# Forest resistance to sea-level rise prevents landward migration of tidal marsh

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## ARTICLE INFO

## ABSTRACT

Little is known about how biotic interactions will influence the distributions of vegetation types under climate change, but these interactions could determine the effectiveness of conservation actions aimed at encouraging ecosystem migration. Tidal marshes are threatened by sea-level rise worldwide unless losses are offset by landward migration. We conducted extensive vegetation surveys within tidal marshes and tested for evidence of ecosystem migration across three scales in adjacent coastal forest in southern New England. We found widespread shifts in tidal marsh vegetation over decadal scales toward a greater extent of flood-tolerant species (e.g. a 5.4% annual increase in *Spartina alterniflora*), but no evidence that coastal forest is changing in a compensatory manner. We found low mortality and high growth rates for trees at the forest edge, suggesting that marsh migration is unlikely in the near term. This apparent mismatch in rates of ecosystem change is likely to result in losses in the extent of high elevation marsh, threatening the persistence of tidal marsh specialists that depend on these areas for reproduction.

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## 1. Introduction

Global shifts in vegetation are expected in response to climate change (Gonzalez et al., 2010), but there is considerable uncertainty about the direction and timing of these shifts for many ecosystems (Pereira et al., 2010; Bellard et al., 2012). One reason for this uncertainty is the increasing evidence that species interactions will have a large influence on the responses of biodiversity to climate change (Davis et al., 1998; Gilman et al., 2010; Wisz et al., 2013; Urban et al. 2012). Species interactions are likely to be especially important when the species competing for space have different life histories, such as at the ecotone of forests and grassy biomes (Bond and Parr, 2010). One such graminoid-dominated biome, tidal marsh, is threatened by sea-level rise (SLR) worldwide (FitzGerald et al., 2008). Tidal marshes may persist, however, if they can migrate landward, replacing other ecosystems (Kirwan and Megonigal, 2013; Schile et al., 2014). There are three major impediments to marsh migration: elevation, human-built coastal protection, and biotic interactions with upland ecosystems at the marsh edge.

Better understanding the potential impediments to migration is important in the short-term for New England's peat-based marshes because they are typically sediment poor and have low accretion rates, which raises doubts about their ability to keep pace with SLR (FitzGerald et al., 2008; Gedan et al., 2011). Marsh loss will likely be greatest in southern New England, which is predicted to experience rates of SLR much higher than the global average (Yin et al., 2009; Boon, 2012, Sallenger et al., 2012). Recent models for southern New England based solely on abiotic factors – SLR, elevation, and accretion – predict substantial losses, especially in high elevation marsh, which is projected to be reduced by 50–70% by 2100 (e.g., Hoover, 2009). However, these projections also suggest that there is enough undeveloped area for migration to mitigate losses. In New England, the highest elevation marsh typically exists above Mean High Water (MHW), closest to the marsh-to-upland boundary (Niering and Warren, 1980). This area of marsh typically floods approximately monthly and is therefore critical habitat for tidal marsh species that require periods without daily flooding for successful reproduction (e.g., Gjerdrum et al., 2008; Bayard and Elphick, 2011).

Observed sea-level trends at tide stations in southern New England range from 2.44 to 2.87 mm/year over the past 50 years (NOAA; www.tidesandcurrents.noaa.gov) and from 1980 to 2009 increases in the rate of SLR have been 3–4 times the global average (Sallenger et al., 2012). Local shifts in marsh vegetation toward communities dominated by flood-tolerant species have been linked to SLR and the associated increase in inundation (Warren and Niering, 1993; Donnelly and Bertness, 2001). It remains uncertain, however, whether these studies are representative of large-scale trends that could pose an urgent threat to the conservation of New England's tidal marshes.

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Perhaps even more uncertain is how biotic interactions will influence the rate of marsh migration, despite recognition that both abiotic and biotic factors are important for determining vegetation communities within tidal marsh ecosystems (Crain et al., 2004; Poulter et al., 2009; Davy et al., 2011; Smith, 2013). The dominant cover at the marsh edge in southern New England is trees, which compete for light and, compared to the graminoid marsh plants that dominate tidal marsh vegetation, have a long life history based on persistence rather than recruitment (Bond and Midgley, 2001). It has been suggested that trees might maintain positive feedbacks that resist a state change from forest to tidal marsh (Brinson et al., 1995), and there is evidence that trees can persist as non-regenerating stands in the face of sea-level rise (Williams et al., 1999). The death of established trees and the subsequent release of tidal marsh plants from competition, therefore, is likely to be one of the most critical, and readily apparent, components of the marsh migration process.

Studies that quantify rates of change at the marsh-upland ecotone are few, but are a powerful tool for understanding whether marsh migration will keep pace with SLR (Smith, 2013; Wasson et al., 2013). Tidal marsh vegetation responds rapidly and predictably to increased inundation (Orson et al., 1998; Warren and Niering, 1993; Donnelly and Bertness, 2001). Vegetation surveys are lacking across broad regions, however, and there is little geographic alignment between studies of vegetation shifts in current marsh and vegetation shifts at the marsh-upland ecotone. Studies with this spatial alignment are needed to determine whether coastal ecosystems as a whole are responding to SLR at the same rate.

Here we explore the hypothesis that tidal marsh and adjacent upland ecosystems are responding to recent sea-level change at different rates, as this temporal mismatch would be an impediment to marsh migration. First, we quantified recent shifts in marsh vegetation. Second, we quantified recent changes in adjacent forest across three scales: 1) forest canopy extent, 2) the proportion of recently-dead trees at the forest-to-marsh boundary, and 3) annual growth rates of dominant tree species, a potential early warning indicator that forests are nearing the tipping point before a dieback event (Camarero et al., 2015).

## 2. Materials and methods

### 2.1. Tidal marsh vegetation change

We first sampled tidal marsh vegetation in 2002–2004 as part of a study designed to describe nest site selection in tidal marsh birds (Gjerdrum et al., 2005). These data came from 55 1-ha plots across twelve marsh complexes in coastal Connecticut, USA (the distribution of sampling locations for all datasets in this paper is shown in Fig. A1). These marsh complexes included several of the largest in the state, and spanned a range of land-ownership types. Plots were randomly selected from within marsh complexes, excluding only areas that were entirely dominated by the non-native *Phragmites australis* or open water. Thus, the data are likely to be representative of natural habitat in Connecticut marshes. In 2013, we resurveyed these plots at the same time during the growing season as the original surveys (mid-July to mid-August), using the same methods. We surveyed each 1-ha plot by estimating the percent cover of all dominant marsh plants within 1-m$^2$ quadrats, the locations for which were chosen by simple random sampling. We excluded from analyses any of the original 1-m$^2$ quadrats that were non-randomly placed at bird nests for Gjerdrum et al. (2005). We searched each quadrat thoroughly for any stems of target marsh plants to ensure accurate estimates for low percent cover estimates. For this paper, we collapsed the percent cover data into presence (>0%) or absence (0%) to facilitate more confident comparisons between 2002–2004 and 2013 and straightforward analyses using logistic models. In 2013, we surveyed at least 36 1-m$^2$ quadrats in each 1-ha plot to quantify the plot-level frequency of occurrence with enough precision to detect change, as determined by an a priori

power analysis. In total, we surveyed 895 in 2002–2004 and 2026 quadrats in 2013. We conducted analyses for the four dominant species: *Juncus gerardii* and *Spartina patens*, which dominate higher elevations with *J. gerardii* typically present in the highest and driest areas; *Spartina alterniflora*, which is found in lower, more frequently flooded areas (Niering and Warren, 1980); and *Distichlis spicata*, which is a pioneer species that colonizes bare patches that are too salty for other species and is often outcompeted elsewhere (Hansen et al., 1976; Crain et al., 2004).

We developed Bayesian hierarchical models using a two-step process. First, we fit an occurrence model using only data from 2002 to 2004 and used the resulting model to make posterior predictions of the expected frequency of occurrence for each 1-ha plot. Then, we compared 2013 data to these predictions in an attempt to falsify the null hypotheses of no change between 2002–2004 and 2013 (Fig. A2). After falsifying these models, we incorporated the 2013 data and expanded the model to include a parameter for change over time. Both the reduced and expanded models included a normal random effect for marsh complex and a log-normally distributed random effect for plot to account for any non-independence caused by spatial autocorrelation. Finally, we included an effect for the frequency of occurrence of *J. gerardii* during the original 2002–2004 survey. This effect should be positive for species for which any gains in occurrence were greater in higher elevation areas, as indicated by a greater initial extent of *J. gerardii* (Niering and Warren, 1980). Code for all statistical analyses and methods for estimating the influence of the 18.6-year lunar cycle (Baart et al., 2011) on the change in marsh plant occurrence are given in the Appendix.

### 2.2. Canopy extent from aerial photos

We obtained 1:12,000-scale Multispectral Coastal Imagery (controlled for tide state) for the northern coast of LIS from the Connecticut Department of Energy and Environmental Protection (http://www.ct.gov/deep/cwp/view.asp?a=2698&q=322898). Existing orthophotography had large georeferencing error (often 18 m root mean squared error; RMSE), which was not adequate for detecting potential forest dieback caused by increased saltwater inundation, which we expected to be a relatively small effect. To improve accuracy, we georeferenced the raw image files at an appropriate resolution. First, we created a grid with 1-ha squares covering Connecticut's entire forest-to-marsh boundary (http://www.clear.uconn.edu) and randomly selected 200 squares. We then georeferenced the raw aerial images only to the extent of a given square, using separate images for each square, which allowed us to significantly improve the precision and accuracy of our images compared to existing orthophotos. We only used squares for which we could achieve an RMSE of <0.5 m, which was assessed using the Orthorectify tool in ArcGIS (ESRI, 2011). In addition to plots that had a georeferencing error of >0.5 m RMSE, we discarded 1) any plots in which development that completely bisects a marsh appeared during the analysis period ($n = 1$) and 2) any plots where we did not feel confident distinguishing *Iva frutescens* from tree cover ($n = 7$). Photos for 37 plots met the above requirements, on which we traced the total area of forest at three time steps with photos clear enough to distinguish the boundary between forest and marsh: 1974, 1990, and 2010. Each plot and time step was traced 10 times non-consecutively by the same observer, and the resulting measurement error was explicitly incorporated into a Bayesian hierarchical model that made it possible to estimate dieback with uncertainty bounds that include measurement error in addition to estimation uncertainty.

### 2.3. Recent tree mortality at the marsh-to-forest boundary

We estimated tree mortality in the zone where marsh migration is projected to occur using data from baseline marsh migration transects established across both the northern and southern coasts of LIS in 2013 (transect coordinates are available at: http://dx.doi.org/10.7910/DVN/VXQLPN). We established transects at the marsh-to-forest boundary and extended them perpendicular to the marsh edge for 100 m or

until we reached either the edge of the area we had permission to survey or a rocky escarpment (Elphick and Field, 2014). We randomly placed 68 transects, across all land ownership types, in areas most likely to be experiencing marsh migration: i.e., slopes at the forest-to-marsh boundary that are <3.5° over the first 10 m according to digital elevation models (Gesch et al., 2002). We augmented this initial data set with 103 transects that were randomly selected along the entire marsh-to-forest boundary of the marsh complexes at: Barn Island WMA (Stonington, CT, USA), Salt Meadow Unit NWR (Westbrook, CT, USA), Rocky Neck State Park, Sunken Meadow State Park (Kings Park, NY, USA), Caumsett State Historic Park Preserve (Huntington, NY, USA), and Wading River Marsh (Riverhead, NY, USA). Our analysis included a site-level random effect, to account for the fact that transects from these marsh complexes were selected using a different sampling scheme than the 68 random transects. The site-level random effect was hierarchically centered on the intercept for the 68 random transects. Allowing the site-level transects to have their own intercepts did not change the results.

We recorded whether each standing tree ($n = 1041$) within 1 m of either side of each transect line was dead (no leaves) or alive (at least some leaves). We do not know when the trees on our transects died, but existing literature on snag falling rates (e.g. Keen, 1955; Russell et al., 2006) suggests little chance that any of the trees still standing died before the first time step of the aerial photo analysis (1974). Along each transect we measured the occurrence of tidal marsh plant species in consecutive 1-m² quadrat for the first 20 m, then every 10 m for the remainder of the transect (Elphick and Field, 2014). For the following analyses, we defined the edge of the marsh as the point on the transect beyond which no tidal marsh specialists (*J. gerardii*, *D. spicata*, *S. patens*, *Salicornia* spp., *Iva frutescens*, *S. alterniflora*, or *Phragmites australis*) occurred. We analyzed tree mortality using Bayesian logistic regression with distance from marsh edge, a random site effect, diameter at breast height (DBH), separate intercepts for the northern and southern coasts (to account for any differences in slope), and a DBH-distance from marsh edge interaction (which could indicate greater mortality of young trees near the marsh edge) as potential predictors. In some cases, the inland-most marsh plants along the transect were found after the initial 20 m causing the marsh edge to fall in the part of the transect with coarser sampling. The resulting uncertainty in this value was explicitly incorporated into the analysis by representing it as a uniform distribution that is bounded by the minimum and maximum possible distances.

### 2.4. Tree growth rates at the marsh-to-forest boundary

At Barn Island WMA (Stonington, CT, USA) and Salt Meadow Unit NWR (Westbrook, CT, USA), we cored all *Quercus* spp., *Acer rubrum*, or *Nyssa sylvatica* >10 cm DBH that were found along the transects used to assess tree mortality rates. These species were chosen because they produce visible growth rings and represent, respectively, the dominant species complex, a common, but less dominant species (the fourth most common species in our dataset), and a wetland-adapted species (Keeley, 1979). We augmented this dataset by coring any trees belonging to the focal species that were the most seaward woody vegetation of the coastal forest and within 10 m of a transect. In total, we cored 15 *Q. alba*, 7 *Q. bicolor*, 20 *Q. velutina*, 1 *Q. coccinea*, 49 *A. rubrum*, and 21 *N. sylvatica*. We took two cores from each tree, perpendicular to each other, and averaged the two time series before analysis.

We took cores with a 4.3 mm diameter Haglöf™ increment borer from approximately 1/2 breast height (~0.7 m) to avoid the influence of the root collar or the first branches. We dried the cores in straws, mounted them on wood molding, and sanded them with a belt sander using progressively finer sandpaper (final polish was at least 400 grit). We scanned cores at 2400 dots per inch using an Epson™ Expression 11000XL Graphic Arts scanner and measured growth rings on the resulting images in ImageJ (Abramoff et al., 2004). During training, technicians measured the same cores repeatedly until the Pearson's correlation between measurements was >0.95.

We created a master chronology using the 20 highest quality cores from each genus (chronologies are available at: http://dx.doi.org/10.7910/DVN/VXQLPN). For developing chronologies, we divided each year's growth by the mean of the 3 years preceding and the 3 years following to diminish the influence of large-scale trends (Speer, 2012). Initially, we compared growth time series by eye. We took a conservative approach to cross-dating and only made changes to a time series when the comparisons identified an error during the measurement process. We also did not take measurements after a break in a core. We then conducted a quantitative assessment of our cross-dating by calculating the Pearson's correlation coefficients between each core and 1) the average of all others (obtaining a single correlation estimate for each core), 2) a sequence of simulated time series in which the observer misses a ring during measurement, with the missed ring sequentially placed after each year in the time series, and 3) a sequence of simulated time series in which the observer measured an extra ring during measurement, with the extra ring sequentially placed after each year in the time series. If the correlation from step 1 was lower than any of the correlations from steps 2 or 3, the core was re-measured. Once the master chronology was completed, we compared each core measured to it first by eye, then using the correlations in steps 1–3 above. As with the master chronology, we only made changes to a time series when the comparisons identified an error during the measurement process. We successfully cross-dated all cores for *Quercus* spp. (which do not produce false or missing rings; Speer, 2012), but cores from *A. rubrum* appeared to be missing growth rings and cores from *N. sylvatica* did not show benchmark narrow rings to use for cross-dating. For both *A. rubrum* and *N. sylvatica*, results should be interpreted as pertaining to the last 20 years that were recorded in cores, which may not always be strictly from 1994 to 2013.

We analyzed tree diameter growth using a Bayesian hierarchical model with random intercepts and slopes for individuals. We modeled baseline growth rates from 20 years ago as a function of DBH, whether or not tidal marsh plants (*P. australis*, *S. alterniflora*, *I. frutescens*, *S. patens*, or *D. spicata*) were present within 1 m of the main stem (Edge-intercept), and Site. For *Quercus* spp. we also included an effect for "red oak" group vs. "white oak" group (Taxon). *Q. bicolor* and *Q. alba* were pooled as the white oak group because we did not find strong evidence for a difference in average growth rates between species (95% confidence interval of difference between means: −0.13, 0.92). Removing *Q. bicolor* cores from the analysis altogether or removing the only *Q. coccinea* vs. lumping it with *Q. velutina* in the red oak group did not affect the results, which are reported with both included. Analysis of *Quercus* spp. also included a Taxon-by-Edge interaction. In addition to the random effect, we modeled the change in growth rates as a function of whether marsh plants were present within 1 m of the main stem (Edge-slope). We also included a first-order autoregressive component (AR1) to account for the effect of growth in year $t$-1 on year $t$. Residuals were log-normally distributed.

### 2.5. Statistical analyses

All analyses were conducted in the software program JAGS (Plummer, 2003) with the R2JAGS package (Su and Yajima, 2012) in R (R Development Core Team, 2015). For each model, we ran three chains for 100,000 iterations after a 20,000-iteration burn-in; we checked convergence by ensuring that each parameter's scale reduction factor was <1.01 (Gelman and Rubin, 1992). Code for all statistical analyses is given in the Appendix.

## 3. Results

### 3.1. Tidal marsh vegetation change

Overall, marsh vegetation showed a shift toward lower-elevation species between 2002–2004 and 2013 (Fig. 1). Frequency of occurrence of *J. gerardii* was consistently lower in the 2013 surveys (Fig. A2), while
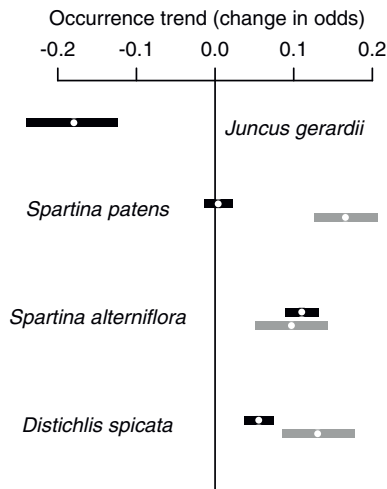
Fig. 1. Annual change in the odds of occurrence for four tidal marsh plant species between 2002–2004 and 2013. Black bars show the 95% credible intervals of the parameter estimates for coast-wide change; white dots are the posterior means. The gray bars show the effects of *J. gerardii* extent on occurrence of the other three species. If the gray interval is completely above zero, there were greater gains in occurrence in areas that had more *J. gerardii* in 2002–2004. Data come from 2921 1-m² quadrats from 55 1-ha plots across 12 marsh complexes in Connecticut, USA.

the occurrence of *S. alterniflora* and *D. spicata* was generally higher. *S. patens* was more common in some plots but less so in others (Fig. A2). Accordingly, the regression coefficients that describe the coast-wide trends were negative for *J. gerardii*, positive for *S. alterniflora* and *D. spicata*, and centered on zero for *S. patens* (Fig. 1). Additionally, the trends for *S. patens*, *S. alterniflora*, and *D. spicata* were more strongly positive in plots that initially had more *J. gerardii*, suggesting that losses for *J. gerardii* were associated with increases for more flood-tolerant species (Fig. 1). The mean change in extent, per 1-ha plot, over the 11-year survey period was −0.084 ha for *J. gerardii*, 0.013 ha for *S. patens*, 0.16 ha for *S. alterniflora*, and 0.10 ha for *D. spicata*. The magnitude of the increase in sea level over the survey period explained by the 18.6-year lunar cycle was small (13.5%) relative to the observed total increase in sea level (Fig. A3).

### 3.2. Canopy extent from aerial photos

We did not find evidence for forest canopy dieback between 1974 and 2010: the mean change over time was in fact positive with narrow credible intervals, suggesting an overall increase in canopy extent (4.6 m²/year; credible interval: 0.50–8.7; Fig. 2). Only nine of the 37
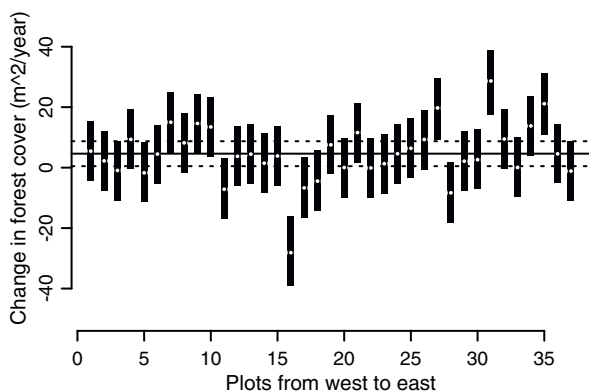


Fig. 2. Change in forest cover (m²/year) at 37 plots in Connecticut, USA, for 1974–2010, organized from west to east. Black bars are plot-level 95% credible intervals and white dots are the mean estimates. The horizontal solid and dotted lines are the mean and 95% credible intervals of the estimated overall trend.

plot-level credible intervals for annual change in forest cover did not overlap zero, and all but one of these showed increases in total forest cover (Fig. 2).

### 3.3. Recent tree mortality at the marsh-to-forest boundary

We did not find strong evidence for greater rates of recent mortality toward the marsh edge, as the effect of distance to marsh overlapped zero (0.0086; −0.0026–0.0200; Fig. 3). The estimated interaction effect between DBH and distance to marsh overlapped zero (−0.00052; −0.0013–0.00030), suggesting that young trees were no more susceptible when near the marsh edge. Thus, we present results for the model with no interaction. The probability of a tree being recently dead was most strongly influenced by DBH (parameter estimate: 0.039; credible interval: 0.022–0.058), approaching no observed mortality for the larger sizes in our dataset (Fig. 3). We also did not find strong evidence that mortality at targeted-site transects differed from 68 randomly-located transects, as the posterior distribution of the standard deviation for the site random effect was close to zero (Fig. A4). It is possible that a standard logistic curve would not be able to adequately describe any abrupt increases in mortality at the immediate marsh edge. We did not, however, find strong evidence for an abrupt increase in mortality at the immediate edge: only 12 of the 85 trees observed <1 m from the marsh edge were dead; all were <38 cm DBH. This degree of
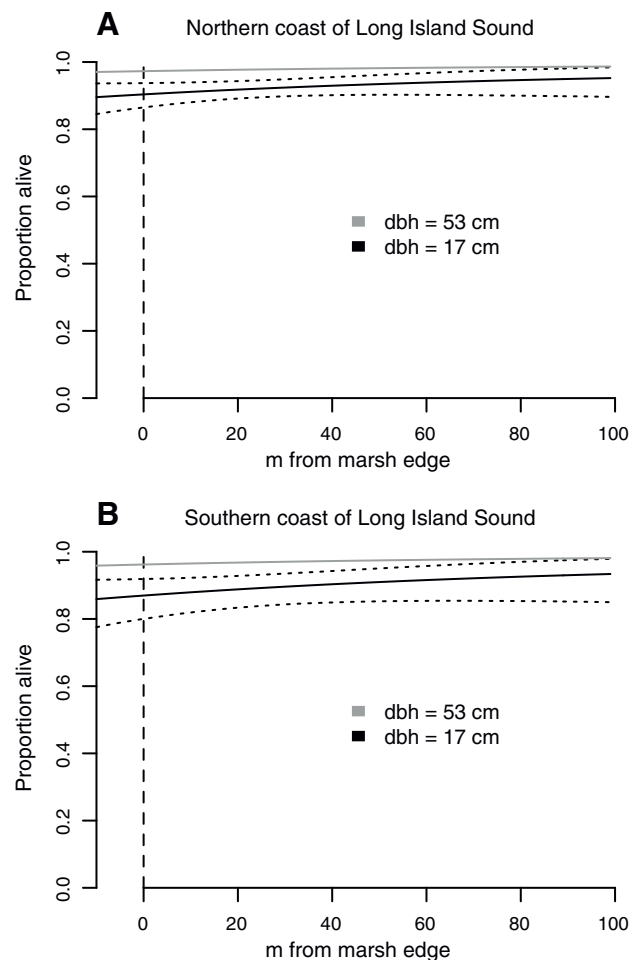


Fig. 3. Recent tree mortality over the first 100 m of the marsh-to-forest boundary on the northern (A) and southern (B) coasts of Long Island Sound (LIS), shown for two sizes: the observed mean DBH (17 cm) and upper 0.95 percentile (53 cm). Dotted lines are 95% credible intervals, which are shown only for observed mean DBH for clarity. Data represented are from 785 trees on the northern coast and 313 trees on the southern coast of LIS.

mortality is within the sampling variation of the Bernoulli distribution predicted by our logistic model.

### 3.4. Tree growth rates at the marsh-to-forest boundary

*Quercus* spp. individuals were growing faster at the marsh edge (within 1 m of marsh plants) than farther into the forest at both of our focal sites (Fig. 4a; 95% credible intervals for edge and interior individuals do not overlap). This result is in contrast to the expectation of slower growth if coastal forest was beginning to die back in response to increased saltwater inundation. *Quercus* growth rates were greater in individuals with larger DBH and were strongly dependent on growth during the previous year, but were not strongly affected by Site, Taxon, or Taxon-by-Edge interaction effects (see Fig. 4b). Growth rates declined over time, as expected for maturing forest, but did not decline faster for trees at the edge (Edge-slope parameter overlaps zero; see Fig. 4c). We found strong evidence for random variation across individuals in both baseline growth rates (intercept) and trends (slope; Fig. 4d). *A. rubrum* and *N. sylvatica* individuals also did not show strong evidence of slower or declining growth at the marsh edge (the posterior probabilities of slower growth at marsh edge are 0.14 and 0.56 respectively; Fig. A5 and Fig. A6).

## 4. Discussion

Our results suggest that coastal forest is more resistant than tidal marsh to observed increases in coastal inundation, and that declines in high elevation marsh vegetation are not being mitigated by landward migration. Over just 11 years we observed large declines in the occurrence of *J. gerardii*, an indicator of the driest areas of marsh, and widespread increases in *S. alterniflora*, a flood-tolerant species. This result extends the geographic scope of inferences from Warren and Niering (1993); Donnelly and Bertness (2001), and Smith (2014), and demonstrates a regional pattern of vegetation shifts toward more flood-tolerant species. There have been strongly increasing trends in measures of sea level that affect marsh ecosystems in our study area during the growing season, likely driven by locally high SLR and changes to meteorological forcing (O'Donnell, 2016). As a result of these trends, tidal marshes are likely being inundated for longer periods of time during the growing season than the changes in annual measures of mean sea level would suggest. Illustrating this potential for significant increases in inundation is the fact that tidal marsh in our study area exists within

a 1-m range in elevation (Hoover, 2009), and the magnitude of the observed increase in MHW is approximately 10% of the tidal range (Mean Range of Tide: 0.78 m; https://tidesandcurrents.noaa.gov/). We found that the magnitude of the 18.6-year lunar cycle was small compared to the increase in sea level over the survey period, ruling out the most likely factor that would cause the changes we observed to be part of a cyclical trend. Another potentially contributing factor is that during 2009–2010, the Northeast USA experienced an extreme jump in sea levels correlated with both a downturn of the Atlantic meridional overturning circulation and a negative value for the North Atlantic Oscillation index (Goddard et al., 2015).

Because *D. spicata* is a pioneer species, the observed increases in its extent might be driven by changes in sediment deposition or winter ice scouring of the marsh surface during the study period, rather than increased flooding from sea-level rise. Two major storms, Irene and Sandy, hit southern New England during our study period and could have dumped sediment or otherwise disturbed the marsh surface (cf. Donnelly et al., 2004). At a large geographic scale, however, Irene and Sandy did not affect the distributions of high elevation or low elevation marsh plant communities (C. Elphick et al. unpublished data).

Because we used only aerial photo plots that could be georeferenced with high precision to estimate changes in the forest edge, plots with clear reference points (e.g., docks, houses, and boulders) are overrepresented in our dataset. This overrepresentation has the potential to bias our overall trend estimate if plots with these features are not representative of the coastline, but we have no evidence of such a bias. The apparent increases in forest cover in some areas on aerial images are likely due to maturation, not encroachment into the marsh, because our study area contains relatively young forest (mean diameter at breast height ~10 cm; Fig. A7).

We found that DBH increases toward the marsh edge (Fig. A7) and that for *Quercus* spp., annual growth rates are higher at the marsh edge, where light competition is lowest, than farther inland. At some point, presumably, the stress from increased saltwater inundation will outweigh the benefits of increased light, but this point clearly has not yet been reached. The timing of marsh migration is likely to be critical for effective conservation planning. One possibility is that coastal forest will eventually reach a tipping point, followed by rapid and widespread tree death when pushed over this tipping point by an extreme storm surge. Predicting such a tipping point is likely limited by our current understanding of the physiological and ecological factors that determine the forest-to-marsh boundary. Specifically, the physiological mechanisms
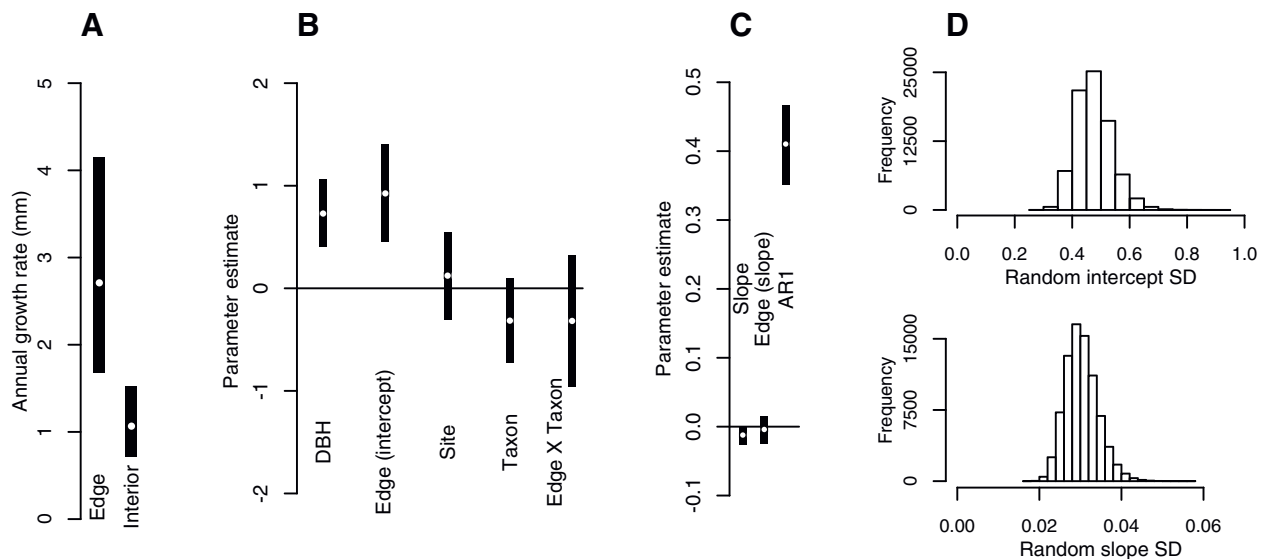


**Fig. 4.** *Quercus* spp. growth rates from 1993 to 2013. A) Estimates of mean annual growth at the marsh edge and in the forest interior (estimated from 43 trees). Black bars are 95% credible intervals and white dots are means. B) and C) Effect sizes of the fixed effects (note different scales). D) Posterior distributions of the random intercept and slope.

of tree death are poorly understood (McDowell et al., 2008), but might play a large role in determining the timing of tree death (Sevanto et al., 2014), and little is known about how marsh plants are excluded from the forest understory.

Smith (2013) found evidence for substantial marsh migration in Delaware Bay – forest retreat of 1.8 m/year – yet we found scant evidence of even declining growth for trees within 1 m of the marsh edge that had marsh plants growing at their base. This discrepancy is likely caused by differences in slope between the two regions, which would influence inundation time and could also potentially result in greater rates of freshwater discharge, lessening the effects of saltwater inundation. In general, the transition from coastal forest to tidal marsh is a complex but poorly understood process that requires changes to salinity and composition of organic and mineral soils, groundwater discharge, and upland community composition (Brinson et al., 1995). Regardless of the mechanisms involved, however, the contrasting results between Smith (2013) and our study highlight challenges ahead for the conservation of southern New England's tidal marshes.

Our results also demonstrate that it is important to consider marsh and coastal forest ecosystems together to make realistic predictions of future marsh extent. Globally, this extent is likely to depend in large part on the responses of the ecosystems that marshes would have to replace. In forested areas, this response could be quite slow because even after recruitment is no longer possible, individuals with life histories based on persistence would have to die before a state change can occur. We found that approximately 93% of the individuals identified on our tree mortality transects are capable of resprouting as adults (based on Tredici, 2001), which suggests the potential for long-term persistence in the face of future stresses. For tidal marshes, data on vegetation change at ecotones will be especially important for understanding changes across large geographic areas: plants are indicators of the flooding regime, which can be costly to measure directly across large areas because of the need for high precision elevation and water level measurements. For other graminoid-dominated ecosystems, such data would provide a better understanding of the potential for losses in extent resulting from being bounded on either side by competition with forests and physiographic limits. This phenomenon is already being observed at high elevations and latitudes (e.g. Walker et al., 2006) and at the ecotone of mangroves and tidal marsh (e.g. Saintilan and Williams, 1999).

Over timescales relevant to conservation, biotic factors, especially competition, might be dominant in determining the extent of tidal marshes. It is not clear whether migration can occur rapidly enough to prevent the extinction of tidal marsh endemics, such as saltmarsh sparrows (*Ammodramus caudacutus*) and diamondback terrapins (*Malaclemys terrapin*). Active management, for example cutting trees at the marsh edge, might be necessary to secure the future of tidal marsh specialists. Research on the effectiveness of these types of management actions should be an urgent priority.

## Acknowledgements

## Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.biocon.2016.07.035. These data include methods for determining the influence of the 18.6-year lunar cycle, the decision rules for tracing canopy extent, code for statistical analyses, supplementary figures (A1-A7), and Google Earth files for the locations of aerial photos and plots for measuring tidal marsh vegetation change. Additionally, the start locations of tree mortality transects and master chronologies for tree cores are available at: doi:10.7910/DVN/VXQLPN.

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