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Community and Landscape Patterns of Forb Pannes: On Two Maine Salt Marshes

Briana Fischella
University of Southern Maine

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Signatures

Author: Briana Fischella Date: 1/31/19

Advisory Committee:

Date: 2/4/2019

(Graduate Advisor)

Date: 5 Feb 2019

Date: 26 Feb 2019

Date:

Chair of the Department of Biological Sciences:

Date: 2/5/2019

Dean of the College of Science, Technology and Health

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Community and Landscape Patterns of Forb Pannes

On Two Maine Salt Marshes

A THESIS

submitted in partial fulfillment of the requirements for the

Degree of Master of Science in Biology

University of Southern Maine

By

Briana Fischella

Advisory Committee:

Dr. Theresa Theodose, Associate Professor of Biology

Dr. Karen Wilson, Associate Research Professor of Environmental Science

Dr. Chris Maher, Professor of Biology, and Associate Dean for Academic Affairs, College of Science, Technology, and Health

2018

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Abstract

Mixed forb pannes of Maine are maintained by waterlogging and are replaced by turf-grass species when drained, elevated, or warmed. These drivers, in particular waterlogging and temperature rise, counteract each other and are representative of in-field abiotic influences such as sea level rise (SLR) and climate warming. Researchers in Maine have studied forb panne landscape distribution, plant communities, and nutrients on salt marshes; however, no one has addressed how forb pannes change over time or mechanisms for this change. My objectives were to 1) remap and statistically compare spatial characteristics and changes undergone in mixed forb pannes of the Little River Salt Marsh in Wells, ME to those previously mapped using GPS and GIS technology, (2) discover small-scale heterogeneity in abiotic and plant community assembly *within*-pannes to better understand in-field species interactions coupled with plant interactions with edaphic variables, and (3) elucidate any edaphic, species and community patterns *between* pannes to determine if they are related to broader geospatial variables previously investigated. At the non-tidally restricted Little River Marsh in Wells, 5% of the marsh was covered in forb pannes in 2005 compared to 4% in 2017, showing slight panne loss over time. However, spatial analysis of panne change between years showed these changes were regional and the southern region of the marsh near the river mouth had higher counts and expansion of forb panne area compared to the 2005 mapping effort. Within-panne edaphic analysis showed temperature and NO_3^- quantities to be higher in interior habitats, whereas NH_4^+ amounts were higher in edge habitats. Salinity, NO_3^- and NH_4^+ were all positive functions of panne area and distance to river, and NO_3^- and NH_4^+ were both inverse functions of distance to urban edge. Edge habitats had higher abundances of *Spartina patens*, a less water tolerant matrix grass, whereas interior forb panne areas had higher abundances of *Spartina alterniflora,* a more water tolerant species. Whereas my hypotheses predicted increased SLR to be the main driver of forb pannes in Maine salt marshes, these two studies suggest forb pannes to be dynamic parts of the marsh, associated with regional differences in marsh inundation time. These results indicate that while rising temperatures may play a role in panne loss in some regions of the Little River Marsh, other regions may experience longer localized tidal inundation associated with expansion of forb panne areas. In the Scarborough Marsh, a suburban marsh of Scarborough, ME, a higher percentage (10%) of the marsh surface was occupied by forb pannes. Whereas no baseline coverage exists for forb pannes on salt marshes in Scarborough, ME, this comparatively high percentage of forb panne cover could indicate a longer tidal inundation period of the marsh and vulnerability of the marsh to increased SLR due to its tidal restriction.

Preface

Salt marsh ecosystems are recognized for their ecological significance, which includes providing habitat for migratory birds and juvenile marine species, extremely high primary production subsidized by upriver nutrients, and production of allochthonous detritus for nearshore waters and bays (Teal 1962; Odum 1971; Boesch and Terner 1984; Shriver et al. 2004). Salt marshes are also recognized for the ecosystem services they provide, including stabilizing coastlines in storm events, sequestering carbon in marsh peat, and filtering runoff from uplands and subsequently protecting nearshore waters (Valiela and Teal 1979; King and Lester 1995; Chmura et al. 2003). Vegetation is the structural, biological and chemical foundation of the salt marsh ecosystem, and this topic of study has received less attention in Maine than in salt marshes of the southern United States. With evidence of a changing climate and increasing sea level rise (SLR) (Walther et al. 2002; Sweet et al. 2017), understanding abiotic influences on Maine's salt marsh plant communities is paramount to maintaining their functions and informing their conservation (Short et al. 2016).

Historic and recent studies have established that southern New England salt marshes display distinct zonation patterns, in which monospecific stands of dominant species are segregated throughout the marsh according to physical variation in tidal inundation and marsh elevation coupled with interspecific competition (Miller and Egler 1950; Niering and Warren 1980; Nixon 1982). Although these salt marsh zonation patterns also occur in northern New England salt marshes, Maine's larger meadow marshes show a different mosaic pattern (Jacobson and Jacobson 1989). Likely due to more gradual changes in elevation across these large meadows, *Spartina patens* and *Juncus gerardii* occur in patchwork patterns on the less frequently inundated high marsh. Ice scouring in winter routinely removes the *Spartina alterniflora* low marsh zone and also portions of the high marsh matrix, and in the high marsh this ice scouring results in short form *S. alterniflora* scattered in depressions often associated with pools (Dionne 1969; Mathieson et al. 1982; Hardwick-Witman 1985). In addition, there exist extensive areas of middle elevation that are sometimes called "rotten spots" (Miller and Egler 1950; Ewanchuk and Bertness 2004b). Mixed forb pannes form in these slightly sunken areas of the high marsh and occupy areas between those dominated by *S. patens, J. gerardii,* and short form *S. alterniflora* (Theodose and Roths 1999; Warren and Neiring 1993; Griffin et al. 2011).

The mixed forb pannes of Maine contain many perennial forb species and so constitute a different plant community from ephemeral forb pannes dominated by the halophyte *Salicornia spp.* Like ephemeral forb pannes, mixed pannes exist as sparsely vegetated patches with exposed sediments, but in Maine mixed forb pannes tend to be larger in area, have higher plant cover, have moister substrates, and are therefore less saline than hypersaline pannes colonized by fugitive annuals (Bertness et al. 1992; Theodose and Roths 1999; Griffin et al. 2011). Mixed forb pannes vary greatly in size even on the same marsh (Griffin et al. 2011) and are almost always associated with pools and nearby stands of short form *S. alterniflora* (Miller and Egler 1950; Warren and Neiring 1993; Griffin et al. 2011). Mixed pannes of Maine are vegetated with a diverse mixture of perennial forbs and graminoids (Miller and Egler 1950; Theodose and Roths 1999; Wilson et al. 2009; Griffin et al. 2011) and this variation in vegetation type makes them in part responsible for the relatively high plant species diversity found in salt marshes along the Gulf of Maine (Gedan and Bertness 2009).

Mixed forb pannes are maintained by high sediment moisture, or waterlogging, which serves as a refuge from competitive graminoids (Ewanchuk and Bertness 2004a). When drained, the marsh matrix graminoid *S. patens* quickly invades and maintains dominance leading to the disappearance of the forb panne (Gedan and Bertness 2009). This behavior is indicative of succession occurring on the marsh and is described by Warren and Neiring (1993) where previous *S. patens* and *J. geradii* stands were converted to mixed forb panne areas, a change that they attributed to increased sea level rise (SLR) on the marsh. Whereas mixed forb pannes are thought to be more permanent features of the salt marshes in Maine (Orson and Howes 1992), this type of large-scale vegetation change suggests these areas are dynamic and responsive to edaphic change, making them good indicators of how SLR and climate change interact to change salt marsh habitat.

These changes of salt marsh vegetation resultant of edaphic change suggest that, with future SLR, Maine salt marshes may experience increased periods of inundation of the marsh platform, which could be more favorable for mixed forb panne formation and maintenance (Ewanchuk and Bertness 2004a). In contrast, warming experiments of pannes result in similar competitive displacement by *S. patens* (Gedan and Bertness 2009). Because Maine marshes may be able to keep up with SLR by accretion, moving inward, and post-glacial rebound, rising temperatures may result in forb panne contraction, fragmentation, or disappearance.

Research on forb panne change over time is lacking for salt marshes in Maine. A remapping of previously mapped forb pannes (Griffin et al. 2011) may inform how SLR and climate change interact to drive forb panne habitat and potential large scale marsh community changes of the future. Moreover, research on spatially located change of forb pannes could inform current edaphic conditions of the marsh.

The vegetation of these pannes has been characterized (Miller and Egler 1950; Theodose and Roths 1999; Griffin et al. 2011), edaphic factors that maintain them has been determined (Ewanchuk and Bertness 2004a; Gedan and Bertness 2009), and spatial distribution has been described (Griffin et al. 2011). However, how vegetation and edaphic factors vary within mixed pannes has not been investigated. Because nutrient availability across the salt marsh is variable (Theodose and Roths 1999; Theodose and Martin 2003) and interspecific competition is dictated by physical stressors (Bertness 1991), nutrient differences, temperature, and sediment moisture within forb pannes may elucidate differences between interior and edge species abundances and further inform how forb panne species are distributed in relation to interacting edaphic variables.

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Chapter 1

Forb Panne Dynamics of the Little River Salt Marsh, Wells, ME, USA

Abstract

Mixed forb pannes of Maine are maintained by waterlogging and are replaced by turf-grass species when drained, elevated, or warmed. These parameters counteract each other and represent in-field sea-level rise (SLR) and climate warming variables. Whereas researchers in Maine have studied forb panne landscape distribution, plant communities, and nutrients, no one has addressed how pannes change over time or mechanisms for this change. The three objectives of this study were to 1) remap the forb pannes of the Little River Salt Marsh in Wells, ME in their entirety 2) use GIS technology to analyze how mapped pannes from 2005 changed over time in terms of number, size, and regional spatial clustering and 3) interpret these changes in light of SLR and climate warming drivers. Mapping of forb pannes in the non-tidally restricted Little River Marsh in Wells, ME showed some panne loss over time, from 5% of the marsh covered in forb pannes in 2005 to 4% in 2017. Panne area loss was due mainly to panne *splitting* as well as to smaller *persistent* pannes and panne *death*. However, the number of forb pannes increased by 412% between the two sampling periods. This increase was due to panne *birth* and *splitting* as well as documented *persistence*. These results indicate that while there were more forb pannes on the marsh, these pannes were smaller and less

extensive in 2017 than in 2005. Spatial analysis showed these changes to be regional as the southern seaward region of the marsh significantly increased in number and size of forb pannes in 2017. Whereas I predicted increased SLR to be the main driver of forb pannes in Maine salt marshes, this study suggests forb pannes to be dynamic parts of the marsh, likely associated with regional differences in marsh inundation time. These results also suggest that while rising temperatures may play a role in panne loss in most regions of non-tidally restricted marshes, hydrologic blockage could result in longer localized tidal inundation leading to expansion of forb panne areas.

Introduction

Salt marshes represent valuable habitat for migratory birds and juvenile marine species and provide extremely high primary production subsidized by upriver nutrients (Teal 1962; Odum 1971; Boesch and Terner 1984; Shriver et al. 2004). These systems are also recognized for the ecosystem services they provide as they are important stabilizers of coastlines in storm events, sequester atmospheric carbon in marsh peat, and filter runoff from uplands subsequently protecting nearshore waters (Valiela and Teal 1979; King and Lester 1995; Chmura et al. 2003). Vegetation is the structural, biological and chemical foundation of the salt marsh ecosystem, and this topic of study has received less attention in northern New England than in salt marshes of the southern United States. With evidence of a changing climate and increasing sea level rise (SLR) (Walther et al. 2002; Sweet et al. 2017), understanding how the salt marsh plant communities of Maine respond to these variables is paramount to maintaining their functions and informing their conservation (Short et al. 2016).

Maine houses large meadow marshes with gradual changes in elevation. These salt marshes display a mosaic pattern of vegetation (Jacobson and Jacobson 1989) that differs from southern New England marshes, which have distinct zonation patterns where monospecific stands of dominant species are segregated throughout the marsh according to physical variation in tidal inundation and marsh elevation (Miller and Egler 1950; Niering and Warren 1980; Nixon 1982). Whereas zonation of low and high marsh habitat is still seen in Maine, across these large meadows patchwork patterns occur on the less frequently inundated high marsh where *Spartina patens* dominates and *Juncus gerardii,* short-form *Spartina alterniflora,* pools, and mixed forb pannes occur in patches across the meadow (Theodose and Roths 1999; Griffin et al. 2011).

Although similar to ephemeral, annual-dominated forb pannes well studied in southern New England, mixed pannes tend to be larger in area, have moister substrates, and lower salinities than hypersaline pannes colonized by fugitive annuals (Bertness 1992; Theodose and Roths 1999). Lower salinities and higher soil moistures are likely due to the higher tides and lower air temperatures of northern New England, and these qualities are also likely responsible for the high diversity of vegetation found in forb pannes (Theodose and Roths 1999; Griffin et al. 2011) which can exist in the less saline environment (Crain et al. 2004). These larger mixed pannes often are associated with pools that are partially ringed by stands of short-form *S. alterniflora* (Miller and Egler 1950; Griffin et al. 2011), and the pannes appear to form partial halos in middle elevations between short form *S. alterniflora* and turf-graminoids *S. patens* or *J. gerardii*. Because they contain a mixture of perennial forbs and graminoids (Miller and Egler 1950; Theodose and Roths 1999; Griffin et al. 2011), mixed forb pannes are responsible for the relatively high plant species diversity found along the salt marshes of the Gulf of Maine (Gedan and Bertness 2009).

These diverse forb pannes are assumed to be relatively persistent habitats of Maine marshes (Ewanchuk and Bertness 2004b), though no study has ever investigated their longevity. Manipulative experiments demonstrate that when drained or elevated, these mixed forb pannes convert to clonal *S. patens* turf

(Ewanchuk and Bertness 2004b), suggesting that waterlogging stress reduces competitive exclusion by fast growing turf graminoids.

Increasing rates of sea level rise (SLR) could enhance waterlogging on Maine marshes, favoring occurrence of forb pannes. Warren and Neiring (1993) invoked such a scenario to explain unusual changes on a Connecticut marsh, where similar mixed forb panne habitats are documented and likely reach the southern-most extent. Their findings showed stands of *J. gerardii* replaced by mixed forb pannes, a finding they attributed to lower marsh surface elevations experiencing greater frequency and duration of tidal flooding.

A warming climate also is predicted to have large-scale impacts on northern New England salt marshes and will likely induce localized responses from forb panne communities as well. Manipulative field experiments conducted along a latitudinal gradient demonstrated how potentially vulnerable diversity is to climate warming (Gedan and Bertness 2009). Gedan and Bertness (2009) used simple plexi-glass greenhouses to elevate air temperature within forb panne areas on Maine salt marshes and areas of diversity on a salt marsh in Rhode Island. In Maine marshes, forb pannes displayed a rapid conversion to marsh matrix species *S. patens,* while the Rhode Island marsh similarly had decreases in plant diversity.

Because potential responses of forb panne communities to warming and SLR conflict (Ewanchuk & Bertness 2004b), it is difficult to predict how global climate change will impact these communities. SLR could favor forb panne expansion into *S. patens* and *J. geradii* turf. Alternatively, increasing temperatures could reduce forb panne area as turf graminoids competitively exclude forb panne species, so that diverse salt marsh communities of northern regions begin to resemble those of lower latitudes, with monocultures of different graminoid species.

Ideally, local responses of forb panne communities to these different global change parameters can be documented with long term monitoring studies. How these communities change could indicate whether SLR or warming is a more influential driver or varies at local or regional scales. Repeated mapping of forb panne peripheries allows visualization of shifts in panne size, with expansion suggesting greater impacts of SLR and contraction indicating greater impacts of warming. In 2005, Griffin et al. (2011) used precision GPS to map all forb pannes on a non-tidally impeded salt marsh, the Little River Marsh, in Wells, Maine. A rationale for this mapping project was the collection of baseline data to be used for documenting changes in the marsh over time. Therefore, the Little River Marsh provides an ideal opportunity to document changes in forb panne area, and to understand relative impacts of SLR and warming temperatures on salt marsh community composition.

The three objectives of this study were to 1) remap forb pannes of the Little River Salt Marsh in their entirety using the same methods as Griffin et al. (2011), 2) use Geographic Information Systems (GIS) technology to analyze how pannes mapped in 2005 have changed over time in terms of number, size, and regional spatial clustering, and 3) interpret these changes in light of SLR and warming drivers.

Based on projected rates of SLR (Sweet et al. 2017), I predicted SLR to be a stronger driver of current forb pannes than climate warming and thus predicted forb pannes of the Little River Marsh in Wells, ME to have increased in number and size over time. I likewise predicted that forb pannes would have overall trends of expansion and that these trends would not be regionally specific, because I assumed SLR and increased inundation periods to be uniform across the marsh surface.

Methods

Study site

The Little River Marsh (43°20'23.4" N, 70°32'28.8" W) is located behind Wells Beach and is typical of a meadow marsh formed behind a protected barrier beach (Fig. 1). The marsh is owned by the Rachel Carson National Wildlife Refuge and is located within the Wells National Estuarine Research Reserve (NERR). The Little River enters the northwestern margin of the marsh, then meanders seawards, creating two peninsulas in the marsh before reaching the sea in the southern portion of the marsh. Low marsh habitats that receive daily inundation are dominated by *S. alterniflora,* although inner edges are often removed by ice scouring. Therefore, most marsh area is classified as high marsh, which receives shorter periods of tidal inundation and is dominated by *S. patens*. Forb pannes are scattered in a patchwork mosaic amongst extensive regions of *S. patens,* intermittent salt marsh pools, and monospecific patches of short form *S. alterniflora, J. gerardii* and occasional *Distichlis spicata*. Within forb pannes, a diversity of perennial and annual forbs occurs as well as some graminoids. Although mixed pannes vary in relative dominance, when pooled together, the dominance rank is as follows: *Plantago maritima, Triglochin maritimum, S. patens, Limonium nashii, S. alterniflora, Agalinis maritima, Glaux maritima, J. gerardii, Salicornia europaea, D. spicata*, and *Puccinellia maritima* (Griffin et al. 2011).

Previous mapping effort

During summer 2005, Griffin mapped all forb panne perimeters at the Little River Marsh in Wells, ME (Griffin et al. 2011, Fig. 2). Griffin et al. (2011) noted forb panne boundaries are at times not discrete and instead fade gradually into surrounding matrix graminoids. They erred on the conservative side by mapping only pannes having >50% forb species with the exclusion of pannes that had a presence of upland species such as *Solidago sempervirens*. They described this method as a structured decision making process, always with the >50% forb cover rule in mind.

Mapping component

To test predictions that forb pannes changed in number and size over time, I mapped forb panne perimeters at the Little River Salt Marsh in Wells, Maine (Fig. 3) in summer 2017, following the same protocol and structured decision making as Griffin et al. (2011). I took GPS data once during the growing season between August 31 and October 22, 2017 with a handheld GeoXT Trimble GPS unit. All data were Real-Time Satellite Based Augmentation System (SBAS) corrected and exported as a shapefile to be processed in ArcGIS (10.5.1). The projection and coordinate system used for the project was the same between sampling years, i.e., Universal Transverse Mercator (UTM) Zone 19N North American Datum 1983 (NAD1983) Continuously Operating Reference Station 1996 (CORS96) with the vertical datum North American Vertical Datum 1988 (NAVD88).

During the creation of composite layers for forb pannes mapped in 2005 and 2017, I identified overlapping polygons that occurred during delineation. To make these data useable, I repaired shapefile geometry and dissolved any multipart polygons. To standardize the data, only 2005 and 2017 forb pannes greater than 1 m^2 were used in analysis. To contextualize 2005 and 2017 forb pannes and check for mapping errors, I used 15.24 cm (6 in) resolution orthoimagery from 2012 (Maine Geolibrary 2012) as a base map.

Forb panne dynamism

To assess how individual forb pannes had changed over time, I replicated methodology of Wilson et al.'s (2009) research on salt marsh pool dynamism. I assigned panne IDs to the 81 forb pannes from the 2005 mapping effort, and used these identifiers for all forb pannes found in the same location in 2017.

To quantify the dynamic processes that allow for changes in forb panne number between the two periods, I specified five events that tracked each 2005 forb panne into 2017, i.e., *birth, life, merge, split,* and *death* (Table 1, see table for pictorial definitions). To quantify these event types in the forb panne data, *birth, merge, split,* and *death* event attributes were assigned either 1 or 0, with 1 representing the occurrence of an event and 0 representing the absence of an event. *Life* represented the number of pannes with the same common ID assignment within a year (with an exception for *merge* event pannes). For example, in places where a panne was absent in 2005 and present in 2017, *birth* was 1, *life* in 2005 was 0, *life* in 2017 was 1, and *merge, split,* and *death* events were all 0. For cases where a panne was present in 2005, but absent in 2017, *death* was 1, *life* in 2005 was 1, *life* in 2017 was 0, with *birth, merge,* and *split* events all 0. Further, in cases where a large 2005 panne fragmented into several small pannes by 2017, *life* in 2005 was 1 and *life* in 2017 was the number of small pannes found in the same location by 2017. In these cases, *split* was 1, and *birth, merge,* and *death* were all 0. For cases where the original 2005 panne did not *split* or *merge,* 2005 and 2017 *life* was quantified as 1, and *birth, merge, split,* and *death* were all 0; I referred to this situation as a *persistence* forb panne (Table 2).

Whereas this method tracked forb panne dynamism over time, it did not address change in individual panne area between the two sampled years or address changes specific to event type.

Event specific changes in forb panne area

To provide a more substantial understanding of how forb pannes changed over time, I also quantified changes in forb panne area specific to event type. For example, I summed the area of all pannes *birth*ed in 2017 to determine the extent to which new pannes accounted for total area in 2017. Likewise for pannes that disappeared by 2017, the total area was used to determine how much area was lost by 2017 from *death* events. For events that required both sampling years for determination, such as *persistence, merge,* and *split* events, I summed area in 2005 and compared this value to the same event's total area in 2017. For example, for *persistence* I compared the total area of pannes in 2005 to that of the same *persistent* pannes in 2017. For *split* events resulting in multiple 2017 pannes, the sum of the common panne areas was used for comparison. This method allowed me to visualize how pannes associated with specific events changed between the two sampled years as well as the degree to which the type of event contributed to total area in a sampling year.

Individual and overall forb panne changes

To further investigate changes in individual panne area between sampling periods, I subtracted individual 2017 panne area (or the sum of the areas in the case of *split* events) from individual 2005 panne area (for *death* pannes, this value was 0). This equation calculates the area change of each panne between sampling years, with positive values indicating panne growth and negative values indicating panne contraction. It also allowed visualization of mean individual change in panne area.

To analyze total change in forb panne number and area between sampling years, I used descriptive statistics including count and total forb panne area to quantify both 2005 and 2017 data. I then digitized the mapped marsh area and used this new layer to calculate total marsh study area, which was then used to calculate percent cover of forb panne area of the marsh.

Spatial variation in panne events

To test predictions about regional forb panne trends and see whether forb panne changes were similar across the entirety of the marsh, descriptive statistics quantifying individual forb panne changes between sampling years were joined to the spatial location of forb pannes in ArcGIS and then analyzed statistically. By spatially locating forb pannes by their event types and area change, clusters of forb pannes on the marsh experiencing statistically significant growth or loss of area could be identified.

To identify marsh sites with heightened forb panne dynamics, a grid was utilized with 100 m^2 grid cells in ArcGIS to delimitate portions of the marsh. Centroids were created in all forb pannes, with each centroid capturing event type and area change data of its respective forb panne. Each grid cell was then joined with the sum total of all forb panne centroids from 2005 and 2017 that fell within it. This process allowed each grid cell to capture the event counts and total area change values of all forb pannes in that grid cell location (Fig. 4, Fig. 5). The spatial binning of dynamic events and area change allowed for a systematic spatial identification of certain regions of the marsh that were hot spots of dynamic events and area change.

Significant spatially clustered events and area change were identified using the Local G Cluster Map tool in Geoda, which is based on the Gi spatial statistic (Getis and Ord 1992; Ord and Getis 1995). The Gi spatial statistic measures the degree of local spatial autocorrelation (1992; Ord and Getis 1995) and uses neighboring locations to identify spatial clustering of like values concentrated in one sub-region of the study area (Anselin 1996). Clusters of high values or hot spots and clusters of low values or cold spots then can be distinguished, and regions of spatial heterogeneity can be indicated objectively (Anselin 1999). Significance for this method was set to $p < 0.05$.

Results

Dynamic trends

Between 2005 and 2017, forb pannes on the Little River Marsh underwent a series of dynamic changes. The number of forb pannes increased by 412% between the two years. This increase was due mainly to panne *birth* and *splitting* as well as to documented *persistence* (Fig. 6). However, total panne area declined by 177% between the years. Panne area loss was due mainly to panne *splitting* as well as smaller *persistent* pannes and panne *death* (Fig. 7, Fig. 8). Thus, while there were more forb pannes on the marsh in 2017, these pannes were smaller and less extensive than in 2005 (Fig. 9, Table 3).

Events undergone by forb pannes from 2005 to 2017 were divided between *splitting, persistence,* and *death,* with *merge* events being rare and *birth* events making up over half of forb pannes documented in 2017. Pannes that *split* made up 43% of the total 334 pannes in 2017, and these pannes experienced a decrease in area between years resulting in a 45% loss of total area from 2005. Pannes that *persisted* declined in total area between the two sampling years, losing 7% of total forb panne area from 2005, whereas pannes that *died* resulted in a 5% loss of the total forb panne area from 2005. Contrary to other results, pannes that *merged* increased in area by 2017, nearly doubling from the total area of those same pannes in 2005. Of the total 334 forb pannes from 2017, 58% were *birth* events. (Table 4, Table 5).

Variation in panne dynamics among marsh sites

Patterns of *birth, death, persistence, split,* and *merge* events were spatially variable over the marsh surface, and spatial statistics found significantly higher quantities of regional dynamic events ($p < 0.05$), or hot-spots clusters, in specific regions of the marsh. Several overlapping hot spot clusters were identified between *merge* and *birth* events in the southern seaward part of the marsh and in this region hot spots of area expansion were also discovered. Some overlap was also seen between hot spot clusters of *splitting* and *death* events identified in the middle and more northern regions of the marsh. Significantly lower quantities of regional dynamic events ($p < 0.05$), or cold spot clusters, were more variable though cold spot clusters for area expansion, *births*, and *merges* were found mainly in the middle and northward regions of the marsh (Fig. 10).

The southern part of the marsh was the only area that experienced *merge* events. The hot spot of pannes that *merged* occurred in the southern seaward part of the marsh, an area extending into the southern tip of the descending peninsula and the southeastern marsh. Moreover, *birth* events seen in this region had larger areas. *Birth* event pannes also had a statistically significant hot spot cluster ($p < 0.05$) in the southern part of the marsh, largely in the southeastern marsh and extending into the mid and southern regions of the ascending peninsula, with a singular cell found just west of the river mouth. *Merge* and *birth* events had three grid cells of overlapping hot-spot clustering.

The statistically significant hot spot cluster for *birth* area was also located in the southern seaward part of the marsh extending up into the middle of the ascending peninsula. Six out of the seven hot spot cluster cells for *birth* area were shared with the hot spot cluster of *birth* events. All three southern-most hot-spot cluster cells for *birth* area were shared with the *merge* event hot spot cluster, and two of these southern-most cells were also shared with the hot spot cluster for total area growth. One of the northern-most hot spot cluster cells for *birth* area was shared with the hot spot cluster for *split* events.

The largest hot spot cluster for panne *death* events was located along the northern tip of the ascending peninsula with two other singular hot spot cluster cells located nearby, east and adjacent to the more northern bow of the Little River. The hot spot cluster for *split* events was located under the *death* event hot spot in the middle region of the ascending peninsula, as well as part of the descending peninsula. One northern-most cell of the hot spot *split* event cluster was shared with the *death* event hot spot cluster. One easternmost hot spot *split* event cluster cell was shared with the *birth* event hot spot cluster as well as the hot spot cluster for *birth* area. Lastly, one southern-most hot spot *split* event cell was shared with the *merge* event hot spot cluster.

Cold spot clusters of pannes that *died* were found in all southern regions as well as the northeast and northwest edges of the marsh. Statistically significant cold spot clusters of *split* events were located sporadically through the east, southwest, and all northern edges of the marsh, and they were generally located near the marsh grid perimeter and thus marsh edge.

Pannes that *merged* had statistically significant cold spot clustering everywhere else on the marsh, except directly surrounding the hot spot cluster in the south. Statistically significant cold spot clusters ($p < 0.05$) of *birth* event pannes were seen in the northern region of the marsh. Cold spot clusters for *birth* area were also located in the northern regions of the marsh.

Area growth had a statistically significant hot spot cluster ($p < 0.05$) in the southern seaward part of the marsh near the river mouth. In the southern part of the hot spot cluster for area growth, three of five hot spot cluster cells were shared with the hot spot cluster for *merge* events and two were shared with hot spot clusters of both *birth* event and *birth* area. A statistically significant cold spot cluster for area change, representing panne area loss, was located in the northwestern part of the marsh adjacent to the northern bow of the Little River Marsh and near the marsh grid border.

Discussion

Based on projected rates of SLR (Sweet et al. 2017), I predicted SLR to be a stronger driver of current forb pannes than climate warming and thus predicted forb pannes of the Little River Marsh in Wells, ME to have increased in number and size over time. Whereas forb panne number did increase over time, size of forb pannes did not, and total forb panne area on the marsh declined by 1% between sampling years. I likewise predicted that forb pannes would have overall trends of expansion and that these trends would not be regionally specific, because I assumed SLR and increased inundation periods to be uniform across the marsh surface. I found that forb pannes had a general trend of area loss over time and areas that experienced forb panne expansion were regionally specific with increase in forb pannes area being clustered in one portion of the marsh.

My findings provide evidence for forb panne habitats as dynamic parts of the marsh and show that mixed forb pannes can be persistent as well as transitory parts of the Maine meadow marsh landscape. Overall trends showed loss of forb panne area and large amounts of forb panne *death* and *splitting* in 2017, which suggests that warming climate has a larger effect on forb panne occurrence than past SLR increases. However, *splitting* and *death* events were spatially variable, with contracting forb panne areas located only in the middle to more northern regions of the marsh, whereas increased panne growth in the form of *merging* and *births* was found largely in the southern seaward region of the marsh near the river mouth.

Due to the known maintenance of forb pannes by waterlogging (Ewanchuk & Bertness 2004a), the non-random spatially located trend of area expansion in the southern seaward region of the marsh suggests a highly waterlogged region. Panne expansion hotspots in the southern region of the marsh could be due to a change in hydrology causing water to become stuck on the marsh surface, perhaps related to a large storm event or could possibly be an early indication of the effects of increasing SLR. High marsh waterlogging also can be a precursor to marsh drowning, and this finding suggests the potential for future loss of this part of the marsh. Future research could monitor these areas over time.

Whereas high rates of *merge* and *birth* events in the southern regions of the marsh potentially indicate a highly waterlogged region, high rates of *death* and *splitting* events located in the middle and more northern regions suggest that waterlogging is decreasing in these regions of the marsh. This trend suggests warming climate has a larger effect on forb panne occurrence here than increased SLR. Alternatively, as elevation gain causes forb pannes to be displaced by graminoid species (Gedan and Bertness 2009), part of this region could still experience slight emergence due to post-glacial rebound from the Laurentide ice sheet that once covered Maine marshes (Dillon and Oldale 1978; Barnhardt et al. 1995).

Whether salt marsh ecosystems will withstand current rates of SLR is a question under scrutiny at present (Kirwan et al. 2010; Fagherazzi et al. 2012). Resilience is determined by a salt marsh's ability to either vertically accrete at rates faster than SLR or to migrate inward (Kirwan et al. 2016). Accretion data taken at three marsh locations on the Little River Marsh between June 2015 and August 2016 (Rachel Carson National Wildlife Refuge, unpublished) show the marsh to have accreted a mean of 2.56 ± 1.13 mm. Whereas accretion rates varied by location between the two years (range 1.28-4.47mm), it may not be enough to keep up with projected rates of SLR. Global mean sea level (GMSL) rise predictions list a high scenario based on current rates of glacier melt of 210 mm by 2030 (Sweet et al. 2017), which even at the highest measurement of 4.47 mm/year would far overcome the marsh surface.

Preliminary events to marsh drowning include increased inundation of the marsh due to elevated SLR coupled with low sediment supply (Mariotti and Carr 2014). SLR increases are exacerbated by hydrologic blockage resultant of historic anthropogenic marsh use, and these blockages result in an increase in marsh pools, which in turn have been associated with waterlogging (MacDonald et al. 2010), thus decreasing marsh resiliency. These findings could be representative of forb panne exapansion seen in the southern seaward region of the marsh. Future research could compare salt marsh pool dynamism on the Little River Marsh to see if high quantities of pool *merge* and *birth* events are positively related to forb panne *merging* and *birth* events.

Whereas both mapping efforts were conducted during summertime peak growth periods, forb pannes in other marsh environments can exist as transitional habitats within one season, which is common in the annual-dominated forb pannes of southern New England (Bertness 1992). Although no conclusive research on a similar phenomenon has occurred with mixed forb pannes in Maine, the possibility exists that slight discrepancies in timing of forb panne perimeter mapping could result in perimeters changing throughout summer.

In conclusion, this study suggests that mixed panne habitats are dynamic and that while *persistent* pannes exist, these habitats are moving and changing through time. Whereas some mixed forb pannes appear to be more permanent parts of the marsh, the high quantities of *splitting* and *death* associated with the overall decrease in forb panne areas seen in the middle and northern regions of the marsh suggest that pannes could be decreasing in these regions due to warmer and drier substrates (Gedan and Bertness 2009). The high frequency of *merging* and *birth* events seen in the southern seaward part of the marsh suggests an increase in waterlogged substrates ideal for panne habitat (Ewanchuk and Bertness 2004a). If so, then plant communities of forb pannes can be utilized to indicate changes in marsh substrate and allow management to develop mitigation plans to prevent marsh loss due to increasing SLR.

Chapter 2

Interior and Edge Plant Community Assembly Of The Salt Marsh Forb Pannes of Maine

Abstract

Mixed forb pannes of northern New England house a diversity of salt marsh vegetation found along the Gulf of Maine. These areas are maintained by waterlogging and replaced by turf-grass species when drained, elevated, or warmed. Whereas studies regarding forb panne landscape distribution, overall plant communities, and nutrients have been conducted, no one has addressed interior gradients of edaphic variables or plant assembly that could indicate community level responses to sea level rise (SLR) and climate warming. My objectives were to 1) determine if edaphic and species gradients exist within pannes 2) if so, determine whether interior and edge species are associated with local edaphic variables such as sediment moisture, temperature, salinity, NH_4^+ and NO_3^-, and 3) map forb pannes and broader geospatial variables of a subsection of the Scarborough Marsh in Scarborough, ME and characterize edaphic variables and species composition with larger scale spatial variables such as panne area, distance to river, distance to pools, and distance to upland edge. Temperature and NO_3^- were higher in interior habitats of forb pannes, whereas NH_4^+ was higher in edge habitats. Salinity, NO_3^- and NH_4^+ were all positive functions of panne area and distance to river, whereas NO_3^- and NH_4^+ were both inverse functions of distance to urban edge. Interior areas had

increased abundances of *Spartina alterniflora,* a water adapted graminoid, and decreased abundances of *Spartina patens*, a less water tolerant matrix grass. In the Scarborough Marsh, an urban and tidally restricted marsh of Scarborough, ME, 10% of the study marsh was occupied by forb pannes. Whereas no base line coverage exists for forb pannes on marshes in Scarborough, Maine, this relatively high percentage of forb panne cover could indicate the susceptibility of the marsh to increased SLR due to its tidal restriction.

Introduction

Salt marsh ecosystems are important ecological habitat for migratory birds and juvenile marine species and possess extremely high primary production subsidized by upriver nutrients, which produces valuable allochthonous detritus for nearshore waters and bays (Teal 1962; Odum 1971; Boesch and Terner 1984; Shriver et al. 2004). These systems are also recognized for the ecosystem services they provide, including stabilizing coastlines in storm events, sequestering carbon in marsh peat, and filtering runoff from uplands and subsequently protecting nearshore waters (Valiela and Teal 1979; King and Lester 1995; Chmura et al. 2003). Vegetation is the structural, biological and chemical foundation of the salt marsh ecosystem and this topic of study has received less attention in northern New England than in salt marshes of the southern United States. With evidence of a changing climate and increasing sea level rise (SLR) (Walther et al. 2002; Sweet et al. 2017), understanding abiotic influences on northern New England's salt marsh plant communities is paramount to maintaining their functions and informing their conservation (Short et al. 2016).

Mixed forb pannes of the salt marshes of Maine house distinct plant communities found in the northeastern United States and perhaps parts of Canada (Chmura et al. 1997; Ewanchuk & Bertness 2004b). These habitats are dominated by perennial species, such as *Plantago maritima* (hereafter *Plantago*) and *Triglochin maritima* (hereafter *Triglochin*), with *Limonium nashii* and sometimes *Glaux maritima* abundant (Griffin et al. 2011). Annual forbs such as *Salicornia spp, Suaeda maritima,* and *Agalinus maritima* are sometimes present, but never more than 10%

relative abundance (Griffin et al. 2011). The only graminoids with high frequency in these pannes are short form *Spartina alterniflora* and *Spartina patens,* but their relative abundance also rarely tops 10% (Theodose and Roths 1999; Griffin et al. 2011). Three other graminoids, *Puccinellia maritima, Juncus gerardii,* and *Distichlis spicata* are infrequent. Whereas some of these species are seen in salt marshes further south, the size and extent of these assemblages are unique to Maine, though they may be present in Canadian salt marshes.

The mixed forb pannes of Maine salt marshes are a diverse plant community maintained by waterlogging (Ewanchuk and Bertness 2004a). When drained, marsh matrix graminoid *S. patens* quickly dominates, leading to the disappearance of the forb panne (Gedan and Bertness 2009). These results suggest that with future sea level rise (SLR), Maine salt marshes may experience increased periods of marsh inundation, which could be more favorable for mixed forb panne formation and longevity (Ewanchuk and Bertness 2004a). In contrast, warming experiments of pannes result in disappearance of the panne and competitive displacement by *S. patens* (Gedan and Bertness 2009). Because Maine marshes may be able to keep up with SLR by a combination of accretion, moving inland, and perhaps post-glacial rebound, rising temperatures may result in decreased diversity of the marsh by forb panne contraction, fragmentation, or disappearance.

Shifts in forb panne size due to increased temperatures or SLR would likely be accompanied by changes in species composition within pannes themselves, particularly at peripheries (Thuiller et al. 2008), creating an edge habitat with species composition that differs from forb panne interiors. Variation in species assembly between the interior and edge of forb pannes could lead to patterns indicative of panne expansion or contraction. If expanding or contracting, edges of forb pannes may house an edge habitat containing different species assemblies from that of interiors.

Edges are ecological features that can exist as gradients or sharp boundaries, but they always are identifiable by their ecologically unique composition (Fagan et al. 1999). Whether that be different species abundances such as is seen in fragmented forests, or the abiotic results of such edges such as decreased humidity on the edge habitats of the Brazilian Amazon (Kapos 1989), edge areas create a distinct habitat, which can help to decipher community interactions and how species behave in relation to slightly varying abiotic inputs (Fagan et al. 1999).

Mixed forb pannes have been documented to be as large as 5081 m^2 (Griffin et al. 2011), and because salt marsh species are so tightly coupled with abiotic variables, there large expanses could hold unique edge habitats not as obvious as distinct graminoid zones. Whereas variation in edaphic factors and species composition has been documented among forb pannes (Theodose and Roths 1999), and stages of revegetation of ice-scoured areas have been monitored (Ewanchuk and Bertness 2003), a more targeted analysis of how edaphic and community parameters vary within existing pannes has not been undertaken. An edge habitat may be particularly important in determining where matrix graminoid species can exist and lead to a more informed understanding of interacting abiotic and species variables in situ.

Research on patterns within forb panne communities is lacking, and identifying internal gradients of species composition and physical edaphic parameters would add to basic research on how these salt marsh plant communities are assembled. Forb panne species distribution in Maine is nonrandom, and forb panne species are associated with larger geospatial variables such as distance from upland edge, distance to nearest pool, distance to river, and panne size (Griffin et al. 2011). However, interior and edge species abundance is largely unknown and spatial methodology coupled with edaphic gradient data has not been undertaken. This work may provide additional insight into how forb panne species are interacting with each other, as well as with edaphic variables.

Because nutrient availability across the salt marsh varies (Theodose and Roths 1999; Theodose and Martin 2003) and interspecific competition is dictated by physical stressors (Bertness 1991), nutrient differences, temperature and sediment moisture within forb pannes may elucidate differences between interior and edge species abundances. Further, examining how nitrogen, sediment moisture and temperature are related to forb panne species abundance informs how plant communities are likely to respond to SLR and climate warming.

I built on the information of forb panne dynamics and investigated variation between interior and edge species and edaphic variables within forb pannes. This work could potentially inform how pannes are shifting, by suggesting which species would respond to SLR and temperature increases, providing indications of future change.

The objectives of this study were to 1) determine if edaphic and species gradients exist within pannes, 2) if so, determine whether interior and edge species are associated with local edaphic variables such as sediment moisture, temperature, salinity, NH_4^+ and NO_3^-, and 3) map forb pannes and broader geospatial variables of a subsection of the Scarborough Marsh in Scarborough, ME and characterize species composition and edaphic variables with larger scale spatial variables such as panne area, distance to river, distance to pools, and distance to upland edge.

Previous work by Theodose (unpublished) determined the Scarborough Marsh to have similar community structure and edaphic variation across forb and graminoid areas as the previously studied Little River Salt Marsh in Wells, ME (Griffin et al. 2011). I chose a subsection of the Scarborough Marsh to study forb pannes because its suburban tidally restricted state is common to northern New England salt marshes. Furthermore, although forb panne vegetation data have been collected for the non-tidally restricted Little River Marsh in Wells, ME (Griffin et al. 2011), no study has assessed forb panne vegetation in a more suburban marsh.

As mixed forb pannes are maintained by waterlogging (Ewanchuk and Bertness 2004a) and have higher temperatures, nutrients, and salinities (Theodose and Roths 1999; Theodose and Martin 2003), I predicted that edaphic and species gradients exist within forb pannes, with interior habitats having higher sediment moisture, temperature, salinity, and nutrients and likewise interiors having higher abundance of waterlogging tolerant species. I also predicted that abiotic and species variables are related to larger spatial variables, with forb pannes closer to rivers edge or pools having higher sediment moisture and likewise higher abundances of waterlogging tolerant plants.

Methods

Study site

All field work took place at a subsection of the Scarborough Marsh in Scarborough, ME (43°32'37.4" N, 70°20'36.8" W). The site is located behind Pine Point Beach near the mouth of the Nonesuch River. This marsh houses a large expanse of panne and pool habitat that is easily accessible via Pine Point Rd (Route 9; Fig. 11). There is no upland edge as this salt marsh is surrounded on its upland side by suburban development and the tidally restrictive Route 9. Whereas this subsection of marsh is more urban, it contains no identifiable ditching or dikes.

Sample design

In May 2017 I conducted a reconnaissance of high salt marsh habitat between Rt. 9 and the Nonesuch River, from just behind the river mouth at Pine Point to 2,000 m upriver. Here, I chose eleven pannes that were accessible on foot and seemed representative of the most common forb pannes on the marsh (Fig. 12). Because some pannes can fade gradually into graminoid species (Griffin et al. 2011), I chose only pannes that had a discrete *S. patens* edge to allow the forb pannes to be appropriately standardized. To test the prediction that edaphic variables follow a gradient, I defined an edge habitat as spanning from the perimeter of the discrete *S. patens* to 0.5 m inward.

Edaphic sampling

To test the prediction that edaphic variables differ between interior and edge forb panne habitats, I collected data on salinity, sediment moisture and sediment temperature data in interior and edge habitats once during every neap tide beginning June 3 and continuing to September 2, 2017. During reconnaissance I haphazardly inserted two salinity tubes: one within 25 cm of the discrete *S. patens* perimeter and one near the relative center of the panne, 1 m interior of the panne perimeter. Salinity tubes are 5 cm diameter PVC pipes stoppered at both ends with several drilled holes that when inserted to approximately a depth of 15cm correspond with the rooting zone of panne plants (Roman et al. 1984). Water enters these tubes and can be drawn periodically and tested for salinity. To measure salinity, I used a plastic pipette to extract all water available in salinity tubes, mixed this sample by inversion to avoid haloclines, then determined salinity in parts per thousand (ppt) using a handheld NaCl refractometer (Pentair Vital Sine™ Salinity Refractometer SR6) measuring to the nearest 1 ppt.

I collected sediment moisture and temperature within pannes haphazardly: for edge data within 0.5 m of the discrete *S. patens* perimeter, and for interior data 1 m interior from the perimeter near the relative center of the panne. Volumetric sediment moisture was measured to the nearest 0.01 cm^3 H_2O/ cm^3 sediment using a Moisture Meter and Probe (Delta-T Devices Theta Meter type HH1 and Delta-T Devices Theta Probe), which measures the dialectic constant of water. Sediment temperature was measured within the first 1-1.5 cm (rooting depth) of marsh sediment to the nearest 0.01 °C using a probe thermometer (Taylor 9841 NSF).

To measure nitrogen availability within edge and interior habitats, I inserted mixed ion exchange resin bags in haphazardly selected locations at the defined interior and edge of each sampling panne. This method provides a relative index of long term N availability within pannes as resin bags collect ions over the entire growing season (Binkley and Matson 1983). Bags were placed in pannes on July 5, 2017 and removed on September 27, 2017. After removal, bags were placed on ice and taken to the University of Southern Maine and immediately frozen to halt microbial activity. Later, resins bags were wiped of debris, and resins were removed and weighed before being extracted with 1M KCl. Extracts were sent to the University of Maine Soil Science Laboratory where NH_4^+ and NO_3^- concentrations were determined by colorimetric analysis. I then calculated extractable NH_4^+ and NO_3^- to the nearest 0.01 µg ion/g resin.

Plant community sampling

I conducted plant community measurements between late July and mid-August 2017 during peak biomass, using a modification of the point plot method (Jonasson 1992). To test predictions about species gradients, I used two 0.5 m grid frames with 25 points each to sample edge and interior species composition, with the edge defined as lying along the *S. patens* perimeter and the interior defined as 1 m inwards towards the relative center. I placed the 0.5 x 0.5 m quadrats haphazardly, two nearest the *S. patens* edge, and two 1 m interior near the relative center of the panne, resulting in 50 points for each habitat. This method allowed increased resolution of vegetation in interior and edge habitats of interest.

From these plot measurements, I determined absolute and relative abundance of each species (Barbour at al. 1987). I used relative abundance data to calculate species diversity and evenness at the edge and interior of each panne. Shannon Diversity Index, H' (Shannon and Weaver 1949), which takes into account both species richness and evenness, was used, as well as the Evar index (range 0-1) as it is independent of species richness (Smith and Wilson 1996).

Spatial variable mapping

To test predictions about effects of spatial variables on edaphic and plant community variables, I located and mapped all forb pannes of the Scarborough Marsh with a Trimble GeoXT GPS unit from July 26 to August 29, 2017. Because forb panne boundaries are at times not discrete and instead fade gradually into surrounding matrix graminoids (Griffin et al. 2011), previous methodology for mapping includes only pannes having >50% forb species, with exclusion of pannes that contained upland species such as *Solidago sempervirens* (Griffin et al. 2011). This method is described as a structured decision making process (Griffin et al. 2011). To replicate the previous mapping effort by Griffin et al. (2011), forb pannes were designated by having >50% forb cover, using the same structured decision making process. Only pannes greater than 1 m^2 were used because smaller pannes were not considered significant forb panne habitat. Sampling points for edaphic variables were also mapped during this time. All data were Real-Time Satellite Based Augmentation System (SBAS) corrected and exported as a shapefile to be processed in ArcGIS (10.5.1). The projection and coordinate system used for the project was Universal Transverse Mercator (UTM) Zone 19N North American Datum 1983 (NAD1983) Continuously Operating Reference Station (CORS96) with the vertical datum North American Vertical Datum 1988 (NAVD88).

During creation of composite layers for mapped forb pannes, I identified overlapping polygons, which occurred during in field mapping of forb panne perimeters. To make these data useable, I repaired the shapefile geometry and dissolved the polygons into single part, a tool in ArcGIS that resolves overlapping delineation. Other features such as pools, river's edge, and urban edge were then digitized. For digitization efforts, I used NOAA 2011 Near Infrared Ortho-rectified Mosaic of Maine: Cutt's Island to Prout's Neck Imagery, available through NOAA's Digital Coast web site, with only the infrared band displayed, making differences between water bodies and marsh apparent (Fig. 13).

Descriptive statistics from all pannes on the marsh included minimum area, maximum area, mean area, and total area. To assess larger scale spatial variables and their relations to species and edaphic variables, distance from panne sampling points to other marsh features such as pools, river's edge, and upland edge, was calculated using the Near Table tool in ArcGIS. Generated distance data were used for all spatial statistical analyses. Lastly, I digitized a polygon of the marsh study area and used its area to calculate percent forb panne cover:

Percent forb panne cover = (total area of forb pannes/total marsh study area) x 100.

Statistical analysis

To test predictions about patterns existing between interior and edge habitats, I statistically compared interior and edge data in JMP using matched pair Wilcoxon signed rank tests (JMP 13.2). Ten pannes with paired interior and edge data were used in analysis as one panne (Plot 3) became overgrown with *J. geradii* halfway through the sampling season and was thrown out. I used linear regression analyses in JMP to compare relationships between vegetation, abiotic and spatial variables (JMP 13.2). Additionally, I used multiple regressions conducted in R to assess individual species as a function of both abiotic and spatial variables, as well as abiotic variables as a function of spatial variables (R 3.3.1 GUI 1.68 Mavericks build). All data were checked for normality and found sufficiently normally distributed. Significance level of $p < 0.05$ was used for all statistical tests. Results are presented as mean ± SE.

Results

Within panne heterogeneity

Abiotic variables differed between edge and interior habitats of forb pannes. Temperature was 4% higher in interior habitats compared to edge (Wilcoxon signed rank test, n = 10 pannes, p = 0.0168, Fig. 14). Sediment nitrogen availability (both NO_3^- and NH_4^+) differed significantly between interior and edge habitats and the two were inversely related. NH_4^+ was 39% higher in edges compared to interior habitats (Wilcoxon signed rank test, n = 10 pannes, $p < 0.0001$, Fig. 15). In contrast, NO_3^- was was 41% higher in interiors (Wilcoxon signed rank test, n = 10 pannes, $p < 0.0001$, Fig. 16). Neither salinity nor sediment moisture differed significantly between interior and edge habitats ($p > 0.05$).

Edge sediment moisture increased with interior sediment moisture across all pannes (Linear regression: n = 10 pannes, $r^2 = 0.4748$, p = 0.0275; Fig. 17). Although not statistically significant ($p > 0.05$), edge salinity and temperature also increased at interiors across pannes. There was no relationship between edge and interior NO_3^- or NH_4^+.

Species composition of edges and interiors

Vegetation varied significantly in species composition in edge and interior panne habitats. *Plantago*, *Triglochin*, *L. nashii*, *S. patens*, and *S. alterniflora* were consistently found throughout all sampling pannes. Absolute abundance of *S. patens* was 29% higher in edge habitats compared to interiors (Wilcoxon signed rank test,

$n = 10$ pannes, $p = 0.0022$; Fig. 18). Conversely, absolute abundance of *S. alterniflora* was 20% higher in interior habitats compared to edge (Wilcoxon signed rank test, $n = 10$ pannes, $p = 0.0387$; Fig. 19). Absolute abundance of *Plantago, Triglochin* and *L. nashii* in interior and edge panne habitats did not differ statistically ($p > 0.05$).

Absolute abundance of interior and edge species showed panne interior and edge *S. patens* to be related, with a statistically significant positive relationship between interior and edge *S. patens* (Linear regression: $n = 10$ pannes, $r^2 = 0.6759$, $p = 0.0035$, Fig. 20). Interior and edge absolute abundance was also statistically significant for *L. nashii* (Linear regression: $n = 10$ pannes, $r^2 = 0.5724$, $p = 0.0113$, Fig. 21). A positive, but not statistically significant relationship ($p > 0.05$), between edge and interior absolute abundance was also present with *S. alterniflora* and *Triglochin,* and inversely with *Plantago*. Diversity, evenness, and species richness showed no trend between interior and edge habitats.

Abiotic and plant relationships

Sediment moisture was positively related to absolute abundance of *L. nashii* (Linear regression: $n = 10$ pannes, $r^2 = 5414$, $p = 0.0153$; Fig. 22). *S. patens* abundance also showed a trend of being inversely related with sediment moisture, and salinity showed a slight positive relationship with *Plantago* and *Triglochin,* but both were not statistically significant ($p > 0.05$). Temperature showed no meaningful trends or statistically significant relationships. NH_4^+ showed a positive non-significant relationship ($p > 0.05$) with *Triglochin* abundance and a negative non-significant relationship ($p > 0.05$) with *L. nashii* abundance.

Spatial patterns and relationships with edaphic and species variables

Forb pannes were plentiful on the Scarborough Marsh and took up a substantial amount of marsh area. A total of 203 forb pannes were mapped, covering a total of 5,554.32 m^2 and comprising 10% of the surveyed area. Mean panne size was 27.36 ± 11.36 m^2 (range 1-2,234.58 m^2). Mean distance to the river's edge was 433.88 ± 185.66 m (range 1-17,081.24 m). Mean distance to the nearest pool was 465.02 ± 187.81 m (range 0.76-17,293.82 m). Mean distance to urban edge was 618.73 ± 184.10 m (range 32-17,114.04 m). However, standard error for river, pool, and urban edge distances were all very high (> 2600), as is expected given the large ranges.

Salinity was a positive function of panne area and distance to river (Multiple regression: n = 10 pannes, $r^2 = 0.598$, $p = 0.03$), whereas NO_3^- and NH_4^+ were both inverse functions of distance to urban edge and positive functions of panne area and distance to river (NO_3^- multiple regression: n = 10 pannes, $r^2 = 0.7461$, $p = 0.02$; NH_4^+ multiple regression: n = 10 pannes, $r^2 = 0.7901$, $p = 0.01$).

Linear regression analyses of spatial variables and species absolute abundances showed several statistically significant relationships. *L. nashii* was more abundant near the river and decreased in abundance with river distance (Linear regression: n = 10 pannes, $r^2 = 0.4478$, $p = 0.03$; Fig. 23). Similarly, *S. patens* was more abundant near pools and declined with pool distance (Linear regression: n = 10 pannes, $r^2 = 0.4786$, $p = 0.03$; Fig. 24). Lastly, *Plantago* was higher in abundance nearer urban edges and increased with distance from the urban edge (Linear regression: n = 10 pannes, $r^2 = 0.4317$, $p = 0.04$, Fig. 25).

Discussion

In line with predictions, statistically significant edaphic and species differences existed between edge and interior habitats of forb pannes. Forb panne interiors had higher temperatures and levels of NO_3^- compared to edges, and edge habitats had higher levels of NH_4^+ compared to interiors. However, soil moisture and salinity did not vary between interior and edge. As forb pannes are identifiable by their more sparse vegetation cover, higher temperatures in interiors are likely due to increased absorption of heat by exposed dark sediments compared to more vegetated areas. Temperature differences may influence arbuscular mycorrhizal (AM) colonization associated with particular salt marsh forb panne species (Burke et al. 2003; Füzy et al. 2008). Arbuscular mycorrhizal fungus (AMF) is typically limited or absent in waterlogged soils (Mason 1928); however, certain species are still present in the salt marsh environment and colonize during drought conditions (Füzy et al. 2008; Wilde et al. 2009). When AMF is suppressed, there are more carbonic exudates in sediment and microbial and bacteria populations associated with nitrogen-fixing increase in biomass and population size (Burke et al. 2002). Thus, temperature could indirectly affect rates of microbial activity by creating periods of drought, which in turn affects abundance of different N compounds. Future research could investigate this phenomenon in Maine forb pannes.

Salinity was a positive function of panne area and distance to river which is likely due to larger areas of more exposed dark substrates and further distance to the river experiencing higher rates of evaporation. NO_3^- and NH_4^+ were also both positive functions of panne area and distance to river and inverse functions of distance to urban edge. These results indicate N compounds may be more abundant in more saline environments. As nitrogen compounds can be utilized by plants as an adaptation to salinity stress (Mansour 2000), this finding is potentially related to some forb species reliance on nitrogen compounds (Storey et al. 1977).

Edge panne habitats had higher absolute abundance of *S. patens* compared to interiors, whereas panne interiors had higher absolute abundance of *S. alterniflora* compared to edges. As *S. alterniflora* is a highly waterlogging adaptive graminoid species (Teal and Kanwisher 1966), the higher abundance of *S. alterniflora* in interiors indicates that interior habitats have more waterlogged substrates than edges do. Likewise, *S. patens* is a graminoid species with limited waterlogging tolerant capabilities (Burdick and Mendelssohn 1990) and also a marsh matrix species. Higher abundance of *S. patens* in edges indicates edge habitats are dryer than interiors of forb pannes are. Higher abundance of *S. patens* in edges and *S. alterniflora* in interiors could indicate interior and edge forb panne habitats as part of an abiotic gradient in which *S. patens* is more competitive in dryer edges and *S. alterniflora* is more competitive in wetter interiors. Higher abundance of *S. patens* in edge habitats could also in part be assisting in the lower temperatures of edge habitats, perhaps due to increased shade created by the turf grass species.

Edge absolute abundance increased with interior absolute abundance for both *S. patens* and *L. nashii.* These results perhaps indicate pannes with overall suitability for either species and could be related to abiotic factors on the marsh surface. Pannes with higher interior and edge absolute abundance of matrix graminoid *S. patens* may be dryer pannes or potentially pannes about to transition to matrix turf species. Conversely, as *L. nashii* abundance was positively related to sediment moisture, forb pannes with higher abundance of *L. nashii* in edge and interior habitats may indicate wetter pannes, or pannes about to transition to short form *S. alterniflora* or pool. Overall suitability of pannes to species based on their waterlogging tolerances enforces predictions of abiotic contributors on species assembly. Moreover, consistently waterlogged areas on the marsh likely result in longer-lived mixed forb pannes.

Statistically significant relationships between spatial variables and species abundance were also found. For example, *L. nashii* was more abundant near the river and decreased in abundance with river distance. Whereas distance to river had no statistically significant relationship with sediment moisture, the relationship of *L. nashii* abundance decreasing with river distance is likely related to the positive relationship between *L. nashii* abundance and sediment moisture. This finding may be more representative of the prolonged hydroperiod of pannes closer to creeks, which allows waterlogging tolerant *L. nashii* to be more competitive, than to maintained high levels of sediment moisture.

Other statistically significant relationships between spatial variables and species abundance included relationships between pools and *S. patens* and between urban edge and *Plantago*. *S. patens* abundance in forb pannes was higher for forb pannes close to pools. This relationship could be an artifact of pools having a higher likelihood of being located in marsh meadows where *S. patens* is the dominant species, versus forb pannes found nearer to the perimeter of the river channel where the dominant graminoid switches to *S. alterniflora* (Bertness and Ellison

1987). The finding of *Plantago* increasing in abundance further away from the upland urban edge is possibly related to other findings on the Little River Marsh, which detailed *Plantago* increasing in abundance closer to pools and rivers (Griffin et al. 2011). Whereas *Plantago* was not significantly related to rivers and pools in this study, the increase in *Plantago* abundance with distance to urban edge could also be a spatial relic, for as distance increases from the upland edge, distance decreases to rivers and pools.

Lastly, forb pannes on the Scarborough Marsh covered 10% of the study marsh, which is double the finding from Griffin et al. (2011) in which forb pannes of the Little River Marsh covered 5% of the study marsh. The Little River Marsh in Wells, ME has no tidal restrictions, whereas the Scarborough Marsh is tidally impeded by Route 9. This tidal impediment likely causes backwash of high tides on to the marsh, and high forb panne cover is probably related to increased inundation of the marsh surface. Future research could focus on forb panne abundance in tidally restricted versus non-tidally impeded salt marshes in Maine to test this hypothesis.

Salt marshes provide valuable ecosystem services to coastal communities and nearshore waters (Valiela and Teal 1979; King and Lester 1995; Chmura et al. 2003). Moreover, the ecological habitat that salt marsh ecosystems provide is important for many species (Teal 1962; Odum 1971; Boesch and Terner 1984; Shriver et al. 2004). Increased forb panne abundance on Maine salt marshes is likely a response to SLR (Sweet et al. 2017) and thus increased marsh inundation. Moreover, increases in waterlogged substrates of the marsh are likely indicators of decreased marsh resilience. With more insight into how plants are distributed within and between forb pannes, this work can help to inform management about how salt marsh vegetation is likely to respond to changes in abiotic variables brought by SLR or climate change.

Conclusion

Salt marshes are valuable ecosystems recognized for both ecological importance to wildlife (Boesch and Turner 1984; Shriver et al. 2004) and ecosystem services such as carbon sequestration and protection of coastlines (King and Lester 1995; Chmura et al. 2003). Existing records of elevation change in salt marshes predict that sea level rise (SLR) will overtake 60% salt marshes worldwide by 2100 (Crosby et al. 2016). I investigated forb pannes of Maine and identified them as potential indicators of edaphic salt marsh change, provided insight into how salt marsh plant species are likely to transition with SLR and warming climate, and elucidated mechanisms by which forb pannes changed over time in a protected salt marsh.

In the first chapter of this thesis, I conclude that mixed forb panne habitats are dynamic parts of the Maine meadow marsh and that while *persistent* pannes exist, these habitats are largely moving and changing through time. My mapping work suggests that decreases in forb panne areas seen in the mid and northern regions of the Little River Marsh are potentially related to warmer and drier substrates (Gedan and Bertness 2009) and that high frequency of *merging* and *birth* events seen in the southern seaward part of the marsh are related to an increase in waterlogged substrates ideal for panne habitat (Ewanchuk and Bertness 2004). These findings suggest that forb pannes indicate edaphic changes in marsh substrate.

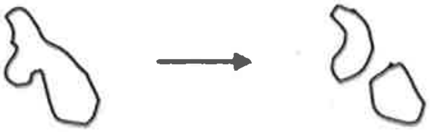
In the second chapter of this thesis, I conclude that mixed forb pannes of Maine exist as diverse habitats that house unique edge and interior habitats with distinct edaphic conditions. Interior and edge habitats also house distinct species arrangements related to edaphic variables and larger spatial variables. My results shed light on the edaphic tolerances of forb and graminoid species.

This research also hypothesizes relatively high percent cover of forb pannes to be associated with tidal restrictions in salt marshes, in which the marsh substrate experiences longer hydroperiod and creates larger areas of waterlogged sediment ideal for creation and maintenance of mixed forb panne habitat. Future research could examine this relationship.

To conclude, my results provide evidence of forb panne marsh communities as indicators of hydrologic change and offers their potential for providing early warnings in salt marshes vulnerable to loss by SLR. The salt marshes of New England have been established as adaptable environments, and the mixed forb pannes of Maine display these same characteristics, transitioning over the marsh surface as substrate conditions change over time.

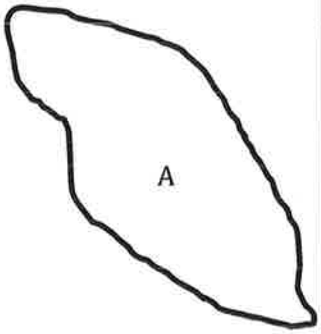
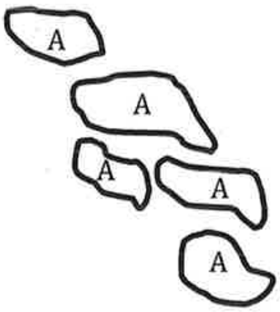
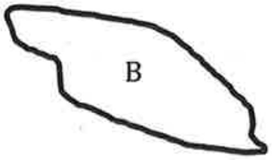
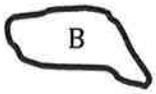
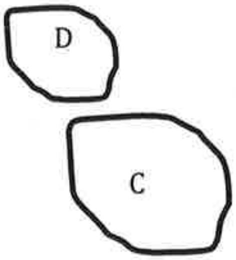
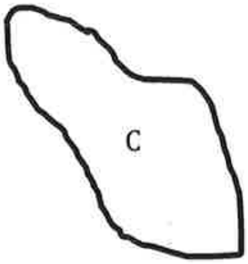
Tables

Table 1: Verbal and pictorial descriptions of forb panne events as observed from 2005 to 2017 in the mapping efforts of the Little River Marsh in Wells, ME.

Forb Panne Event	Verbal Description	Pictorial Description 2005 2017
Birth	Spontaneous appearance of a forb panne on the marsh surface that cannot be explained by *splitting* or *merging*, such that a new forb panne was observed.	
Persistence	Persistence of a forb panne on the marsh surface between sampling periods.	
Merge	The process of two or more forb pannes coalescing to form one larger forb panne. The number of pannes coalescing determines the total number of *merge* events.	
Split	The process of a forb panne fragmenting into two or more other pannes. The number of resulting pannes determines the total number of *splitting* events	
Death	Disappearance of a forb panne that cannot be explained by *merging* or *splitting* processes, such that a forb panne seen in one sampling year was not observed in the next.	

*Nomenclature scheme borrowed and modified from Wilson et al. (2009)

Table 2: Quantitative and pictorial descriptions of a *split* event (Panne A), *persistence* (Panne B), and a *merge* event (Panne C), with pictorial assignments of common panne IDs that were used to track individual panne events from the 2005 to 2017 mapping efforts of mixed forb pannes on the Little River Marsh in Wells, ME. Single year events such as *birth* and *death* are left out for brevity.

Event Type	Quantitative Descriptions				
	2005	**2017**			
	life	*life*	*merge*	*split*	*death*
Panne A	1	5	0	1	0
Split					
Panne B	1	1	0	0	0
Persistence					
Panne C	2	1	1	0	0
Merge					

*Nomenclature scheme borrowed and modified from Wilson et al. (2009)

Table 3: Descriptive statistics including count, area, and percent cover of forb pannes from the 2005 and 2017 mapping efforts of mixed forb pannes on the Little River Marsh in Wells, ME.

Forb Panne Count, Area, and % Cover Comparison		
Descriptive Statistic	**2005**	**2017**
Count	81	334
Minimum area (m^2)	7	1
Maximum area (m^2)	5081	4247
Mean area (m^2)	500	69
Total area (m^2)	40520	22880
% of marsh as pannes	5	4

Table 4: Descriptive statistics including count, area and area difference of *death* and *birth* events derived from the 2005 and 2017 mapping efforts of mixed forb pannes on the Little River Marsh in Wells, ME.

Descriptive Statistic	**Event**	
	***death* 2017**	***birth* 2017**
Count	28	193
Mean area (m^2)	165	26
Minimum area (m^2)	7	1
Maximum area (m^2)	910	636
Total area (m^2)	2219	5059
Area difference (m^2)	-2219	5059

Table 5: Descriptive statistics including count, area and area difference of *persistence, merge,* and *split* events from the 2005 and 2017 mapping efforts of mixed forb pannes on the Little River Marsh in Wells, ME.

Descriptive Statistic	**Event**					
	***persistence* 2005**	***persistence* 2017**	***merge* 2005**	***merge* 2017**	***split* 2005**	***split* 2017**
Count	23	23	5	2	25	142
Mean area (m^2)	327	196	415	2626	1052	322
Minimum Area (m^2)	25	3	76	1005	28	9
Maximum Area (m^2)	1823	1656	984	4247	5081	2082
Total Area (m^2)	7510	4505	2074	5252	26304	8041
Diff. of Means (m^2)		-131		2211		-730
Area Difference (m^2)		-3005		3178		-18263

Figures

Figure 1: Map of the Little River Marsh, Wells, ME. Labels indicate ascending and descending peninsulas created by the Little River, the river mouth of the Little River, as well as the Wells barrier beach, behind which the Little River Marsh forms. Imagery courtesy of MEGIS and Maine Geolibrary.

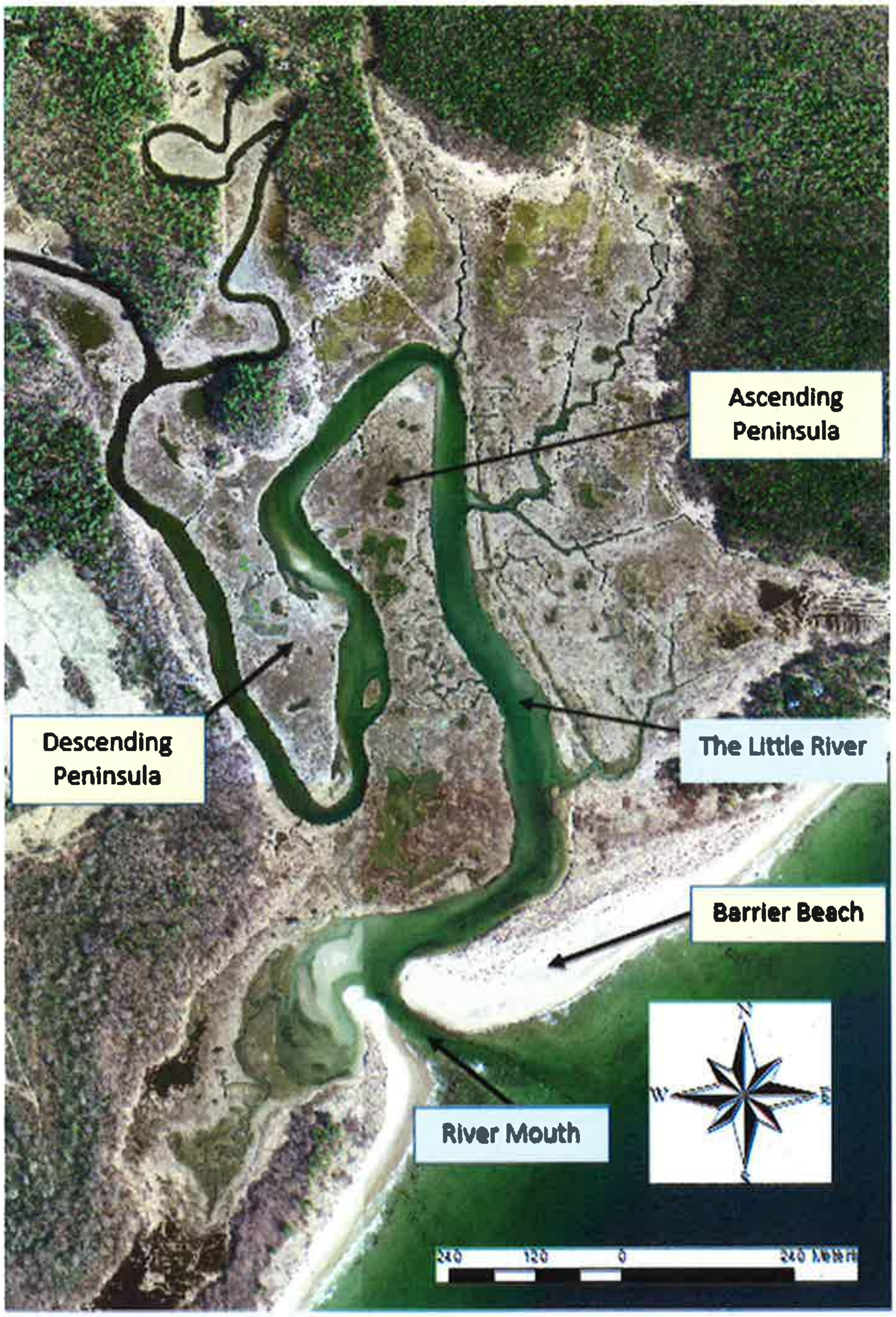


Figure 2: 2005 forb pannes of the Little River Marsh, Wells, ME mapped by Griffin et al. (2011). Imagery courtesy of MEGIS and Maine Geolibrary.

Figure 3: 2017 forb pannes of the Little River Marsh, Wells, ME mapped by Fischella (this study). Imagery courtesy of MEGIS and Maine Geolibrary.

Figure 4: Flow diagram of grid methods allocating forb panne data to grid cells for spatial analysis of forb panne change over time on the Little River Marsh, Wells, ME.

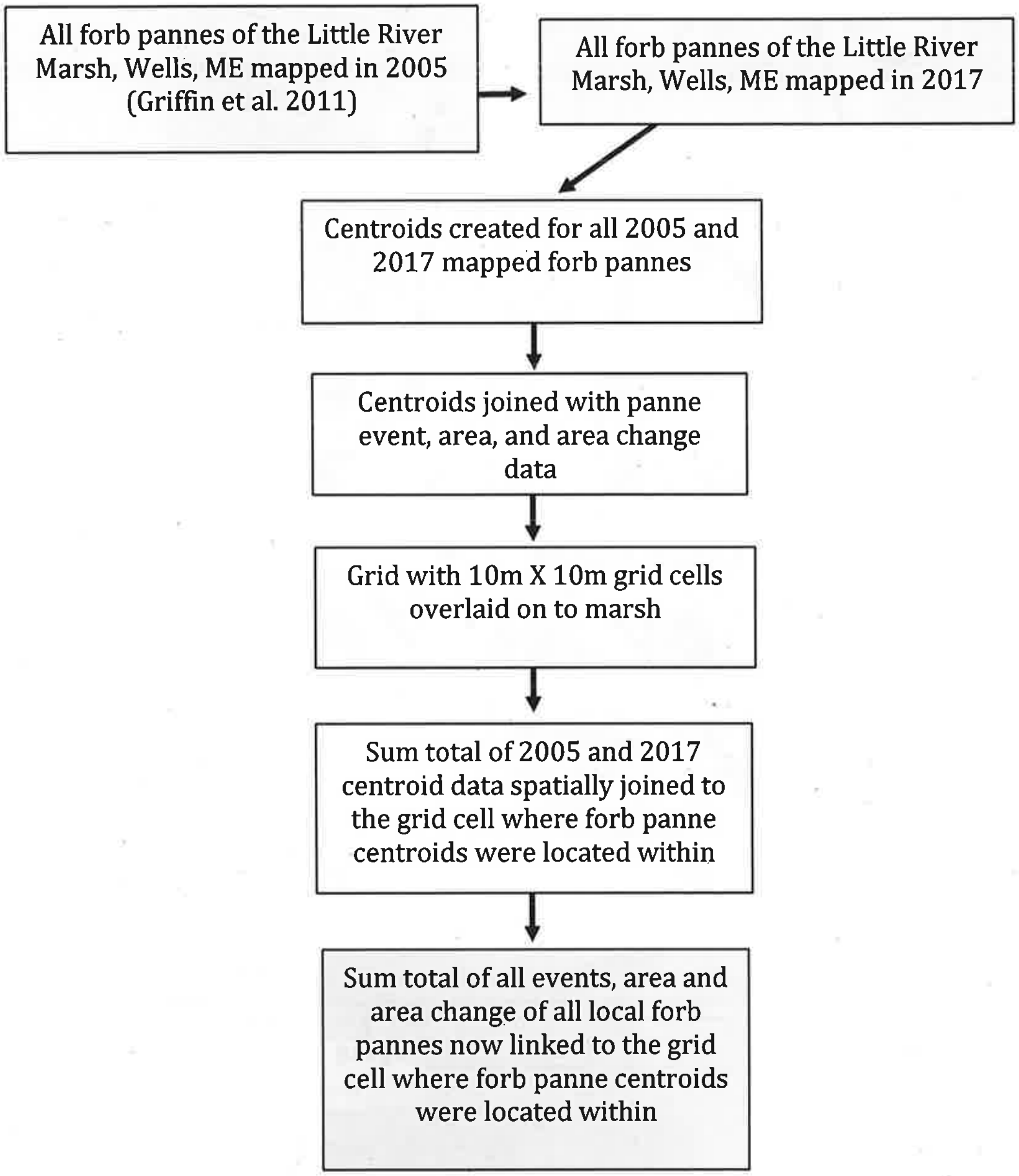


Figure 5: Grid with 10 X 10 m grid cells overlaid on to 2005 & 2017 forb pannes and their generated centroid points, Little River Marsh, Wells, ME.

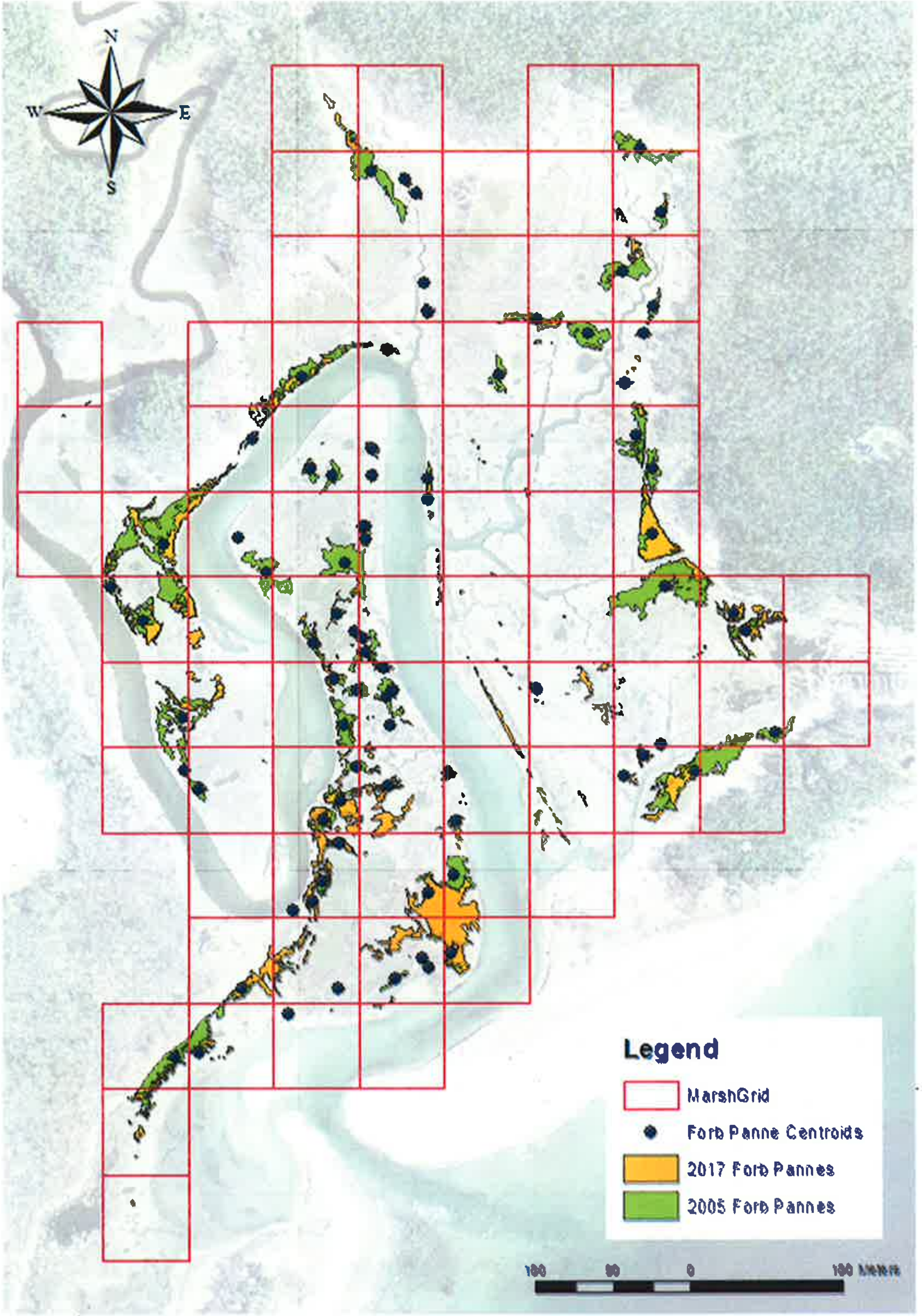


Figure 6: Counts of event types of forb pannes in years 2005 and 2017, Little River Marsh, Wells, ME.

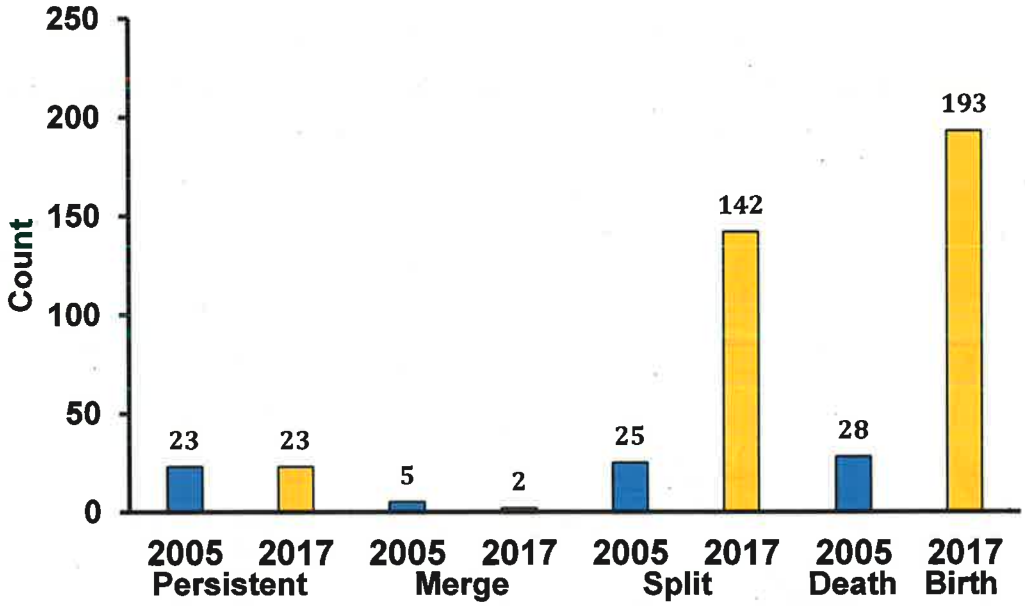


Figure 7: Comparison of total area (m^2) of event specific forb pannes in 2005 and 2017, Little River Marsh, Wells, ME.

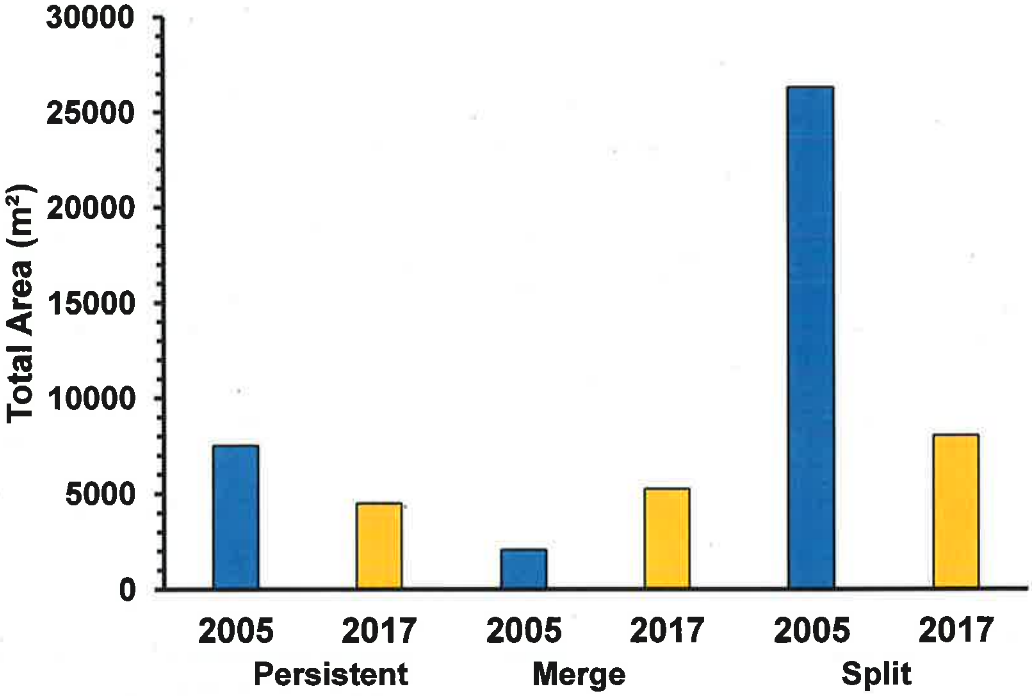


Figure 8: Total area (m^2) of forb pannes with *birth* and *death* events in 2017, Little River Marsh, Wells, ME.

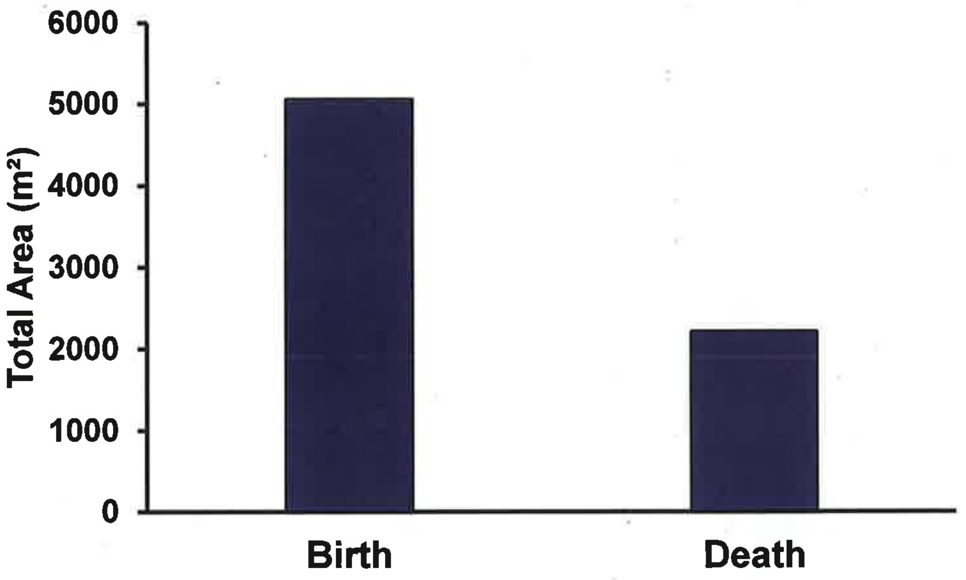


Figure 9: Comparison of total forb panne area (m^2) in 2005 and 2017, Little River Marsh, Wells, ME.

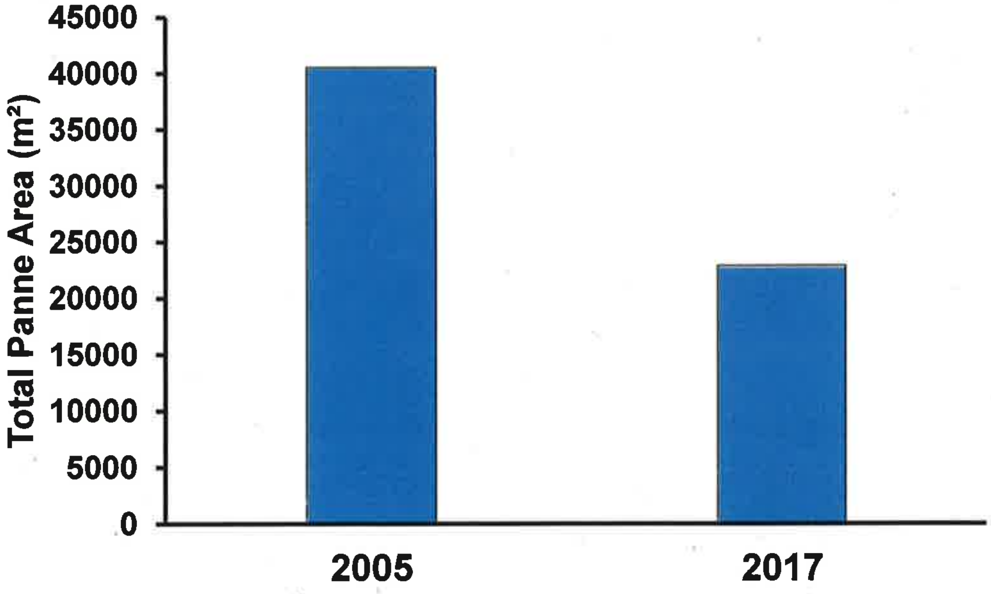


Figure 10: Local G Cluster maps of forb panne change on the Little River Marsh in Wells, ME. Displaying in red, hot spots, or statistically significant clusters of high regional rates of events and area change and in blue, cold spots, or statistically significant clusters of low regional rates of events and area change. Event data were obtained by counts of the specific events that pannes underwent in each grid cell between 2005 and 2017. Area change was calculated by 2017 area - 2005 area, where red hot spots indicate areas of overall panne expansion and blue cold spots indicate areas of overall panne loss. Significance set as $p < 0.05$. Uncolored grids are not statistically significant. Base map courtesy of Carto.

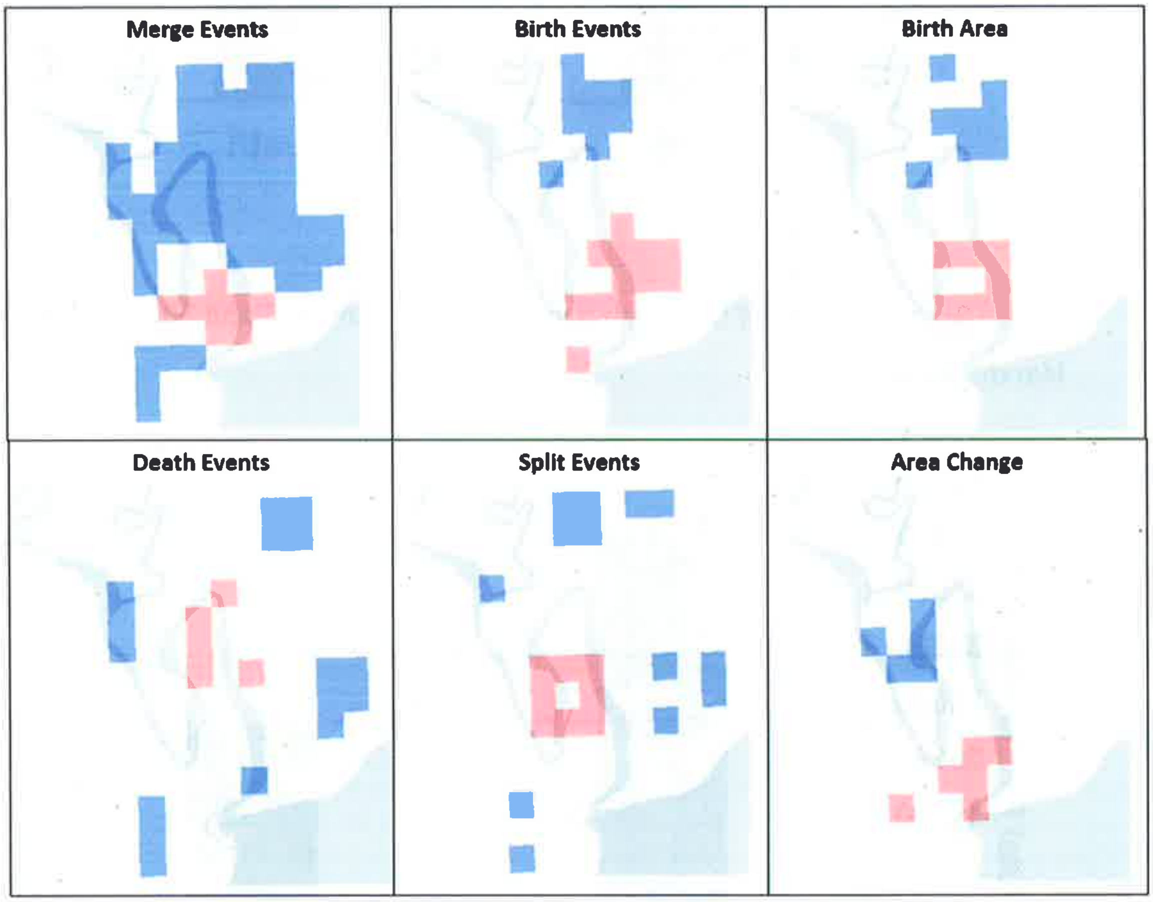


Figure 11: Map of the Scarborough Marsh in Scarborough, ME, located behind Pine Point Beach near the mouth of the Nonesuch River. Study marsh site is indicated by red box.

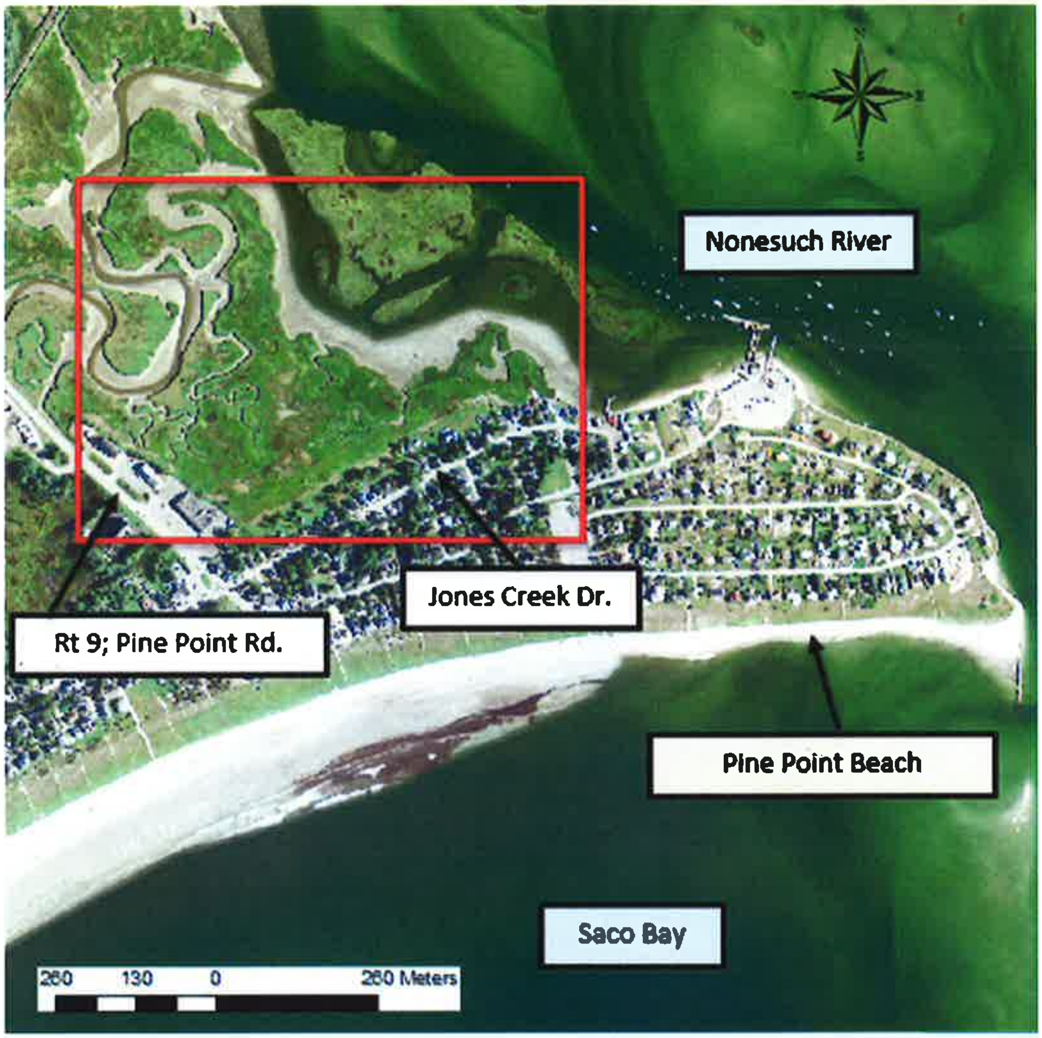


Figure 12: Map of forb pannes and sampling plots mapped by Fischella from July 26 to August 29, 2017, Scarborough Marsh, Scarborough ME.

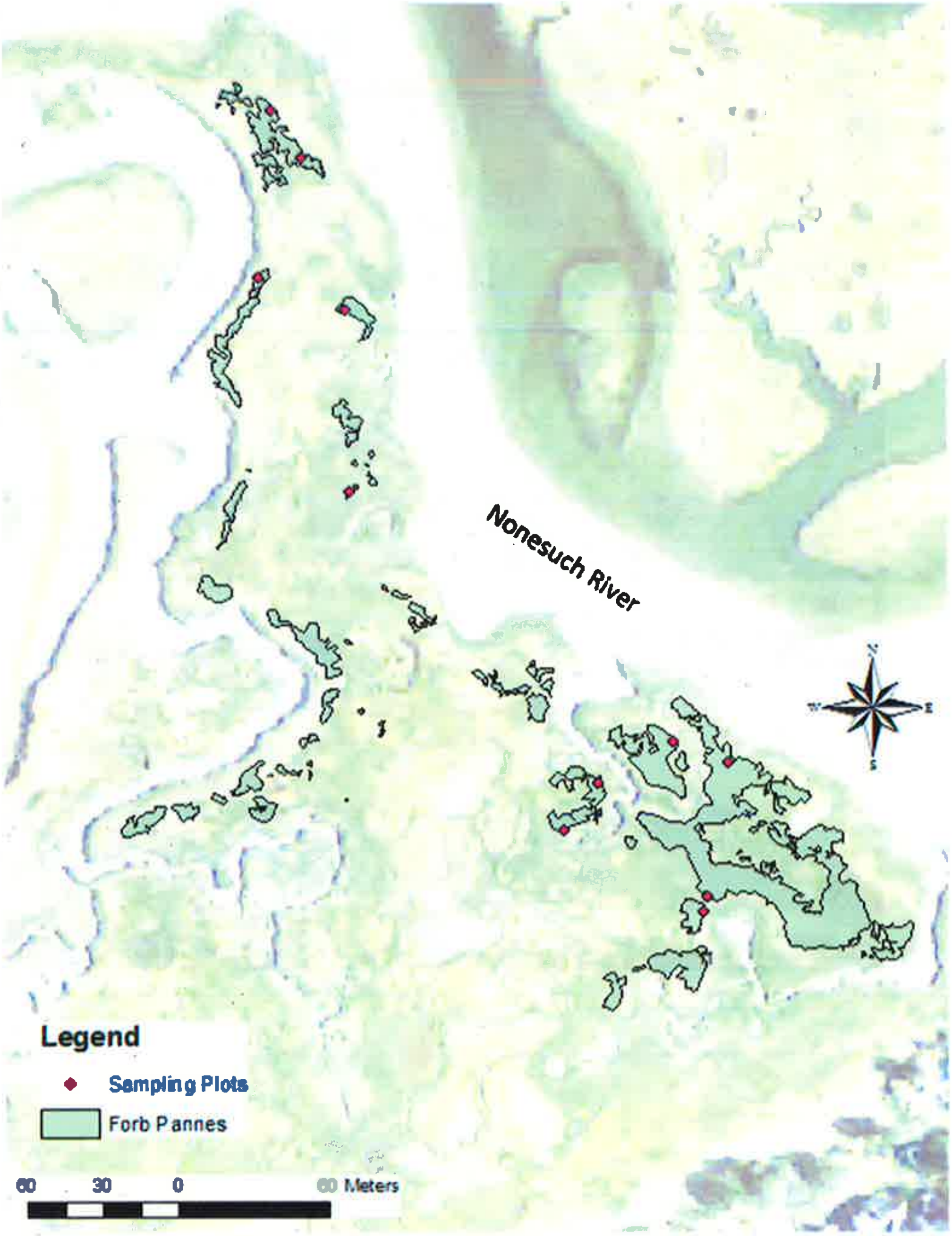


Figure 13: Map of forb pannes and sampling plots of Scarborough Marsh, Scarborough, ME, mapped by Fischella from July 26 to August 29, 2017 and digitized spatial variables including river edge, pools, and urban edge, which were delineated from 2011 NOAA CIR imagery. CIR imagery was used to display spatial variables as it makes clear the differences between standing water and marsh.

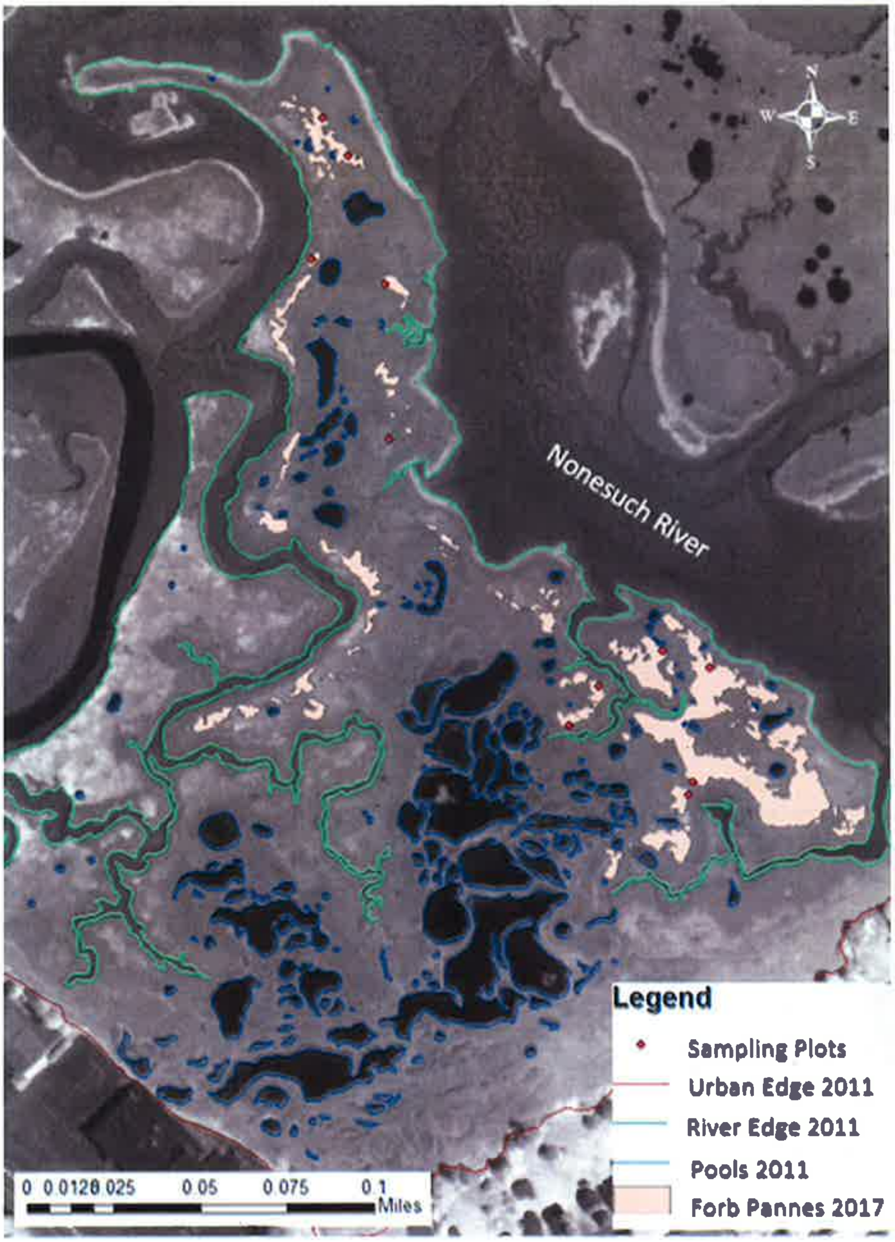


Figure 14. Comparison of mean (±SE) sediment temperature (°C) in edge and interior habitats of each sampling plot throughout the summer, Scarborough Marsh, Scarborough, ME. Y-axis begins at 20°C to better visualize differences.

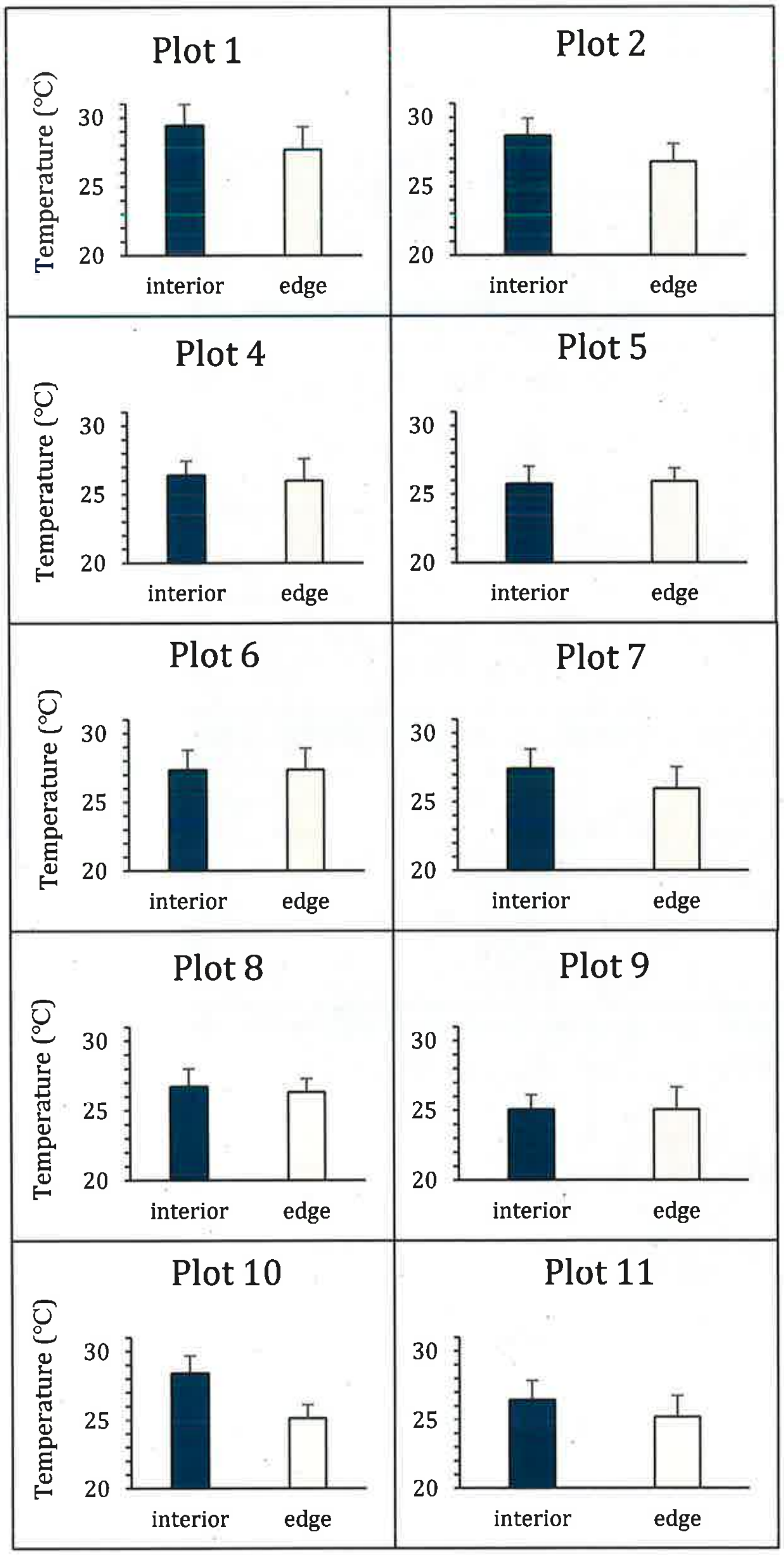


Figure 15. Comparison of NH_4^+ (µg) in edge and interior habitats of each sampling plot. Nutrient quantities were obtained via inserted resin bags, which provide a measurement of nutrient availability throughout the summer, Scarborough Marsh, Scarborough, ME.

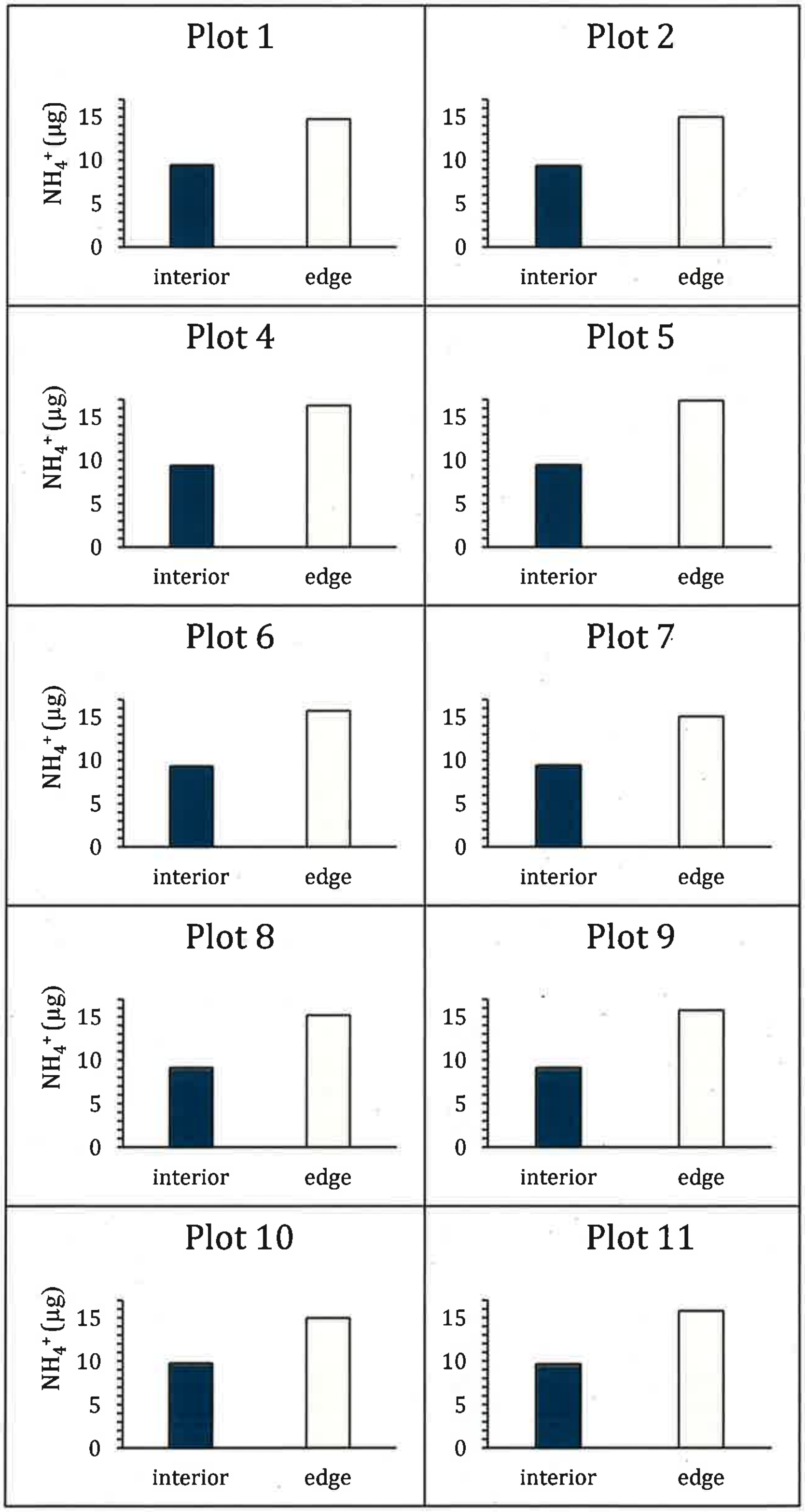


Figure 16. Comparison of NO_3^- (μg) in edge and interior habitats of each sampling plot. Nutrient quantities were obtained via inserted resin bags, which provide a measurement of nutrient availability throughout the summer, Scarborough Marsh, Scarborough, ME.

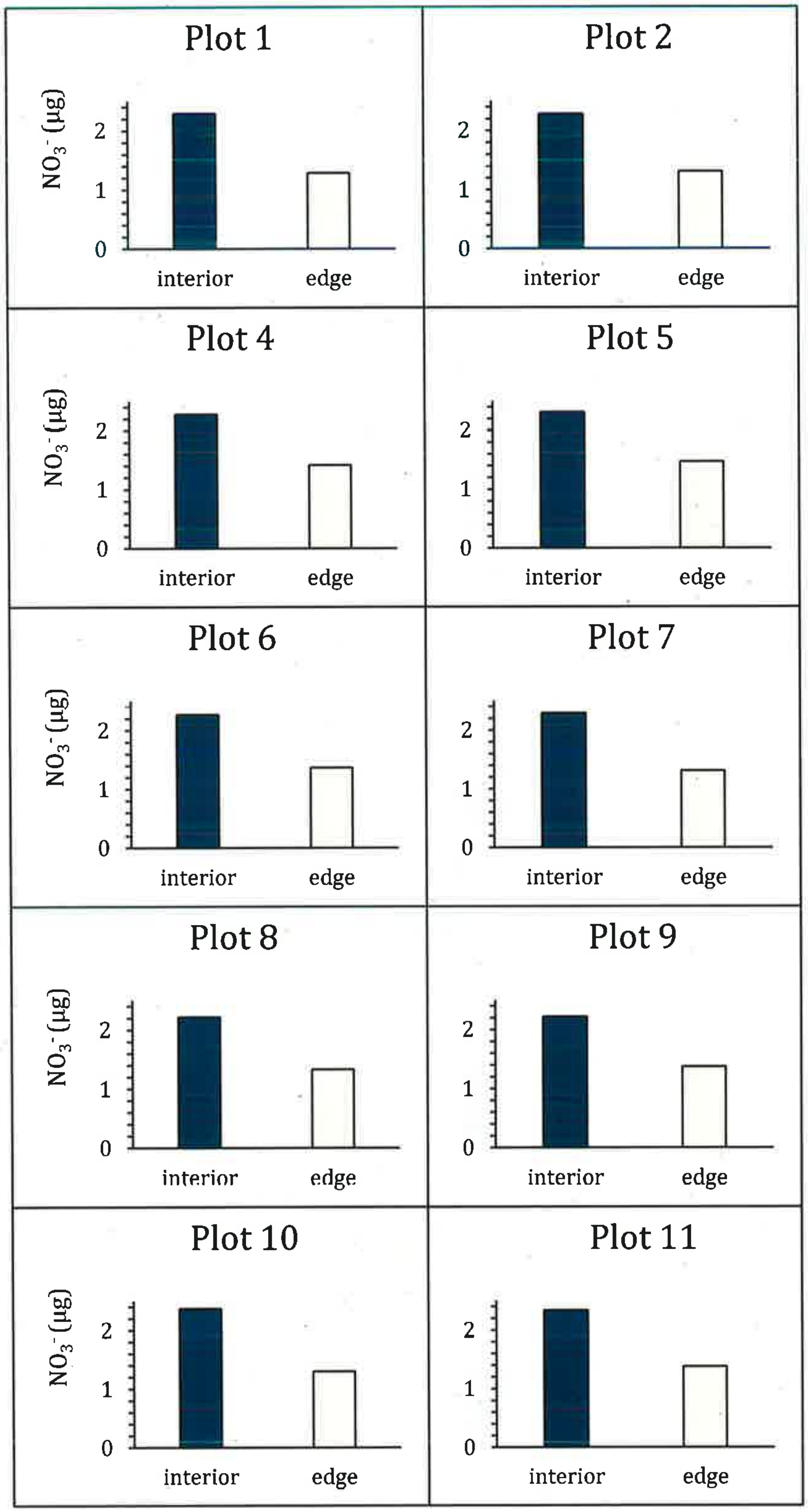


Figure 17: Relationship between mean interior and edge sediment moisture (cm^3 water/ cm^3 sediment) of sampling pannes throughout summer, Scarborough Marsh, Scarborough, ME. Whereas n = 10 pannes, only six points are visualized due to overlap in moisture values.

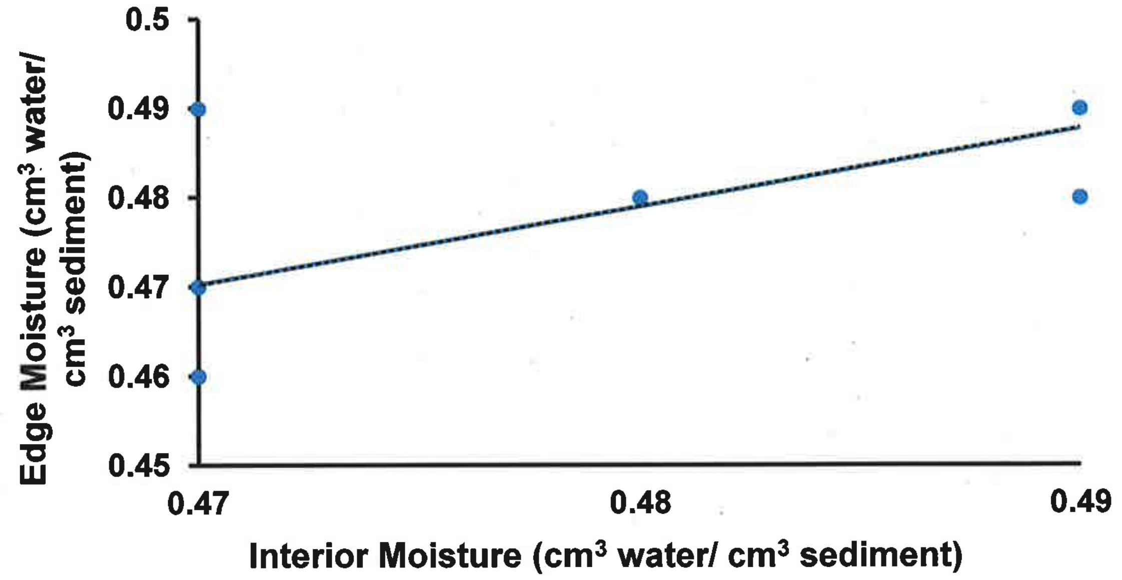


Figure 18. Comparison of percent absolute abundance of *S. patens* in edge and interior habitats of each sampling plot. Data were collected July-August 2017, Scarborough Marsh, Scarborough, ME.

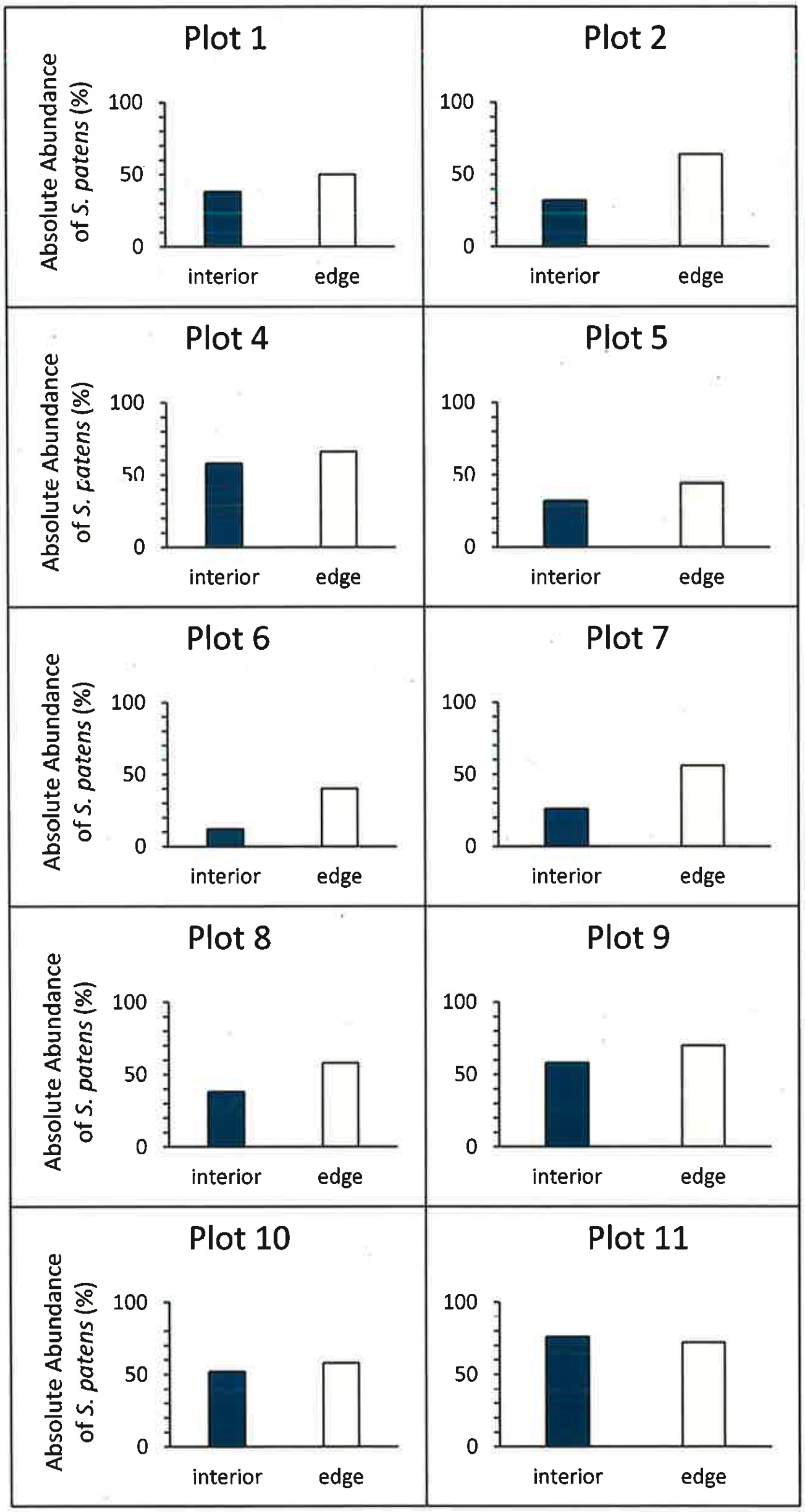


Figure 19. Comparison of absolute abundance of *S. alterniflora* in edge and interior habitats of each sampling plot. Vegetation data were collected July-August 2017, Scarborough Marsh, Scarborough, ME.

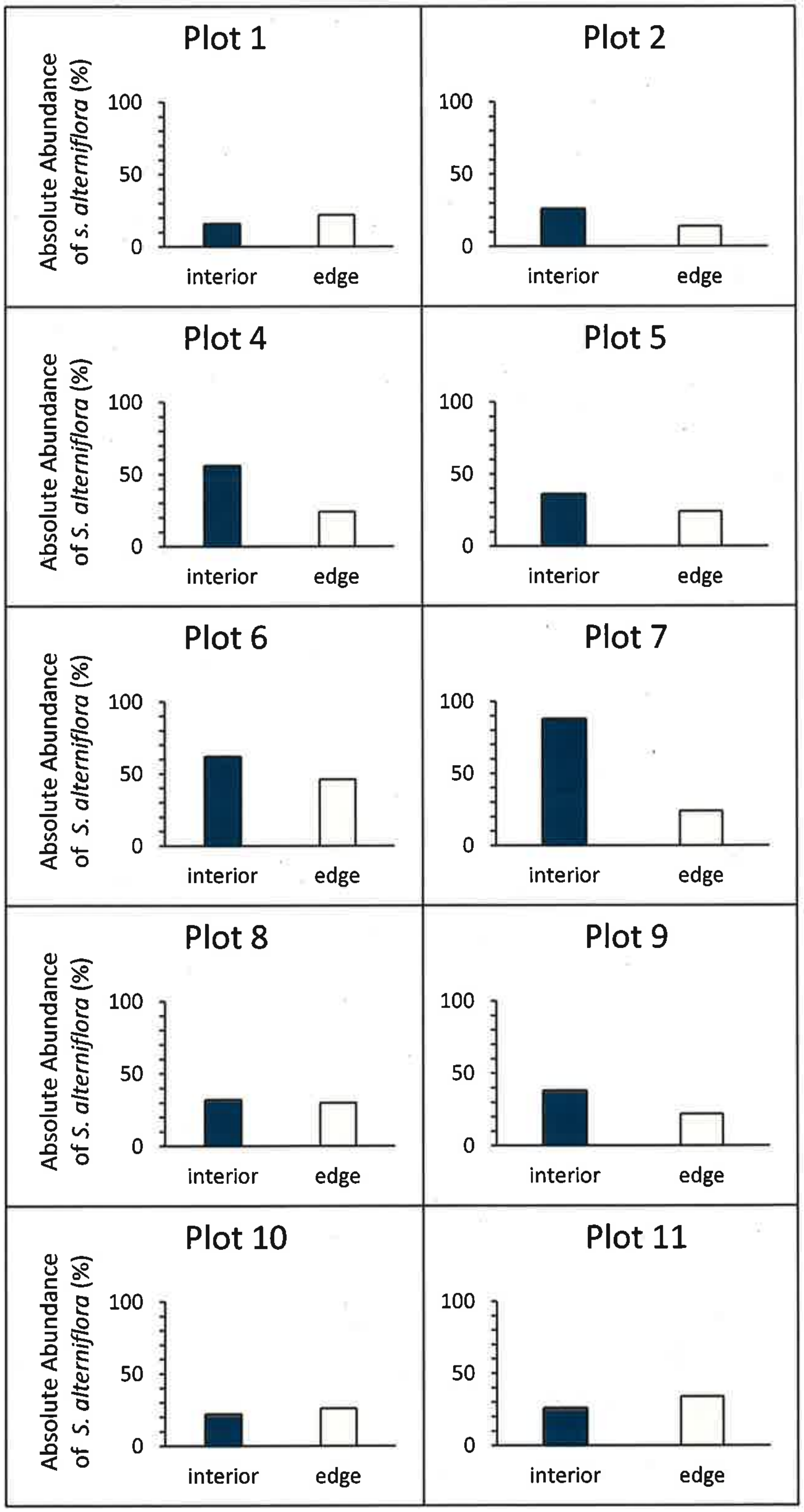


Figure 20: Relationship between percent absolute abundance of *S. patens* (%) in interior and edge habitats across sampling pannes. Vegetation data were collected July-August 2017, Scarborough Marsh, Scarborough, ME.

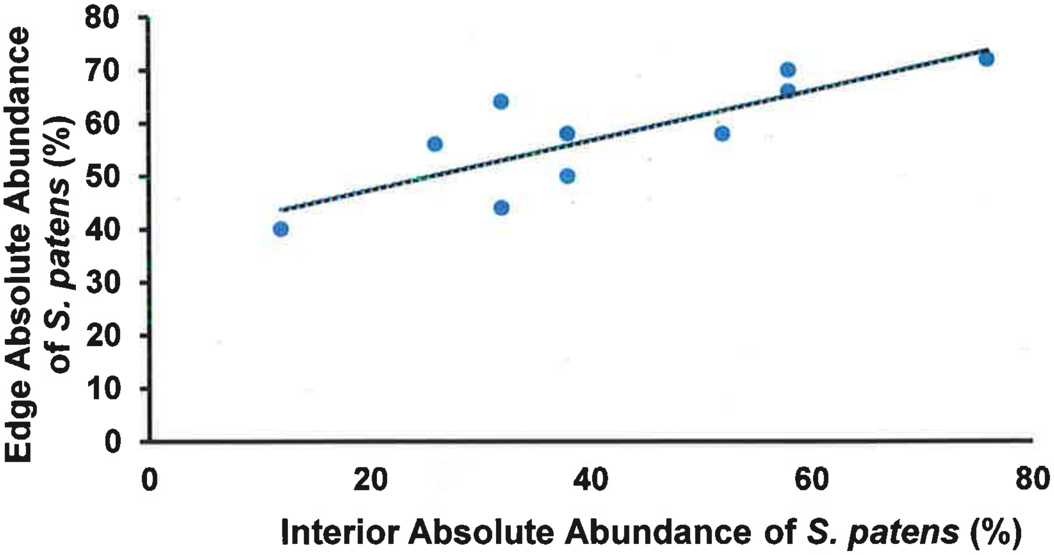


Figure 21: Relationship between percent absolute abundance of *L. nashii* (%) in interior and edge habitats across sampling pannes. Vegetation data were collected July-August 2017, Scarborough Marsh, Scarborough, ME.

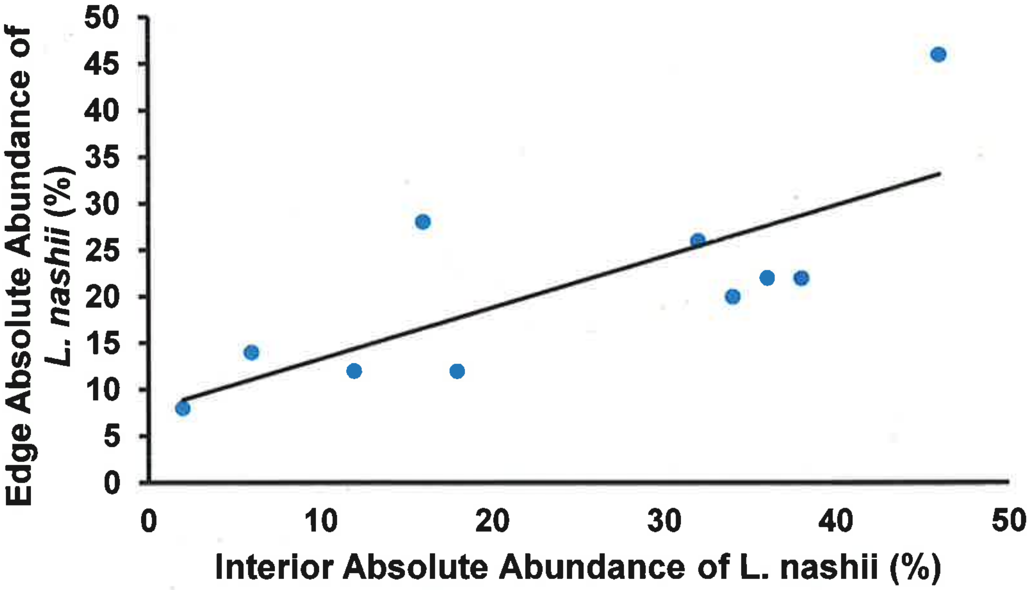


Figure 22: Relationship between sediment moisture (cm^3 water/ cm^3 sediment) and percent absolute abundance of *L. nashii* (%) across sampling pannes. Vegetation data were collected July-August 2017, and edaphic data were collected throughout summer 2017, Scarborough Marsh, Scarborough, ME. Due to the small range of variation in sediment moisture, the x axis was started at the lowest moisture value (0.47) to better visualize differences.

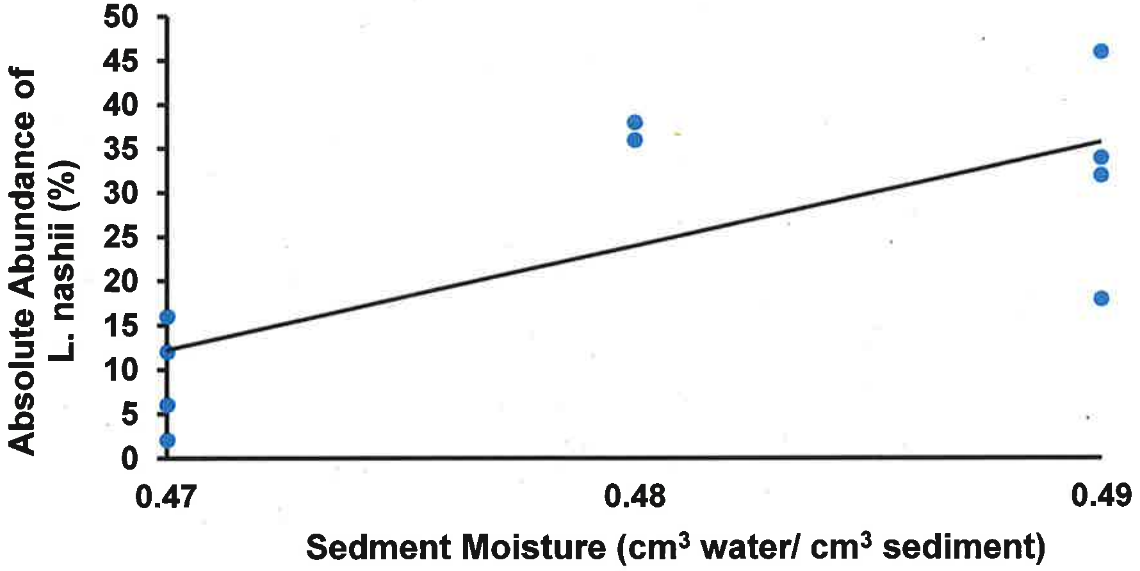


Figure 23: Relationship between forb panne distance to river (m) and percent absolute abundance of *L. nashii* (%) across sampling pannes. Vegetation data were collected July-August 2017, and spatial data were digitized from 2011 NOAA CIR imagery, Scarborough Marsh, Scarborough, ME.

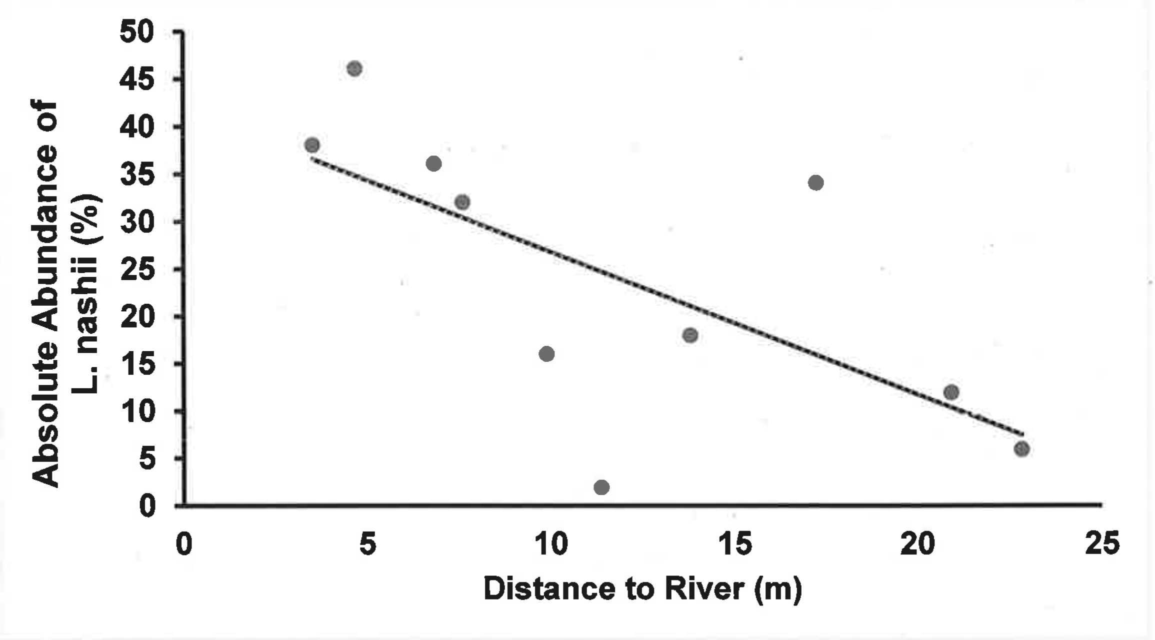


Figure 24: Relationship between forb panne distance to nearest pool (m) and percent absolute abundance of *S. patens* (%) across sampling pannes. Vegetation data were collected July-August 2017, and spatial data were digitized from 2011 NOAA CIR imagery, Scarborough Marsh, Scarborough, ME.

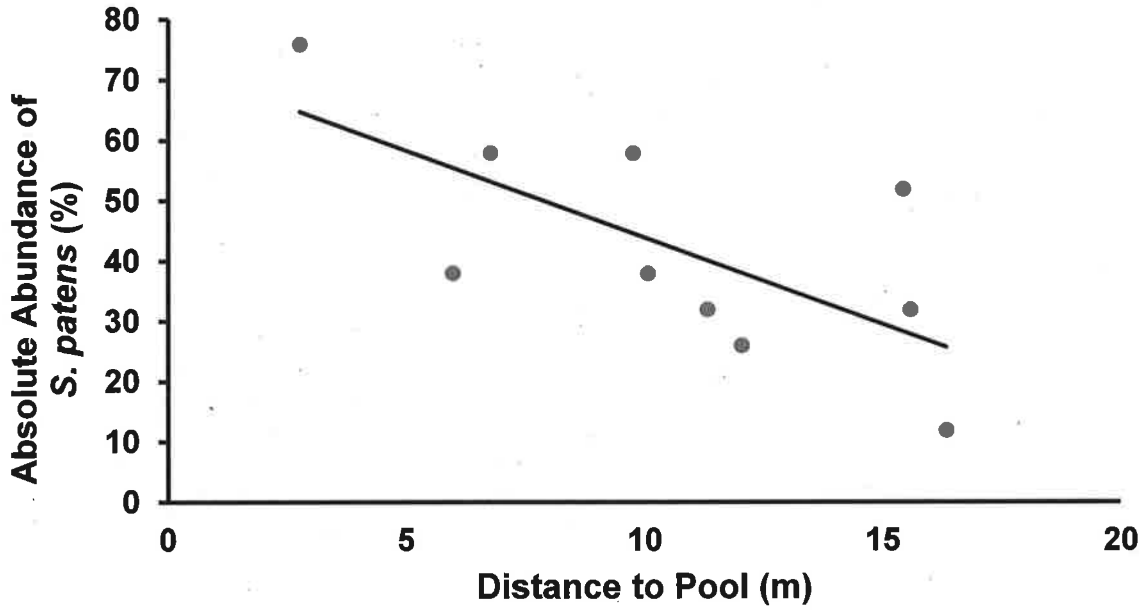
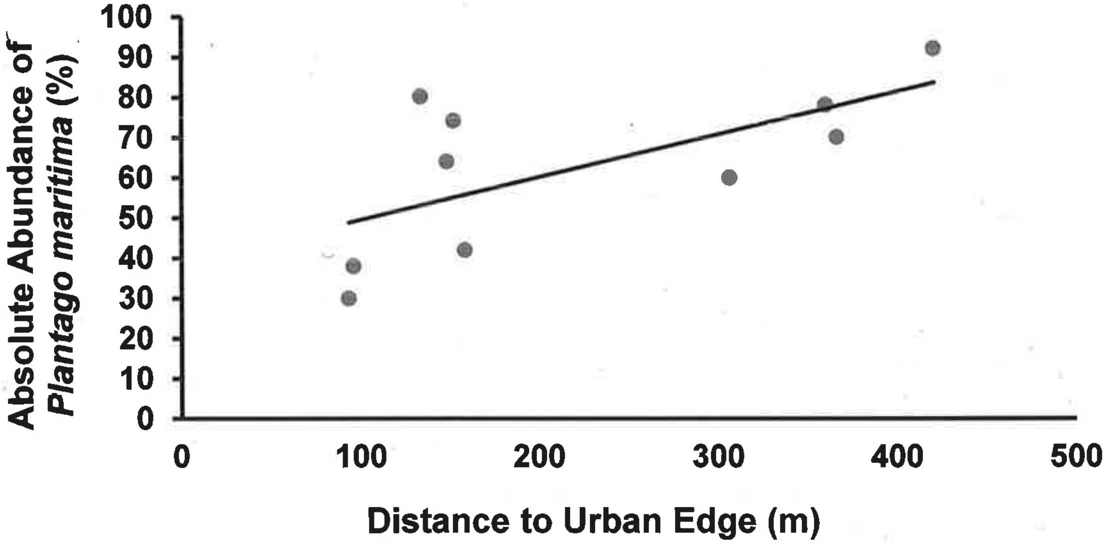


Figure 25: Relationship between forb panne distance to urban edge (m) and percent absolute abundance of *Plantago maritima* (%) across sampling pannes. Vegetation data were collected July-August 2017, and spatial data were digitized from 2011 NOAA CIR imagery, Scarborough Marsh, Scarborough, ME.



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Appendix

Tracked events of all 2005 forb pannes in 2017.

Panne ID	***Merge***	***Split***	***Life* 2005**	***Life* 2017**	***Death***
1	0	1	1	10	0
2	0	1	1	2	0
3	0	1	1	2	0
4	0	1	1	6	0
*5	1	0	1	0	0
6	0	1	1	2	0
7	0	0	1	1	0
8	0	1	1	6	0
9	0	0	1	1	0
10	0	1	1	8	0
11	0	0	1	1	0
12	0	1	1	3	0
13	0	0	1	1	0
14	0	1	1	4	0
15	0	0	1	1	0
16	0	0	1	1	0
17	0	1	1	8	0
18	0	1	1	2	0
19	0	0	1	1	0
20	0	1	1	13	0
21	0	1	1	7	0
22	0	1	1	11	0
23	0	1	1	7	0
24	0	1	1	3	0
25	0	0	1	1	0
29	0	0	1	1	0
30	0	0	1	1	0
31	0	0	1	1	0
32	1	0	3	1	0
33	0	0	1	1	0
*34	1	0	1	0	0
35	1	0	2	1	0
36	0	1	1	2	0
*37	1	0	1	0	0
39	0	0	1	1	0
40	0	0	1	1	0
43	0	0	1	1	0
44	0	1	1	2	0
48	0	1	1	3	0
49	0	1	1	2	0
50	0	1	1	2	0
51	0	1	1	2	0

54	0	1	1	2	0
55	0	0	1	1	0
61	0	0	1	1	0
63	0	0	1	1	0
68	0	1	1	3	0
71	0	0	1	1	0
74	0	0	1	1	0
76	0	1	1	2	0
77	0	0	1	1	0
80	0	0	1	1	0
81	0	0	1	1	0
26	0	0	1	0	1
27	0	0	1	0	1
28	0	0	1	0	1
38	0	0	1	0	1
41	0	0	1	0	1
42	0	0	1	0	1
45	0	0	1	0	1
46	0	0	1	0	1
47	0	0	1	0	1
52	0	0	1	0	1
53	0	0	1	0	1
56	0	0	1	0	1
57	0	0	1	0	1
58	0	0	1	0	1
59	0	0	1	0	1
60	0	0	1	0	1
62	0	0	1	0	1
64	0	0	1	0	1
65	0	0	1	0	1
66	0	0	1	0	1
67	0	0	1	0	1
69	0	0	1	0	1
70	0	0	1	0	1
72	0	0	1	0	1
73	0	0	1	0	1
75	0	0	1	0	1
78	0	0	1	0	1
79	0	0	1	0	1
80	0	0	1	1	0
81	0	0	1	1	0

*Starred pannes indicate lesser contributors to *merges*, where their life in 2017 became 0. The largest contributors to *merges* keep the panne ID and their Life 2005 is denoted by how many pannes formed the *merge* to make its life in 2017 a value of 1.