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

Christopher R. Field *, Carina Gjerdrum [1], Chris S. Elphick

Department of Ecology and Evolutionary Biology and Center for Conservation and Biodiversity, University of Connecticut, 75 N. Eagleville Road, Unit 3043, Storrs, CT 06269-3043, USA

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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.

* Corresponding author at: Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Road, Unit 3043, Storrs, CT 06269-3043, USA.
E-mail address: christopher.field@uconn.edu (C.R. Field).
[1] Current address: Environment Canada, 45 Alderney Drive, Dartmouth, Nova Scotia B2Y 2 N6, Canada.

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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

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