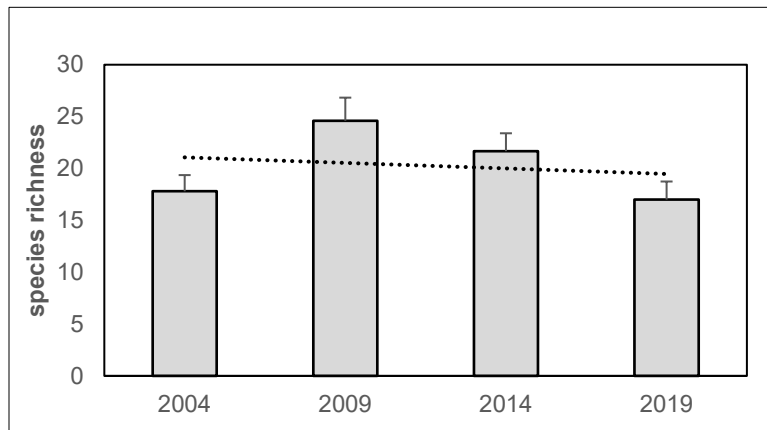


Figure 10. Mean species richness by year among the 15 IS sites (2004–2019).

Table 3. Species richness in 2004 and 2019 by site and magnitude of change (15 original IS sites).

Species	2004	2009	2014	2019	Change	% Change
HHA	11	20	15	15	4	36%
HHB	19	23	22	16	−3	−16%
HHC	21	39	31	24	3	14%
LSA	15	21	15	14	−1	−7%
LSB	14	19	16	13	−1	−7%
NPA	12	19	17	11	−1	−8%
NPB	25	41	35	29	4	16%
NPC	11	15	20	15	4	36%
PLA	17	28	28	21	4	24%
PLB	27	36	26	29	2	7%
PLC	10	20	15	10	0	0%
RPA	27	33	29	23	−4	−15%

Table 3 (continued). Species richness in 2004 and 2019 by site and magnitude of change (15 original IS sites).

Species	2004	2009	2014	2019	Change	% Change
RPB	14	17	17	9	-5	-36%
SMA	19	16	16	9	-10	-53%
SMB	25	22	23	17	-8	-32%
mean	18	25	22	17	-1	-3%
SE	1.6	2.2	1.7	1.7	1.2	7%

Additional IS sites

In the 22 additional IS sites established in 2009, ANOSIM indicates a significant floristic change since 2009 ($R=0.18$, $p=0.01$) (Figure 11). The shift was largely due to an increase in woody shrubs (*V. macrocarpon*, *K. angustifolium*, and *M. pensylvanica*) and pitch pine (*Pinus rigida*) (Table 4).

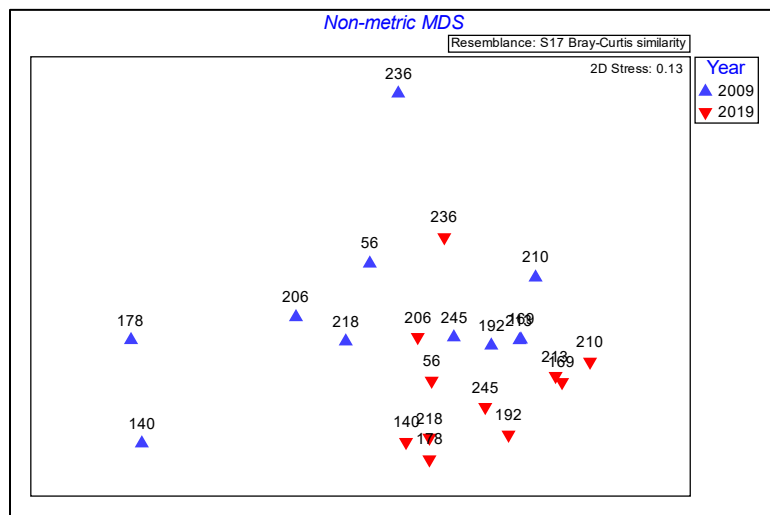


Figure 11. nMDS of floristic composition of additional IS sites (first established in 2009) in 2009 and 2019.

Table 4. SIMPER results from analysis of species composition change between 2004 and 2019 in the additional IS sites (SS=sub-shrub, GR=graminoid, SH=shrub, TR=tree).

Species	Growth form	2009	2019	%Cum Var
<i>Vaccinium macrocarpon</i>	SS	0.20	0.59	23.48
<i>Kalmia angustifolium</i>	SH	0.06	0.16	33.02
<i>Pinus rigida</i>	TR	0.04	0.17	41.92
<i>Morella pensylvanica</i>	SH	0.08	0.17	50.00
<i>Juncus greenei</i>	GR	0.08	0.03	55.46
<i>Cladium mariscoides</i>	GR	0.01	0.08	60.19
<i>Juncus canadensis</i>	GR	0.01	0.06	63.51
<i>Salix cinerea</i>	TR	0.02	0.04	66.66
<i>Toxicodendron radicans</i>	SH	0.02	0.04	70.00

A sampling of the 40 additional sites, in which vegetation was broadly surveyed by ranked abundance, yielded results similar to the IS sites. As a group, plant community composition in these wetlands was not statistically different in 2019 than in 2004 (ANOSIM R=0.023, p=0.09) (Figure 12). Nonetheless, some of the individual species changes followed patterns observed in the IS wetlands. For example, *Pinus rigida*, *Vaccinium macrocarpon*, and *Vaccinium corymbosum* have also become more prominent, while *Juncus greenei* was diminished in importance.

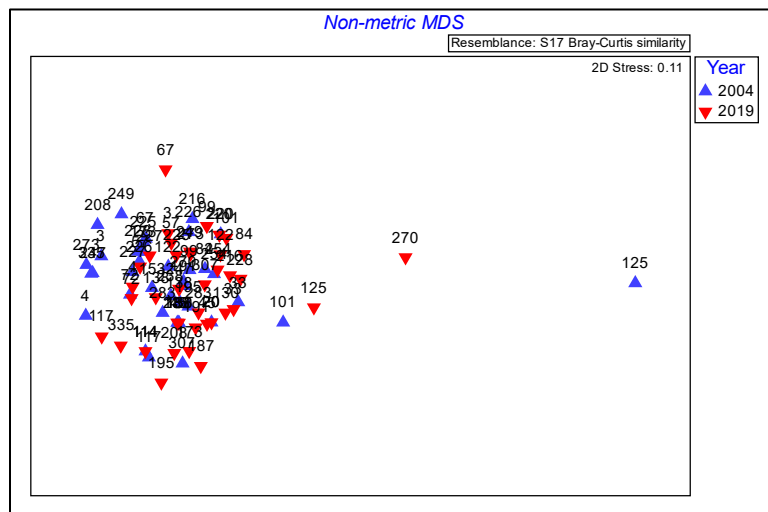


Figure 12. nMDS of floristic composition in the non-IS sites in 2004 vs. 2019.

Table 5. SIMPER results from analysis of species composition change (whole-wetland surveys, dominant 3 species) between 2004 and 2019 in the non-IS sites (FB=forb, SS=sub-shrub, GR=graminoid, SH=shrub, TR=tree).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Pinus rigida</i>	TR	0.66	0.82	11.1
<i>Vaccinium macrocarpon</i>	SS	0.84	1.16	20.5
<i>Morella pensylvanica</i>	SH	0.79	0.26	29.6
<i>Kalmia angustifolia</i>	SH	0.45	0.47	37.3
<i>Juncus greenii</i>	GR	0.45	0.26	43.5
<i>Vaccinium corymbosum</i>	SH	0.21	0.39	49.2
<i>Scirpus cyperinus</i>	GR	0.08	0.37	53.6
<i>Toxicodendron radicans</i>	SH	0.18	0.24	57.8
<i>Salix</i> sp.	GR	0.18	0.21	61.6
<i>Juncus canadensis</i>	GR	0.16	0.16	64.7
<i>Drosera rotundifolia</i>	FB	0.26	0.00	67.3
<i>Scirpus pungens</i>	GR	0.08	0.16	69.8

Species composition change at individual IS sites (2004–2019)

Twelve of the fifteen sites exhibited significant changes in floristic composition between 2004 and 2019.

HHA

Wetland vegetation at HHA has changed dramatically between 2004 and 2019 (ANOSIM $R=1$; $p<0.01$) (Figure 13). During this time, the graminoid community (consisting largely of *Juncus* spp.) was replaced by the subshrub *Vaccinium macrocarpon* (Table 6) There was also expansion of *Morella pensylvanica* shrubs at this site.

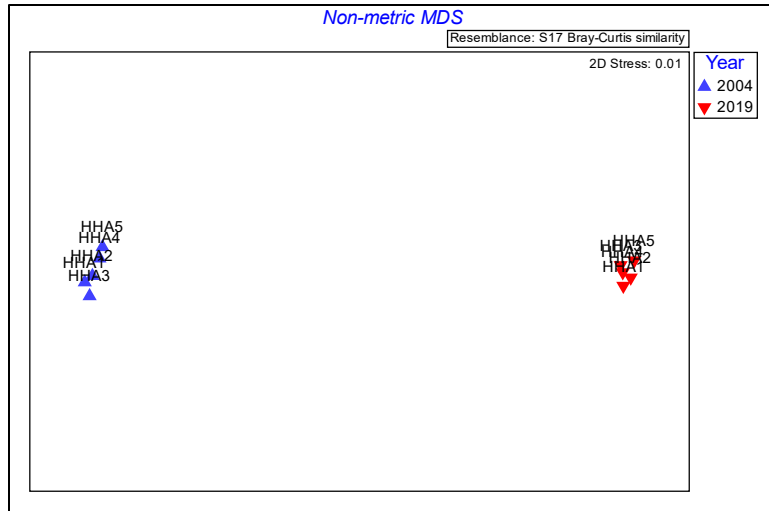


Figure 13. nMDS of floristic composition by transects at HHA in 2004 and 2019.

Table 6. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at HHA (FB=forb, SS=sub-shrub, GR=graminoid, SH=shrub, TR=tree).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Vaccinium macrocarpon</i>	SS	0.00	0.79	37.28
<i>Juncus greenei</i>	GR	0.56	0.01	63.16
<i>Morella pensylvanica</i>	SH	0.11	0.26	71.65

HHB

Plant communities in 2004 and 2019 at this site were significantly different (ANOSIM $R=0.47$, $p=0.02$) (Figure 14). Similar to HHA, increases in *Vaccinium macrocarpon*, *Cladium mariscoides*, and *Scirpus cyperinus* mostly accounted for the floristic shift (Table 7). Conversely, *Juncus canadensis* and *Deschampsia flexuosa* declined between surveys.

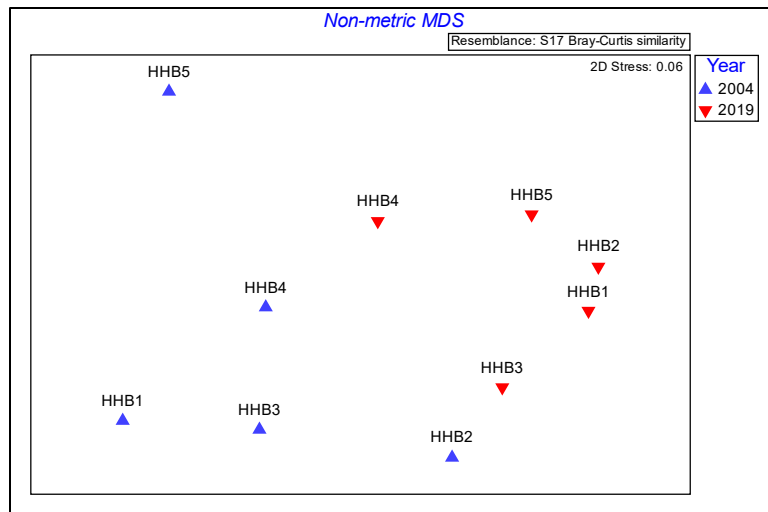


Figure 14. nMDS of floristic composition by transects at HHB in 2004 and 2019.

Table 7. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at HHB (FB=forb, SS=sub-shrub, GR=graminoid, SH=shrub, TR=tree).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Vaccinium macrocarpon</i>	SS	0.49	0.81	24.6
<i>Cladium mariscoides</i>	GR	0.04	0.25	41.5
<i>Scirpus cyperinus</i>	GR	0.09	0.11	51.0
<i>Morella pensylvanica</i>	SH	0.11	0.15	58.7
<i>Juncus canadensis</i>	GR	0.09	0.0	65.5
<i>Deschampsia flexuosa</i>	GR	0.11	0.08	71.4

HHC

There was a significant difference between plant community composition in 2004 vs. 2019 (ANOSIM $R=0.49$, $p=0.05$) (Figure 15). Transect HHC5 was omitted from the analysis as it has been buried by a migrating sand dune. Notwithstanding, higher abundances of *Vaccinium macrocarpon*, *Cladium mariscoides*, *Schoenoplectus pungens*, and *Morella pensylvanica* accounted for most of the cumulative dissimilarity between surveys (Table 8).

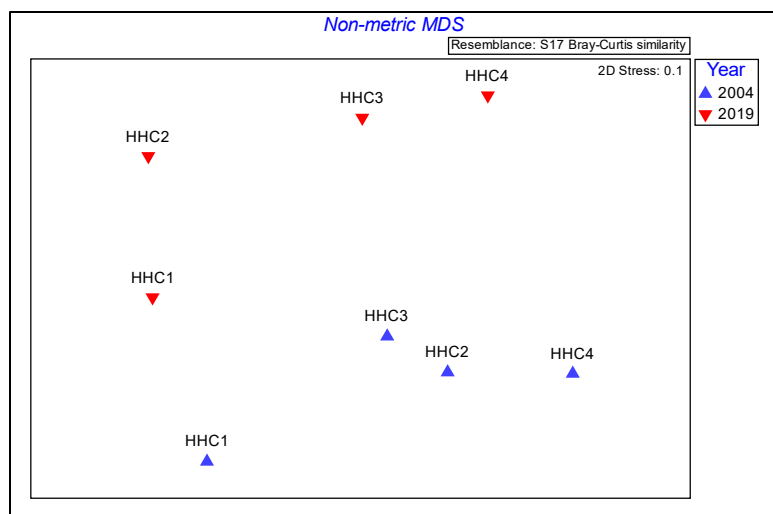


Figure 15. nMDS of floristic composition by transects at HHC in 2004 and 2019.

Table 8. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at HHC (FB=forb, SS=sub-shrub, GR=graminoid, SH=shrub, TR=tree).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Vaccinium macrocarpon</i>	SS	0.71	0.90	16.1
<i>Cladium mariscoides</i>	GR	0.55	0.70	31.7
<i>Schoenoplectus pungens</i>	GR	0.08	0.18	46.5
<i>Morella pensylvanica</i>	SH	0.09	0.14	53.2
<i>Toxicodendron radicans</i>	SH	0.06	0.12	59.7
<i>Rubus hispida</i>	SH	0.13	0.06	65.8
<i>Kalmia angustifolia</i>	SH	0.04	0.08	71.2

LSA

At LSA, taxonomic disparities in transect vegetation between survey years was obvious (ANOSIM $R=0.46$, $p<0.01$) (Figure 16). Sizeable increases in *Vaccinium macrocarpon*, *Salix cinerea*, and *Morella pensylvanica* occurred between 2004 and 2019, coupled with reductions in *Ammophila breviligulata* and *Deschampsia flexuosa* (Table 9).

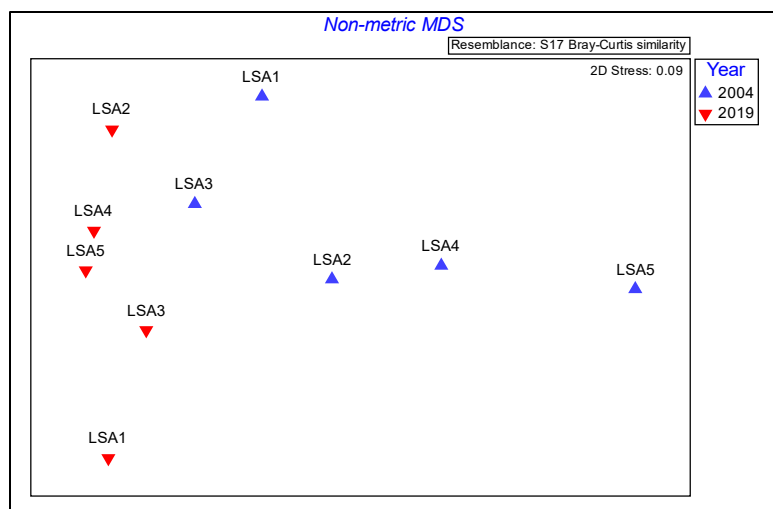


Figure 16. nMDS of floristic composition by transects at LSA in 2004 and 2019.

Table 9. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at LSA (FB=forb, SS=sub-shrub, GR=graminoid, SH=shrub, TR=tree).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Vaccinium macrocarpon</i>	SS	0.13	0.54	20.2
<i>Ammophila breviligulata</i>	GR	0.33	0.06	34.7
<i>Salix cinerea</i>	TR	0.13	0.32	48.3
<i>Morella pensylvanica</i>	SH	0.24	0.39	57.3
<i>Deschampsia flexuosa</i>	GR	0.15	0.05	64.2
<i>Pinus rigida</i>	TR	0.07	0.11	70.1

LSB

The vegetation at LSB also shifted between 2004 and 2019, as indicated by the separation of the transects by year in Figure 17 (ANOSIM $R=0.58$, $p<0.01$). This change was primarily due to an expansion of *Vaccinium macrocarpon* and *Morella pensylvanica*, and a decline in *Pinus rigida*, *Juncus greenei*, and *Deschampsia flexuosa*. (Table 10)

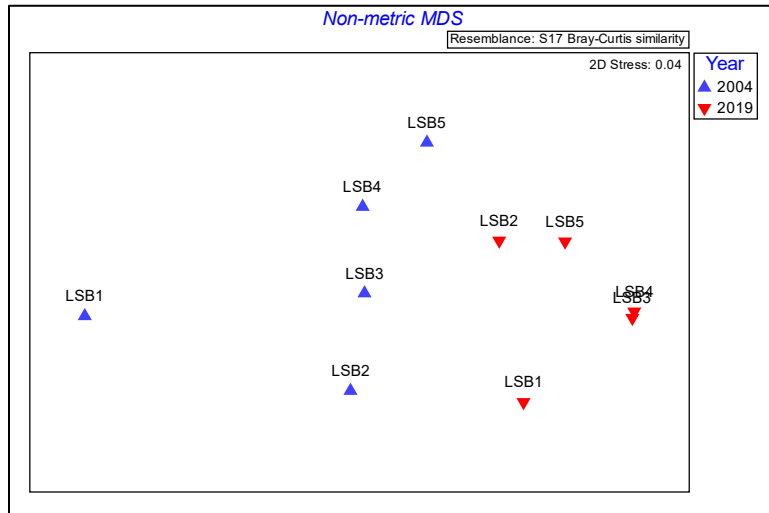


Figure 17. nMDS of floristic composition by transects at LSB in 2004 and 2019.

Table 10. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at LSB (FB=forb, SS=sub-shrub, GR=graminoid, SH=shrub, TR=tree).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Vaccinium macrocarpon</i>	SS	0.20	0.74	29.7
<i>Morella pensylvanica</i>	SH	0.34	0.64	48.6
<i>Pinus rigida</i>	TR	0.19	0.16	56.8
<i>Juncus greenei</i>	GR	0.12	0.06	64.5
<i>Deschampsia flexuosa</i>	GR	0.14	0.05	71.1

NPA

Vegetation along the NPA transects was highly variable by transect to begin with, but no significant changes were observed between survey years (ANOSIM $R=-0.052$, $p=0.59$) (Figure 18).

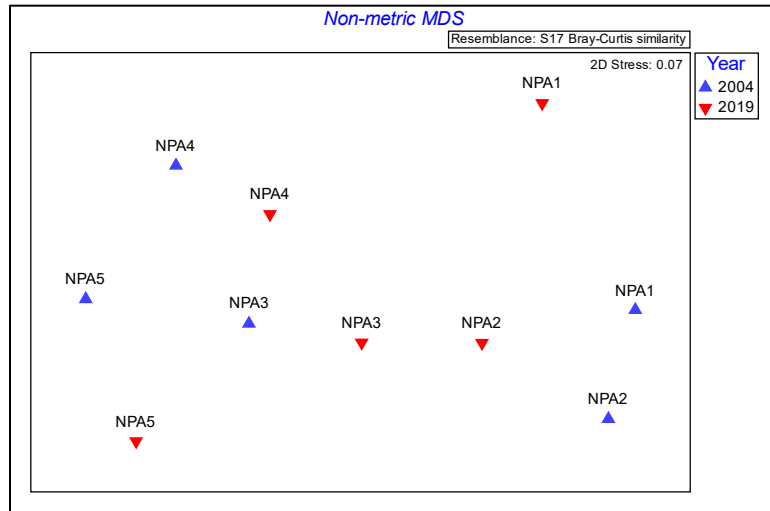


Figure 18. nMDS of floristic composition by transects at NPA in 2004 and 2019.

NPB

NPB experienced an increase in *Vaccinium corymbosum*, concurrent with reductions in *Rubus hispida* (common name) and *Triadenum virginica* (common name). Abundances of *M. pemsyvainca* and *V macrocarpon* were similar in 2004 and 2019, but their spatial distributions were altered, all of which contributed to significant dissimilarity between surveys (ANOSIM $R=0.69$; $p=0.01$) (Figure 19, Table 11).

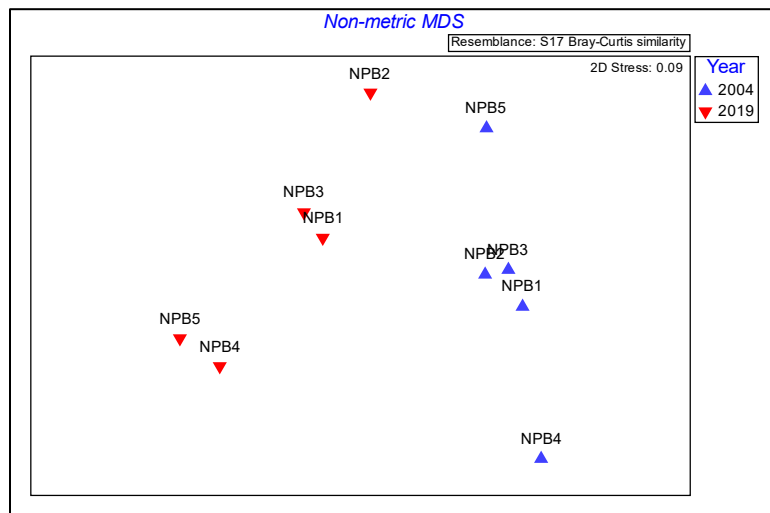


Figure 19. nMDS of floristic composition by transects at NPB in 2004 and 2019.

Table 11. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at NPB (TR=tree, SH=shrub, SS=subshrub, GR=graminoid, FB=forb).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Vaccinium corymbosum</i>	SS	0.00	0.34	17.7
<i>Rubus hispida</i>	SH	0.31	0.12	27.2
<i>Vaccinium macrocarpon</i>	SS	0.50	0.57	36.3
<i>Triadenum virginica</i>	FB	0.18	0.01	45.4
<i>Morella pensylvanica</i>	SH	0.21	0.23	50.5

NPC

A large separation in ordinal space illustrates floristic differences between 2004 and 2019 (ANOSIM $R=0.61$; $p=0.01$) (Figure 20). This shift was driven by the spread of *Pinus rigida* and *Morella pensylvanica*, contrasted by a decline in *Juncus greenei* and *Deschampsia flexuosa* (Table 12).

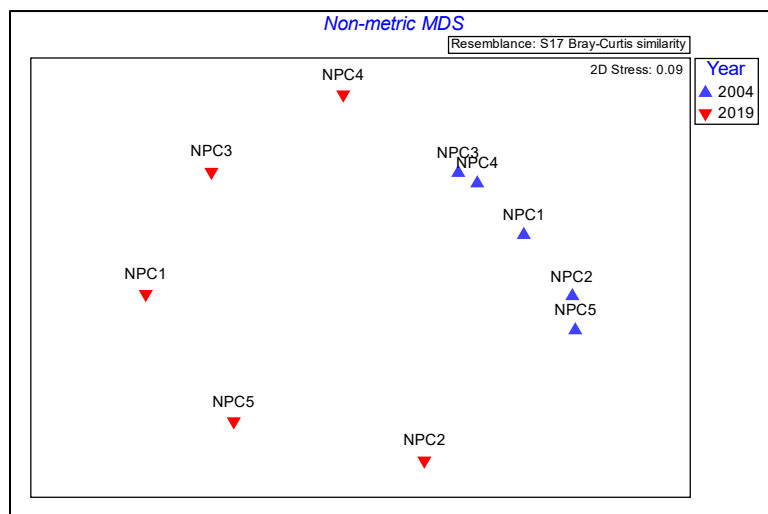


Figure 20. nMDS of floristic composition by transects at NPC in 2004 and 2019.

Table 12. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at NPC (TR=tree, SH=shrub, SS=subshrub, GR=graminoid, FB=forb).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Pinus rigida</i>	TR	0.00	0.41	25.4
<i>Juncus greenei</i>	GR	0.48	0.14	47.3
<i>Deschampsia flexuosa</i>	GR	0.39	0.15	63.9
<i>Morella pensylvanica</i>	SH	0.15	0.19	77.2

PLA

Similar to site NPA, there were relatively minor shifts in transect vegetation and the plant community in 2019 was statistically similar to that in 2004 (ANOSIM $R=-0.07$; $p=0.64$) (Figure 21).

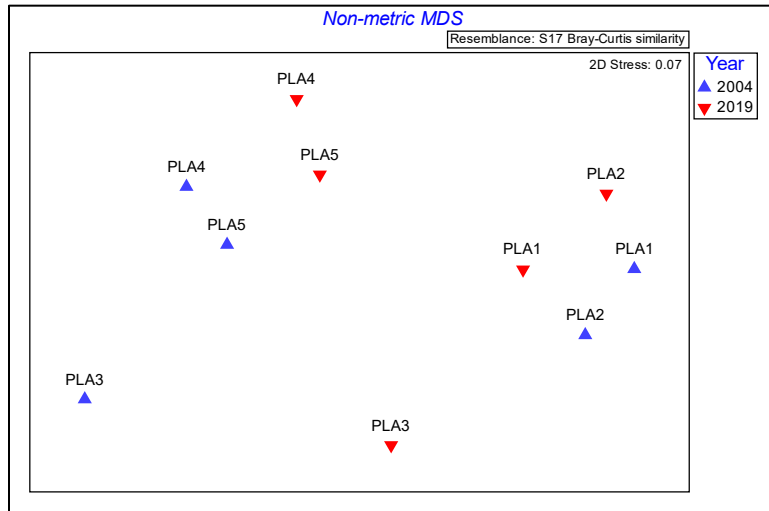


Figure 21. nMDS of floristic composition by transects at PLA in 2004 and 2019.

PLB

At PLB, dune slack vegetation in 2004 statistically similar to that in 2019 (ANOSIM $R=-0.07$; $p=0.63$) (Figure 22).

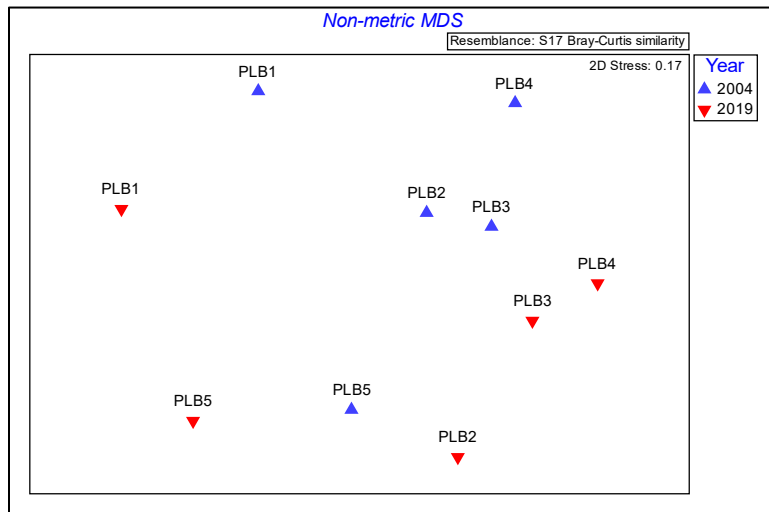


Figure 22. nMDS of floristic composition by transects at PLB in 2004 and 2019.

PLC

Similar to PLB, PLC exhibited no statistically significant shift in plant species composition since 2004 (ANOSIM $R=0.02$; $p=0.38$) (Figure 23).

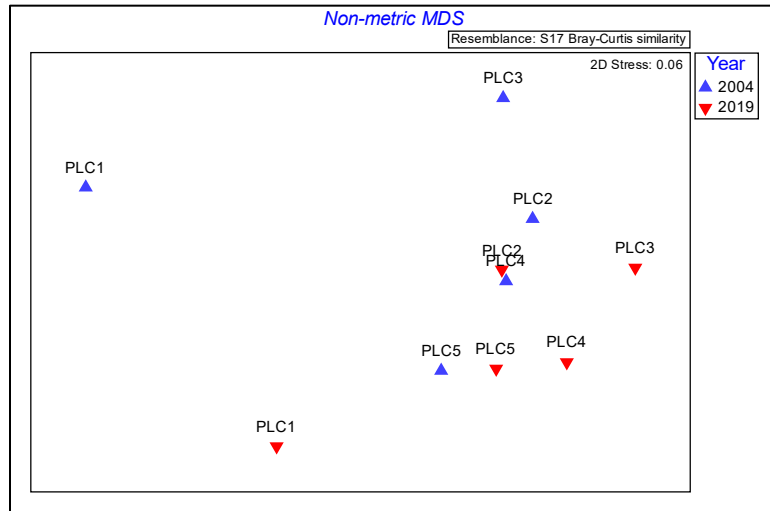


Figure 23. nMDS of floristic composition by transects at PLC in 2004 and 2019.

RPA

This site is adjacent to a salt marsh and sea level rise between 2004 and 2019 has resulted in pulses of salt water delivered to this wetland during storm events and extreme high tides. This has dramatically altered the wetland vegetation (ANOSIM $R=0.88$; $p=0.01$) (Figure 24). Since 2004, *Vaccinium macrocarpon*, *Toxicodendron radicans*, *Pinus rigida*, *Cladium mariscoides*, *Gaylussacia baccata*, and *Morella pensylvanica* have virtually disappeared, being replaced by invasive *Phragmites australis* (Table 13).

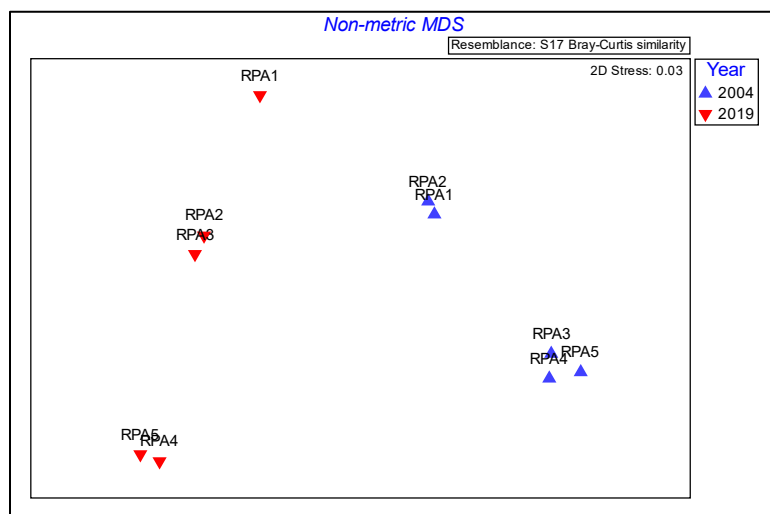


Figure 24. nMDS of floristic composition by transects at RPA in 2004 and 2019.

Table 13. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at RPA (TR=tree, SH=shrub, SS=subshrub, GR=graminoid, FB=forb).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Vaccinium macrocarpon</i>	SS	0.61	0.09	24.8
<i>Phragmites australis</i>	SH	0.30	0.64	42.4
<i>Toxicodendron radicans</i>	SH	0.22	0.13	50.6
<i>Pinus rigida</i>	TR	0.17	0.01	58.2
<i>Cladium mariscoides</i>	GR	0.13	0.00	64.6
<i>Gaylussacia baccata</i>	SH	0.11	0.00	69.6
<i>Morella pensylvanica</i>	SH	0.10	0.01	73.9

RPB

A significant difference in plant communities emerged between 2004 and 2019, mostly due to a reduction in *Vaccinium macrocarpon*, *Pinus rigida*, and *Kalmia angustifolia*, while *Vaccinium corymbosum* expanded (ANOSIM $R=0.22$, $p=0.03$) (Figure 25, Table 14). The disappearance of *Kalmia angustifolia* from RPB5, where it was fairly abundant in 2004, is the reason for the large gap in ordinal space in the nMDS plot below.

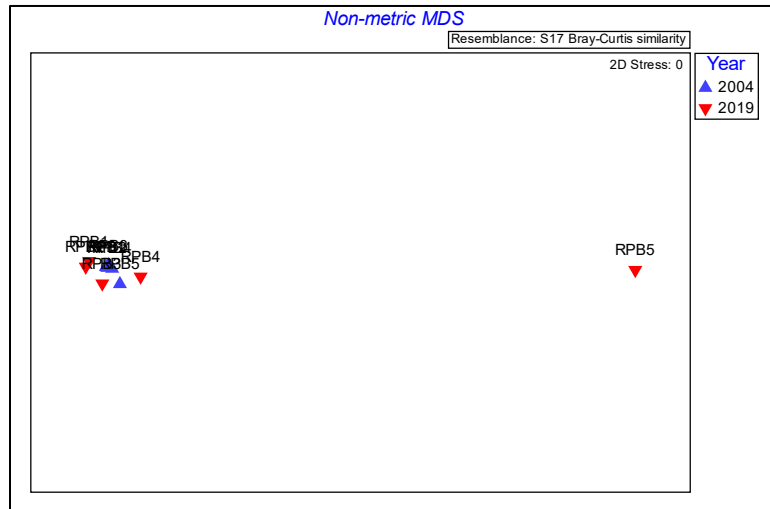


Figure 25. nMDS of floristic composition by transects at RPB in 2004 and 2019.

Table 14. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at RPB (TR=tree, SH=shrub, SS=subshrub, GR=graminoid, FB=forb).

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Vaccinium macrocarpon</i>	SS	0.67	0.61	24.6
<i>Pinus rigida</i>	TR	0.41	0.37	42.5
<i>Vaccinium corymbosum</i>	SH	0.13	0.31	58.9

SMA

The wetland plant community in SMA exhibited significant change between 2004 and 2019 (ANOSIM $R=0.61$; $p=0.01$) (Figure 26). This site is unique in that it periodically receives a large amount of salt spray from the ocean, which raises salinity levels enough to influence the vegetation. Anecdotal there is also a large amount of sand deposition onto this site from the nearby bluffs. Regardless, the vegetation in SMA experienced a large increase in *Agrostis hyemalis*, a smaller increase in *Toxicodendron radicans*, and a precipitous decline in both *Ammophila breviligulata* (common) and *Erechtites hiericifolia* (common) (Table 15).

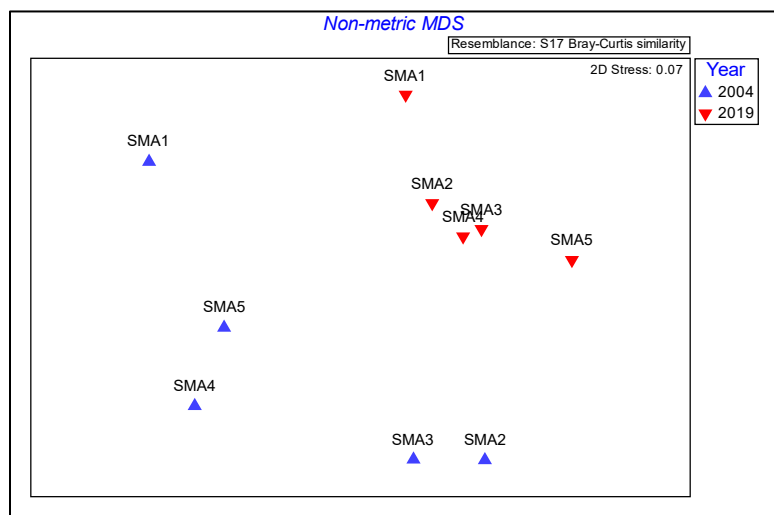


Figure 26. nMDS of floristic composition by transects at SMA in 2004 and 2019 (TR=tree, SH=shrub, SS=subshrub, GR=graminoid, FB=forb).

Table 15. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at SMA.

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Agrostis hyemalis</i>	GR	0.28	0.95	33.1
<i>Toxicodendron radicans</i>	SH	0.55	0.65	46.7
<i>Ammophila breviligulata</i>	GR	0.19	0.00	55.9
<i>Erechtites hiericifolia</i>	FB	0.18	0.00	64.7
<i>Phragmites australis</i>	SH	0.22	0.22	72.2

SMB

At this site, plant communities in 2019 were statistically different than in 2004 (ANOSIM $R=0.44$, $p=0.01$) (Figure 27). The years between 2004 and 2019 saw an increase in *Morella pensylvanica*, *Vaccinium macrocarpon*, *Toxicodendron radicans*, and *A. breviligulata*. Conversely, *Deschampsia flexuosa*, *Agrostis hyemalis*, *Dichanthelium acuminatum*, and *Euthamia tenuifolia* disappeared (Table 16)

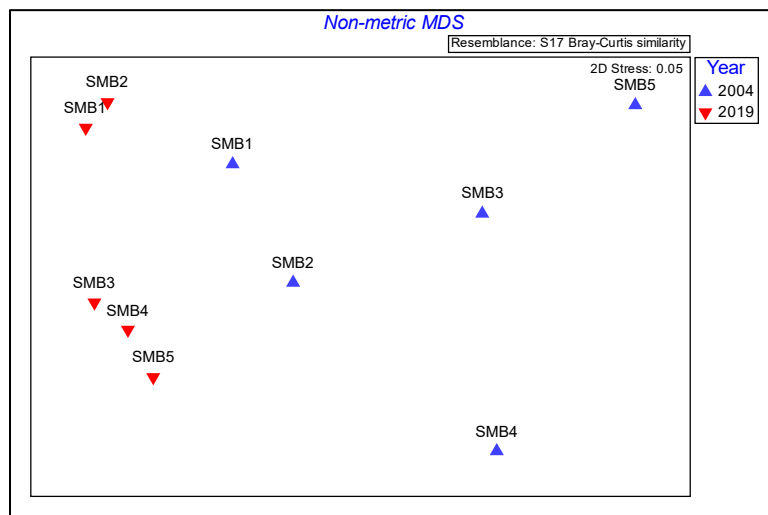


Figure 27. nMDS of floristic composition by transects at SMB in 2004 and 2019 (TR=tree, SH=shrub, SS=subshrub, GR=graminoid, FB=forb).

Table 16. SIMPER results indicating the species with the largest contribution to floristic dissimilarities between 2004 and 2019 at SMB.

Species	Growth form	Ab-2004	Ab-2019	%Cum Var
<i>Morella pensylvanica</i>	SH	0.11	0.32	14.0
<i>Vaccinium macrocarpon</i>	SS	0.34	0.51	26.5
<i>Ammophila brevilingulata</i>	GR	0.12	0.22	38.3
<i>Deschampsia flexuosa</i>	GR	0.21	0.04	49.8
<i>Toxicodendron radicans</i>	SH	0.13	0.19	58.2
<i>Agrostis hyemalis</i>	GR	0.08	0.00	63.5
<i>Dichanthelium acuminatum</i>	GR	0.07	0.00	68.5
<i>Euthamia tenuifolia</i>	FB	0.08	0.01	73.2

When the above sites were analyzed collectively as grouped by growth form, a distinct community trend emerged (Table 17). Clearly, the wetlands are losing the “open” character as shrubs and trees encroach into these depressions at the expense of graminoids, forbs, and sub-shrubs like *V. macrocarpon* (cranberry).

Table 17. Mean midpoint percentages of vegetation grouped by growth form in 2004 vs. 2019 and the absolute and percent difference between survey years.

Growth form	2004	2019	Diff	%Diff
graminoid	4.6%	1.5%	-3.1%	-67%
forb	1.1%	0.5%	-0.6%	-57%
subshrub	72.9%	33.5%	-39.5%	-54%
Shrub ¹	1.7%	2.8%	1.1%	64%
Tree ¹	0.8%	3.1%	2.3%	281%

¹ Growth forms that are increasing in abundance, also shown shaded in gray.

Trends in select key species

All transects all sites

From this and previous analyses, there are five taxa that account for much of the floristic change within dune slack wetlands. With only four data points (representing each of the four surveys completed thus far), there is not yet much statistical power to detect trends. However, *Juncus greenei* exhibited a significant decline with a very high correlation coefficient (Figure 28). The same was true for *Pinus rigida* and *Vaccinium corymbosum*, except the trend was opposite as these species increased over time. *Cladium mariscoides* and *Vaccinium macrocarpon* also exhibited reductions, but with extremely low abundance values in 2009 that added substantial variability to any temporal trends (Figure 28). Regardless, graminoid, forb, and subshrub vegetation is gradually succumbing to increasing abundances of woody shrubs and trees in a predictable pattern of succession (Berendse et al. 1998).

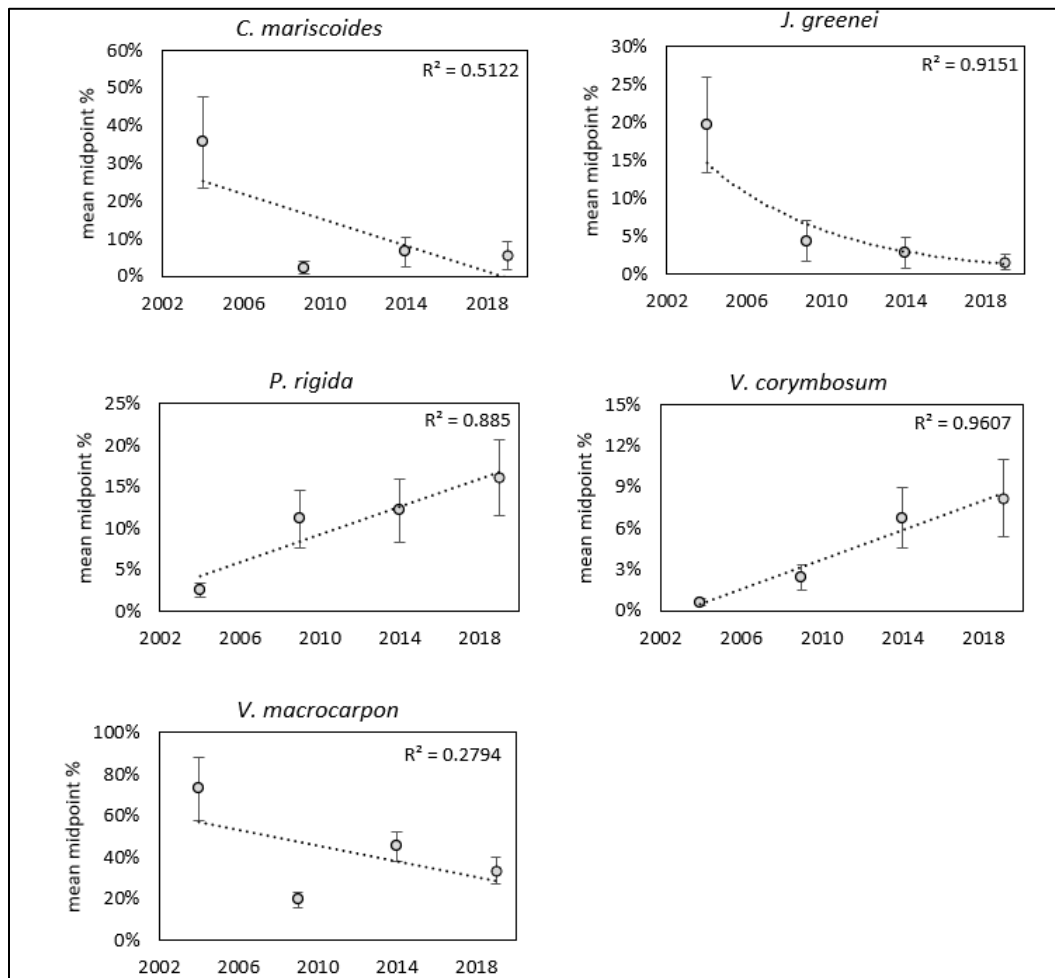


Figure 28. Temporal trends in the cover of key graminoid vs. shrub vegetation in the IS sites between 2004 and 2019.

Environmental parameters

Porewater

Although no porewater samples were collected in 2009, data from the other 3 survey years indicates that porewater pH may be generally decreasing, as is typical for these types of wetlands (Berendse et al. 1998). On the other hand, porewater conductivities exhibited high variability and no temporal trend (Figure 29).

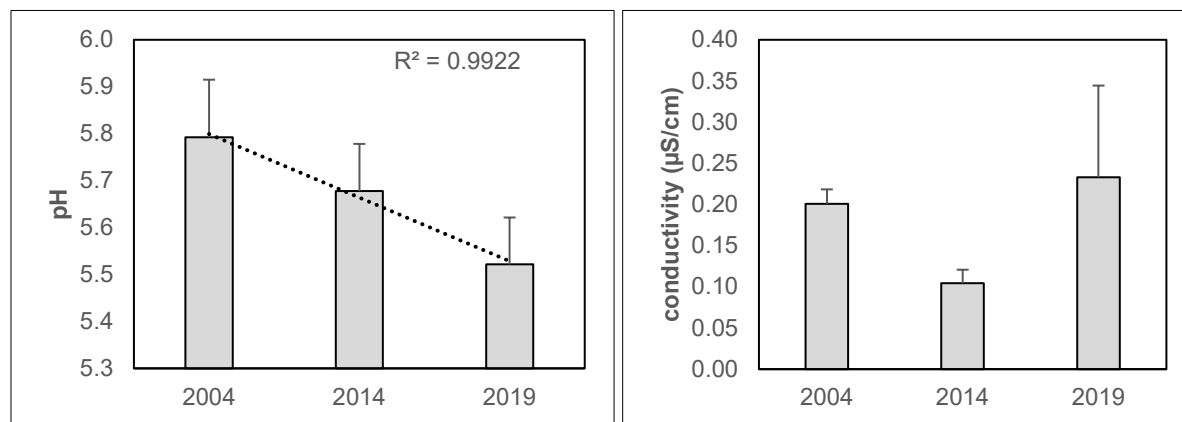


Figure 29. Porewater pH (left) and conductivity (right) by survey year (no porewater collected in 2009; error bars are standard errors of means).

Soil Properties

The organic content of soils from the 15 original IS sites shows no change from 2004 to 2014, followed by a large increase in 2019 (Figure 30). A more detailed inspection of the data reveals that there were considerable increases in organic matter content of soil cores from NPA, PLB, and RPA. Omission of those sites, however, still reveals a sizeable increase among the other sites. Soil organic matter generally increases with succession. However, sand deposition and hydroperiod both influence this process. In dry years a portion of soil organic matter is lost through oxidation, whereas accumulation occurs under increased flooding during wet years. Notwithstanding, hat more surveys are needed to properly evaluate this variable as a component of the long-term dune slack monitoring protocol.

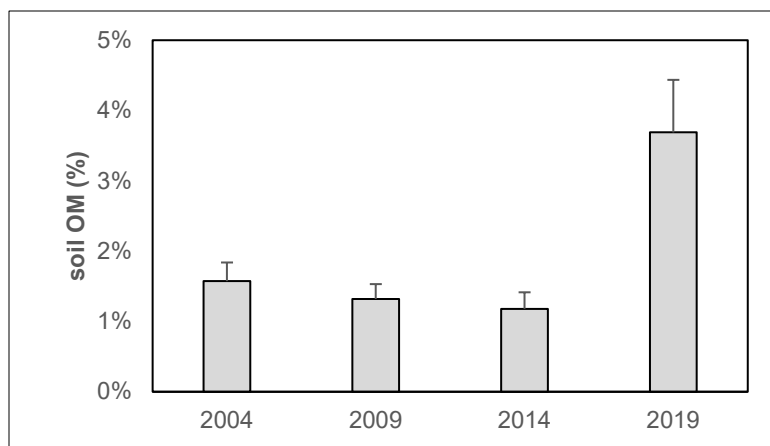


Figure 30. Mean percent soil organic matter (OM) in cores from the 15 original IS sites by survey year (error bars are standard errors of the means).

Local climate between 2004 and 2019

Between 2004 and 2019, mean daily air temperature during the growing season (Chatham, MA) exhibited a significant rising trend (Figure 31), although there is substantial interannual variability. The years when surveys were conducted were relatively cool in comparison to many other years up until 2014.

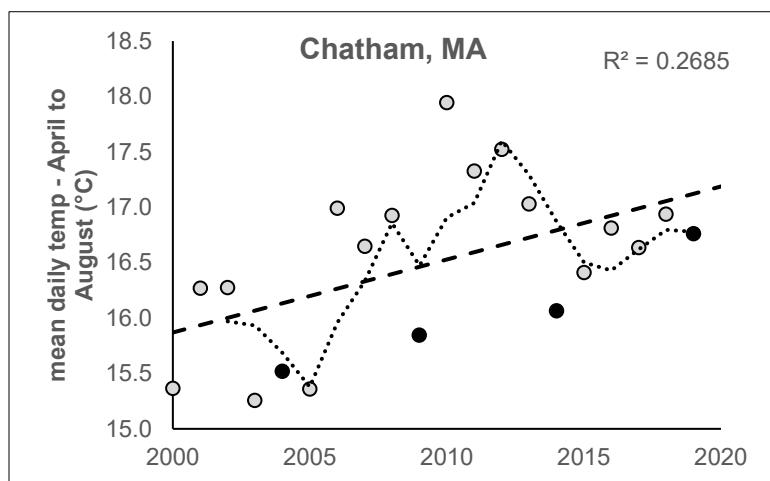


Figure 31. Mean daily air temperature (Chatham) between 2000 and 2019 (solid black circles indicate dune slack survey years) with the 3-year running average of this variable (dotted line).

Figures 32 and 33 illustrate precipitation patterns from 2000–2019. Variability in total annual and growing season precipitation illustrates the lack of any statistically significant trends.

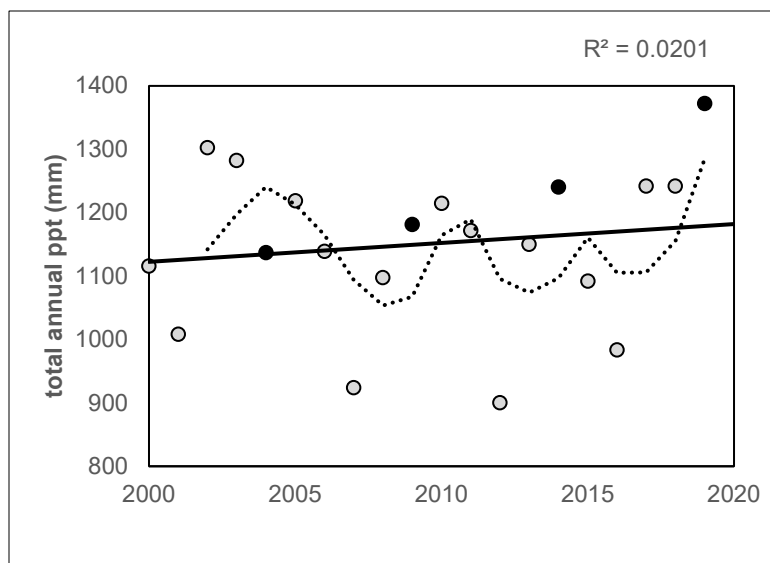


Figure 32. Total annual precipitation (ppt) from 2000–2019 (Chatham, MA) (solid black circles indicate dune slack survey years; dotted line is the 3-year running average of ppt).

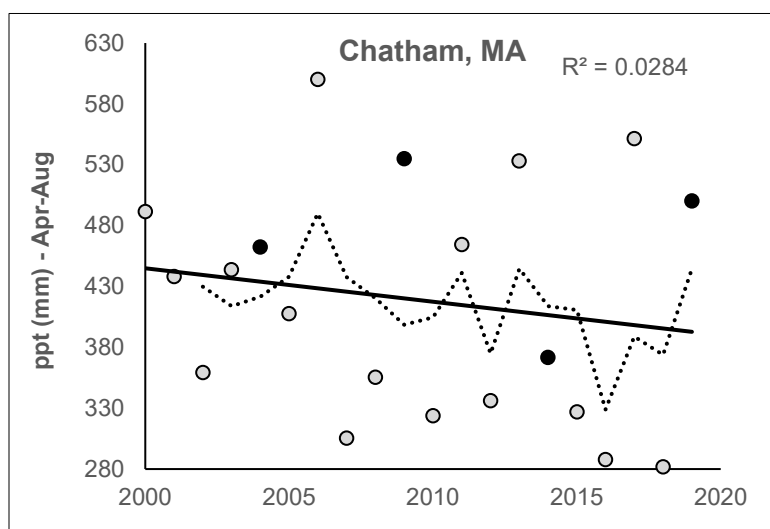


Figure 33. Total growing season (April–August) precipitation (ppt) from 2000–2019 (Chatham, MA) (solid black circles indicate dune slack survey years; dotted line is the 3-year running average of ppt).

Groundwater levels from a USGS monitoring well in the Province Lands (MA-PZW 78) show that the freshwater lens has risen over time (Figures 34), ostensibly due to SLR (as has previously been documented in numerous groundwater wells through CACO; see Smith and Medeiros 2018). Although individual sites have unique hydrologic characteristics much of the time, a rising water table will theoretically affect the hydroperiod of many wetlands in the form of increased flooding depth/duration. However, other effects of climate change may play an antagonistic role given that evaporation and evapotranspiration both increase with temperature and the latter will increase greatly with the proliferation of large woody vegetation, particularly trees.

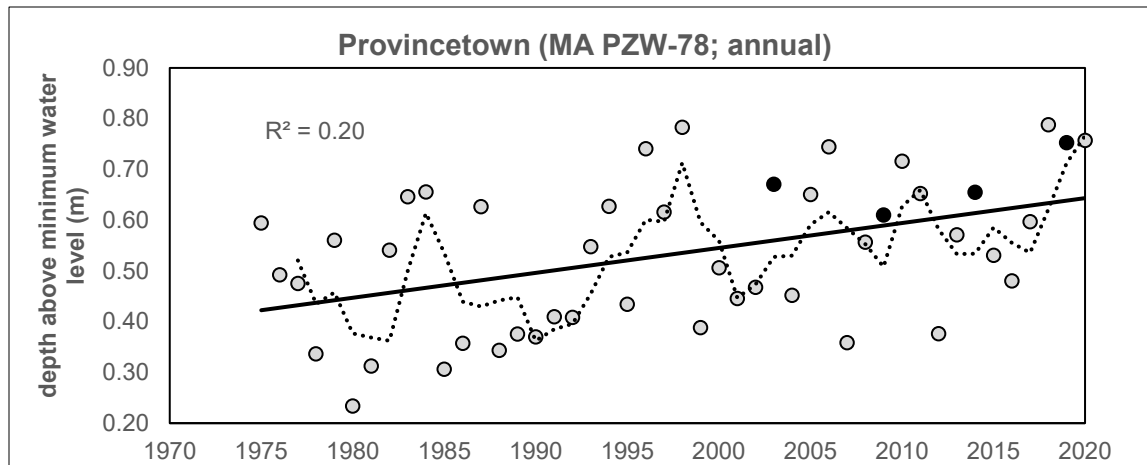


Figure 34. Mean annual groundwater elevations (relative to lowest reading) between 1975 and 2020 in Provincetown, MA (solid black circles indicate dune slack survey years; dotted line is the 3-year running average of ppt).

While it is difficult to relate the above trends in climate variables to floristic change in dune slack wetlands, they do indicate that these critical factors regulating plant growth and wetland hydroperiod are shifting, and this will influence these systems in numerous ways.

Discussion

CACO's Ecosystem Monitoring program has yielded valuable information by which to understand vegetation structure and composition in dune slack wetlands, and how it is changing in response to both natural and anthropogenic factors. Since the inception of monitoring in 2004, there have been significant shifts in the flora of these systems. Wetland age (and stage of succession) primarily determines the vegetative character of these systems since standing water is around for just long enough to exclude terrestrial vegetation but too short to exert much selective pressure among hydrophytic taxa (Smith et al. 2008). Graminoid, forb, and sub-shrub vegetation (the latter being mostly cranberry), which typically dominate newly formed wetlands, are gradually replaced by woody shrubs and trees as they evolve from open- to closed-canopy systems (Table 17). By monitoring dune slack vegetation over a decadal time scale, these changes are now quite predictable. In fact, has dune slack wetlands provide excellent natural laboratory for understanding successional processes.

Some of the unique flora in open, graminoid-dominated wetlands (e.g., sundews, orchids) will disappear as woody vegetation expands. Furthermore, opportunities for new wetlands to form in the wake of dune migration are decreasing as vegetation continues to stabilize the landscape. On the other hand, groundwater levels have exhibited a long-term rise, which is partially attributed to sea level rise (Smith and Medeiros 2018). This will presumably create new wetlands where the water table becomes elevated enough to intersect with the ground surface.

The future status of dune slack wetlands depends on many other climatic and landscape-level processes. Shifts in the amounts and timing of rainfall, trends in groundwater elevations, and rising air temperatures will all have complex interactive effects. Disturbances like high wind/storm events can deposit large amounts of sand into wetlands. Alterations in precipitation patterns, air temperatures, evaporation, and evapotranspiration will influence hydroperiod and soil properties. Moreover, the creation of new dune slack wetlands is becoming increasingly limited by stabilization of the surrounding landscape by colonizing plants. In addition, dune slack wetlands will all continue to change and undergo succession. These processes can be observed in aerial photographs across the entire dunes landscape (both terrestrial and wetland habitat), across which bare, or sparsely vegetated sand dunes (light colored terrain) are quickly colonized (dark colors) (Figure 35).

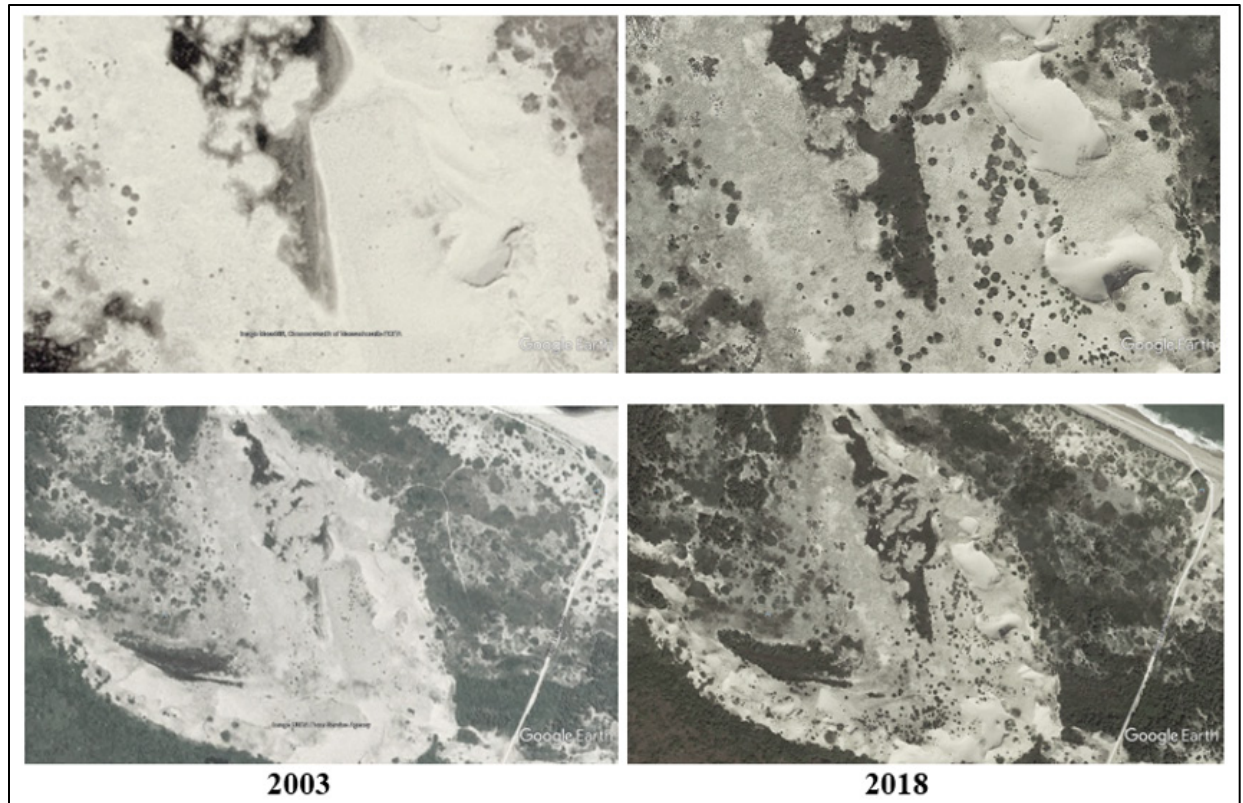


Figure 35. Aerial images of a dune slack wetland in 2003 (top left) and in 2018 (top right). Bottom photos are scaled out for a larger view of the landscape.

Finally, eradication of *P. australis* should be considered as a future management goal for the few wetlands that contain it. The monitoring data show that it is becoming more abundant. *Salix cinerea* (gray willow) and *Lythrum salicaria* (purple loosestrife) are other species that could also be treated in the future.

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