

Assessment of Plant Community Characteristics in Natural and Human-Altered Coastal Marsh Ecosystems

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5 ***Assessment of Plant Community Characteristics in Natural and Human-Altered***
6 ***Coastal Marsh Ecosystems***

7
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21 **Abstract** Salt marsh ecosystems provide many critical ecological functions, yet they are
22 subject to considerable disturbance ranging from direct human alteration to increased
23 inundation due to climate change. We assessed emergent salt marsh plant characteristics
24 in the Tuckerton Peninsula, a large expanse (~2,000 ha) of highly inundated habitat along
25 the southern New Jersey coast, USA. Key salt marsh plant parameters were monitored in
26 the heavily grid-ditched northern segment, Open Marsh Water Management (OMWM)
27 altered central segment, and the shoreline altered southern segment of the peninsula in the
28 summer months of 2011 and 2013. Plant species composition and three metrics of
29 abundance and structure (maximum canopy height, percent areal cover, and shoot
30 density) were examined among marsh segments, along transects within segments,
31 seasonally by month, and between years. Despite seasonal or annual variability, the
32 northern segment of the marsh differed in plant species composition from the central and
33 southern segments. This difference was partly due to greater percent areal cover in the
34 northern segment of such upper marsh species as *Spartina patens* and *Distichlis spicata*.
35 *S. patens* also exhibited higher shoot densities in the northern segment than the central
36 segment. Despite the higher abundance of upper marsh species, marsh surface elevations
37 were lower in the northern segment than in the central or southern segments, suggesting
38 the influence of altered hydrology due to human activities. Understanding current
39 variation in the emergent salt marsh vegetation along the peninsula will help inform
40 future habitat change in other coastal wetlands of New Jersey and the mid-Atlantic region
41 subject to natural and anthropogenic drivers.
42

43 **Keywords:** Tuckerton Peninsula, salt marsh habitat, marsh plant communities, species
44 composition, climate change effects
45
46

47 **Introduction**

48 Coastal salt marshes are an important native habitat (Chapman 1974; Mitsch and
49 Gosselink 2015) and have long been key systems for studying community and ecosystem
50 level processes (Ewanchuk and Bertness 2004). Salt marshes are generally comprised of
51 only a few dominant species from low to high marsh elevations across a gradient of tidal
52 flooding, salinity, and physical stressors (Adam 1990; Adam et al. 2008; Bertness and
53 Ewanchuk 2002; Levine et al. 1998). Combined human activities and climate change are
54 having a dramatic effect on the structure, function and species composition of salt marsh
55 ecosystems (Day et al., 2008).

56

57 Though fairly simple in structure, salt marshes provide an array of vital ecological
58 functions and services. They constitute important nursery habitat for many estuarine and
59 marine fishes, including those of recreational and commercial importance (Meixler et al.
60 2005). They also provide feeding and refuge areas for numerous invertebrates, havens
61 for migratory birds, and are favored habitats for various amphibian, reptilian, and
62 mammalian species (Able and Hagen 2000; Kennish et al. 2012; Peterson and Turner
63 1994). In short, salt marshes are areas of strikingly high biodiversity (Strayer and
64 Findlay 2010). In addition, these vital coastal habitats act as a buffer from storm activity
65 by dissipating physical energy, creating a natural flood zone, and reducing the risk of
66 inundation in adjacent watersheds which could pose a hazard to some coastal
67 communities (Boorman 1992; King and Lester 1995). Coastal salt marshes are sites of
68 intense nutrient cycling and carbon sequestration (blue carbon), thereby simultaneously
69 improving water quality, acting as carbon sinks, and filtering contaminants that could

70 impact nearby estuarine waters (Temmerman et al. 2013). Further, the organic matter
71 concentrated in salt marshes constitutes an important food source for a wide variety of
72 commercially important fish and shellfish species (Boorman 1999).

73

74 Despite their many benefits, salt marshes along the east coast of North America are
75 experiencing substantial change and degradation (Gedan et al. 2011; Kirwan and
76 Megonigal 2013). Anthropogenic alterations, specifically in highly developed coastal
77 areas, are common (Hartig et al. 2002) and result from a wide range of activities such as
78 parallel grid ditching, Open Marsh Water Management (OMWM), hardening and
79 compression of the shoreline, hydrologic modification, extension of bulkheads,
80 landfilling, pollution, agriculture, urbanization, resource extraction, introduction of alien
81 species, and recreation (Kennish et al. 2014a; Strayer and Findlay 2010).

82

83 In addition to these direct human alterations, impacts to salt marshes due to climate
84 change are also of considerable concern. Anthropogenic impacts have already replaced
85 past shorelines (expansive marshes bordered by forest) with the current highly varied mix
86 of semi-natural and highly engineered shore zones (Strayer et al. 2012); these losses are
87 expected to continue with rising sea level and climate-induced change (Gedan et al. 2011;
88 IPCC 2014). Although accretion of sediments and organic matter in the future may occur
89 at a rate sufficient to maintain marsh elevation in the face of rising sea level, the current
90 salt marsh accretion rate in the area of our study, the Tuckerton Peninsula salt marsh
91 system (0.17 cm yr^{-1} ; Velinsky et al. 2011), appears to be insufficient to maintain its
92 elevation over the long term. With sea-level rise projected to average 45 cm in this

93 region of New Jersey by 2050 (Miller et al. 2013), salt marsh habitat will be vulnerable to
94 conversion either as mud/peat/sand flats (unconsolidated shore) or open water. The
95 future character and ecological health of this salt marsh system and east coast shorelines
96 in general may require management of a very different quality than in the past.

97

98 Given the impending effects of climate and anthropogenic changes along the New Jersey
99 coast, this is an important time in which to study alterations in the region's salt marshes.

100 A major weakness in our knowledge and management of these hazards in salt marsh
101 communities is the dearth of locations that have been studied (Adam 2015; Ewanchuk
102 and Bertness 2002; Mitsch and Gosselink 2015), with a particular focus on plant
103 community change through space and time along the New Jersey coast (Kennish et al.
104 2014b). Further, monitoring of salt marsh composition and function under a framework
105 of global climate change is essential to the development of models to predict future
106 changes. Predictions from models will likely play an important role to support
107 management and planning decisions for adaptation and conservation of estuarine
108 ecosystems (IPCC 2007, 2014).

109

110 In this study, we investigated how the species composition and vegetation structure of the
111 Tuckerton Peninsula salt marsh system differed among salt marsh areas subject to
112 different sources of human and natural disturbance. Specifically, we assessed species
113 composition, maximum canopy height, percent areal cover, and shoot density of the salt
114 marsh vegetation in three segments of the Tuckerton Peninsula across the growing
115 seasons of two nonconsecutive years. Our goals were to evaluate differences among

116 marsh segments, variation within each segment, and seasonal or annual changes over
117 time. We put our results in the context of the anthropogenic and natural drivers of change
118 in the system. As such, this contribution is important as it adds to the national and global
119 databases of case studies on natural and human-altered coastal marsh ecosystems.

120

121 **Methods**

122 Study site

123 The study area, Tuckerton Peninsula, forms a large expanse (~20 km²) of highly
124 inundated and dissected salt marsh habitat (Figure 1) typical of most coastal marshes in
125 the region (Kennish 2001). Extensive *Spartina alterniflora* Loisel. (smooth cordgrass)
126 salt marshes border broad areas (~33.8 km²) of Little Egg Harbor to the north and the
127 Mullica River-Great Bay Estuary to the south. Other common species include *S. patens*
128 (Aiton) Muhl. (salt marsh hay), *Distichlis spicata* (L.) Greene (spike grass), *Limonium*
129 *carolinianum* (Walter) Britton (lavender thrift), and *Salicornia* spp. L. (glasswort). The
130 area has experienced significant interior salt marsh loss due to an expanding channel
131 network and pond development, a process described by Kirwan et al. (2008). In addition,
132 shoreline erosion and rising sea level are causing significant loss of salt marsh habitat,
133 measured at 1.6 m y⁻¹ between 1995 and 2008 (Kennish et al. 2014b) along the southern
134 shoreline of the peninsula, and these factors are contributing to slow submergence of the
135 marsh platform. If this trend continues, the peninsula will be among the first salt marsh
136 platforms along the central New Jersey coast to be eliminated by sea-level rise and
137 erosion (Kennish et al. 2012; Kennish et al. 2014a).

138

139 The Tuckerton Peninsula is within the Jacques Cousteau National Estuarine Research
140 Reserve (JCNERR) which encompasses more than 465 km² of aquatic and terrestrial
141 habitats along the south-central New Jersey coastline. The reserve contains more than
142 130 km² of salt marsh habitat. Human development in the region is low (<3%), making
143 the Mullica River-Great Bay Estuary one of the least disturbed estuarine systems in the
144 Northeastern corridor.

145

146 Data collection

147 The Tuckerton Peninsula was divided into three segments (northern, central, and
148 southern) for this study, with three sampling transects (each ~200 m in length)
149 established in each segment. Along each of the nine transects, 10 plots (1 m² in area)
150 were sampled monthly during the peak salt marsh growth period (June-September 2011
151 and June, July, and September 2013; Figure 1). Transects 1-3 occur in the northern
152 segment, which is heavily impacted by surface alteration (grid ditching) of the marsh
153 surface (i.e., direct anthropogenic alteration). Transects 4-6 are located in the central
154 segment, an area impacted by OMWM. Transects 7-9 lie in the southern segment, where
155 the salt marsh habitat is most susceptible to current and wave activity, erosion, and sea-
156 level rise (i.e., climate change impacts). Transect locations within each segment were
157 chosen based on accessibility.

158

159 Sampling plots were located with a differentially-corrected Global Positioning System
160 (GPS) and marked with PVC stakes driven into the marsh surface. For each of the nine
161 transects, the 10 sampling plots were marked at evenly spaced intervals of 20 m. RTK

162 GPS (Real-Time-Kinematic Global Positioning) data were collected at each of the plots.
163 Marsh elevation above mean sea level for each plot was obtained from digital elevation
164 model data (10 m x 10 m) from the New Jersey Department of Environmental Protection.

165

166 We followed the non-destructive sampling protocols of Moore (2011) for emergent salt
167 marsh habitat, consistent with field protocols commonly used in the National Oceanic
168 and Atmospheric Administration's (NOAA) National Estuarine Research Reserve
169 Program. A 0.25 m² metal quadrat was placed on the marsh surface at each sampling plot,
170 and data were recorded on maximum canopy height, percent areal cover, and shoot
171 density for each species. Maximum canopy heights (in cm) were measured for the
172 dominant species based on the length of the longest leaf (Moore 2011). Percent areal
173 cover estimates were determined using a standardized reference guide based on cover
174 estimate values with 5% intervals (Moore 2011). The number of stems or shoots of each
175 species in the quadrat was counted to determine its density. For particularly dense plots,
176 the quadrat was subsampled for shoot density by counting the total number of shoots in
177 0.0625 m² of the quadrat.

178

179 Data analysis

180 We used non-metric multidimensional scaling (NMDS) to show variation within or
181 among marsh segments and through time (months or years) based on percent areal cover
182 of plant species. Analyses were run using PC-ORD version 7.0. With either plot or
183 transect as the sampling unit, we ran NMDS analyses using Sorensen (Bray-Curtis)
184 dissimilarity matrices of untransformed percent areal cover interval data for all plant

185 species occurring in more than two plots or transects. We then analyzed differences in
186 species composition among factors (segments, transects, years, and months) using
187 repeated measures nonparametric multivariate analysis of variance, with plot as the
188 sampling unit and transect nested within segment. The repeated measures analysis
189 employed Adonis (Vegan library, R version 3.11) to test differences over time and
190 interactions with time (i.e., the repeated measure), and nested.npmanova (in the
191 BiodiversityR package of R) to test the main effect of segment or transect. This analysis
192 also used Sorensen (Bray-Curtis) dissimilarity matrices of untransformed percent areal
193 cover data, through 999 permutations. Because the repeated measures analysis identified
194 interactions between segment and time (month or year), we also used Adonis to test the
195 effect of segment for months individually.

196

197 In addition to these multivariate analyses for the salt marsh community as a whole, we
198 also analyzed relationships between response variables (maximum canopy height, percent
199 areal cover, and shoot density) and explanatory variables (spatial and temporal) both
200 across all species and for each species individually. Normality of each response variable
201 was tested using the Shapiro-Wilk test of normality in SAS version 9.3 (SAS Institute,
202 Cary, NC), and all variables were found to be non-normal. We transformed maximum
203 canopy height using a square root and applied a power transformation of 0.25 to percent
204 areal cover and shoot density following the suggestion from the Box-Cox procedure in
205 SAS.

206

207 Because we have multiple response variables, we explored the possibility of using
208 repeated measures multivariate analysis of variance (RM-MANOVA in SAS) for our
209 analysis. However, RM-MANOVA was not feasible because missing data in our design
210 (for two months in 2013) leads to bias in the analysis. Also, while RM-MANOVA can
211 account for correlated responses in space or from the same plot over time, it cannot
212 simultaneously account for the significant transect effect we detected for some response
213 variables and species. We then explored the possibility of using nonparametric tests
214 (Adonis and nested.npmanova) for analyses of multiple response variables but as of yet,
215 we are unaware of a way to test random effects using these analytical methods.

216

217 In contrast to RM-MANOVA or nonparametric alternatives, linear mixed models can
218 incorporate both missing data and random effects in the design. They are limited to
219 univariate models, however; a single mixed model cannot include correlated response
220 variables. We tested the strength of the correlation among our three response variables
221 and found that maximum canopy height is weakly correlated with the other two variables
222 ($r = 0.04$ for shoot density and $r = 0.22$ for percent areal cover). This weak relationship
223 held true when tested by individual months as well. The correlation between shoot
224 density and percent areal cover was higher ($r = 0.61$), therefore requiring a Bonferroni
225 correction to mitigate any increase in familywise error rate.

226

227 Thus, we used a linear mixed model (PROC MIXED in SAS) to examine the effects of
228 the explanatory variables on each of the transformed response variables, both across
229 species and for each of the seven species individually. The design for all mixed models

230 included transect nested within segment; latitude, longitude and marsh elevation as
231 random effects; and repeated measures for plots over time. Post hoc Tukey-Kramer tests
232 were performed for multiple comparisons in all mixed models. We used a first-order
233 autoregressive covariance structure, and denominator degrees of freedom were computed
234 using the KENWARDROGER option. Thus, we controlled for variance among transects;
235 latitudes, longitudes and marsh elevations; and repeated measures over time. We tested
236 for spatial autocorrelation separately for all three response variables using transect within
237 segment and plot within transect and segment as random factors, and repeated sampling
238 within plots with transect as the subject with an autoregressive covariance structure. We
239 found no spatial correlations for any of the response variables; thus, we did not include
240 this in the model. When response variables for a species showed no effect of transect,
241 latitude, longitude, or marsh elevation, we removed the selected random effect from the
242 model for that species. The Bonferroni correction compensates for increased Type I error
243 by testing each individual hypothesis at a significance level of α/m , where $\alpha = 0.05$ and
244 m is the number of hypotheses. In our case, $m = 3$, therefore significant differences were
245 determined in this study at $\alpha = 0.0167$ after applying the Bonferroni correction. Species
246 with few data points often could not compute; these were noted in the results in Tables 1
247 and 2.

248

249 **Results**

250 *Species patterns*

251 Seven species of marsh plants were found in plots within transects sampled in the study
252 area. *S. alterniflora* was the dominant species, the only species occurring in all of the

253 sampling transects in both 2011 and 2013. *L. carolinianum* and *Salicornia* spp. occurred
254 in all three segments during both years, though not all transects. *Morus rubra* L. (red
255 mulberry) was almost entirely found only in the northern segment, and *S. patens* was not
256 observed in the southern segment. *D. spicata* occurred in all three segments in 2011, but
257 was missing from the central segment in 2013. *Symphytotrichum tenuifolium* (L.) G.L.
258 Nesom (perennial saltmarsh aster) was found in all segments in 2011, but only in the
259 northern segment in 2013.

260

261 ***Spatial and temporal variation in community composition***

262 For June, July, August, and September of 2011 and September of 2013, plant community
263 composition differed between the northern marsh segment and the other two segments
264 (Figures 2 and 3a), as indicated by repeated measures nonparametric multivariate analysis
265 of variance of percent cover data. This difference was driven by two of the three
266 transects in the northern segment (Figure 3b), largely by the high abundance of *S. patens*
267 in these transects. Plant community composition shifted over time, by month ($F=17.98$,
268 $p=0.001$; Figure 3c) and year ($F=44.83$, $p=0.001$; Appendix A). Differences in
269 community composition among segments also depended on time: the main effect of
270 segment interacted with both month ($F=2.25$, $p=0.006$) and year ($F=4.23$, $p=0.003$). For
271 individual months, the plant community differed among marsh segments (i.e., the
272 northern segment differed from the other two segments (Figure 2, Appendix A)) in June
273 ($F=12.00$, $p=0.001$), July ($F=13.85$, $p=0.001$), August ($F=9.84$, $p=0.001$), and September
274 ($F=6.66$, $p=0.001$) of 2011 and September of 2013 ($F=10.98$, $p=0.001$). Differences in

275 community composition among transects were independent of time, either for month
276 ($F=11.36$, $p= 0.01$) or year ($F=4.14$, $p=0.02$).

277

278 *Across-species differences*

279 In contrast to the community-level analysis utilizing multivariate techniques, analyses
280 across all species (using linear mixed models for maximum canopy height, total percent
281 cover, or mean shoot density; Table 1) demonstrated no consistent differences among
282 segments for any of the three response variables. Differences in maximum canopy height
283 among marsh segments interacted with sampling year in two ways, however: (1) within
284 the year 2013, maximum canopy height was higher in the northern segment (43.4 ± 0.2
285 cm) than the central segment (27.6 ± 0.2 cm); and (2) within the central segment,
286 maximum canopy height was higher in 2011 (34.7 ± 0.1 cm) than in 2013 (27.6 ± 0.2
287 cm). Maximum canopy height varied by month with a significant increasing trend from
288 June through September, whereas total percent areal cover followed a significant
289 decreasing trend over the same period. Differences in mean shoot density among marsh
290 segments interacted with sampling month with density largely decreasing from June to
291 September.

292

293 *Spatial and temporal variation for individual species*

294 In analyses of species individually (linear mixed model analyses; Table 2), only shoot
295 density for *S. patens* differed significantly among marsh segments. Shoot density for *S.*
296 *patens* was higher in the northern segment (223.8 ± 11.8 shoots/m²) than the central
297 segment (59.2 ± 20.8 shoots/m²); *S. patens* did not occur in the southern segment. Only

298 *S. alterniflora* exhibited significant differences between years for shoot density (2013
299 higher; 81.6 ± 0.1 shoots/m² compared with 48.7 ± 0.1 shoots/m²) and percent areal cover
300 (2013 higher; 36.4 ± 0.01 % compared with 28.5 ± 0.01 %).

301

302 For *S. alterniflora*, maximum canopy height and percent areal cover changed through the
303 growing season, with maximum canopy height increasing from June (34.7 ± 0.1 cm)
304 through September (42.1 ± 0.1 cm), and percent areal cover decreasing from June ($38.4 \pm$
305 0.01%) through September ($26.6 \pm 0.01\%$). For *L. carolinianum*, maximum canopy
306 height also predominantly increased with progression through the growing season.

307 Differences in maximum canopy height of *Salicornia* spp. among marsh segments
308 interacted with sampling month with increasing canopy heights through the growing
309 season to August and then decreasing; heights in the northern segment were generally
310 highest and heights in the southern segment lowest. Differences in shoot density of *S.*
311 *patens* and *S. alterniflora* among marsh segments also interacted with sampling month
312 with largely decreasing values through the growing season and higher values in the
313 central segment compared to the northern segment for *S. patens*. *S. alterniflora* exhibited
314 fluctuating values through the growing season and highest values in the central segment
315 followed by the southern and northern segments, respectively. For individual marsh
316 species, differences among marsh segments did not vary by sampling year.

317

318 ***Analysis of explanatory factors***

319 Marsh surface elevation above mean sea level, latitude, and longitude explained some of
320 the observed variation in maximum canopy height, percent areal cover, and shoot density

321 for individual plant populations, reflecting the sensitivity of individual species to
322 different factors of change (Table 2). The factor with the strongest relationship to plant
323 response was marsh elevation, which differed among segments ($F = 370.32$, $p < 0.0001$),
324 with the northern segment exhibiting significantly lower elevation (1.8 ± 1.0 m)
325 compared to the central (3.0 ± 0.1 m) and southern segments (3.0 ± 0.1 m). Marsh
326 elevations along transects within the northern marsh segment varied from ~1-3 m, while
327 elevation remained constant around 3 m within the central and southern segments.
328 Differences in marsh elevation among segments were reflected in analyses of plant
329 species abundance and vegetation structure (Table 2). For example, for *Spartina patens*,
330 maximum canopy height was greater at lower marsh surface elevation. For *Salicornia*
331 spp., *Spartina patens*, and *Symphyotrichum tenuifolium*, percent areal cover was
332 generally higher at higher marsh elevations; while for *Spartina alterniflora*, shoot density
333 was higher at higher marsh elevations.

334

335 **Discussion**

336 Analysis of salt marsh plots revealed important differences in the vegetation of the
337 Tuckerton Peninsula among the three study segments. Despite seasonal or annual
338 variability over time, the northern segment of the marsh differed in plant species
339 composition from the central and southern segments (Figure 2); this difference was partly
340 due to greater percent areal cover (e.g., *S. patens*, *D. spicata*) and shoot density (e.g., *S.*
341 *patens*) for plant species typical of upper salt marsh communities. Differences in species
342 composition and vegetation structure between the northern segment of the marsh and the
343 central and southern segments may reflect drier conditions from parallel grid ditching

344 activities in the northern segment (Adam 2015, Day et al. 2008), relative to OMWM in
345 the central segment or sea-level rise and wave action in the southern segment. It is
346 important to note that other factors such as intra-segment differences (i.e., development
347 next to select transects), circulation and sedimentation patterns, underlying
348 hydrogeomorphic characteristics, or historical differences in elevation may also be at
349 play. It is likely that both human and natural drivers are playing a role; however, our
350 study design does not allow us to make this distinction clearly. Future investigations of
351 the Tuckerton Peninsula salt marsh should include physico-chemical measures to better
352 elucidate drivers of observed vegetation patterns within this complex system.

353

354 *Vegetation patterns and drivers of change*

355 Overall, our analyses of marsh species composition and vegetation structure suggest that
356 hydrologic and edaphic conditions differ across our sites, as has been shown in other salt
357 marsh systems (Adam 2015; Mitsch and Gosselink 2015). Hydrology and
358 geomorphology of the northern segment of the Tuckerton Peninsula salt marsh system
359 were heavily altered by parallel grid ditching decades ago to drain standing water and
360 reduce natal habitat for mosquito larvae, while concurrently enabling aquatic mosquito
361 larvae predators to access their prey (Gedan 2015). By this process, fewer pannes
362 formed, and the salt marsh surface was not as “wet” as unditched areas in the central and
363 particularly the southern segment of the peninsula. Similarly, Lathrop et al. (2000) and
364 Lathrop and Bognar (2001) reported far more pool habitat in unditched than ditched salt
365 marshes of the nearby Barnegat Bay-Little Egg Harbor Watershed.

366

367 The drying out of marsh surfaces can change plant community structure, function, and
368 species characteristics; emergent salt marsh plant communities can be altered
369 considerably by hydrological modification of the marsh surface (Kent 1994). Species
370 physiological tolerances to environmental stressors such as tidal inundation and anoxia
371 determine in large part salt marsh plant distribution patterns (Adam 2015; Bertness and
372 Ellison 1987; Emery et al. 2001). Higher marsh zones are relatively less stressful for
373 perennials than are conditions in the lower marsh zones where waterlogging and anoxia
374 are common (Emery et al. 2001). Marsh dewatering associated with parallel grid
375 ditching can lead to the conversion of more typical salt marsh vegetation (*S. alterniflora*,
376 *S. patens*, *D. spicata*) to plant communities characteristic of a drier, well-drained
377 condition (e.g., marsh shrubs) (Wolfe 2005). Our analysis suggests that, while marsh
378 shrubs were not yet abundant in the northern section of the Tuckerton Peninsula marsh,
379 ditching activities may be supporting a drier, upper marsh community there relative to
380 other surrounding areas.

381

382 Variation in water level, indicated in this study by marsh surface elevation, is a major
383 driver of vegetative spatial patterns in salt marsh systems generally (Bertness and Ellison
384 1987). In the Tuckerton salt marsh system, marsh surface elevation was a significant
385 explanatory factor for species such as *S. patens* and *Salicornia* spp. (Table 2). Dominant
386 plant species in the northern segment were more typical of an upper marsh community
387 (e.g., *Salicornia* spp., *D. spicata*, *M. rubra*, etc.). Species in this area may be adapted to
388 less frequent inundation, fewer waterlogged soils, and more stable conditions overall, and
389 less tolerant of extreme physical disturbance and interspecific competition (Bertness and

390 Ellison 1987; Pennings et al. 2005). One possible explanation for these observed
391 vegetation patterns would be the position of the northern marsh segment at the landward
392 side of the peninsula, where it is reasonable to expect higher marsh elevations, drier
393 conditions, and a corresponding plant community typical of the upper marsh.

394

395 Despite its upper marsh vegetation, however, the northern marsh segment had lower
396 surface elevations than the other two segments. There are a number of possible
397 explanations for the presence of upper marsh species despite lower elevations in the
398 northern marsh segment. For example, the northern segment may have had lower
399 elevation historically (despite being on the landward side) and correspondingly wetter
400 conditions; it may therefore have been ditched heavily to dry the area. Ditching may
401 have led to drier conditions that allowed the northern segment to support upper marsh
402 species. Alternatively, ditching may have caused the lower marsh elevations in the
403 northern segment by exposing the marsh surface to drying. This would likely increase
404 decomposition and subsidence rates, thereby lowering the marsh surface relative to the
405 unditched segments (Vincent et al. 2013). These processes would allow the northern
406 segment to support upper marsh species despite the lower elevations. In either scenario,
407 lower surface elevations in the northern segment compared with the other two segments
408 suggest that ditching has altered area hydrology significantly, supporting an upper marsh
409 plant community at elevations that might more typically support a lower marsh plant
410 community. The northern segment may also have supported an upper marsh community
411 historically, but likely with higher marsh surface elevations pre-ditching. Future
412 investigations of the Tuckerton Peninsula salt marsh should assess water depths and

413 inundation patterns throughout the growing season to elucidate the hydrologic drivers of
414 vegetation patterns.

415

416 In lower marsh plant communities in the central and southern marsh segments,
417 dominance of *S. alterniflora* rather than *S. patens* may reflect natural drivers of marsh
418 variation, human activities that have increased inundation, or a combination. Because it is
419 removed from adjoining upland areas, the central segment is somewhat more likely than
420 the northern segment to support a lower marsh plant community. However, the pattern of
421 tidal creeks in the Tuckerton Peninsula results in the vegetation not necessarily
422 conforming to an expected gradient from land to estuary. Additionally, the central
423 segment has undergone considerable OMWM, a mosquito-control technique supplanting
424 grid ditching that results in more frequently flooded and waterlogged areas particularly
425 near tidal creeks. While grid ditches are connected to tidal creeks on the marsh platform,
426 OMWM features are not, and they do not drain pannes and pools on the marsh surface as
427 do grid ditches; instead, sheet flow over the marsh surface delivers estuarine water to
428 reservoirs and canals (Kent 1994). In the southern segment, OMWM practices have not
429 been applied, but shoreline erosion due to sea-level rise and wave action is prevalent
430 (Kennish et al. 2014b). *S. alterniflora* was dominant in areas of OMWM, a finding also
431 documented by Elsey-Quirk and Adamowicz (2016), and in areas subject to sea-level
432 rise, wave action, and therefore increased likelihood of inundation. The success of *S.*
433 *alterniflora* in areas of OMWM (central segment) and in areas experiencing sea-level rise
434 and wave action (southern segment) is reasonable, given that dense stands of *S.*
435 *alterniflora* generally dominate in the intertidal zone or lower marsh communities

436 adjacent to tidal creeks and bays (Mitsch and Gosselink 2015; Tiner 1999), though other
437 explanations are possible.

438

439 A study of plant species composition in relation to hydrology in created ditches and ditch
440 plugs in New England salt marshes (roughly analogous to parallel grid ditching and
441 OMWM, respectively) and natural creeks and pools demonstrated similar patterns to
442 those observed in the Tuckerton Peninsula (Vincent et al. 2013). In this New England
443 study, *S. patens* was dominant in created ditched zones, and *S. alterniflora* was almost
444 absent, while the reverse was true in ditch plugs, comparatively (Vincent et al. 2013).

445 We found a similar trend with *S. patens* dominant in the ditched northern segment, and *S.*
446 *alterniflora* dominant in the OMWM habitat of the central segment. Higher water levels
447 in ditch plugged habitat were cited as partly responsible for the dominance of *S.*
448 *alterniflora* observed in the New England salt marsh study (Vincent et al. 2013), not
449 unlike the results we found in our OMWM habitat.

450

451 Overall, the spatial transition from *S. patens*-dominated marsh in the northern segment to
452 *S. alterniflora*-dominated marsh in the central and southern segments may indicate a
453 combination of natural and anthropogenic drivers. Observed vegetation patterns may
454 reflect responses to the different types of management or disturbance in these zones,
455 which often include marked shifts in plant species abundance and distribution,
456 particularly of the dominant forms (Day et al. 2008; Kirwan and Megonigal 2013;
457 Kirwan et al. 2008). Vegetative transitions across space may partly reflect a natural shift

458 from upper to lower marsh as well, but the boundaries may be shifted due to human-
459 induced disturbances.

460

461 ***Implications for management***

462 With continued sea-level rise and shoreline erosion of the Tuckerton Peninsula, careful
463 consideration of management strategies may be needed to mitigate marsh habitat loss and
464 increase sustainability of the system. Sea-level rise and shoreline erosion are most
465 notably affecting the southern segment of the marsh system; however, the lower marsh
466 surface elevations in the northern segment, likely due to ditching, increase concern about
467 rising sea levels coming into direct contact with the upper marsh plant community,
468 putting this area at greater risk. Measures that may be considered to sustain the marsh
469 include the use of living shorelines to stabilize marsh edges (Bilkovic and Mitchell 2017;
470 Bilkovic et al. 2016; Rella et al. 2017; Sutton-Grier et al. 2015), the application of thin-
471 layer deposition of sediment on the marsh platform to increase vertical accretion (Ford et
472 al. 1999; Mendelssohn and Cohn 2003; Tong et al. 2013), and hydrological restoration to
473 facilitate greater tidal flow and sediment delivery to the marsh surface (Durey et al.
474 2012). In addition, the planting of marsh grasses at strategic locations could build out
475 damaged marsh habitat (Moody et al. 2017). Such actions may help to retard loss of
476 marsh lands in our narrow study area and other similar peninsulas. Effective long-term
477 management plans are necessary to support the ecosystem services of the salt marsh
478 system so vital to the resilience of natural and built communities in the area.

479

480

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488

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683

684 **Figure Captions**

685

686 **Fig. 1** Map of the Tuckerton Peninsula salt marsh system. Note location of nine transects
687 for sampling salt marsh vegetation in this study. Boundaries between northern, central
688 and southern marsh segments are drawn. Inset shows location of the peninsula with
689 respect to the State of New Jersey. From Kennish et al. (2016).

690

691 **Fig. 2** Non-metric multidimensional scaling (NMDS) plot showing nine field transects
692 sampled in the Tuckerton Peninsula salt marsh from June through September 2011,
693 grouped by (a) marsh segment (1-3), (b) transect (1-9), and (c) month (6-9). For each
694 transect, percent areal cover estimates for each species were averaged across 10 plots.
695 Segments 1, 2, and 3 represent the northern, central, and southern segments of the marsh,
696 respectively, and Figure 1 shows the distribution of transects within each segment. Plant
697 species included DISSPI (*Distichlis spicata*), LIMCAR (*Limonium carolinianum*),
698 MORRUB (*Morus rubra*), SALSPP (*Salicornia* spp.), SPAALT (*Spartina alterniflora*),
699 SPAPAT (*Spartina patens*), and SYMTEN (*Symphyotricum tenuifolium*). Final stress
700 was 0.073.

701

702 **Fig. 3** Non-metric multidimensional scaling (NMDS) plot showing 90 field plots sampled
703 in the Tuckerton Peninsula salt marsh in August 2011, grouped by marsh segment.
704 Segments 1, 2, and 3 represent the northern, central, and southern segments of the marsh,
705 respectively. Plant species included DISSPI (*Distichlis spicata*), LIMCAR (*Limonium*
706 *carolinianum*), SALSPP (*Salicornia* spp.), SPAALT (*Spartina alterniflora*), and

707 SPAPAT (*Spartina patens*). Final stress was 0.047. Plot-level NMDS plots for June,
708 July, and September 2011 and September 2013 (not shown) demonstrated segment
709 groupings similar to August 2011.

710

711

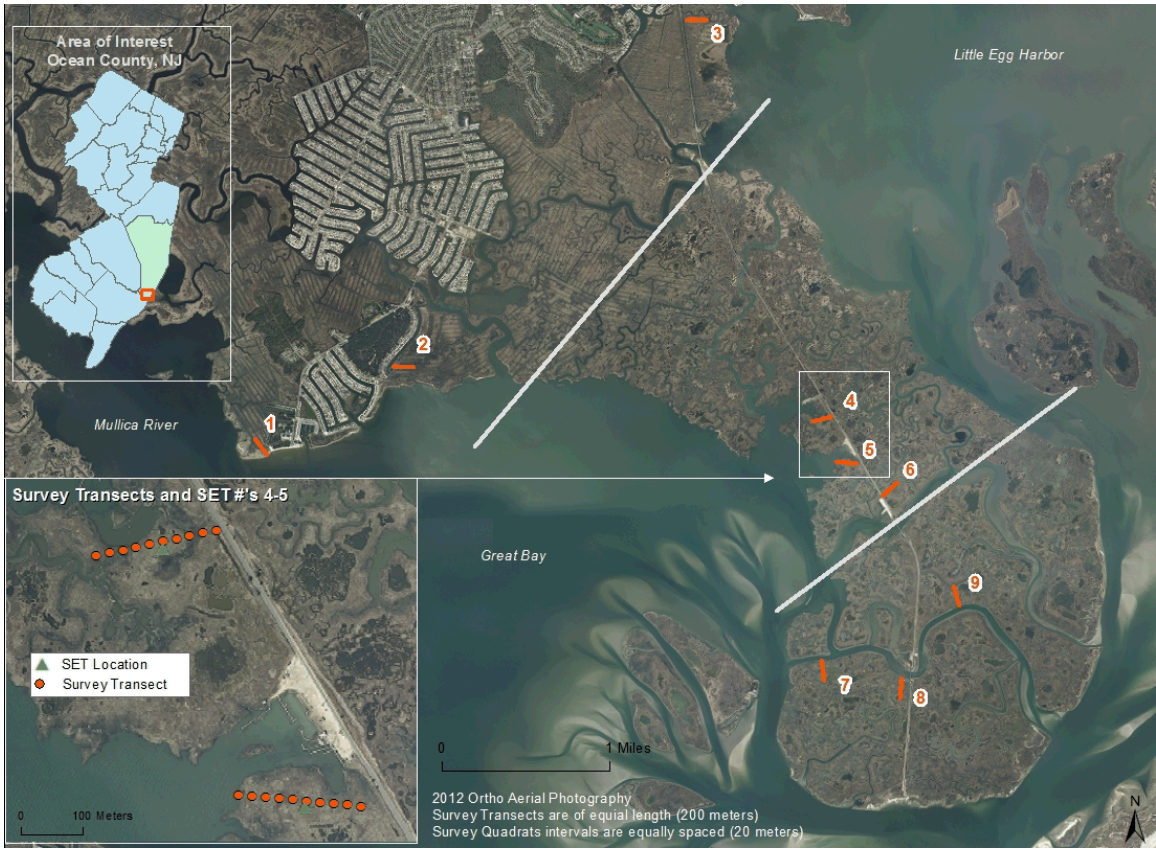


Figure 1.

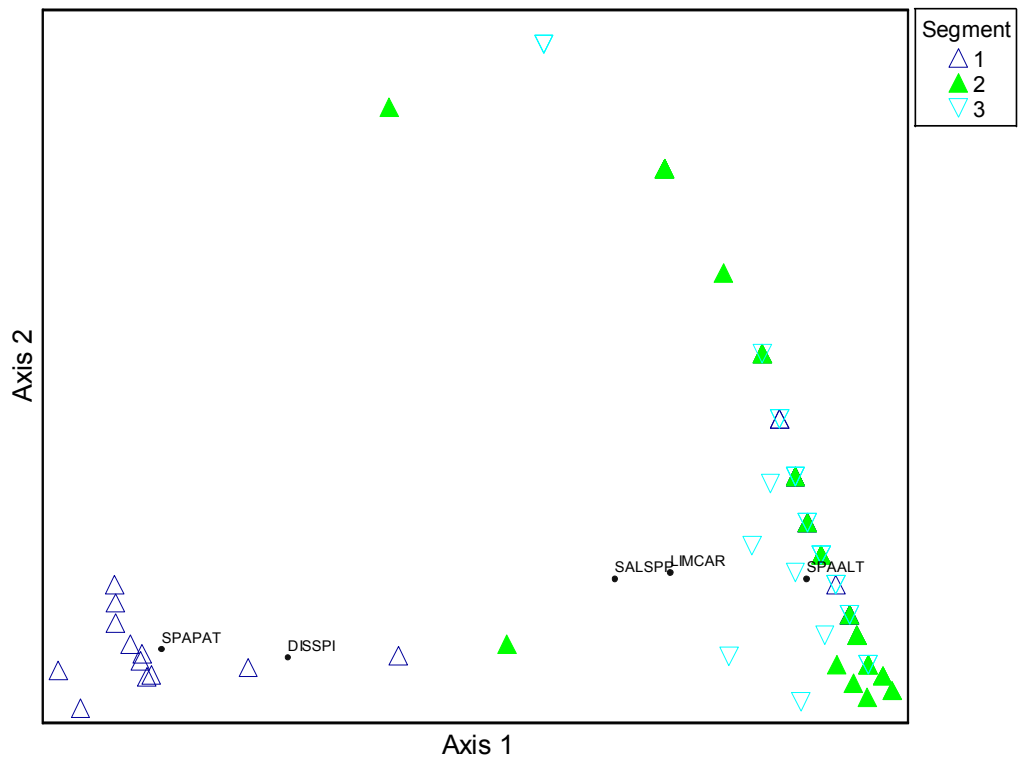


Figure 2.

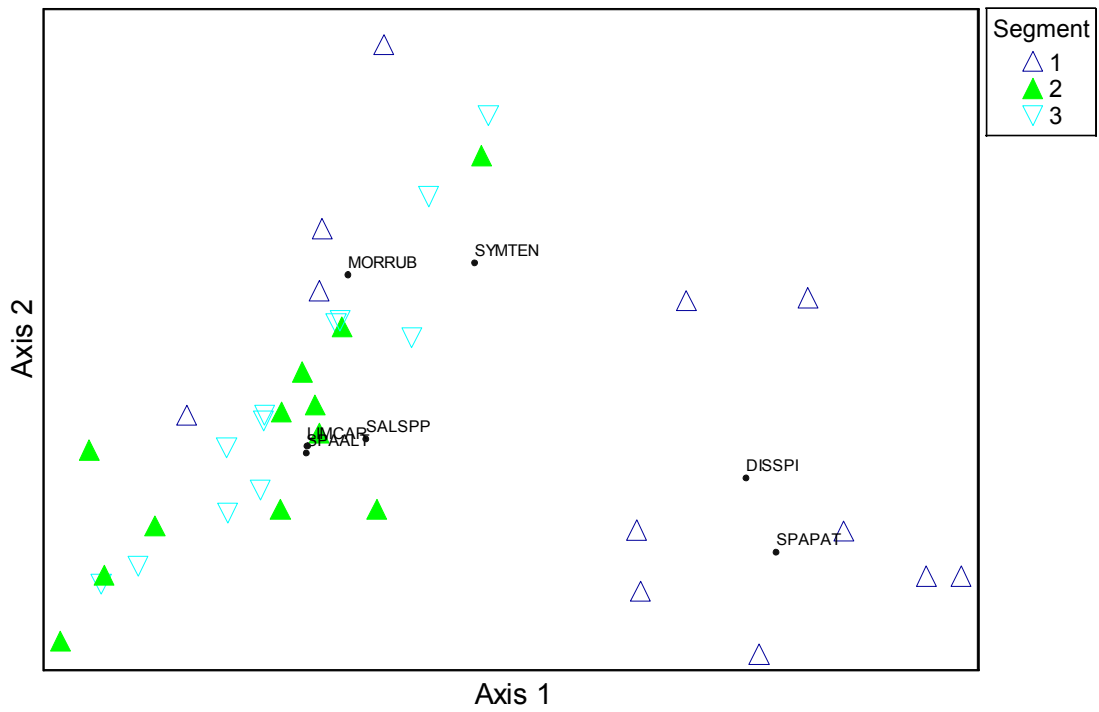


Figure 3a.

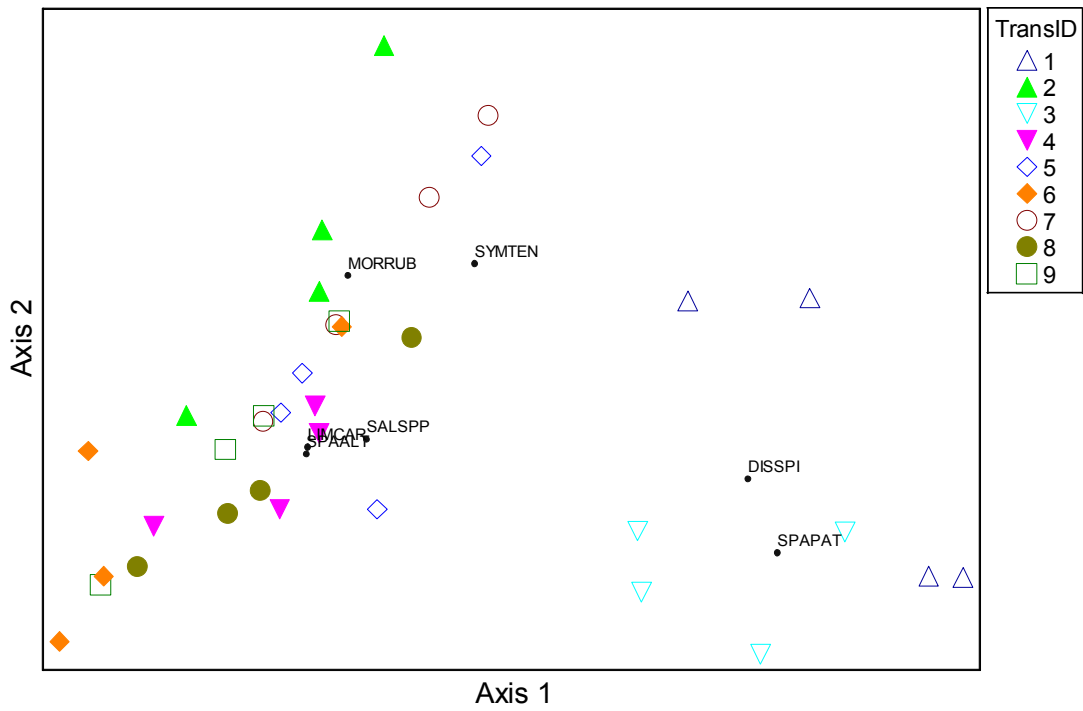


Figure 3b.

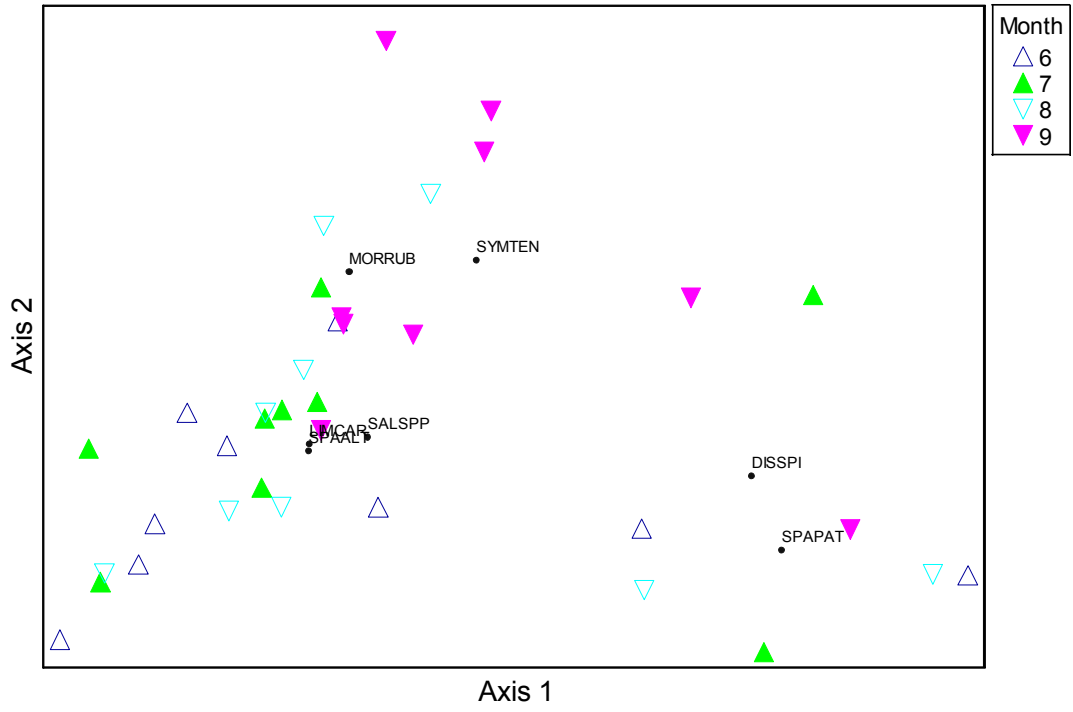


Figure 3c.

Table 1. Linear mixed model results for combined species for maximum canopy height, percent areal cover, shoot density and explanatory factors (segment, year, month, segment*year, and segment*month). A period indicates that the statistic could not be computed. Significant P-value results at $\alpha = 0.0167$ are bolded.

Response variable	Covariances					Segment				Year				Month				Segment*Year				Segment*Month				
	Trans- ect	Lat- itude	Long- itude	Marsh elevation	AR(1)	Residual	Num df	Den df	F value	P-value	Num df	Den df	F value	P-value	Num df	Den df	F value	P-value	Num df	Den df	F value	P-value	Num df	Den df	F value	P-value
Maximum canopy height	0.3117	0.4819	0.3728	.	0.407	0.9972	2	6.14	2.46	0.1644	1	681	13.19	0.0003	3	505	12.82	<0.0001	2	680	5.99	0.0026	6	505	0.68	0.6677
Percent areal cover	0.01803	.	.	.	0.6075	0.2584	2	6.06	0.75	0.5102	1	761	0.77	0.3806	3	594	21.37	<0.0001	2	758	2.46	0.0859	6	593	1.69	0.1205
Shoot density	0.7398	4.2118	2	108	0.86	0.4249	1	679	0.51	0.4744	3	573	16.68	<0.0001	2	676	3.68	0.0256	6	572	12.68	<0.0001

Table 2. Linear mixed model results for individual species for maximum canopy height, percent areal cover, and shoot density, and explanatory factors (segment, year, month, segment*year, and segment*month). A period indicates that the statistic could not be computed. Significant P-value results **0.0167** are bolded.

Dependent factor	Assemblage	Covariances					Segment				Year				Month				Segment*Year				Segment*Month				
		Trans-ect	Lat-itude	Long-itude	Marsh elevation	AR(1)	Residual	Num df	Den df	F value	P-value	Num df	Den df	F value	P-value	Num df	Den df	F value	P-value	Num df	Den df	F value	P-value	Num df	Den df	F value	P-value
Maximum canopy height	<i>Distichlis spicata</i>	0.04	<0.01	.	.	-0.10	0.24	2	33	1.59	0.22	1	45	3.68	0.06	3	47	1.67	0.19	1	45	0.14	0.71	4	44	0.18	0.95
Maximum canopy height	<i>Limonium carolinianum</i>	0.58	.	.	.	0.40	0.54	2	12	0.55	0.59	1	13	5.84	0.03	3	21	5.19	0.01	1	13	1.71	0.21	5	21	0.76	0.59
Maximum canopy height	<i>Morus rubra</i>	0.96	7.79	1	5	0.00	0.96	3	5	1.80	0.26
Maximum canopy height	<i>Salicornia spp.</i>	.	.	.	0.15	0.86	0.60	2	20	0.82	0.45	1	65	2.09	0.15	3	43	28.46	<0.0001	2	64	1.14	0.33	6	42	5.42	0.0003
Maximum canopy height	<i>Spartina alterniflora</i>	0.12	0.63	0.14	.	0.06	0.52	2	6	3.60	0.09	1	247	3.64	0.06	3	267	11.57	<0.0001	2	248	1.01	0.37	6	281	1.25	0.28
Maximum canopy height	<i>Spartina patens</i>	0.02	0.02	0.01	<0.01	0.10	0.18	1	11	6.33	0.03	1	38	1.19	0.28	3	30	1.31	0.29	1	38	5.86	0.02	3	30	0.72	0.55
Maximum canopy height	<i>Symphytotricum tenuifolium</i>	0.01	0.01	.	.	0.67	0.11	2	1	7.27	0.25	1	1	58.35	0.08	2	1	2.53	0.41
Percent areal cover	<i>Distichlis spicata</i>	0.34	0.09	2	35	1.85	0.17	1	57	0.25	0.62	3	44	0.11	0.95	1	57	0.25	0.62	4	40	0.1	0.98
Percent areal cover	<i>Limonium carolinianum</i>	0.60	0.02	2	19	0.67	0.52	1	33	0.11	0.75	3	27	0.22	0.88	1	33	0.11	0.75	5	27	0.3	0.91
Percent areal cover	<i>Morus rubra</i>	<0.0001	0.28	1	10	0.89	0.37	1	10	0.60	0.46	3	10	0.84	0.50
Percent areal cover	<i>Salicornia spp.</i>	.	.	.	<0.01	0.38	0.01	2	17	0.46	0.64	1	59	0.86	0.36	3	64	1.18	0.33	2	59	1.12	0.33	6	63	1.03	0.41
Percent areal cover	<i>Spartina alterniflora</i>	0.02	.	.	.	0.51	0.11	2	6	3.87	0.08	1	375	14.64	0.0002	3	314	12.76	<0.0001	2	375	1.89	0.15	6	317	1.92	0.08
Percent areal cover	<i>Spartina patens</i>	<0.01	<0.01	14.34	<0.0001	-0.18	0.11	1	2	1.51	0.34	1	56	0.01	0.91	3	24	2.06	0.13	1	56	0.01	0.91	3	24	1.24	0.32
Percent areal cover	<i>Symphytotricum tenuifolium</i>	.	.	<0.0001	<0.01	0.00	0.04	2	1	0.00	1.00	1	1	0.33	0.67	3	1	0.00	1.00	1	1	0	1.00
Shoot density	<i>Distichlis spicata</i>	0.57	1.00	2	28	3.20	0.06	1	53	1.42	0.24	3	44	1.63	0.20	1	53	0.07	0.79	4	40	0.74	0.57
Shoot density	<i>Limonium carolinianum</i>	0.20	.	25.65	.	0.58	0.36	2	1	0.34	0.77	1	26	0.95	0.34	3	24	0.92	0.44	1	26	0.01	0.94	5	24	0.77	0.58
Shoot density	<i>Morus rubra</i>	<0.0001	0.13	1	6	1.20	0.32	3	3	0.51	0.71
Shoot density	<i>Salicornia spp.</i>	0.22	.	.	.	0.71	0.43	2	4	0.01	0.99	1	80	0.26	0.61	3	49	0.27	0.85	2	79	0.40	0.67	6	47	0.82	0.56
Shoot density	<i>Spartina alterniflora</i>	0.13	.	.	<0.0001	0.56	1.55	2	4	3.80	0.13	1	383	30.59	<0.0001	3	324	0.80	0.4927	2	383	1.46	0.23	6	326	10.83	<0.0001
Shoot density	<i>Spartina patens</i>	.	.	8.49	.	-0.60	1.46	1	58	15.00	0.0003	1	51	0.27	0.61	3	37	3.00	0.04	1	51	2.21	0.14	3	37	5.19	0.004
Shoot density	<i>Symphytotricum tenuifolium</i>	-0.27	0.91	2	1	0.40	0.74	1	1	0.02	0.91	2	1	0.06	0.94

Appendix A. Non-metric multidimensional scaling (NMDS) plot showing 90 field plots sampled in the Tuckerton Peninsula salt marsh in September 2011 and September 2013, grouped by year. Plant species included DISSPI (*Distichlis spicata*), LIMCAR (*Limonium carolinianum*), SALSPP (*Salicornia* spp.), SPAALT (*Spartina alterniflora*), and SPAPAT (*Spartina patens*). Final stress was 0.069.

