

# Upslope development of a tidal marsh as a function of upland land use

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## Abstract

To thrive in a time of rapid sea-level rise, tidal marshes will need to migrate upslope into adjacent uplands. Yet little is known about the mechanics of this process, especially in urbanized estuaries, where the adjacent upland is likely to be a mowed lawn rather than a wooded natural area. We studied marsh migration in a Long Island Sound salt marsh using detailed hydrologic, edaphic, and biotic sampling along marsh-to-upland transects in both wooded and lawn environments. We found that the overall pace of marsh development was largely unaffected by whether the upland being invaded was lawn or wooded, but the marsh-edge plant communities that developed in these two environments were quite different, and some indicators (soil salinity, foraminifera) appeared to migrate more easily into lawns. In addition, we found that different aspects of marsh structure and function migrated at different rates: Wetland vegetation appeared to be a leading indicator of marsh migration, while soil characteristics such as redox potential and surface salinity developed later in the process. We defined a 'hydrologic migration zone', consisting of elevations that experience tidal inundation with frequencies ranging from 20% to 0.5% of high tides. This hydrologically defined zone – which extended to an elevation higher than the highest astronomical tide datum – captured the biotic and edaphic marsh-upland ecotone. Tidal inundation at the upper border of this migration zone is highly variable over time and may be rising more rapidly than mean sea level. Our results indicate that land management practices at the upland periphery of tidal marshes can facilitate or impede ecosystem migration in response to rising sea level. These findings are applicable to large areas of tidal marsh along the U.S. Atlantic coast and in other urbanized coastal settings.

*Keywords:* foraminifera, indicators, Long Island Sound, migration, sea-level rise, soil salinity

*Received 1 April 2016 and accepted 9 June 2016*

## Introduction

Global sea-level rise (SLR) is now faster than at any point in the last 2000 years, and further acceleration of SLR will occur during this century, as ocean waters continue to warm and land-based ice continues to melt (Church *et al.*, 2013; Kemp *et al.*, 2015; DeConto & Pollard, 2016). These high rates of SLR will undoubtedly impact all coastal ecosystems in some way, but the dynamic responses of these ecosystems are still poorly understood (Passeri *et al.*, 2015).

Per unit area, tidal wetlands (marshes and mangroves) provide the highest ecosystem service value of any global biome except coral reefs (Costanza *et al.*, 2014), and their loss would endanger marsh-dependent species (Bayard & Elphick, 2011) and increase the vulnerability of coastal communities to flooding (Shepard *et al.*, 2011). In responding to SLR, tidal marshes benefit from geomorphic feedbacks that stabilize their relative

elevation and help them survive in place (Morris *et al.*, 2002; Kirwan & Megonigal, 2013; Kirwan *et al.*, 2016). However, these feedbacks may fail at high rates of SLR, and marsh loss has already been observed at some locations, in part due to co-occurring stressors such as herbivory, low sediment availability, and high nutrient loading (Delaune *et al.*, 1983; Holdredge *et al.*, 2009; Deegan *et al.*, 2012; Anisfeld *et al.*, 2016; Schultz *et al.*, 2016).

At the same time, SLR also presents an opportunity for marshes to expand at their upland edge through landward (lateral) migration – an opportunity that is likely to be critical to marsh survival in the coming decades. Consequently, managers are increasingly incorporating marsh migration into coastal planning. To support this effort, many studies are forecasting future marsh area (and associated ecosystem services) by combining SLR projections with coastal elevation data using SLAMM (Sea Level Affecting Marshes Model) or other models (Craft *et al.*, 2009; Feagin *et al.*, 2010; Geselbracht *et al.*, 2011; Rogers *et al.*, 2012; Linhoss *et al.*, 2015). These models implicitly assume that, once sea level rises to a given elevation, marshes – with essentially full structure and function – will quickly occupy the available space.

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Yet relatively little is known about the processes by which coastal ecosystems expand landward in response to SLR: How quickly does migration happen? Does this rate depend on the adjacent land use? Do different aspects of ecosystem structure and function appear at different rates? Answering such questions is essential to accurately predict future ecosystem distributions and establish coastal management practices that can maximize ecosystem services.

Few studies have directly examined marsh migration, and these have generally looked at migration into natural landscapes dominated by woody vegetation (Williams *et al.*, 1999; Denslow & Battaglia, 2002; Desantis *et al.*, 2007; Saha *et al.*, 2011; Smith, 2013; Wasson *et al.*, 2013; Raabe & Stumpf, 2015). These studies have documented significant inland marsh migration over the last several decades, although in several cases, migration has been slowed by the resistance of coastal forests to salt stress (Williams *et al.*, 1999; Denslow & Battaglia, 2002; Desantis *et al.*, 2007), as predicted by Brinson *et al.* (1995) in their conceptual model of marsh migration.

The landscape for migration in many urbanized estuaries is quite different from the forested landscapes emphasized in these studies. Specifically, maintained lawns and other managed land uses are common at the upland borders of many marshes. Given the human influence on the upland landscape – and the potential to better manage this landscape to facilitate migration – we sought to understand how marsh migration is affected by the land use in the bordering upland.

We hypothesized that migration by marshes into lawns would occur more rapidly than migration into wooded uplands, because of two factors: (1) growth of marsh plants into lawns is less likely to be impeded by shading and a heavy litter layer; (2) compared to trees, lawn grasses are likely to respond more quickly to salt and flooding stress due to their more rapid turnover and shallower roots. In addition, we hypothesized that marsh development at the upland border is a gradual process, with different components of the ecosystem migrating at different rates.

To address these hypotheses, we used a variety of biotic and abiotic indicators to assess the extent of marsh development during the migration of a Long Island Sound (LIS) marsh into both wooded and lawn uplands. LIS is an excellent place to study marsh migration, as it is a hotspot for both SLR (Sallenger *et al.*, 2012) and urbanization (Wolfe *et al.*, 1991). It therefore serves as an appropriate case study for tidal marshes in many of the most vulnerable regions of the U.S. Atlantic coast.

## Materials and methods

### Approach and study site

Our study uses a space-for-time substitution (Pickett, 1989) to understand marsh migration. We take a snapshot of marsh development along a series of marsh-to-upland transects and interpret differences among transects as reflecting differences in the extent of marsh migration.

Our logic is illustrated in Fig. 1. Some parameters (e.g., soil salinity) are expected to show a relatively smooth transition from marsh to upland (Fig. 1a), while others (e.g., the presence of wetland plants) are likely to show threshold behavior (Fig. 1b). In both cases, we predict that the lawn transects will show more ‘marsh-like’ characteristics farther into the upland than the wooded transects, reflecting a faster upslope migration.

The study took place at Sherwood Island State Park in Westport, CT (Fig. 2), which offered plentiful areas of marsh-upland ecotone for study, including lawn and wooded areas. More detail on this site is provided in Anisfeld *et al.* (2016) and Schultz *et al.* (2016). Our analysis of processes at the marsh-upland boundary consisted of three components: hydrologic analysis, transect sampling, and point sampling.

### Hydrology

The frequency of tidal inundation – controlled by the elevation of the marsh surface relative to tidal hydrology – is a master

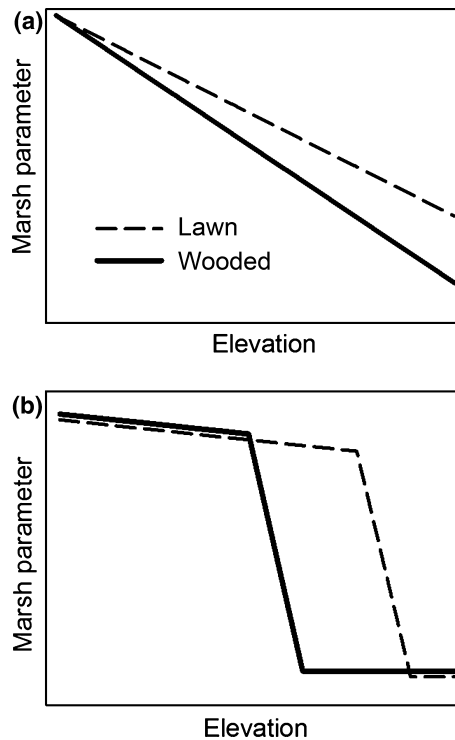
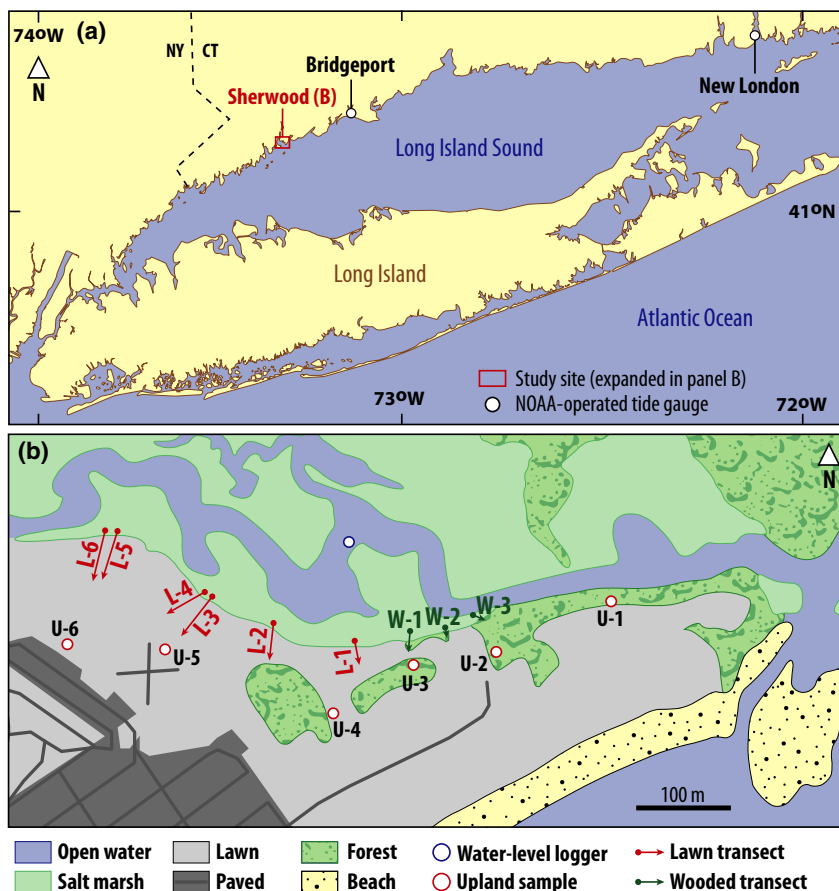


Fig. 1 Conceptual diagram of hypothesized difference between marsh migration into lawn (dashed line) vs. woods (solid lines), for (a) smoothly varying parameters and (b) threshold parameters.



**Fig. 2** Map of study site. (a) Location of study site at Sherwood Island State Park on the Connecticut coast of Long Island Sound. Locations of the Bridgeport and New London tide gauge stations are shown. (b) Position of marsh-to-lawn (L-1 to L-6) and marsh-to-woodland (W-1 to W-3) transects within the study site. Also shown are the locations of upland reference samples (U-1 to U-6) and a water-level logger deployed to characterize the local tidal regime.

variable controlling soil properties and the distribution of marsh flora and fauna. We focus here on the tidal inundation of the marsh-upland ecotone, specifically the elevations that are flooded with frequencies ranging from 0.5% to 20% of high tides, which we define as the ‘hydrologic migration zone’.

To determine tidal hydrology at our site, a water-level logger (Solinst Levelogger, Georgetown, ON, Canada) was deployed in the main tidal creek (Fig. 2b) and surveyed in to the North American Vertical Datum of 1988 (NAVD88) using a total station and a Real-Time Kinematic Global Positioning System (RTK-GPS). Water levels were recorded every 5 min during two time periods: May 22 to August 14, 2013 and May 14 to December 3, 2015. Recorded water levels were corrected for atmospheric pressure and water density. For each tidal cycle during these periods, maximum water levels were extracted from the dataset and plotted against the corresponding high tide measured at the nearby Bridgeport NOAA station (station 8467150; Fig. 2a). The correlation between the two high-tide data sets (local and Bridgeport) was then used to translate any Bridgeport high tide into its local equivalent.

As a check on this approach, we installed an additional water-level logger on the marsh (at a known elevation) from

July 24 to December 3, 2015. We extracted high-tide water levels for tides that flooded the logger by at least 3 cm ( $n = 88$ ) and compared those measured high-tide water levels to the water levels predicted by the Bridgeport correlation approach discussed above.

We used the Bridgeport correlation, together with NOAA Bridgeport high-tide data, to construct a synthetic high-tide data set for our study site for the years 2006 to 2015. Local flooding frequency (the percentage of high tides that reach or exceed a given elevation) was calculated from this data set. The relatively long (10-year) time period was used to accurately represent the unusually high tides that are of greatest relevance at the marsh-upland ecotone and that may occur as a result of storms or monthly- to annual-scale perturbations of prevailing atmospheric and oceanographic circulation patterns. We also evaluated temporal variation in flooding frequency by constructing elevation-flooding curves for each calendar year over the period 2006–2015.

For reference, three tidal datums were calculated for our site: mean high water, MHW (the average, across the synthetic 2006–2015 data set, of all high-tide water levels); mean higher high water, MHHW (the average, across the synthetic data set,

for all tides designated by NOAA as 'higher high'); and highest astronomical tide, HAT (the NOAA value for HAT at Bridgeport for the epoch 1983–2001, converted to the equivalent local water level).

We also assessed the rate of SLR at the upper and lower boundaries of the hydrologic migration zone (i.e., at 0.5% and 20% flooding frequencies). To do this, we used NOAA data from the New London tide gauge (station 8461490; Fig. 2a), because it has the longest record of high-tide water levels in LIS. For each year in the period of record (1979–2015), we calculated annual elevations of the 20% and 0.5% flooding frequencies, and compared their increase over time to the increase in annual MHW and annual mean sea level (MSL).

### Transect sampling

A series of marsh-upland transects was occupied during summer 2013 (Fig. 2b). Transects were chosen to include two types of marsh-upland transition: 'wooded' transects ( $n = 3$ ), extending into wooded upland areas (mostly *Juniperus virginiana*) and 'lawn' transects ( $n = 6$ ), extending into mowed lawns. (The larger number of lawn transects was designed to allow an experimental 'no-mow' treatment in half of these transects, but the work reported here was carried out before or shortly after implementation of the no-mow regime.)

Two measurements were carried out along the transects. First, surface elevations (NAVD88) were measured every 0.5 to 1 m (lateral distance) using a total station to reference each point to a local benchmark of known elevation. The slope of the land surface within the migration zone (i.e., from 20% to 0.5% flooding frequency) was calculated for each transect.

Second, the borders between different plant communities along the transect were located, where plant communities were defined as follows:

- Zone 1 (low marsh): *Spartina alterniflora* was present
- Zone 3 (upland): upland plants were present
- Zone 2 (high marsh/border): neither *S. alterniflora* nor upland plants were present.

We defined upland plants as those classified as 'facultative' (FAC) or 'facultative upland' (FACU) in the 2014 National Wetland Plant List ([http://wetland\\_plants.usace.army.mil/](http://wetland_plants.usace.army.mil/)). The list of plants identified in the field is found in Table 1. Elevations of the plant community boundaries were calculated by interpolating linearly between surveyed points. Elevations were converted to flooding frequencies using the elevation-flooding curve described above.

### Point sampling

We conducted more detailed sampling at 5 points (A–E) along each transect. Two points were positioned in the marsh proper, at flooding frequencies of 55% (A) and 33% (B), while three points were positioned in the migration zone, at flooding frequencies of 17% (C), 7.4% (D), and 2.2% (E). At each point, we sampled edaphic and biological parameters (Table 2) that are often used to define the existence of tidal marsh (e.g., Cui *et al.*, 2011; Reddy *et al.*, 2013; Tiner, 2013; Veldkornet *et al.*, 2015).

At each point, percentage vegetative cover (by species) was quantified in a 0.36 m<sup>2</sup> quadrat, soil redox potential was measured using a Hanna Instruments (Woonsocket, RI, USA) ORP probe (converted to the standard hydrogen electrode by addition of 200 mV), and two sediment samples were collected.

The first sediment sample was a core (diameter = 5.5 cm, length = 25 cm) collected with a gouge corer. Cores were returned to the lab, dried, and weighed. Dry bulk density was calculated as dry mass divided by core volume. The sediment was then ground to a fine, homogenized powder, and a subsample was ashed at 400 °C for 20 h to determine organic content by loss on ignition (LOI). In addition, 25 g of ground sediment was mixed with 25 g of water and shaken for 1 h to create a 1 : 1 paste. The paste was centrifuged for 15 min at 4600 RPM, and the salinity of the supernatant was measured using a conductivity probe.

The second sediment sample was a surface sample (0–1 cm) for foraminiferal analysis, collected by hand. Vegetated tidal marshes in Connecticut (and other regions) are occupied by agglutinated foraminifera (Edwards *et al.*, 2004; Wright *et al.*, 2011), and their presence is limited to environments and elevations experiencing some marine influence (Horton & Edwards, 2006). The samples were placed in a vial containing buffered ethanol (25%) and rose Bengal stain to promote preservation of foraminifera tests (including calcareous forms) and to allow differentiation between individuals that were living and dead at the time of collection (Walton, 1952). In the laboratory, these samples were wet-sieved, and the foraminifera-bearing fraction (63–500 µm)

**Table 1** Wetland indicator status of plants identified in this study

Plant	Wetland Indicator Status
<i>Spartina alterniflora</i>	OBL
<i>Juncus gerardii</i>	OBL
<i>Salicornia maritima</i>	OBL
<i>Limonium carolinianum</i>	OBL
<i>Spartina patens</i>	FACW
<i>Distichlis spicata</i>	FACW
<i>Iva frutescens</i>	FACW
<i>Phragmites australis</i>	FACW
<i>Plantago maritima</i>	FACW
<i>Baccharis halimifolia</i>	FACW
<i>Solidago sempervirens</i>	FACW
<i>Atriplex patula</i>	FACW
<i>Spergularia marina</i>	FACW
<i>Symphyotrichum subulatum</i>	FACW
<i>Cyperus esculentus</i>	FACW
<i>Panicum virgatum</i>	FAC
<i>Festuca rubra</i>	FACU
<i>Lotus corniculatus</i>	FACU
<i>Lonicera morrowii</i>	FACU
<i>Digitaria</i> spp.	FACU
<i>Lolium perenne</i>	FACU

OBL, obligate; FACW, facultative wetland; FAC, facultative; FACU, facultative upland.

**Table 2** Summary of indicators used to define the presence of tidal marsh

Parameter	Units	Expected change from marsh to upland	Reference
Edaphic			
Soil salinity	psu	Decrease	Tiner (2013)
Organic content	%	Decrease	Tiner (2013)
$E_h$	mV	Increase	Tiner (2013)
Bulk density	$g\ cm^{-3}$	Increase*	Reddy <i>et al.</i> (2013)
Biological			
Wetland species	%†	Decrease	Tiner (2013)
Plant diversity	Number of species	Increase	Tiner (2013)
Foraminifera	Abundance index (0–2)	Decrease	Edwards <i>et al.</i> (2004)

\*Cui *et al.* (2011) found a decrease.

†Cover of wetland species (FAC and FACU) as a percent of total plant cover (excluding bare soil).

was retained and suspended in water. Representative subsamples were pipetted into gridded trays, and agglutinated foraminifera were counted (total assemblage being live plus dead) under a binocular microscope. Their abundance was classified using an index that acknowledges that the concentration of agglutinated foraminifera in surface sediment samples declines sharply at the marsh-to-upland transition (Wright *et al.*, 2011; Edwards & Wright, 2015). Although a small number of foraminifera are commonly found at elevations about the 'highest occurrence of foraminifera', they do not represent an *in situ* and viable assemblage. Samples that yielded  $\geq 25$  individuals in 1 tray were termed 'abundant'. Samples with  $< 25$  individuals in 1 tray, but  $\geq 25$  individuals in 4 trays were termed 'present'. Samples with fewer than 25 foraminifera in 4 trays were termed 'absent'. Mean abundance was calculated for each elevation and land use by assigning numerical values to each abundance category (abundant = 2; present = 1; absent = 0). We opted not to identify foraminifera to the species level to maximize the number of samples that could be analyzed and because the assemblages at these high tidal elevations were unlikely to vary among samples or transects.

For reference, six additional points that were clearly above any tidal influence (upland points, designated U) were sampled for redox potential and soil properties as described above, but not for vegetation.

#### Soil water content and salinity

To follow up on initial observations, we conducted additional soil sampling on 10 dates between May and August 2015 (every 1 to 2 weeks). On each date, soil volumetric water content (%) and salinity (dS/m) in the top 10 cm were measured with a handheld probe (Decagon Instruments GS-3 with ProCheck, Pullman, WA, USA) at points C, D, and E in each transect and at one upland point for reference. Despite the fact that the mow and no-mow treatments were now under way, they were still combined into a 'lawn' category, because we did not expect mow status to affect water content or salinity, and there were no significant differences in these parameters between the two treatments.

#### Statistical methods

We conducted multivariate analysis using general linear models (GLMs) to assess the effects of elevation and land use on edaphic and biological properties. The first GLM used the four edaphic parameters shown in Table 2 as response variables and included two levels of land use (lawn and wooded) and six levels of elevation (A, B, C, D, E, and U). For the second GLM, response variables were the three biological parameters shown in Table 2; this GLM included only 5 levels of elevation, as vegetation was not measured at the upland (U) points.

To analyze the 2015 soil water content and salinity, we used a two-way ANOVA for each parameter at each elevation, with land use and date as factors.

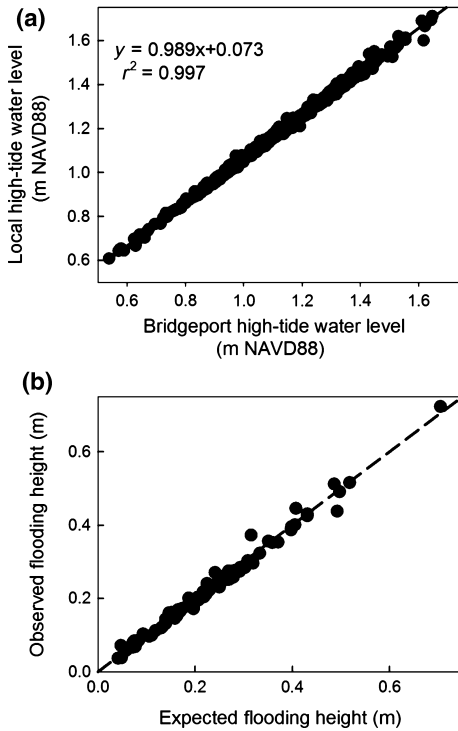
## Results

#### Hydrology

The correlation between high-tide water levels at Bridgeport and at our site was excellent and did not change between 2013 and 2015 (Fig. 3a). The predictive ability of our approach was likewise excellent (Fig. 3b), with a mean error (observed minus predicted) of  $-3.4 \pm 1.6$  mm ( $n = 88$ ).

The elevation-flooding curve (Fig. 4) demonstrates that the hydrologic migration zone at our site (defined as the area with tidal flooding frequency ranging from 0.5% to 20%) occupies an elevation range of about 0.47 m, from 1.31 m NAVD88 (the elevation that floods on 20% of high tides) to 1.78 m NAVD88 (flooding on 0.5% of high tides). The upper boundary of the migration zone was 0.21 m above HAT (1.57 m, 3.2% flooding frequency), demonstrating the importance of deviations from astronomical tides in controlling flooding frequencies at higher elevations.

The interannual variation in the elevation-flooding curves was large (Fig. 4, inset). For example, the elevation that was flooded on 10% of high tides for the 2006–2015



**Fig. 3** Hydrologic data. (a) Relationship between local and Bridgeport high tides, with best-fit line; (b) Observed vs. predicted flooding heights ( $n = 88$ ), with 1 : 1 line for reference.

period as a whole had annual flooding frequencies that ranged from 6.2% (in 2007) to 14.5% (in 2011).

Another measure of the ‘clumping’ of the highest tidal events is reflected in the time between flooding events for a given elevation. For the 0.5% elevation (1.78 m NAVD88), the time between flooding events

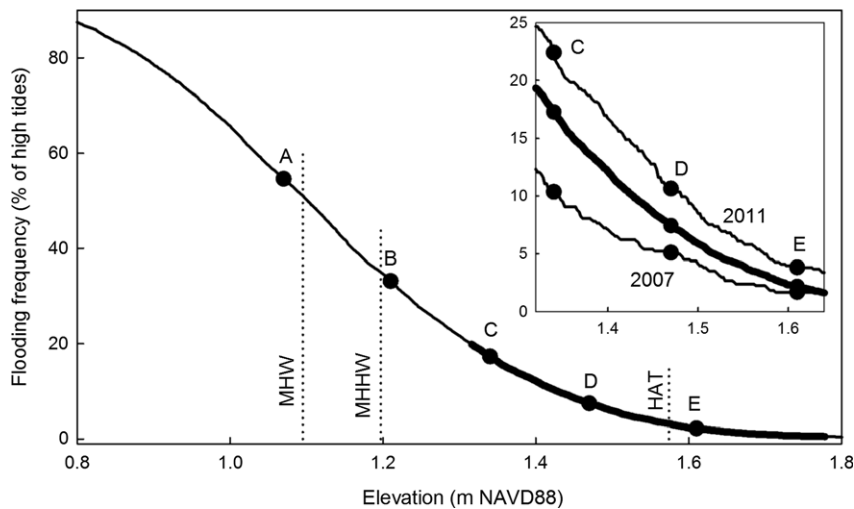
averaged 105 days (35 events over a 10-year period), but ranged from less than 1 day (i.e., flooding on two consecutive high tides) to more than a year between flooding events.

Sea-level rise (1979–2015) in the marsh migration zone was somewhat different from that at lower elevations (Fig. 5). Specifically, MSL, MHW, and the elevation of the 20% flooding frequency all rose at rates between 4.2 and 4.4 mm yr<sup>-1</sup> over this time period, while the 1% flooding frequency rose at a rate of 5.7 mm yr<sup>-1</sup>. In addition, the SLR signal at the upper edge of the migration zone was noticeably more variable than at lower elevations, as indicated by a lower  $r^2$  (uppermost line in Fig. 5).

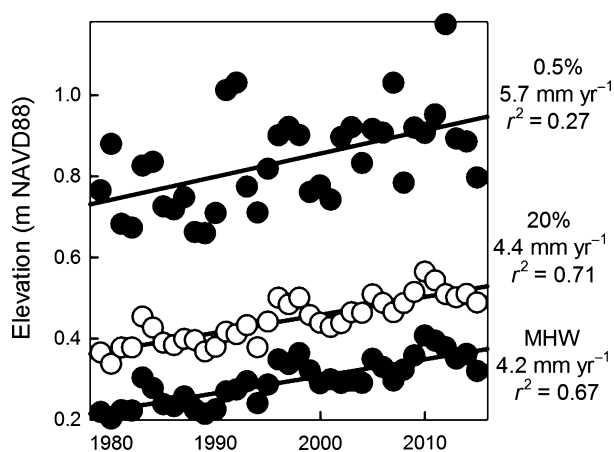
*Transects*

Our transects (Fig. 6) demonstrate several relevant features. First, the lawn transects generally did not have a simple and gradual rise in elevation from marsh to upland, but rather were punctuated by berms or ditches. These features are likely part of the long history of human manipulation of this site (and almost all others in LIS), although their exact origin is unknown. Based on observations of water flow in the field, we are confident that these noncontinuous berms do not prevent tidal water flow into the areas behind them.

Second, the wooded transects were uniformly much steeper (higher slope) than the lawn transects (Fig. 6). Note that average slopes for each transect were defined for the elevation range 1.31–1.78 m NAVD88 (the migration zone), including berms and ditches where relevant, with the exception of Lawn4, where we began



**Fig. 4** Elevation-flooding curve for our site (2006–2015), with the five sampling points shown (flooding frequencies: A = 55%, B = 33%, C = 17%, D = 7.4%, E = 2.2%). Darker trace shows the hydrologically defined migration zone (0.5–20% flooding frequency). Inset shows two annual curves compared to the 10-year average. Note that the difference between 2007 and 2011 reflects interannual variability, not sea-level rise.



**Fig. 5** Rate of rise (1979–2015) in the elevations of MHW, the 20% flooding frequency, and the 0.5% flooding frequency, with best-fit lines, slopes, and  $r^2$  values. Data from NOAA New London tide gauge. For MSL (data not shown), slope = 4.4 mm yr<sup>-1</sup> and  $r^2$  = 0.70.

the slope calculation at the lowest point landward of the large berm.

Third, all six of the lawn transects had sections that were mowed regularly by park staff (until implementation of the no-mow treatment in three of the transects). Mowing extended as low as 1.24 m NAVD88 (29%

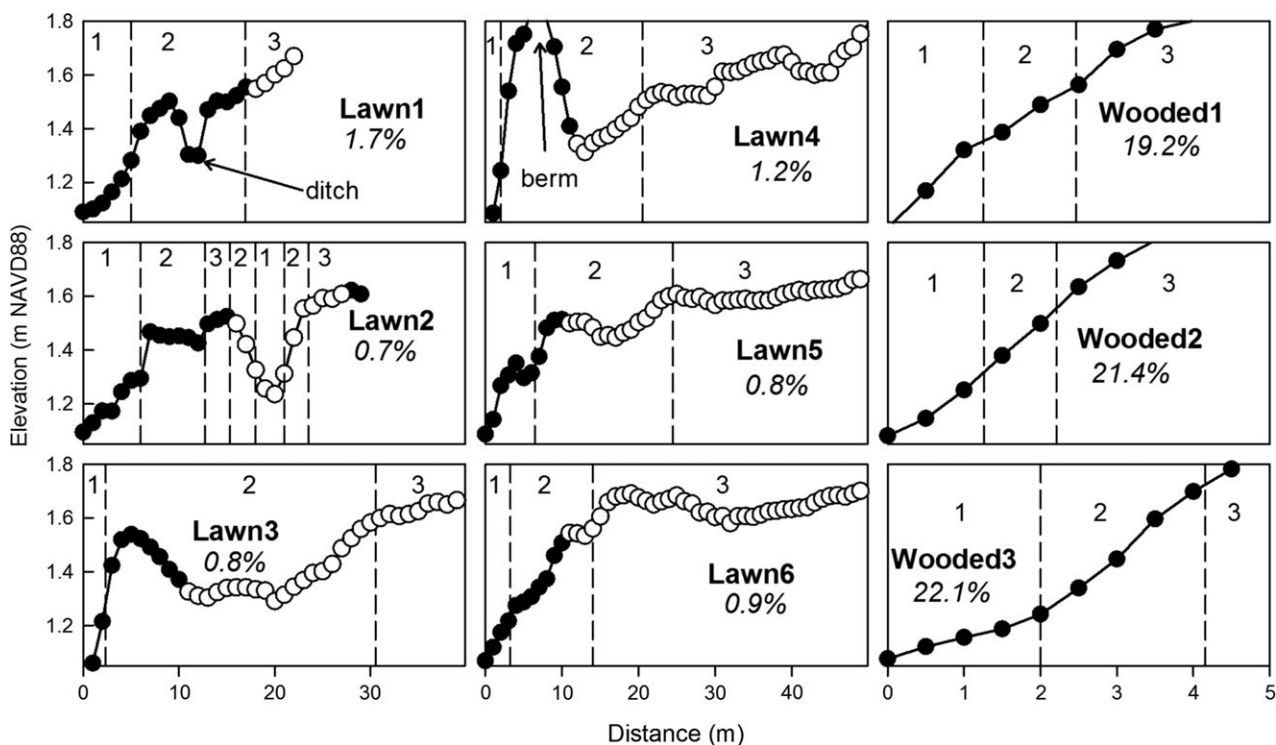
flooding frequency) in one of the transects and extended into zone 2 (high marsh/marsh border) in five of the six transects.

Fourth, as expected, plant communities changed with elevation, from zone 1 (low marsh, dominated by *S. alterniflora*) at the lowest elevations, through zone 2 (high marsh/marsh border, dominated by wetland plants other than *S. alterniflora*), to zone 3 (upland) at the highest elevations. It should be noted that zone 3 was defined by the first appearance of upland plants, but this zone often included some wetland plants as well. (Percent cover was quantified for point samples, below, but not for the transects.)

The transitions between zones took place at fairly consistent elevations. The transition between zones 1 and 2 corresponded to a flooding frequency of  $22.5 \pm 1.4\%$  ( $n = 11$ , due to multiple transitions in transect Lawn2), while the transition between zones 2 and 3 took place within the hydrologic migration zone, at a flooding frequency of  $3.8 \pm 0.6\%$  ( $n = 11$ ).

#### Point sampling

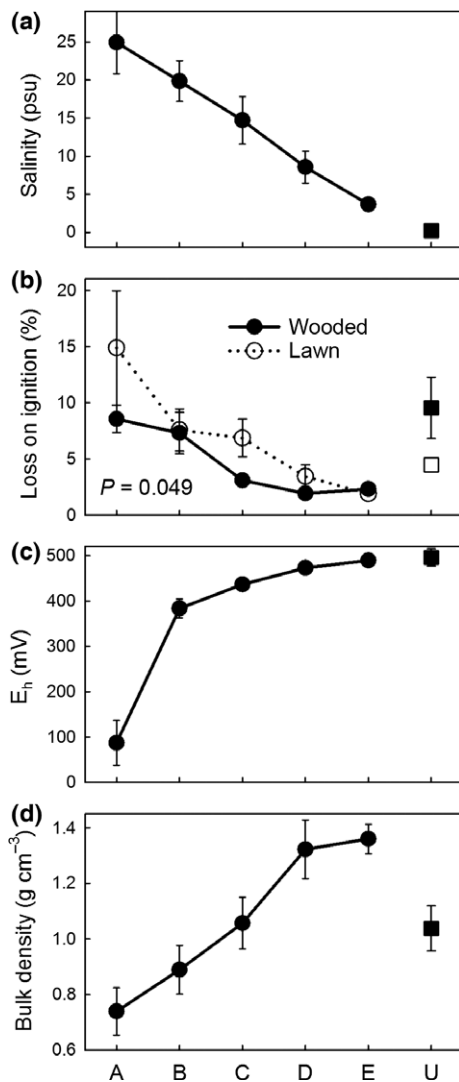
Contrary to our hypothesis, most of the edaphic parameters did not vary significantly between lawn and wooded environments (GLM,  $P > 0.05$ ); the only



**Fig. 6** Transect results: elevations and plant communities. Numbers indicate vegetation zones (1 = low marsh; 2 = high marsh/marsh border; 3 = upland). Open circles represent mowed points. Numbers shown in percent are the slopes, calculated over the hydrologic migration zone.

exception was LOI, where the difference was marginally significant ( $P = 0.049$ ). All of the edaphic parameters did vary significantly with elevation (Fig. 7; GLM,  $P < 0.05$ ). Soil salinity and organic content (LOI) both generally decreased with elevation, as expected, although the organic content of the wooded upland samples was quite high.  $E_h$  and bulk density generally increased with elevation, although the upland points (U) had an intermediate bulk density, most likely because of a different parent material due to the history of fill at this site (Anisfeld *et al.*, 2016).

Foraminiferal abundance was strongly affected by both elevation and land use, as well as the interaction



**Fig. 7** Edaphic properties as a function of elevation (mean and standard error, SE). A through E are points of increasing elevation along our transects, while U are upland points. Where differences by land use were not significant, the average across all transects is shown. Where differences were significant,  $P$  values are shown.

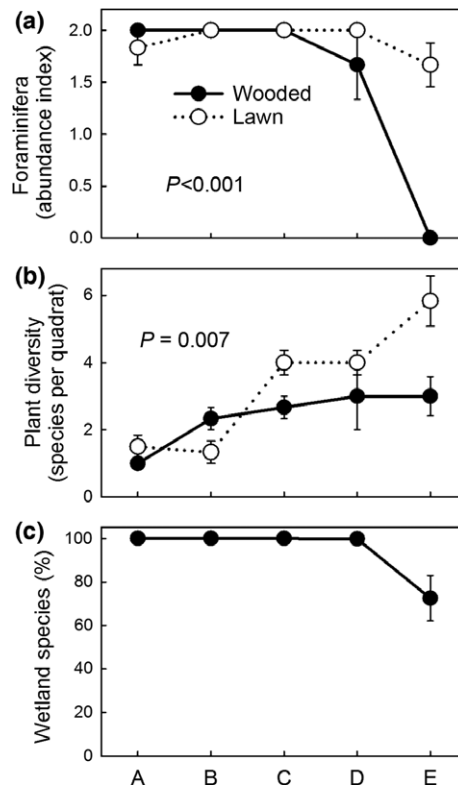
between them (Fig. 8a): in the lawn transects, foraminifera were abundant even at the highest elevations, while all three wooded transects had no foraminifera at their highest points (E).

Plant diversity was significantly different in the lawn transects compared to the wooded ones, especially at the highest elevation point, where the lawn quadrats had almost twice as many species as the wooded quadrats (Fig. 8b).

Wetland plant cover (as a percent of total plant cover) declined at higher elevations, but was not significantly different between land uses (Fig. 8c). However, a closer examination of the plant communities shows clear differences by land use (Fig. 9). *S. patens*, *D. spicata*, and *J. gerardii* dominated the lawn transects, while the wooded transects had much higher cover of *P. australis*, *B. halimifolia*, and bare soil.

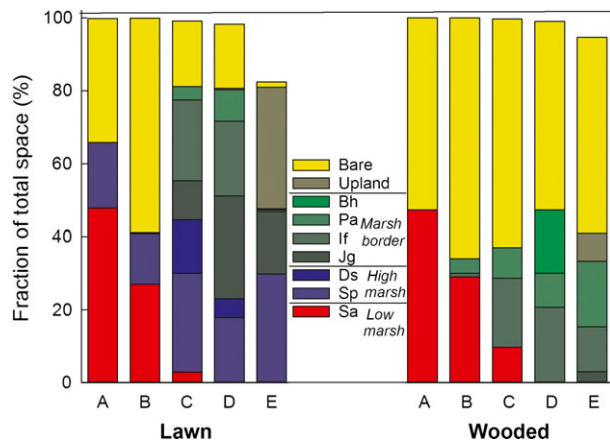
#### Soil water content and salinity

Near-surface soil water content and salinity, measured periodically with a handheld probe over the summer of 2015, were consistently higher at lawn transects



**Fig. 8** Biological properties as a function of elevation and land use (mean and SE). A through E are points of increasing elevation along our transects. Where differences by land use were not significant, the average across all transects is shown. Where differences were significant,  $P$  values are shown.





**Fig. 9** Average vegetation distribution for lawn and wooded transects. Plant abbreviations as follows: Sa = *Spartina alterniflora*; Sp = *Spartina patens*; Ds = *Distichlis spicata*; Jg = *Juncus gerardii*; If = *Iva frutescens*; Pa = *Phragmites australis*; Bh = *Baccharis halimifolia*; upland = all FAC and FACU plants; bare = bare soil.

compared to wooded ones (Fig. 10). This difference was significant (ANOVA,  $P < 0.05$ ) for three of the six comparisons. This contrasts with the lack of land-use effect on the salinity content of the cores (Fig. 7a), most likely because the 2015 sampling had greater temporal coverage and was focused on surface soil, where differences are more likely.

## Discussion

### Does land use affect marsh migration?

Our results mostly do not support the hypothesis (Fig. 1) that marsh migration proceeds faster/farther in lawn areas compared to wooded areas. Specifically, there were no significant land-use effects on most of our measured parameters, including zonation patterns (Fig. 6), soil characteristics (Fig. 7), and the abundance of wetland plants in the ecotone (Fig. 8c).

Despite this overall conclusion, wooded and lawn transects did differ in two important ways. First, the wetland plant communities occupying the ecotone were quite different between the two land uses. The dominance of *P. australis* and bare soil in the wooded transects (Fig. 9) – along with the lower plant diversity in these transects (Fig. 8b) – means that lawns arguably facilitate a more ecologically beneficial transition zone than wooded areas. The differences in the plant communities between the two land uses can probably be attributed to some combination of shading in the wooded transects (which tends to favor bare soil and disfavor *S. patens* and *D. spicata*) and mowing in the lawn transects (which tends to disfavor tall and woody

wetland plants such as *P. australis*, *I. frutescens*, and *B. halimifolia*).

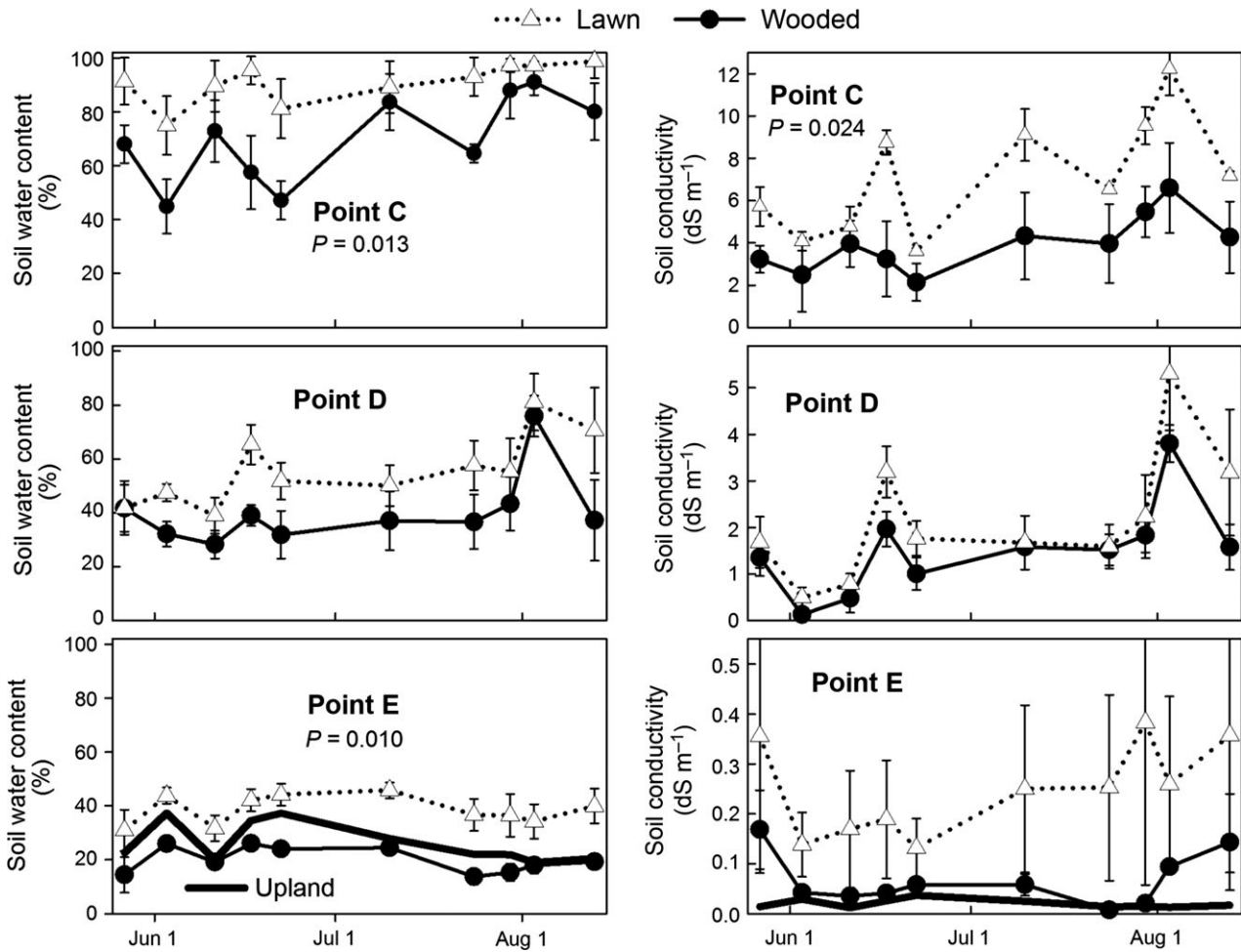
Second, the lawn transects were more ‘marsh-like’ than the wooded transects in their foraminiferal abundance (Fig. 8a) and in their near-surface water content and salinity (Fig. 10). However, we believe that this may be an artifact of the different land slopes in the two transect types. Specifically, the higher slopes in the wooded transects mean that these transects may drain away the occasional saltwater pulse more readily than the low-slope transects, resulting in a drier, less saline soil and a less conducive environment for foraminifera. The higher slopes found in the wooded transects are not a coincidence, of course: managers tend to mow lower-slope areas, which prevents woody growth. Still, it would be useful in future work to try to distinguish between these separate driving forces by locating low-slope wooded transects (or high-slope lawns).

An important caveat to our approach lies in the nature of the space-for-time substitution. Specifically, an alternative interpretation of Fig. 1 is that land-use differences in marsh-edge characteristics reflect static differences in landscape features, rather than differences in development over time. Only adding in the time element will resolve this uncertainty.

### Where does the marsh end and the upland begin?

Similar to previous studies (Cui *et al.*, 2011; Veldkornet *et al.*, 2015), our results suggest that the location of the border between the marsh and the upland depends on what parameter you are examining. For example, our point E was clearly marsh-like in some aspects but not in others: Point E experienced tidal inundation every 24 days (on average) over the last 10 years, but also repeatedly experienced dry periods lasting more than 3 months. Point E was indistinguishable from an upland soil in terms of redox status, but had higher core salinity than the upland (Fig. 7). Vegetation at point E was dominated (>50%) by salt marsh species, but foraminifera were low or nonexistent (Fig. 8).

This observation implies that we should not expect full-blown marshes – with their full complement of ecosystem services – to instantaneously move upslope in response to SLR. Rather, different elements of marsh structure and function are likely to appear at different times at a given elevation. This ecological trajectory is similar to observations made in the context of marsh creation (Craft *et al.*, 2002, 2003) and restoration (Anisfeld, 2012). More research into the order of appearance of these different elements – and their relationship to ecosystem services – is necessary, but our results suggest that the presence of wetland vegetation may be a leading indicator of marsh development (Fig. 8), while



**Fig. 10** Soil water content (left panels) and conductivity (right panels) at points C, D, and E in summer 2015 (mean and SE,  $n = 6$  for lawn, 3 for wooded). Where differences between lawn and wooded transects were significant ( $P < 0.05$ , ANOVA), a  $P$  value is shown. In bottom panels, values for an upland point are shown as a darker line. Note different scales on the three different conductivity axes.

redox status would be a lagging indicator. Soil salinity is a more complex indicator: while 25 cm cores at point E had higher salinities than upland cores (Fig. 7), surface salinity measurements were similar to those at an upland point, at least for our wooded transects (Fig. 10).

#### *The importance of hydrology*

Sea-level rise is the driving force behind marsh migration, but few studies have examined in detail the relationship between tidal hydrology and the biotic and abiotic patterns at the marsh-upland ecotone. One exception is Wasson *et al.* (2013), who found evidence that variation in inundation at the upland edge was driving the movement of plant communities.

Our results illustrate that tidal hydrology at the upland edge is highly variable over time (Fig. 4 inset

and Fig. 5). For example, a point at the upper edge of the migration zone (average flooding frequency of 0.5%, or 3.5 flooding tides per year) can go for over a year without being flooded; indeed, this occurred 3 times in the 10-year period that we studied. To some extent, this variability is tied to the interannual variability in MSL, which results from perturbations of prevailing atmospheric and oceanographic circulation patterns (Goddard *et al.*, 2015; McCarthy *et al.*, 2015); this interannual variability is coherent throughout LIS (Kemp *et al.*, 2015) and across larger regions (Sallenger *et al.*, 2012). However, the variability at the upland edge can also be driven by individual storm events. For example, 2007 was a year of relatively low MSL (lowest annual MSL between 2005 and 2015 in LIS), but it had an above-average number of flooding events at the upper edge of the migration zone (5, compared to the average of 3.5). Of these 5 flooding events, 4 occurred on

consecutive days in April 2007, when spring tides coincided with an extratropical storm (nor'easter) impacting the East Coast. These types of events undoubtedly bring pulses of saltwater to soils and vegetation that do not normally receive it, and may be important in initiating marsh migration.

Our data also suggest that SLR at the upland edge may be faster than at lower elevations (Fig. 5; higher slope for uppermost line), perhaps due to growing storminess or increasing tidal range. However, the scatter in the data – resulting from the smaller number of flooding events at higher elevations – means that this conclusion is necessarily tentative. Nonetheless, this finding is consistent with results from two recent studies: Talke *et al.* (2014) found that the annual maximum storm tide in New York City has risen more rapidly than MSL, and Mawdsley *et al.* (2015) found that both the New York City and New London tide gauges have seen significant increases in mean tidal range.

While our 'hydrologic migration zone' of 20% to 0.5% flooding frequency was arbitrarily defined, it does appear to capture the relevant portion of the landscape, as indicated by two observations. First, as noted above, point E, at 2.2% flooding frequency, clearly occupied an intermediate position between true marsh and true upland. Second, the transition between vegetation zones 2 and 3 (defined by the first appearance of upland plants) occurred at a flooding frequency of  $3.8 \pm 0.6\%$ , well within our migration zone. Interestingly, our migration zone is consistent with the ecotone defined by Wasson *et al.* (2013) on the basis of plant communities. Specifically, their ecotone, as measured in 2001, covered the elevation range from 0.6% to 13% flooding frequency (calculated from data provided by K. Wasson). Further studies are necessary to determine how widely applicable these thresholds are.

#### *What does the future hold for coastal wetlands in urbanized areas?*

Understanding the fate of coastal ecosystems in a time of accelerated SLR requires studies that integrate hydrologic, morphological, and ecological tools to investigate the complex, nonlinear responses of these ecosystems (Passeri *et al.*, 2015). This is even more true in systems – like LIS – that are highly impacted by local and regional human pressures, including changing sediment availability, high nutrient loading, and upland development.

Tidal wetlands in these urbanized areas are particularly valuable, but also particularly vulnerable, especially given that upland migration may be precluded in some cases by barriers such as roads and other infrastructure. Our work suggests that, in the quite common

situation where the marsh backs onto a mowed lawn, urbanized marshes may be able to migrate at least as rapidly as their less-developed counterparts. The historic mowing of these sites appears to have been beneficial to marsh migration in that it has prevented dominance by woody upland plants and *P. australis*, and thus has allowed high plant diversity at the marsh-upland ecotone. However, continued mowing of the ecotone may be detrimental to further marsh development.

Regular mowing by park managers took place at point E in all six of our lawn transects, and even extended into zone 2 in five of the transects (Fig. 6), meaning that the plants being mowed were exclusively marsh plants. This reflects the fact that soils at these elevations behave in many ways like upland soils (e.g., high bulk density), and tidal inundation is episodic and easy to miss. (Even a detailed digital elevation model would not provide an accurate picture of tidal inundation, as point E is located above the published value of HAT.) At a casual glance, a mowed lawn of *J. gerardii* is not that different from a lawn of upland grasses, so park managers may be slow to adjust their mowing patterns to SLR, thus inadvertently inhibiting full development of marsh vegetation (especially woody plants such as *I. frutescens*) and associated ecosystem services.

We strongly encourage managers to terminate mowing practices in areas with flooding frequencies greater than 1%, and we have had positive responses from managers at state parks in Connecticut. Despite the historic benefits provided by the practice, now is the time to cease mowing and allow marshes to more fully develop in these areas.

#### Acknowledgements

We thank Connecticut Sea Grant for funding (award NA14OAR4170086, subaward 47940). We are very grateful to the staff at Sherwood Island State Park, especially James Beschle, for their cooperation and assistance with this work. For assistance in the field and laboratory, we thank Jonathan Cooper and Yale students Michelle Camp, Bunyod Holmatov, Allison Khoe, Jamie O'Connell, Rebecca Schultz, and Kevin Sherrill. We thank Pincelli Hull for microscope use and Brad Erkkila, Helmut Ernstberger, Troy Hill, and Jonas Karosas for laboratory guidance. This study benefitted from conversation with Alex Felson and comments from two anonymous reviewers. We thank Kerstin Wasson for sharing hydrology and elevation data from her study in Elkhorn Slough. This work is a contribution to PALSEA2 and IGCP Project 639, 'Sea-level change from minutes to millennia'.

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