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# A Threatened Ecosystem in a Human-Dominated Landscape: Tidal Marsh Conservation in the Face of Sea-Level Rise

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# A Threatened Ecosystem in a Human-Dominated Landscape: Tidal Marsh Conservation in the Face of Sea-Level Rise

Christopher R. Field, PhD

University of Connecticut, 2016

Biological conservation is a crisis-driven discipline that is inextricably linked to its broader social, political, and economic context. Historically, conservation research has often been conducted within ecology disciplines and with limited links to this broader context, which has contributed to a gap between research and its real-world implementation. One impediment to creating stronger interdisciplinary links is that it requires the integration of many types of data from across a range of disciplines. Owing to the difficulty of such integration, questions related to the relative importance of different types of knowledge in conservation decision-making have remained largely unexplored. The answers to these questions, however, are fundamental to the identity of conservation biology as a discipline and have implications for both early-career and late-career conservation scientists, including appropriate training during graduate school and opportunities for cross-disciplinary collaboration and research. I collected data from a range of sources to explore the role of different information for understanding issues related to the conservation of Long Island Sound's tidal marshes, a human-dominated ecosystem that is threatened by sea-level rise. By integrating analyses of abiotic, ecological, and social data, I found that 1) there were diminishing returns for incorporating greater statistical complexity and geographic representation of sampling sites when estimating population parameters, 2) high resolution data on tide heights was important for understanding extinction risk in saltmarsh sparrows (*Ammodramus caudacutus*), 3) data on rates of vegetation change were important for understanding ecological impediments to landward marsh transgression, 4) data on the behavioral intentions of coastal landowners were important for understanding the likely

effectiveness of conservation strategies for encouraging marsh transgression, and 5) better data on land costs have greater potential than other types of data to improve the effectiveness of spatial planning aimed at encouraging marsh transgression. These results highlight the importance of clearly defining the socio-ecological context within which conservation is taking place and the value of accumulating evidence for understanding the relative importance of different types of data in conservation. They also raise questions about the persistence of tidal marshes, and marsh-breeding species such as saltmarsh sparrows, over the next century of sea-level rise.

A Threatened Ecosystem in a Human-Dominated Landscape: Tidal Marsh Conservation in the  
Face of Sea-Level Rise

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B.S., University of Connecticut, **2007**

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Doctor of Philosophy Dissertation

A Threatened Ecosystem in a Human-Dominated Landscape: Tidal Marsh Conservation in the  
Face of Sea-Level Rise

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### *Chapter 6*

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# **Quantifying the importance of geographic replication and representativeness when estimating demographic rates**

## **Abstract**

Demographic rates are rarely estimated over an entire species range, limiting empirical tests of ecological patterns and theories and casting doubt on the representativeness of studies that use data from a small portion of a range. The uncertainty that results from using demographic rates from just a few sites is especially pervasive in population projections, which are critical for a wide range of questions in ecology and conservation. We estimated survival, fecundity, and population growth rates at 21 sites distributed across much of the saltmarsh sparrow's (*Ammodramus caudacutus*) breeding range. We then investigated the consequences of sub-sampling our dataset, using five sampling scenarios that represent a variety of biases in study design to examine their effects on the global mean and variance of growth rates. We found spatial variation in demographic rates, but no large systematic patterns. Simulations that estimated the global mean and variance of growth rates using subsets of the data suggested that at least 10-15 sites were required for reasonably unbiased estimates, but that sampling at the full 21 sites offered diminishing returns.

## **Introduction**

Estimates of survival rates and fecundity are used to address a wide range of questions in theoretical and applied ecology, yet little is known about how these demographic rates vary over species ranges (Sagarin et al. 2006). Spatial variation in vital rates is a fundamental parameter for a wide range of ecological and evolutionary processes, including: species range limits (Gaston 2009); meta-population dynamics (e.g. Guo et al. 2004, Jongejans and De Kroon 2005, Raithel et



al. 2010); population viability (e.g Stacey and Taper 1992); and trait and life history evolution (e.g. Bronikowski and Arnold 1999, Kolb et al. 2007). In many of these areas of study, empirical tests lag behind theoretical advances, which has impeded progress in addressing basic ecological questions and in some cases has led to the wide acceptance of largely untested assumptions (Sagarin and Gaines 2002). The gap between theory and empirical tests presumably arises from the fact that collecting data on demographic rates across large areas is expensive and time-consuming. Estimating annual survival, in particular, requires many years of continuous data collection using many of the common methods (e.g. mark-recapture methods; Lebreton et al. 1992). A pressing, but largely untested, question is how often investment in collecting demographic data over an entire species range would be a fruitful use of research or conservation funding, or whether sampling from just a few sites, as is typically done, is adequate for quantifying demographic rates for most species.

Here, we evaluate data from a 4-year, range-wide demographic study of saltmarsh sparrows (*Ammodramus caudacutus*). Saltmarsh sparrows are an ideal model system for quantifying demographic rates across their range because they are found exclusively in the narrow fringe of tidal marshes in eastern North America. The ranges of coastal species can be treated as one-dimensional in many circumstances, which simplifies tests for biogeographic patterns (Sagarin and Gaines 2002). We collected data on apparent annual survival from 21 sites distributed across a large proportion of the saltmarsh sparrow range (sampling covered approximately 4.3 degrees of latitude: 39.365 to 43.661 decimal degrees; Figure 1), including near their northern limit, where they hybridize with their sister taxon, Nelson's sparrow (*Ammodramus nelsonii*). In total, 3648 individuals were used to estimate annual survival. We combined these survival estimates with fecundity data collected from the same sites over the

same years (Ruskin et al. 2015) to estimate site-level survival, fecundity, and growth rates across the species range, including a rigorous quantification of spatial variation. Studies with demographic data over such a large part of a range are rare (Brewer and Gaston 2003, Samis and Eckert 2007), and few studies have estimated growth rates.

We then used the resulting growth rate estimates to address two questions: 1) How representative are smaller, more typical, datasets in making inferences about range-wide growth rates? 2) How does the spatial configuration of the sampling sites influence these inferences? To address these questions, we conducted simulations that sub-sample the available site estimates to represent smaller datasets across different scenarios for spatial biases in sampling design.

## **Methods**

### *Field methods*

To estimate annual survival, we conducted standardized mist-netting at 21 plots in major marsh complexes (referred to as “sites” below) from New Jersey to Maine, USA (Table 1). We surveyed most plots in 2011-2014; see Table 1 for specific years each plot was surveyed. Plots were 1-28 ha and divided into 1-5 subplots that were surveyed using two or three arrays of six, 12-m mist-nets in a continuous string. We surveyed each subplot on three separate days, cycling through the subplots such that each was visited once before the next round of visits. The survey period at each site began between mid-May and early June, with lower latitude sites starting earlier, and corresponded with the period in which most individuals at a plot could reasonably be assumed to be resident. We made three visits to each subplot, and did not sample later than mid-August. Each visit consisted of three hours of mist-netting that was completed by 11:00. We did not conduct mist-netting during rain, heavy fog, or strong winds. We captured sparrows

passively and by field crews walking in a line to flush birds into the net array at regular intervals throughout the 3-hour netting period. We fitted captured birds with United States Geological Survey-issued aluminum bands and a site-specific color band (see SI Appendix 1, 2). We aged each individual based on plumage and determined the sex by looking for a brood patch or cloacal protuberance. We released all birds after measuring and scoring for body condition and plumage features.

We augmented mark-recapture data from systematic surveys by targeted mist-netting of adult (one year old or older) birds at nests at all sites, banding nestlings shortly before they fledged from nests that we were monitoring at all sites, mist-netting birds during spring and fall migration at select sites, and capturing birds at migration and wintering sites south of our main study area (Borowske 2015). Some individuals caught on study sites as adults may have been captured previously during migration or as nestlings; however, this subset of individuals comprised less than 5% of our total dataset.

For fecundity data collection, we conducted systematic nest searches of subplots when they were visited for standardized mist-netting and at regular intervals until the end of the nesting period (late-August through late-September depending on site). We visited nests and recorded contents every 1-5 days until they fledged or failed. Nest fate (success, flooding, or depredation) was assigned based on evidence at the nest using a standardized protocol (see SI Appendix 3), and we censored nest visit data to account for uncertainty in nest assignment (*sensu* Stanley 2004). See Ruskin et al. (2015) for additional details on the field methods.

### *Statistical methods - survival*

We estimated apparent annual survival of adults using the complete-data likelihood of Cormack-Jolly-Seber (CJS) models (Lebreton 1992; Schofield et al. 2009; Reed et al. 2014). Like other CJS models, the complete-data likelihood approach accounts for imperfect detection of marked individuals by using estimates of capture probability ( $p$ ) to correct estimates of apparent survival ( $S$ , combined emigration and mortality). The complete-data likelihood approach allows one to include latent variables and encounter data obtained outside of the primary sampling scheme, potentially improving estimates of  $S$  (Schofield et al. 2009, Reed et al. 2014). Since our approach is Bayesian, the full posterior distributions of derived parameters are easily obtained by specifying them in the model code. We obtained the posterior distributions for 1) the predicted upper and lower 95% credible intervals of the site effect (back-transformed), 2) the posterior distribution of the standard deviation of the spatial random effect, and 3) the posterior prediction of the distribution of survival rates across the species range.

We modeled systematic variation in both  $S$  and  $p$  using logistic regression. We initially modeled variation in  $S$  using sex (male = 1) and random site and year effects. The model did not converge, however, when using random effects for both site and year. A model with just the random year effect, however, showed that there was not strong evidence for annual variation in survival (year effects and their standard deviation are close to zero; Figure S1). In contrast, the random site effect was strongly supported (see Figure S2) and therefore retained.

Treating site as a random effect made it possible to obtain the best site-level estimates of survival while protecting against over-fitting by taking advantage of the shrinkage (cf. Schaub & Kéry 2008, Lipksy et al. 2010) that results from assuming that sites arise from a common distribution. We modeled variation in  $p$  using sex (male = 1) and study plot size. We included plot size to account for any differences in capture rate caused by small differences in the area

that was being surveyed. We did not have any reason to expect spatial variation in capture rates, beyond that accounted for by the plot effect, because tidal marsh habitat is relatively homogenous across the range and we used the same standardized protocol each site (see SI Appendix 1, 2). We standardized the plot variable by subtracting the mean and dividing by two standard deviations (Gelman 2008).

Saltmarsh and Nelson's sparrows cannot always be positively identified in the field, creating a subset of unknown-species individuals from their hybrid zone, which extends from northern Massachusetts into Maine (Walsh et al. 2015). Ignoring this subset has the potential to bias estimates of apparent survival, in the same way that ignoring unknown-sex individuals can bias parameter estimates (cf. Nichols et al. 2004). To avoid this bias, for birds caught in the hybrid zone, we used a two-step process to 1) reduce the size of the unknown subset using linear discriminant function analysis (LDA) for species assignment and 2) explicitly incorporate uncertainty for individuals that could not be assigned with confidence using the LDA. Because they found, using molecular methods, that it was not possible using structural or plumage metrics to reliably distinguish hybrid backcrosses from members of their parental species using morphometric data, Walsh et al. (2015) developed an LDA that assigns species to a "Saltmarsh" group and a "Nelson's" group based on plumage and morphology. Of the individuals that we positively identified to species in the field, 99.8% of males and 99.7% of females corresponded with the LDA classifications for Saltmarsh group vs. Nelson's group. Individuals that could not be identified with certainty in the field were classified using a reduced LDA using measurements taken on every individual (so that we would not have to drop individuals from the analysis): wing chord (LDA coefficient for males: 0.145; females: 0.488), weight (1.055; 0.496), and tarsus length (-0.146; -0.279). We used a conservative approach when assigning individuals to avoid

bias from misclassification: individuals were only assigned with certainty if their LDA value fell within the range that had zero misclassifications ( $> 26$  for Saltmarsh group;  $< 25$  for Nelson's group). Following Schofield et al.'s (2009) method for dealing with covariate uncertainty, we coded the remaining individuals as being of uncertain species identity and explicitly incorporated that uncertainty by treating species identity as a Bernoulli random variable with  $pi$  being the prior probability of an unknown individual belonging to the Saltmarsh group:

$$\text{Eq. 1: } \mathbf{species} \sim \text{Bernoulli}(pi)$$

We defined  $pi$  as the proportion of Saltmarsh group individuals in the hybrid zone (0.69) from Walsh et al. (2015). Unknown-species individuals were assigned a 1 or 0 (Saltmarsh group = 1) at each step of the MCMC algorithm with a frequency determined by the prior,  $pi$ , and the model likelihood, according to Bayes theorem. This indicator variable, *species*, was used as an index in the model code to remove individual  $i$  from the likelihood of the Saltmarsh group model (and add it to a Nelson's group model with independent parameters) when  $species_i = 0$  (code is provided in SI).

### *Statistical methods – reproductive parameters*

We estimated reproductive parameters using data from Ruskin et al. (2015). These data were re-analyzed in a Bayesian mode of analysis to facilitate drawing from their posterior distributions to propagate uncertainty through the population simulations described below. We estimated daily nest failure probabilities using logistic regression with a site-level random effect and a random date effect, which allowed estimation of site-specific effects of date on nest failure

probability. We estimated re-nesting probability using logistic regression with effects for date and latitude to account for any systematic geographic trends, since the data could not support a site-level random effect. For other parameters (see Figures 2 and 3), we used range-wide estimates. We modeled the number of offspring lost before fledging using Poisson regression with an effect for clutch size (code is provided in SI).

We fit models for survival and reproductive parameters using JAGS (version 3.2.0, Plummer 2003) in R (R Core Team 2013, <http://www.R-project.org/>) with the R2jags package (Su and Yajima 2012, <http://CRAN.R-project.org/package=R2jags>). We used uninformative distributions for all priors (specified in the model code in the SI). We ran three chains for 100,000 iterations after a 25,000-iteration burn-in; the potential scale reduction factors (Brooks and Gelman 1998) for all parameters were <1.01.

#### *Statistical methods – fecundity and population growth rates*

We estimated fecundity and population growth rates at each site over the time period of our sampling, 2010-2014, using individual-based simulation models that propagate uncertainty from both parameter estimation and demographic stochasticity. First, we drew values for the demographic parameters from their posterior distributions (taken from the survival and fecundity analyses described above and from Ruskin et al. 2015; see Figures 2 and 3 for the values of each parameter). Using this set of parameter values, we simulated the populations at each site for 5 years, as outlined in Figure 3, and from these simulations calculated 1) the number of females fledged/female/year and 2) compound annual growth rates. R code for the population simulations is available at <https://github.com/chrisf22/saltmarsh-sparrow/>. We repeated this process for 1000

draws of demographic parameters to quantify the variation in fecundity and growth rates that arises from parameter uncertainty and demographic stochasticity.

We modeled only females because they are critical to the demography of saltmarsh sparrows, which have a sex ratio that is heavily skewed toward males (Hill et al. 2013). Our simulations assumed that annual variation in fecundity and survival parameters were not correlated. The resulting estimates are site-level growth rates in the absence of immigration – i.e. estimates incorporate births, deaths, and emigration (a component of apparent annual survival). We did not expect immigration to have a large influence on growth rate estimates, as saltmarsh sparrows have high site fidelity (DiQuinzio et al. 2001).

We considered five sub-sampling scenarios to quantify the potential consequences of sampling fewer sites on estimates of the global mean growth rate and its variance (Figure 4). For each scenario, we sequentially varied the number of sites from 3 to 21 by 1) adding sites from south to north, 2) adding sites from north to south, 3) adding sites inwards from the edge toward the center of the range, 4) adding sites from the center of the range outwards, and 5) randomly selecting sites from across the range. For each scenario, we randomly drew from the distribution of growth rates for each site included in that scenario, and calculated the mean and standard deviation of growth rates by fitting a normal distribution using the R package MASS (Venables and Ripley 2002). This process was repeated 100,000 times for each scenario to quantify uncertainty arising from estimating growth rates. We confirmed the assumption of normality for growth rates across the range using quantile-quantile plots.

## **Results**



We found clear variation in survival by site: the difference between the predicted upper and lower 95% credible intervals of the site effect and the standard deviation of the spatial random effect were both clearly non-zero (Figure S2). The posterior 95% prediction interval of the distribution of survival rates across the species range spanned 0.25 to 0.67 (Figure S2); mean survival rate was 0.44 for females (95% credible interval: 0.37 – 0.52) and 0.49 (0.42 – 0.56) for males. The parameter estimate for the effect of plot size on capture rate was negative (-0.67; -1.0 – -0.31), suggesting that we were able to more completely sample smaller plots. The parameter estimate for the effect of sex (male = 1) was positive for survival, but overlapped zero (0.21; -0.075 – 0.48), and negative for capture rate (-0.79; -1.2 – -0.37), suggesting that males had lower capture rates than females.

The mean estimate of the number of females produced by each female each year (no. females/female/year) was above one for all but 2 sites, but the confidence intervals for all overlapped 1 (Figure 5). The median number of females produced/female/year across all sites was 1.15 (0.83 – 1.52); with site estimates ranging from 0.92 (0.59 – 1.30) to 1.38 (1.06 – 1.71). The 95% credible interval for the difference between the highest and lowest observed fecundity was 0.12 – 0.82 (mean: 0.46).

The mean estimates of annual population growth rates were positive for only four sites (Figure 5). In general, the confidence intervals were largely overlapping between sites. The growth rate estimates across sites ranged from -0.20 (-0.36 – -0.055) to 0.099 (-0.031 – 0.21), with a sample median of -0.075 (-0.25 – 0.076). The 95% credible interval for the difference between high and lowest observed growth rates was 0.16 – 0.45 (0.29). Plots of survival, fecundity, and growth rates by latitude showed no evidence of systematic trends (e.g. latitudinal,

greater abundance at the center of the range, or declines at the range edge) that would warrant additional model complexity (Figure 5).

For all subsampling scenarios, the confidence bounds of mean growth rate began to converge on the bounds obtained using the full 21 sites after between 10 and 15 sites were used (Figure 6). The confidence bounds of the standard deviation of growth rates were more variable across and within subsampling scenarios, but were still largely within the bounds of the estimate from the full 21 sites after approximately 15 sites were used. None of the sub-sampling scenarios were clearly better or worse than others at estimating mean growth rate, especially when considering the large confidence bounds. Before converging on the estimate obtained from the full dataset, all scenarios were biased to some degree, with random sampling being the least biased. Confidence in knowing the direction of the population trend (the point after which the 95% confidence bounds no longer overlapped zero) occurred after fewer sites for scenarios 1 and 5 (12 and 10 sites respectively) compared to scenarios 2, 3, and 4 (19, 20, and 18 sites respectively).

## **Discussion**

Despite wide confidence bounds on annual fecundity and growth rates, we had enough precision to detect site-level differences and rule out the presence of large systematic trends, such as that expected under the “abundant center” hypothesis, which states that abundance (and therefore either emigration, immigration, survival, or fecundity) is expected to be higher in the center of a species range (Gaston 2009). One reason for the wide bounds is that the uncertainty from estimating the reproductive parameters and survival were propagated through to the final estimates in our individual-based simulation, resulting in a more complete description of

uncertainty than is commonly reported. Our models also do not predict lower growth rates for the hybrid zone compared to the core of the range, even though our survival estimates include some hybrid individuals at those sites. Our results are qualitatively similar to existing studies of demographic rates across a species range. Brewer and Gaston (2003) found significant spatial variation with no decline in demographic rates at the range edge for the holly leaf-miner (*Phytomyza ilicis*). Samis and Eckert (2007) also found variable demographic rates, but with evidence for higher rates at the range center for 1 of the 2 species of coastal dune plant studied. Too few studies have quantified demographic rates across species ranges however, to draw any conclusions about general patterns or factors that might explain variation among studies.

We found strong evidence of spatial variation in survival rates across the saltmarsh sparrow range. More research is needed to determine if this spatial variation can be explained by landscape variables. Finding landscape variables that explain variation in survival is likely to be difficult, however, because such a large component of annual survival is determined outside of breeding sites for migratory species. For saltmarsh sparrows, it is likely that most of the variation in annual survival is explained by mortality during migration (Borowske 2015).

Estimates of the global mean and variation of growth rates were relatively stable across subsampling scenarios, although there was more bias when fewer sites were included. How much bias is acceptable will depend on the nature of the question being asked. Still, with our dataset, we would have been able to determine that the mean growth rate for saltmarsh sparrows is negative by sampling half as many sites (if we randomly sampled sites), demonstrating that there were diminishing returns. More sites would have been required if the mean growth rate estimate was not largely non-zero, highlighting the influence of the strength of the population

trend in determining the number of sampling sites needed to determine its direction with confidence.

Once 10-15 sites were included, geographic bias in sampling design did not make a practical difference for estimating global growth rates, especially in light of the inherent uncertainty in the parameter estimates, suggesting that for some species it is appropriate to have confidence in global population models that use geographically biased data. Nonetheless, our results do suggest that relying on demographic data from just a few sites is likely to lead to biased results when extrapolating across a species range. We suspect that for most questions in theoretical and applied ecology, the uncertainty in estimates of demographic parameters is likely to be more relevant than the degree of bias we found when at least 10 sites were included. More intensive sampling at the site level could improve precision, but there will always be considerable parameter uncertainty with designs like CJS, which require that the parameter of interest is adjusted for detection or capture rate, and many of our sites were sampled as completely as could be expected without causing disturbance that could bias estimates in other ways. Moreover, the confidence intervals in our sub-sampling scenario are somewhat narrower than in some situations because we made site-level estimates using borrowing strength from other sites.

Quantifying demographic rates for coastal and restricted range species is one way to narrow the gap between empirical and theoretical advances in species range ecology, but caution should be exercised when generalizing results to species with larger and more geographically variable ranges. The lack of broad patterns in demographic rates across the saltmarsh sparrow range could result from being habitat specialists, relying on a restricted, relatively homogenous, habitat type throughout their annual cycle (Greenlaw and Rising 1994). More empirical data on

demographic rates across taxonomic groups and species range types would benefit a broad range of areas of research across ecology, evolution, and conservation.

## Figures and tables

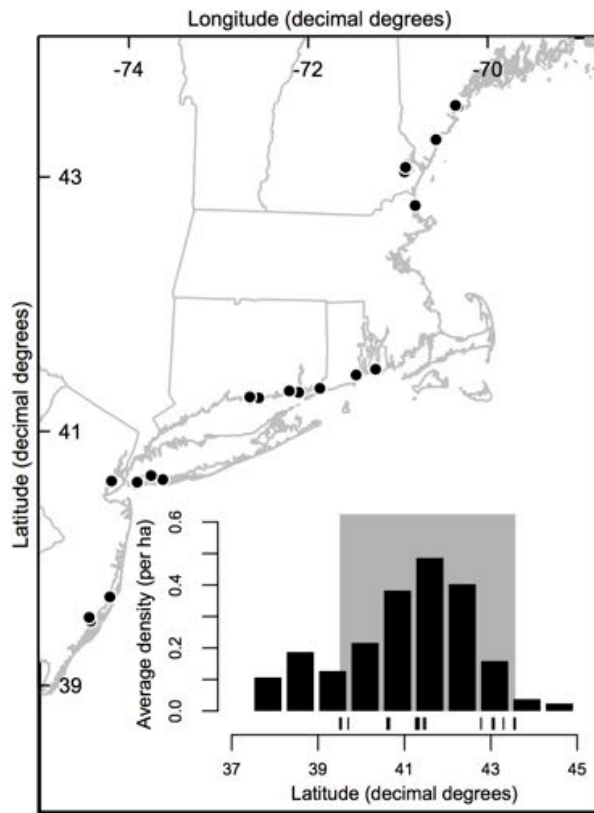


Figure 1. The distribution of demographic sampling plots (black circles on map; tick marks along inset histogram). The inset shows average saltmarsh sparrow density by latitude (from Wiest et al. 2015). The latitudinal distribution of our sampling plots, shaded in gray in the histogram, encompasses the core of the species range.

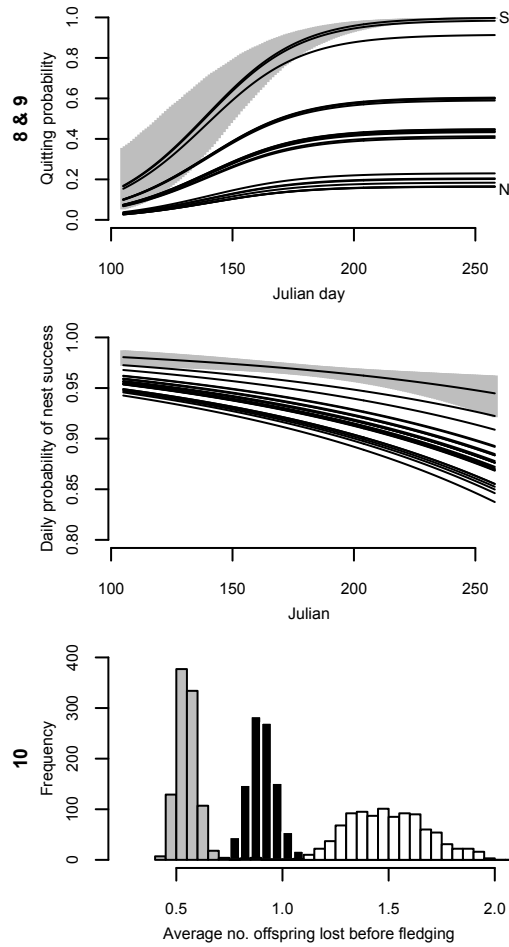
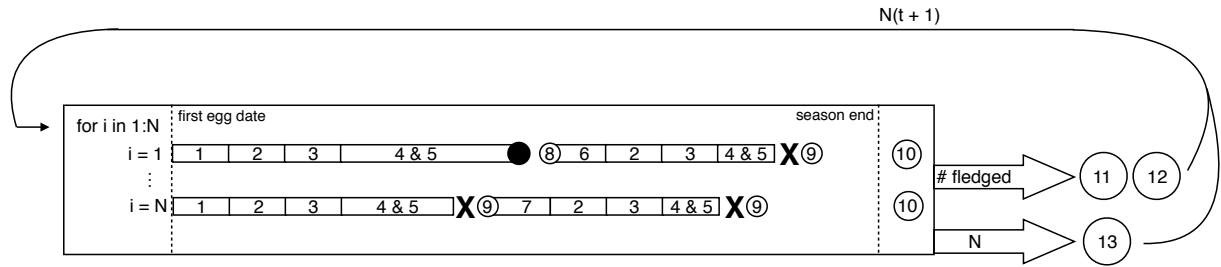


Figure 2. Reproductive parameters used in the population simulations. Top: Probability of ending re-nesting attempts over days since January 1. Lines are for each site, from south to north. 95% credible interval is shown for just the southern-most site for clarity. Middle: Daily probability of nest success over days since January 1. Separate lines are shown for each site; for clarity, 95% credible interval is shown just for the site with the highest nest success. Bottom: Posterior distributions of the average number of offspring lost from the clutch before fledging, shown for starting clutch sizes of three (gray), four (black), and five (white).



Index	Parameter	Mean	Standard Error	Individual variation	Distribution	Source
1	Days until initiation	3	NA	NA	Poisson	Expert opinion
2	Nest building days	[0, 0.25, 0.25, 0.5]	NA	NA	Multinomial	DeRagon 1988
3	Egg laying days (based on clutch size)	[0, 0, 1.60, 2.12, 0.43]	[0, 0, 0.15, 0.15, 0.18]	NA	Multinomial	Estimated from data in Ruskin et al. 2015
4	Egg incubation days	10.97	0.2	1.18	Normal	Estimated from data in Ruskin et al. 2015
5	Nestling days	9.7	NA	0.8	Normal	Hill 1968, DeRagon 1988
6	Days until renesting (after success)	17	NA	1	Normal	DeRagon 1988
7	Days until renesting (after failure)	2	1.02	NA	Poisson	Estimated from data in Ruskin et al. 2015
8	Quitting probability (after success)	See Figure 2	See Figure 2	NA	Binomial	Estimated from data in Ruskin et al. 2015
9	Quitting probability (after failure)	See Figure 2	See Figure 2	NA	Binomial	Estimated from data in Ruskin et al. 2015
10	No. of offspring lost before fledging	See Figure 2	See Figure 2	NA	Multinomial	Estimated from data in Ruskin et al. 2015
11	Sex ratio	0.41	0.038		Normal	Hill et al. 2013
12	First year survival (as a proportion of adult survival)	0.5	0.13	NA	Normal	Expert opinion
13	Adult survival	See Figure 5	See Figure 5	NA	Binomial	Estimated from data

Figure 3. Conceptual diagram of the population simulation used to estimate demographic parameters for saltmarsh sparrow populations throughout the species range. The fate of each female's nesting attempts is simulated over a 154-day breeding season (April 15 through September 15) and the resulting reproductive output combined with survival estimates to determine the female population size (N) at time t+1. Numbers link parameters listed in the first column of the table to those in the diagram, which represents alternative sequences of nest fates for N females. Each female's sequence is broken down into potential reproductive stages as the breeding season progresses; two hypothetical sequences are shown. Solid black circles represent



fledged nests and black Xs represent failed nests. Daily nest failure probabilities (see Figure 2) start affecting nest attempts during egg laying (3). In the table, the mean column refers to the mean estimate for that parameter; multiple values are given when the parameter is based on multinomial probabilities. The standard error column refers to estimation uncertainty, which is incorporated whenever parameters were estimated from our dataset or uncertainty was reported in the source study. The individual variation column refers to the standard deviation for each parameter observed across individuals. The distribution column gives the statistical distributions used to represent estimation uncertainty and/or individual variation for each parameter. For distributions that do not have separate variance terms (i.e. Poisson, multinomial, or binomial), individual variation is assumed to be the sampling variation of that distribution. R code for the population simulation is available at <https://github.com/chrisf22/saltmarsh-sparrow/>.

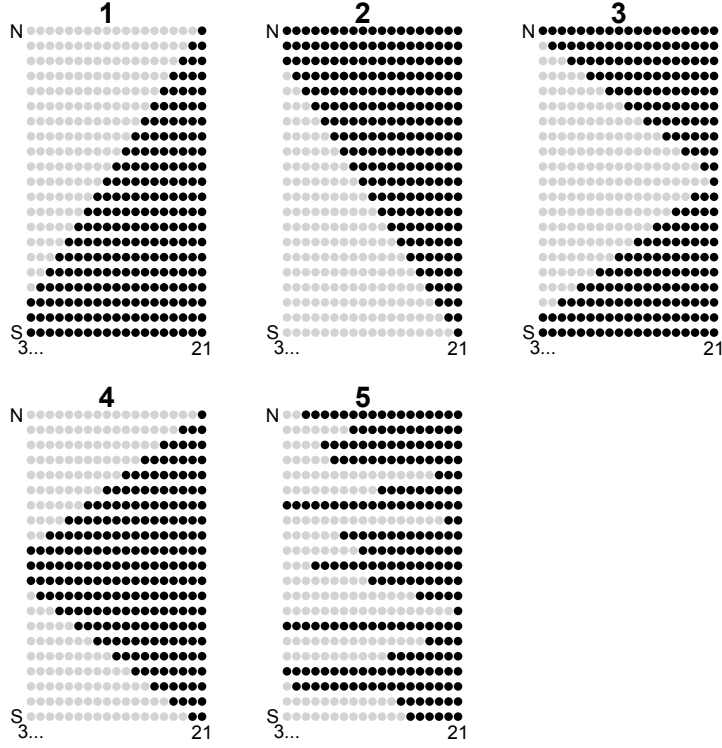


Figure 4. Diagram of five sub-sampling scenarios used to simulate less representative datasets.

Bold numbers are scenario references used for reporting results in Figure 6. Each column of circles represents the sites used for a scenario (denoted by black circles; grey circles are excluded sites) from south (S) to north (N). Within each group, we estimated parameter values with sub-samples of 3 (the minimum required to calculate the standard deviation) through 21 sites, shown along the horizontal axis.

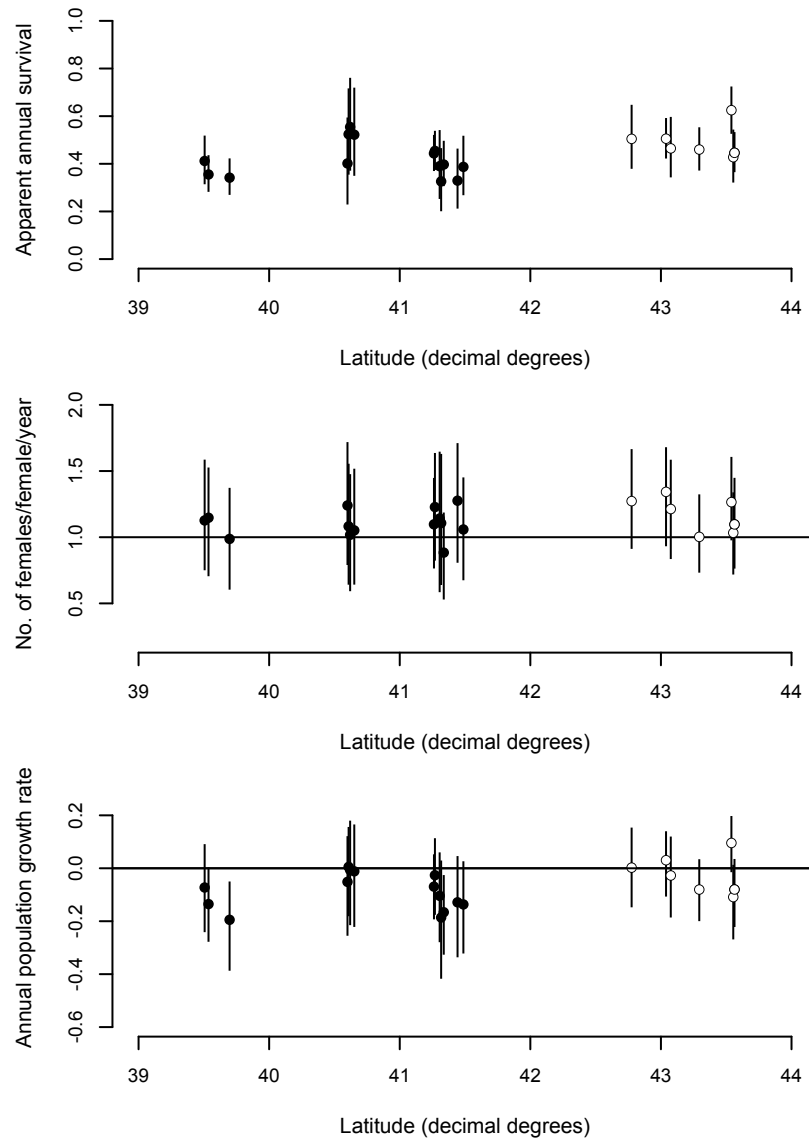


Figure 5. Estimated demographic parameters for 21 sites distributed across the latitudinal range of saltmarsh sparrow. Means for each site are represented by a dot; white dots are sites in the hybrid zone. Vertical lines are 95% credible intervals. Top: Annual female survival rates. Middle: Fecundity (number of females/female/year); horizontal line is shown at 1 for reference. Bottom: Compound annual growth rates; horizontal line is shown at 0 (no population growth or decline).

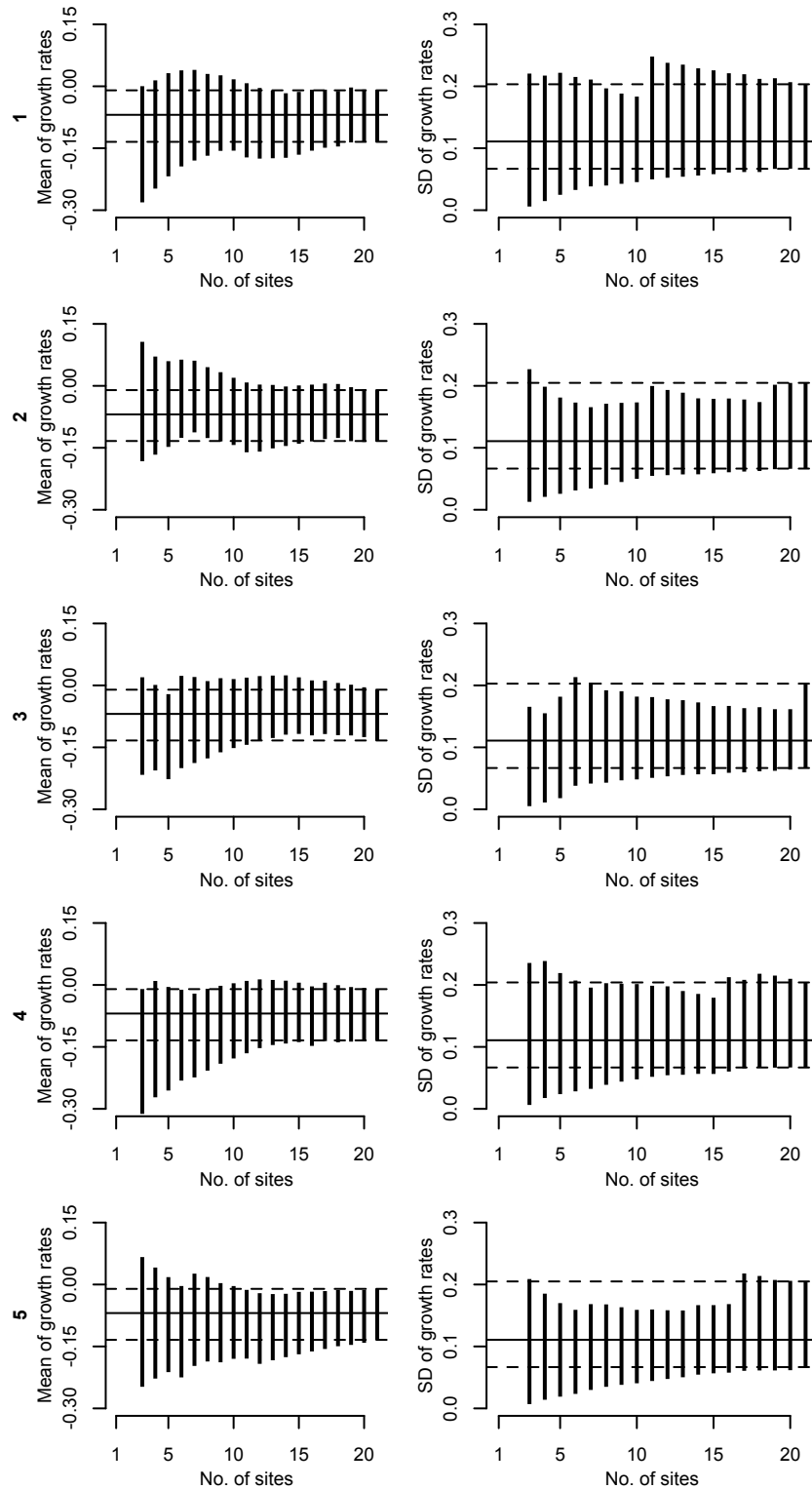


Figure 6. Global mean and standard deviation of growth rates for five sub-sampling scenarios.

Bold numbers on the vertical axis reference the scenarios illustrated in Figure 4. Black bars are

the 95% confidence intervals. Horizontal solid and dashed lines are the mean and 95% confidence interval that was estimated using all 21 sites (the right-most bar in each graph).

Table 1. Demography study sites at which mark-recapture data for saltmarsh sparrows were collected. Number of unique individuals captured at each study site is given for Saltmarsh Sparrow (SALS) and Saltmarsh x Nelson's Sparrow hybrids (HYBRID).

Latitude	Longitude	Marsh complex name	No. of banded SALS	No. of banded HYBRID	Plot size (ha)	Years surveyed	No. of nests (from Ruskin et al. 2015)
39.50598823	-74.42564887	Oyster_Creek	178	0	19	2011-2014	30
39.53554518	-74.44253256	Mullica_Wilderness	372	0	17	2011-2014	69
39.69698951	-74.21126457	ATT	377	0	14	2011-2014	68
40.59975147	-73.90725924	Four_Sparrow_Marsh	22	0	1	2012-2014	15
40.60848309	-74.19277382	Sawmill_Creek	54	0	4	2012-2014	25
40.62011387	-73.62124797	Marine_Nature_Study_Area	39	0	4	2012-2014	9
40.65182314	-73.75157351	Idlewild	64	0	3	2012-2014	6
41.26211791	-72.5520973	Hammonasset	442	0	13	2010-2014	48
41.26940894	-72.65164296	East_River	379	0	19	2010-2014	38
41.30556173	-72.10669055	Waterford	30	0	3	2011-2013	1
41.31700371	-72.21177681	Pattagansett	42	0	8	2011-2013	4
41.33702643	-71.8703894	Barn_Island_WMA	253	0	23	2010-2014	32
41.4425439	-71.46571031	John_H_Chaffee_NWR	94	0	12	2011-2014	25
41.48726854	-71.24917593	Sachuest_Point_NWR	80	0	4	2011-2014	18
42.77556486	-70.80810268	Parker_River_NWR	307	0	28	2013-2014	26
43.03915478	-70.9269943	Chapmans_Landing	287	19	12	2011-2014	127
43.07542386	-70.91539007	Lubberland_Creek	97	0	8	2012-2014	25
43.29366458	-70.57620127	Eldridge_Marsh	218	29	11	2011-2014	59
43.53970539	-70.35444111	Jones_Creek	285	204	17	2012-2014	78
43.55398384	-70.32848703	Nonesuch_River	87	82	14	2011-2014	28
43.56329844	-70.35844569	Scarborough_Marsh	236	195	10	2011-2014	56

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### Supplementary Information

JAGS code for the model of apparent annual survival:

```
#random site effect if species = 1 (Saltmarsh group)
for(i in 1:21){
  site[i, 2] ~ dnorm(0, tau2[2])
}
```

```
#random site effect if species = 0 (Nelson's group); there are only 6 sites with
individuals that could be Nelson's group
for(i in 1:6){
  site[i, 1] ~ dnorm(0, tau2[1])
}
```

```
#when species = 1, there is no possibility of site being 7:21, so set equal to zero to
make exporting the vector easier
for(i in 7:21){
  site[i, 1] <- 0
}
```

```
#for priors specified below, the s loop is to specify which species-specific parameters
should be used (1 = Nelson's; 2 = Saltmarsh)
#priors for the variance parameters of the random site effect
for(s in 1:2){
  sd2[s] ~ dunif(0, 1000)
  tau2[s] <- 1/(sd2[s]*sd2[s])
}
```

```
#variance for random year effect
for(s in 1:2){
  sd[s] ~ dunif(0, 1000)
  tau[s] <- 1/(sd[s]*sd[s])
}
```

```
#priors for the effect of sex on p (Bsexp) and S (BsexS)
for(s in 1:2){
  Bsexp[s] ~ dnorm(0, 0.001)
  BsexS[s] ~ dnorm(0, 0.001)
}
```

```
#priors for the effect of plot on p
for(s in 1:2){
  Bplot[s] ~ dnorm(0, 0.001)
}
```

```

#random year effect; 5 years
for(i in 1:5){
  for(s in 1:2){
    year[i, s] ~ dnorm(0, tau[s])
  }
}

#separate intercepts for Saltmarsh and Nelson's
for(s in 1:2){
  CSmu[s] ~ dnorm(0, 0.001)
  Cpmu[s] ~ dnorm(0, 0.001)
}

#prior for sex ratio
for(s in 1:2){
  sexratio[s] ~ dunif(0, 1)
}

#for 2878 individuals
for(i in 1:2878){
  #prior for unknown sex individuals (male is sex = 1)
  sex[i] ~ dbin(sexratio[species[i] + 1], 1)
  #species_prior is read in as data; 1 for all certain Saltmarsh group and 0.69 for unknown
  species
  species[i] ~ dbin(species_prior[i], 1)
  #firstcapture_aux is a vector of the first captures
  #for 5 years
  for(z in (firstcapture_aux[i]+1):5){
    #logistic regression equation for apparent survival
    logit(R[i, z]) <- CSmu[species[i]+1] + BsexS[species[i]+1]*sex[i] + year[z, species[i] + 1]
    #dead birds stay dead
    S[i, z] <- A[i, z-1]*R[i, z]
    #matrix A indexes whether individuals are alive or dead
    A[i, z] ~ dbin(S[i, z], 1)
    #logistic regression equation for capture probability
    logit(q[i, z]) <- Cpmu[species[i]+1] + Bsexp[species[i]+1]*sex[i] + Bplot[Spp[i]+1]*plot[i]
    # capturing an individual depends on whether it is alive (A) and the capture probability
    p[i, z] <- q[i, z]*A[i, z]
    data[i, z] ~ dbin(p[i, z], 1)
  }
}

```

JAGS code for the model of daily nest survival:

```

#prior for random site effect
sd ~ dunif(0, 1000)
tau <- 1/(sd*sd)

#prior for random date effect
sd2 ~ dunif(0, 1000)
tau2 <- 1/(sd2*sd2)
#mean of random date effect
B ~ dnorm(0, 0.001)
#prior for intercept
int ~ dnorm(0, 0.001)

#random site and date effects
#random site effect is centered on zero; random date effect is centered on B
for(i in 1:21){
  site[i] ~ dnorm(0, tau)
  C[i] ~ dnorm(B, tau2)
}

#for 796 nests
for(i in 1:796){
  #total_nest_days is a vector of the number of days each nest was active
  for(t in 1:total_nest_days[i]){
    #logistic regression equation
    logit(mu[i, t]) <- int + C[Site[i]]*(date[i]+(t-1)) + site[Site[i]]
    #data are Bernoulli distributed
    nest_fate_matrix[i, t] ~ dbern(mu[i, t])
  }
}

```

JAGS code for the model of quitting probability:

```

#prior for latitude effect
B ~ dnorm(0, 0.001)
#prior for date effect
B2 ~ dnorm(0, 0.001)
#prior for intercept
int ~ dnorm(0, 0.001)

#for 613 nests
for(i in 1:613){
  #logistic regression equation

```

```

logit(mu[i]) <- int + B*lat[i] + B2*date[i]
#data are Bernoulli distributed
quitting_prob[i] ~ dbern(mu[i])
}

```

JAGS code for the model of brood size at fledging:

```

#prior for intercept
int ~ dnorm(0, 0.001)
#prior for effect of clutch size
B ~ dnorm(0, 0.001)

#for 325 nests
for(i in 1:325){
#regression equation with log link
log(lambda[i]) <- int + B*clutch[i]
#the number of chicks lost from nest before fledging is Poisson distributed
chicks[i] ~ dpois(lambda[i])
}

```

R code for sub-sampling scenarios:

```

#load the MASS package for estimating means and standard deviations
library(MASS)

#site_growth_rates is a matrix with 21 rows (for each site) and columns for each
iteration of the population simulation

#for mean of growth rates
#for each of five scenarios
for(w in 1:5){
#create a blank scenario-by-site matrix
index_mat = mat.or.vec(5, 21)
#North to South
index_mat[1,] <- c(1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21)
#South to North
index_mat[2,] <- rev(c(1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20,
21))
#from the edges in
index_mat[3,] <- c(1, 21, 2, 20, 3, 19, 4, 18, 5, 17, 6, 16, 7, 15, 8, 14, 9, 13, 10, 12, 11)
#center of range out
index_mat[4,] <- c(11, 10, 12, 9, 13, 8, 14, 7, 15, 6, 16, 5, 17, 4, 18, 3, 19, 2, 20, 1, 21)

```

```

#random
index_mat[5,] <- sample(1:21, 21)
#load "index" with the correct scenario
index <- index_mat[w, ]
#starts at 3 sites
#create a blank number of sites-by-number of iterations matrix
mean_est = mat.or.vec((length(index)-2), 100000)
#for 100000 iterations
for(z in 1:100000){
  for(i in 1:(length(index)-2)){
    #create a temp vector that indexes which value from the vector of simulations to draw
    temp <- sample(1:length(site_growth_rates[21, ]), 2+i, replace=TRUE)
    #create a temp matrix with only the sites being considered at this step in the scenario
    temp_site <- site_growth_rates[index[1:(2+i)], ]
    #pull iteration of simulation vector to get a vector with one value for each site
    temp_site <- diag(temp_site[, temp])
    #fit a normal distribution and get the mean and its standard error
    a <- fitdistr(temp_site_logit, "normal")
    #save mean and error of mean to object
    mean_gr <- a$estimate[1]
    sd_gr <- a$sd[1]
    #draw one value from the standard error
    b <- rnorm(1, mean_gr, sd_gr)
    mean_est[i, z] <- b
  }
}

#for standard deviation of growth rates
#for each of five scenarios
for(w in 1:5){
  #create a blank scenario-by-site matrix
  index_mat = mat.or.vec(5, 21)
  #North to South
  index_mat[1,] <- c(1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21)
  #South to North
  index_mat[2,] <- c(1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21)
  #from the edges in
  index_mat[3,] <- rev(c(1, 21, 2, 20, 3, 19, 4, 18, 5, 17, 6, 16, 7, 15, 8, 14, 9, 13, 10, 12,
  11))
  #center of range out
  index_mat[4,] <- c(11, 10, 12, 9, 13, 8, 14, 7, 15, 6, 16, 5, 17, 4, 18, 3, 19, 2, 20, 1, 21)
  #random
  index_mat[5,] <- sample(1:21, 21)
  #load "index" with the correct scenario

```

```

index <- index_mat[w, ]
#starts at 3 sites
#create a blank number of sites-by-number of iterations matrix
sd_est = mat.or.vec((length(index)-2), 100000)
#for 100000 iterations
for(z in 1:100000){
  for(i in 1:(length(index)-2)){
    #create a temp vector that indexes which value from the simulation chain to draw
    temp <- sample(1:length(site_logit[21, ]), 2+i, replace=TRUE)
    #create a temp matrix with only the sites being considered at this step in the scenario
    temp_site <- site_growth_rates[index[1:(2+i)], ]
    #pull iteration of simulation chain to get a vector with one value for each site
    temp_site <- diag(temp_site[, temp])
    #fit a normal distribution and get the standard deviation and its standard error
    a <- fitdistr(temp_site_logit, "normal")
    #save mean and error of sd to object
    mean_logit <- a$estimate[2]
    sd_logit <- a$sd[2]
    #draw one value from the standard error
    b <- rnorm(1, mean_logit, sd_logit)
    sd_est[i, z] <- b
  }
}

```



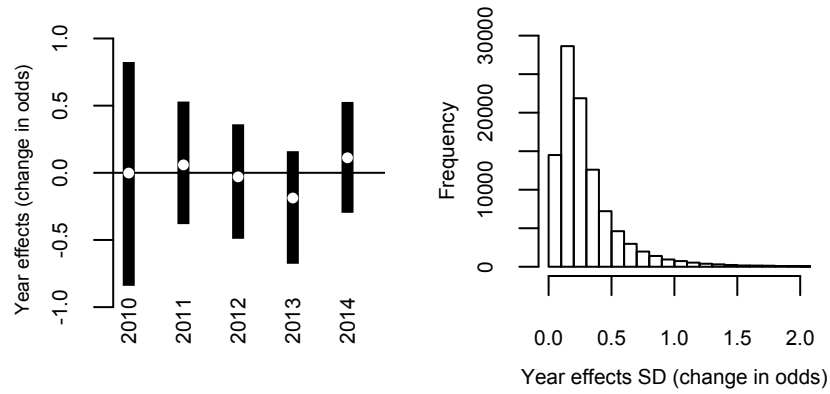


Figure S1. Results for the random year effect in our model of apparent annual saltmarsh sparrow survival without a spatial random effect. Left: Year effects for 2010-2014. Black bars show 95% credible intervals and white dots show the means. Right: The posterior distribution of the standard deviation of the random year effect. A large part of the density is close to zero, suggesting a weak effect.

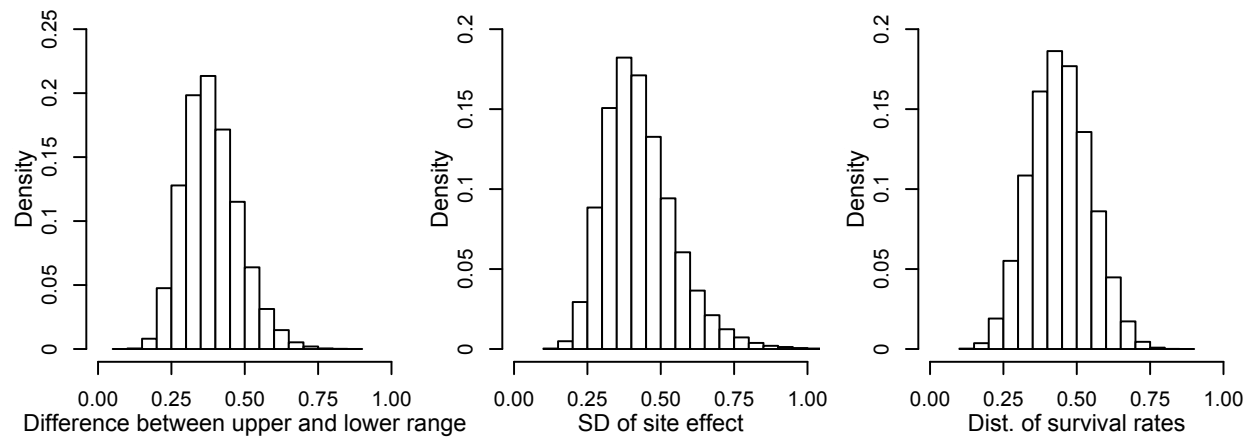


Figure S2. Three quantifications of spatial variation in apparent annual survival in saltmarsh sparrows. Left: The posterior distribution of (left) the difference between the predicted upper and lower 95% credible intervals of the site effect (backtransformed); (middle) the standard deviation of the spatial random effect; and (right) the distribution of survival rates across the range.

## High resolution tide projections reveal extinction threshold in response to sea-level rise

### Abstract

Sea-level rise will affect coastal species worldwide, but models that aim to predict these impacts are typically based on simple measures of sea level that do not capture its inherent complexity, especially variation over timescales shorter than one year. Coastal species might be most affected by floods that exceed a critical threshold, however, and the frequency and duration of floods may be more important than mean sea level. The potential for non-linear population responses or biological thresholds to flooding merits further research, but in many cases will require greater resolution in sea level than is often used. We created population projections for a threatened songbird, the saltmarsh sparrow (*Ammodramus caudacutus*), in a region where sea level is predictable with high accuracy and precision. We show that incorporating the timing of semidiurnal high tide events throughout the breeding season, in addition to mean sea-level rise, predicts a reproductive threshold and affects estimates of extinction risk. This threshold is likely to cause a rapid demographic shift that threatens the persistence of saltmarsh sparrows beyond 2060. Our results suggest that the variation and complexity of climate-driven variables could be especially important for predicting population responses to sea-level rise.

### Introduction

Global sea levels will rise over the next century, threatening coastal species worldwide (Harley et al. 2006; Hoegh-Guldberg and Bruno 2010). Even with no future carbon emissions, coastal specialists face over 0.5 m of sea-level rise (SLR) over the next century, with more than 1 m possible (Schaeffer et al. 2012). Models developed to better understand and predict the effects of

SLR on coastal species are common (e.g. Ellison and Stoddart 1991; Galbraith et al. 2002), but often rely on simple measures of sea level, such as globally-averaged trends in Mean Sea Level. Sea level, however, is the sum of complex drivers, including astronomical, meteorological, physical, and geomorphological components (Parker 2005). Consequently, in any given area, sea level has substantial systematic (including cyclical) and stochastic variation over timescales ranging from decades to hours (Chelton and Davis 1982; Fukumori et al 1998).

Increasing evidence suggests that understanding the effects of climate change on biodiversity will require incorporating more information about climate variability, rather than basing inference simply on average values (Katz and Brown 1992; Stenseth et al. 2002). Specifically, studies may need to include event-focused, as opposed to trend-focused, analyses (Jentch et al. 2007) and multiple components of climate variables, especially the variance (Nadeau and Fuller 2015). Variation in sea level and the timing of this variation could be especially important for species threatened by SLR because frequency and severity of events such as storm surges could have a large effect on population viability (e.g. Van De Pol 2010). Moreover, the combined influence of multiple variables that interact to determine sea level, such as SLR and storm surge, could lead to response thresholds (Harley et al. 2006) and non-linear biotic responses (e.g. Hsieh et al. 2005). The potential for such nonlinearities is often overlooked (Andersen et al. 2009; Monac and Helmuth 2011), even though the responses of complex ecological systems to changes in the physical climate are not necessarily proportional (Burkett et al. 2005), and knowledge of potential thresholds is relevant to management and policy (Hsieh et al. 2005).

There is a need to investigate whether incorporating the complexity of sea level prediction alters inferences about the behavior of coastal systems and the viability of coastal

species. One challenge to incorporating this complexity, however, is that downscaled climate variables are often too coarse spatially or temporally to be biologically relevant for many species (Potter et al. 2013). While an increasing number of studies are addressing how the spatial resolution of climate variables affects inferences about species responses (e.g. Franklin et al. 2013), much less research is focused on the importance of temporal resolution (Early and Sax 2011). We suspect greater temporal resolution will be critically important for understanding SLR effects on ecosystems given the wide variation in sea level, even over daily timescales.

We address this challenge here by developing population projections for a songbird that is threatened by SLR in a region where precise and temporally high-resolution predictions of sea level are possible: Long Island Sound (LIS), USA. Saltmarsh sparrows (*Ammodramus caudacutus*) are tidal marsh specialists, for which nest failure is tightly correlated with tide height because high sea levels cause eggs and nestlings to float out of the nest (Humphreys et al. 2007; Bayard and Elphick 2011). In LIS, 95% of the variation in sea level is caused by the astronomical component of tides (Wong 1990), which can be predicted with high accuracy and temporal resolution using tidal constituents. To take advantage of these high-resolution predictions of sea level, we developed a novel statistical analysis that uses a latent variable specification to estimate sparrow nest survival probabilities over 12-hour time intervals (the approximate time between high tides in LIS), even when the data are at a much coarser resolution.

We use these population projection models to address two main questions: 1) How does the timing of high tides within the saltmarsh sparrow breeding season affect estimates of extinction risk in the face of SLR? 2) Does incorporating more realistic sea level information alter estimates of the potential for population thresholds or rapid shifts?

## Methods

To complete a nesting cycle, saltmarsh sparrows require approximately 23 days without tides high enough to cause nest failure (DeRagon 1988; Greenlaw and Rising 1994), making them particularly sensitive to “high spring tides”, which occur approximately every 29.5 days (during new or full moons). Saltmarsh sparrows do not actively synchronize their breeding to lunar cycles, and tides several days before and after new or full moons can be high enough to cause nest failure (Elphick et al. unpublished data). SLR has the potential to increase the length of time that tides around full and new moons have a substantial influence on nest failure rates, effectively closing the 23-day window needed for successful reproduction.

We took advantage of the predictability of tides in LIS to create population projections for saltmarsh sparrow populations with 12-hour temporal resolution. In doing so, we quantified the range of normal variation and trends in the meteorological component of tides, and the fine-scale relationship between saltmarsh sparrow nest survival and tide height. We also estimated trends and potential non-linearities in the occurrence of suitable breeding windows and in fecundity. Finally, we simulated the effects of eliminating the cyclical nature of extreme tides in order to estimate how these cycles influence estimates of extinction risk.

### *Astronomical, meteorological, and local components of tide*

We obtained the harmonic constituents and observed sea level data (relative to Mean Sea Level; 1979-2011) for the New London, Connecticut, USA tide station (the station most central and closest to the study plots described below) from the National Oceanic and Atmospheric

Administration's (NOAA) Tides and Currents web site (<http://tidesandcurrents.noaa.gov>). We calculated the astronomical component of tide height as (from Parker 2005):

$$tide\ height_t = \sum_{i=1}^{34} C_{amplitude_i} * f_{it} * \cos(C_{speed_i} * t + ((V_{it} - u_{it}) - C_{phase_i}))$$

where tide height above Mean Sea Level at time  $t$  depends on the amplitude, phase, and speed (the  $C$  parameters) of the 34 harmonic constituents (Table S1),  $i$ , for the New London tide station. We used the 'oce' package (Kelley et al. 2015) for R (R Development Core Team 2015) to obtain, for each harmonic constituent, the astronomical phase,  $V$ , the lunar cycle phase modulation,  $u$ , and the lunar cycle amplitude correction,  $f$ .

We removed any trend in the observed sea level data that was contributed by the contemporary rate of global SLR (0.54 mm/year; Vermeer and Rahmstorf 2009). We then subtracted the astronomical component, as calculated above, from these de-trended data. The resulting difference between the observed height and astronomical predictions is caused by the meteorological influence on tidal forcing, including seasonal variations in Mean Sea Level, and the local rate of SLR (relative to global SLR). The combined effect of these components is hereafter referred to as the non-tidal fluctuations in tide height. We modeled non-tidal fluctuations during an approximation of the saltmarsh sparrow breeding season (May 1 through August 31) in a Bayesian hierarchical framework that estimated trends across years as well as within seasons. This framework made it possible to estimate the full posterior distributions for the model's variance parameters. Obtaining the full uncertainty for variance parameters was important because the meteorological component of sea level is stochastic; therefore projections are based on statistical descriptions of the normal range of variation and the central tendency. We accounted for this variation explicitly by propagating it in the population simulations described below.

We modeled the baseline non-tidal fluctuation from 1979-2011 as a linear equation (see SI for model code; intercept is “S”, slope is “beta\_year”) with normally-distributed yearly variation (standard deviation of yearly variation is “sd\_year”). We accounted for any within-season trends in Mean Sea Level from the year-specific baseline described above, “**alpha**”, with year-specific trend coefficients, “**beta**”. These trend coefficients were normally distributed around a common mean, “beta\_mu”, with standard deviation “sd\_slope”. Residual variation in non-tidal fluctuations was normally distributed with standard deviation “sd”. Autocorrelation function plots of high tide heights suggested autocorrelation at lag one, so we included a first-order autoregressive component, “gamma”. Katz and Brown (1992) suggest that trends in the variance of climate variables are often more important than trends in the mean. In the context of the tide height, a trend in the variance of non-tidal fluctuations would result in an increasing frequency of tides capable of causing nest failure, even with no change in the mean. We did not *a priori* expect trends in the variance, and we detected no strong trend over time in the variance parameter, sd, which was close to zero (mean: 0.00039; credible interval: -0.0012 – 0.0020). We checked that this model produced reasonable predictions by estimating the 95% posterior prediction intervals from the model fit using only data from 1979-2011, and adding the astronomical components to these estimates to get predictions for tide height above Mean Sea Level. These predictions were then compared to observed high tide heights in 2012, 2013, and 2014.

#### *Sea-level rise and accretion*

The influence of SLR on saltmarsh sparrow nest success could potentially be offset by the vertical accretion of the marsh surface, depending on the rate of accretion. We estimated the



median accretion rate, while accounting for uncertainty, from published studies within the same region as our demographic plots in coastal Connecticut, USA (median estimate: 3.3 mm/year, standard error: 0.19; Harrison and Bloom 1977; Orson et al. 1987; Warren and Niering 1993; Anisfeld et al. 1999; Anisfeld and Hill 2012). In our population projections, we assumed that accretion rate will stay constant into the future. This is likely to be a reasonable scenario, if slightly conservative, as 1) both accretion rates and the contribution from inorganic matter are declining in southern New England (Carey et al. 2015), presumably as a result of declining sediment supplies (Weston 2013); 2) the sample of accretion rates used to estimate the median is biased toward lower elevation marsh, which has higher accretion rates than the higher elevation marsh (Redfield 1972; FitzGerald et al. 2008) that supports the majority of saltmarsh sparrows nests (Greenlaw and Rising 1994; Gjerdrum et al. 2008); and 3) there is increasing evidence from southern New England that accretion in higher elevation marsh is not keeping pace with the current rate of SLR (Warren and Niering 1993; Donnelly and Bertness 2001; Field et al. 2016a).

We used the highest and lowest global SLR projections (A1F1 and B1) from Vermeer and Rahmstorf (2009). A1F1 and B1 are emissions scenarios used by the Intergovernmental Panel on Climate Change that represent intensive fossil-fuel use/rapid economic growth and a high level of environmental consciousness/sustainable development, respectively (IPCC 2014). Our population simulations assume that the difference between local and global SLR observed from 1979-2011 remains constant into the future. This also is likely to be conservative, as our study area is expected to experience SLR rates above the global mean (Yin et al. 2009; Sallenger et al. 2012).

#### *Demographic parameters*

Between 2002 and 2009, we collected data on saltmarsh sparrow nest success at 119 1-ha plots that were widely distributed across coastal Connecticut (Gjerdrum et al. 2008; Meiman et al. 2012; Elphick et al. 2015). In 2010, we monitored sparrow nest success at five larger plots (between three and 23 ha) using the same protocol as these previous studies (locations for all plots are shown in Fig. S1). We conducted systematic nest searches at regular intervals throughout the nesting period. We visited nests and recorded their contents approximately every three days until they fledged or failed. We used a Bayesian logistic regression model to estimate the survival probability of individual eggs or nestlings through diurnal high tides, as recorded in the sea level data described above. Visits to monitor nests took place three days apart, and occasionally longer when visits were not possible because of weather or other logistical constraints. To obtain survival probabilities at a finer scale, we indexed the model so that the survival probability between visits (which is what we observed) was the product of the probabilities of surviving each high tide that occurred between visits (which are unobserved latent variables; code is provided in SI). This approach made it possible to obtain the probability of each chick or egg surviving a single high tide. To account for the potential non-independence of eggs or nestlings from the same nest, we included a nest-level, normally-distributed random effect. This random effect also accounted for any differences in survival probability among nests that would be caused by small variations in the height of nests off the ground. We excluded from the analysis any nests that had visits longer than six days apart because the fate of eggs and nestlings from these nests could not be determined with confidence. For nests included in the analysis, we determined fate at each visit using evidence for flooding or depredation according to a standardized protocol (SI Appendix 1) that allowed for uncertain nest assignments, which were recorded as NA and explicitly incorporated as missing data in the nest survival model (see code

in SI). We used 674 nests in the analysis. Once the influence of tide height was accounted for, we did not find strong evidence for a residual trend in daily nest success over the time period covered by our dataset (mean of trend coefficient: 0.057; 95% credible interval: -0.016 – 0.135). Accordingly, this variable was not retained in the model used for predictions.

We used estimates of annual survival for females from Field et al. (2016a): the value for a typical site was 0.44 (0.37 – 0.52), and the (logit transformed) standard deviation of variation across sites was 0.61 (0.56 – 0.67). Reproductive parameters other than nest survival are from Field et al. (2016a) and Ruskin (2015), and are described in Figs. 1 and 3.

We lack data on how demographic parameters would change with population sizes much larger than the current size, so we took a conservative approach in which the population was considered density independent unless it increased to three times the starting size. Beyond this point, baseline nest success probability was gradually reduced according to a logistic curve that increased as population size increased beyond the three times threshold (this curve is shown in Fig. 1 and the code is available at <https://github.com/chrisf22/saltmarsh-sparrow-IBM>).

We fit models for local sea-level trend and nest survival probability using JAGS (version 3.2.0, Plummer 2003) in R with the R2jags package (Su and Yajima 2012). We used uninformative distributions for all priors (specified in the model code in the SI). We ran three chains for 100,000 iterations after a 25,000-iteration burn-in; the potential scale reduction factors (Brooks and Gelman 1998) for all parameters were less than 1.01.

### *Population simulation*

Our general approach was to create a population simulation with as much realism as possible, with limits to complexity being driven by data limitations instead of modeling considerations.

This realism made it possible to capture the way in which the timing of extreme high tides affects population trajectories. We created an individual-based simulation that tracks the fate of each female in the population and any female offspring they produce. We modeled only females because they are critical to the demography of saltmarsh sparrows, which have a sex ratio that is heavily skewed toward males (Hill et al. 2013). The core of this simulation follows the nesting attempts of females over a 123-day breeding season (May 1 through August 31), after which estimates of annual survival determine how many individuals will breed the following year (i.e., we assume no non-breeding adults). Nest survival probability was based on the predicted height of peak tides from above and the relationship between nest survival and tide height. A conceptual model of the population simulation is shown in Fig. 2 and the full list of reproductive parameters is given in Figs. 1 and 2. In each year of the simulation, the Mean Sea Level component of tide height was increased by the rate of SLR minus the rate of accretion.

We propagated uncertainty from both parameter estimation and demographic/environmental stochasticity throughout the model. First, we drew values for the demographic and non-tidal fluctuation parameters from their posterior distributions. Using this set of parameters, we simulated the heights of non-tidal fluctuations and the population over 80 years, beginning in 2014. We repeated this process for 1000 draws of the parameters to obtain 1000 replicate populations. We calculated the 5th and 95th percentiles of these replicate populations to quantify the variation in population size that arises from parameter uncertainty and demographic/environmental stochasticity.

We used a starting population of 1500 females, approximately one-third of the estimated total population size in our study region (Wiest et al. 2016), to account for the skewed sex ratio. R code for the population simulations is available at <https://github.com/chrisf22/saltmarsh->

[sparrow-IBM](#). We ran population simulations for the sea-level scenarios with greatest and least acceleration, A1F1 and B1. In addition to population size, we calculated, for each iteration of the simulation, which years had at least one 23-day window without a high tide that would cause failure for greater than 95% of eggs and nestlings. This threshold (1.05 m above Mean Sea Level, as estimated by the nest survival model described above) represents the point beyond which reproduction would be essentially impossible. We also ran simulations for each SLR scenario in which we ordered each year's predicted tide heights from lowest to highest, beginning at the start of the season. Changing only the order of tides isolates the influence of the cyclical timing of spring and extreme tides on nest failure, because the product of the daily nest survival probabilities in a given season remains constant, but the cyclical nature of tide height is removed. Ordering tides from lowest to highest creates the greatest potential for a suitable breeding window, thereby ensuring a best case scenario. We compared these results to those initially obtained to quantify the influence of the cyclical nature of tide height on extinction risk.

We quantified the magnitude of potential non-linear shifts in fecundity by estimating the deviation of the full population simulation from linear extrapolations of fecundity: First, for each model iteration, we fit a regression equation of linear change in fecundity (females/female) over time using the initial 25 years of fecundity projections from the population simulations. 25 years was long enough to estimate a trend, but short enough to avoid including any threshold responses to sea level (see Fig. 4). We used the coefficients from these linear equations to estimate the date when reproduction would stop (i.e., the first year in which fecundity equals zero), assuming that fecundity continues to decline linearly. For each model iteration, we then calculated the difference between this prediction and the first year without reproduction as estimated from the full population simulations.

## Results

### *Non-tidal fluctuations and nest survival modeling*

We found strong evidence for an overall increase in the height of non-tidal fluctuations (above astronomical predictions) from 1979-2011 (beta\_year: 0.45 cm/year; 95% credible interval: 0.36 – 0.54; Table S2) with considerable annual variation (sd\_year: 2.1; 1.5 – 2.9). The height of non-tidal fluctuations increased between May and August (beta\_mu: 0.063 cm/day; 0.057 – 0.069), but there was not much variation in the magnitude of this trend among years (sd\_slope: 0.0049; 0.00042 – 0.011). As expected, there was a strong first-order correlation between successive high tides (gamma: 19; 18 – 19). The normally-distributed variation in non-tidal fluctuations over the course of a season had narrow credible intervals (sd: 6.1 cm, 6.0 – 6.2). Observed high tides in 2012-2014 fell within the 95% posterior prediction intervals 97% of the time (Fig. 3), indicating that our model is able to predict future tide heights accurately.

We found a very strong negative effect of tide height on the survival probability of nest contents (-3.9 on a logit scale; -4.2 – -3.6; Fig. 1). The standard deviation of the nest-level random effect was 1.8 (1.6 – 2.0), suggesting considerable variation in survival probability among nests.

### *Population simulations*

Our models predict a steep drop in the likelihood of 23-day windows without reproduction-stopping high tides: the proportion of model iterations, in each year, that had at least one such window dropped from 95% to less than 5% within the span of 13 years for the A1F1 scenario and 14 years for B1 (Fig. 4). Within each simulated population trajectory, the time for this

window to permanently close (the number of years between the first year without at least one window and the last year that had at least one window) was never more than 16 years, and for both SLR scenarios, the mode was an immediate threshold (zero years; Fig. 4). In our simulations, fecundity dropped to zero sooner than the predictions of a linear model of fecundity 91% of the time for both SLR scenarios, and this deviation from the initial linear trend was could be on the order of decades (Fig. 6).

Despite the large variation and a mean increase in population size among simulation iterations for the first 20 years, all iterations converged to extinction within a relatively narrow range of dates (Fig. 5), with no simulated populations persisting beyond 2064. The date range for quartiles was particularly narrow (Fig. 5). For both SLR scenarios, the majority of model iterations had a positive initial population trajectory (A1F1: 77%, B1: 75%), but none had positive growth after 2030 (Fig. 5). Uncertainty grew in the first 10 years, but then declined rapidly, suggesting that the initial population trajectory had little influence on extinction estimates (Fig. 6).

SLR scenario had very little influence on median time to extinction (1 year difference) or population trajectory (Fig. 5). For A1F1, the scenario with the higher rate of SLR, mean time to extinction was 30 years from 2014 (upper 5th and lower 95th percentiles: 18, 42; median: 31).

All simulated populations went extinct within 5 years after the first year without a 23-day window. The year in which the populations dropped below 100 individuals always occurred on or before the last 23-day window, suggesting a clear threshold beyond which there is less than a 5% probability of persistence: A1F1: 2057, B1: 2058. Ordering the high tides in each year increased the mean time to extinction by 11 years for A1F1 (Fig. 6), and 12 years for B1.

## Discussion

We found that cyclical astronomical processes have the potential to interact with SLR, via tide heights, to create a threshold beyond which saltmarsh sparrow reproduction is impossible. Evidence for this threshold includes a steep drop in the presence of suitable breeding windows, non-linear and rapid shifts in fecundity, and a narrow range of estimated extinction dates, in spite of significant variation in population trajectory before the threshold is reached. Moreover, the order of tide heights had a larger influence on estimated extinction date than emission scenario, further demonstrating the value of the high temporal resolution of our population models for elucidating important population dynamics.

The potential for this threshold creates a serious conservation challenge as major population changes could happen over timescales of only a few years, which is likely not enough time to implement effective conservation strategies, especially under realistic funding scenarios. An additional challenge for conservation planning is that saltmarsh sparrow populations may increase in the short term, but population size may not be a useful measure of extinction risk given the possibility for non-linear population responses. Population size and trend, however, are commonly used in species risk assessments such as the International Union for the Conservation of Nature Red List and the U.S. Endangered Species Act.

The pervasiveness and ubiquity of SLR-related change in coastal areas suggests potential for SLR-induced thresholds across a wide range of coastal taxa, especially for species that rely on intertidal areas for reproduction (e.g. Seavey et al. 2011; Thorne et al. 2012). Our simulations suggest a very low probability of persistence beyond 2060 for the LIS population of saltmarsh sparrows. Given that the species' global population breeds only in tidal marshes and that rates of SLR are similar throughout the species range, we do not expect other regions to have



substantially different extinction risks, or for there to be many refugia from SLR. The narrow range for time to extinction in each scenario (despite the large variation in population sizes in the first years of the simulations) and the large influence of a reproduction threshold suggest that extinction estimates are unlikely to be sensitive to limitations in our understanding of current population size or density dependence.

Two factors that could reduce extinction risk, but that were not incorporated into our simulations, are adaptation and/or tidal marsh transgression into the upland (Gedan et al. 2011). We lack data on the potential for adaptation, which could take the form of selection for increased nest height or choice of higher elevation marsh plants as nesting substrate. Current evidence suggests, however, that there is little existing variation in these nesting traits (see Greenlaw and Rising 1994; Humphreys et al. 2007; Gjerdrum et al. 2008), which would limit the potential for evolutionary change over such a short time span. The potential for marsh transgression in LIS also appears to be low over the decadal timescales relevant here due to the steep slope at the marsh-to-upland boundary and competition from resilient coastal forest (Field et al. 2016a) and human infrastructure (Gittman et al. 2015).

While our models predict a high probability of extinction within 30 years, these estimates could be optimistic: SLR in LIS is predicted to be higher than the global average used in our population simulations (Yin et al. 2009; Sallenger et al. 2012), and our projections do not account for habitat loss – in particular a shift from high-elevation to low-elevation marsh plants – as a result of increased inundation. This habitat shift appears to be happening already (Warren and Niering 1993; Donnelly and Bertness 2001; Field et al. 2016a).

The phenomenon of ecological changes being driven by an increasing trend in maximum tide height during one part of the year, rather than the comparatively smaller trend in annual

Mean Sea Level, has been demonstrated in other systems (Van De Pol 2010; Wasson et al. 2013). This phenomenon reinforces the importance of incorporating changes in sea level variance, as well as mechanistic models of the biotic responses to climate change. The increasing trend we observed in the tide gauge data is likely being driven primarily by high rates of local SLR and tidal forcing from wind (O'Donnell 2010; O'Donnell 2016).

By focusing on a geographic area with rich data for both abiotic climate-driven variables and ecological processes, we were able to obtain narrow credible/prediction intervals for key parameters and model the potential behavior of this system with a high level of precision. By projecting tide height into the future and incorporating the relationship between tide height and nest survival into our models, we avoided the assumption that vital rates will stay constant, a common criticism of population viability analysis (Coulson et al. 2001). Projecting the present-day estimates of vital rates would have resulted in positive initial population trajectories for the majority of model iterations, severely underestimating extinction risk. Our analysis does assume that the relationship between tide height and nest survival probability remains the same. In the absence of rapid evolution or increased plasticity, however, we consider this assumption to be reasonable, as we were able to quantify the mechanistic relationship between tide height and nest survival across the full range of nest survival probabilities, from 0% to 100%.

Our study demonstrates the utility of study systems that allow for high precision predictions for providing insight into what level of detail is necessary for developing models that contain enough realism to inform conservation strategies and policy. Better understanding and identifying the potential for thresholds will be critical for developing these strategies because 1) rapid thresholds are, by their nature, hard to manage for (Lindegren et al. 2012), and 2) biological thresholds in response to climate change have now been shown in agricultural systems

(Schlenker and Roberts 2009), terrestrial systems (Chen et al. 2015), and marine systems (Monaco and Helmuth 2011), suggesting that they might be more common than previously assumed. More research on the potential for thresholds and non-linear responses is needed in coastal areas worldwide, where the transition from terrestrial to marine ecosystems will have largely unknown effects on the physical (Cooper and Pilkey 2004) and biological (Field et al. 2016a) drivers of ecosystem change over the next century.

## Figures and tables

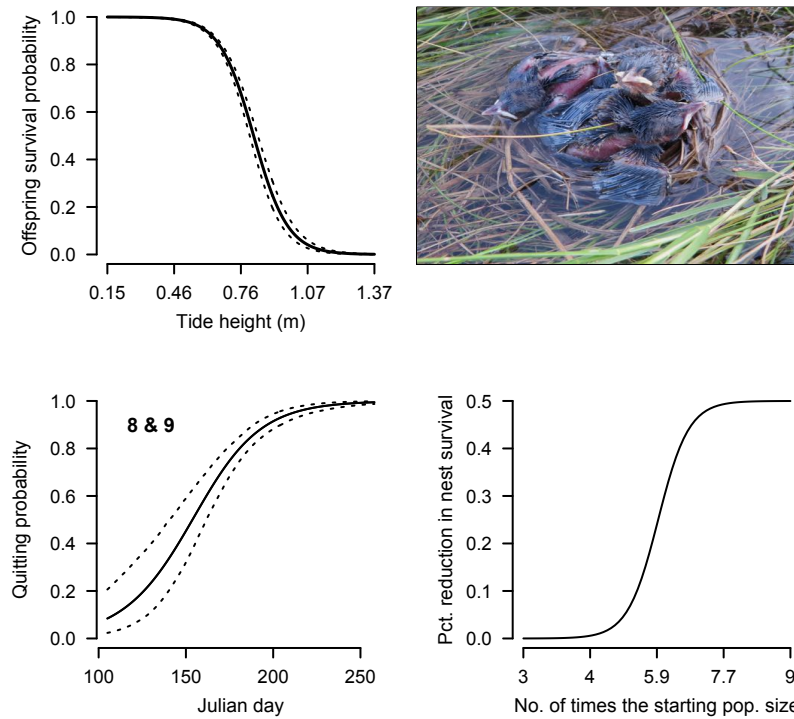


Fig. 1. Demographic parameters used for saltmarsh sparrow population simulations. Dotted lines show the 95% credible intervals. Top left: Offspring survival probability through a high tide is influenced by tide height (above Mean Sea Level;  $n = 674$  nests). Bottom left: Probability of ending nesting attempts for the season (“quitting”) after a failed or successful nest is influenced by days since January 1 (from Field et al. 2016b). The numbers 8 and 9 in the axis label refer to the conceptual model shown in Fig. 2. Top right: Picture of a high tide flooding a nest, the main cause of nestling mortality. Bottom right: In our simulations, we assumed no density dependence until the population size reaches three times the starting population and that it then increases according to a logistic curve to a maximum of a 50% reduction in daily nest survival.

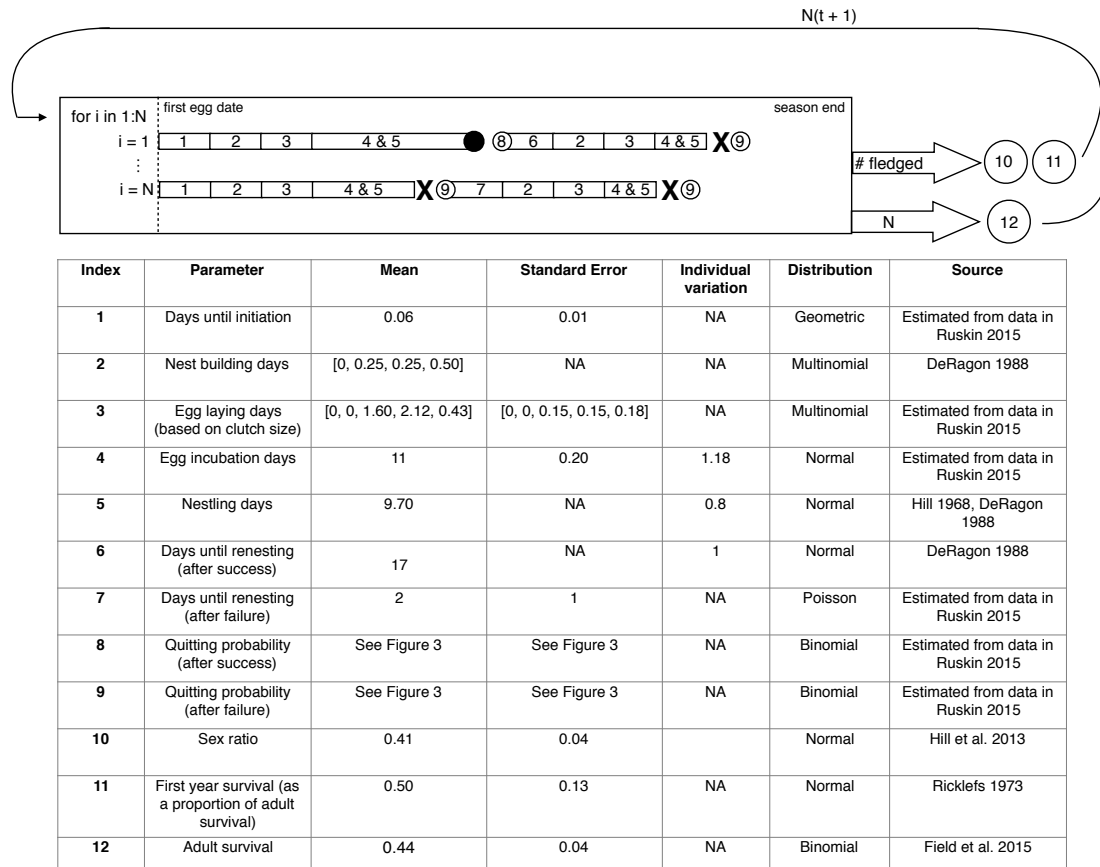


Fig. 2. Conceptual diagram of the simulation used to project population viability in saltmarsh sparrows. The fates of each female's nesting attempts are simulated over a 123-day breeding season (May 1 through August 31) and the resulting reproductive output combined with survival estimates to determine the female population size ( $N$ ) at time  $t+1$ . Numbers link parameters listed in the first column of the table to those in the diagram, which represents alternative sequences of nest fates for  $N$  females. Each female's sequence is broken down into potential reproductive stages as the breeding season progresses; two hypothetical sequences are shown. Solid black circles represent nests that produce fledglings and black Xs represent failed nests, which occur when all of the eggs or nestlings die. Daily nest failure probabilities (see Figure 3) start affecting nest attempts during egg laying (3). In the table, the mean column refers to the

mean estimate for a given parameter; multiple values are given when the parameter is based on multinomial probabilities. The standard error column refers to estimation uncertainty, which is incorporated whenever parameters were estimated from our dataset or uncertainty was reported in the source study. The individual variation column refers to the standard deviation for each parameter observed across individuals. The distribution column gives the statistical distributions used to represent estimation uncertainty and/or individual variation for each parameter. For distributions that do not have separate variance terms (i.e. Poisson, multinomial, or binomial), individual variation is assumed to be the sampling variation of that distribution. R code for the population simulation is available at <https://github.com/chrisf22/saltmarsh-sparrow-IBM>.

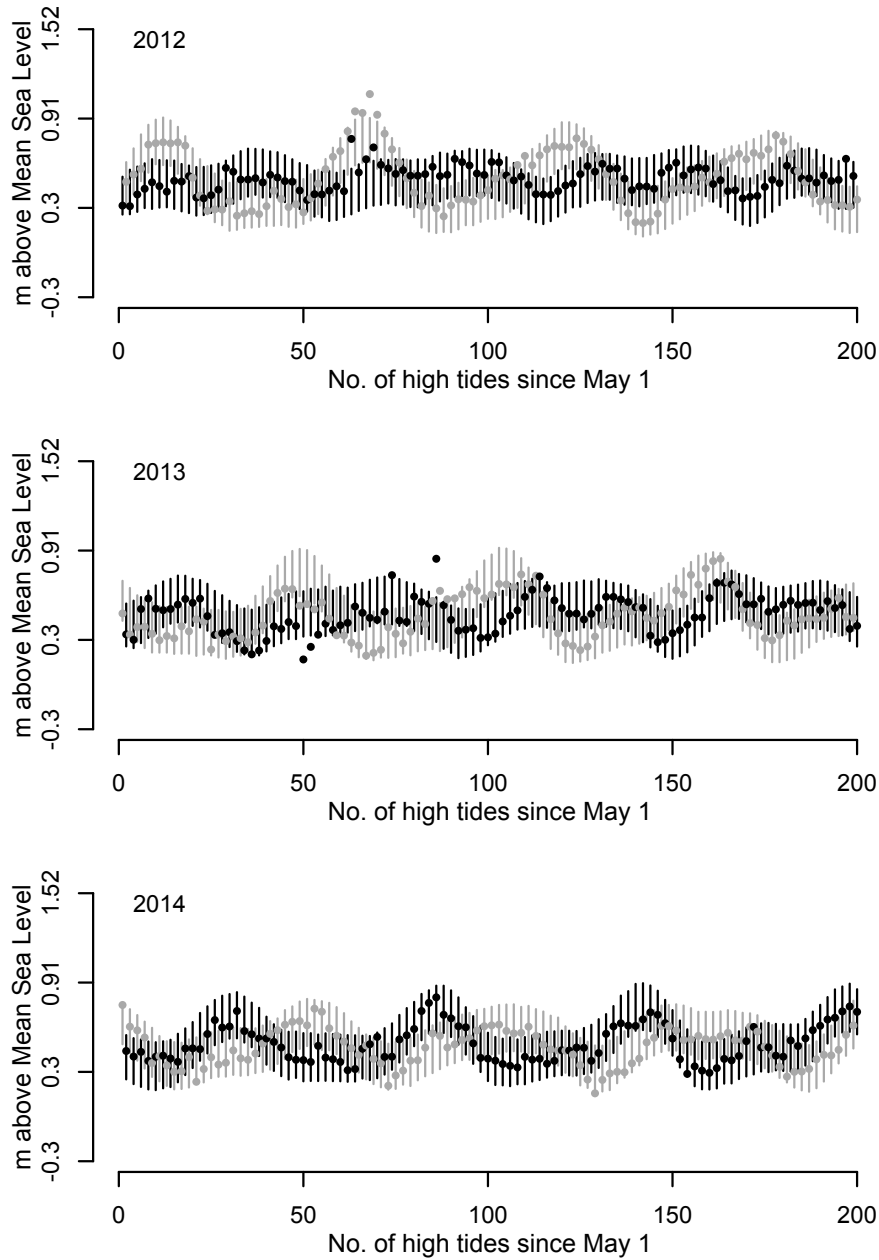


Fig. 3. 95% posterior prediction intervals (black and gray bars) from the local sea-level trend model compared to the observed tide heights (dots) in 2012 (top), 2013 (middle), and 2014 (bottom). We alternated colors to enable visualizing how our predictions capture the differences in height between successive high tides (known as the diurnal inequality). Only 2% of observed tides lie outside the predicted ranges.

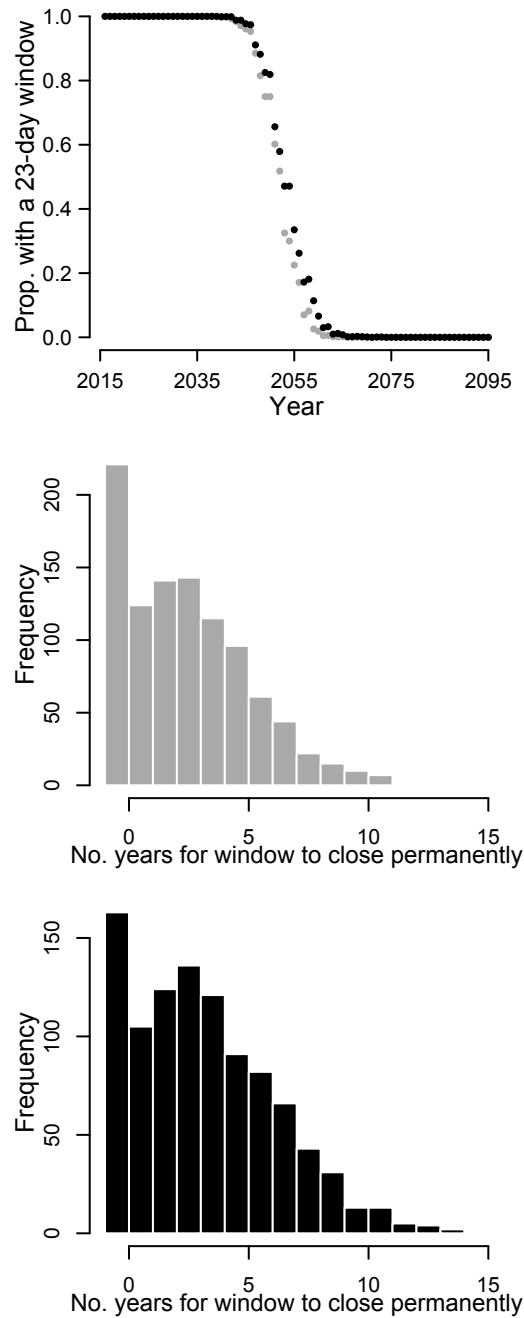


Fig. 4. Top panel: The proportion of iterations that have at least one 23-day window without a tide that would cause failure for at least 95% of eggs and nestlings. Black dots are the B1 scenario and gray dots are the A1F1 scenario. Middle and Bottom panels: Histograms, for 1000



model iterations, of the number of years between the first year without at least one 23-day window and the last year with at least one 23-day window (gray is the A1F1 scenario; black is the B1 scenario).

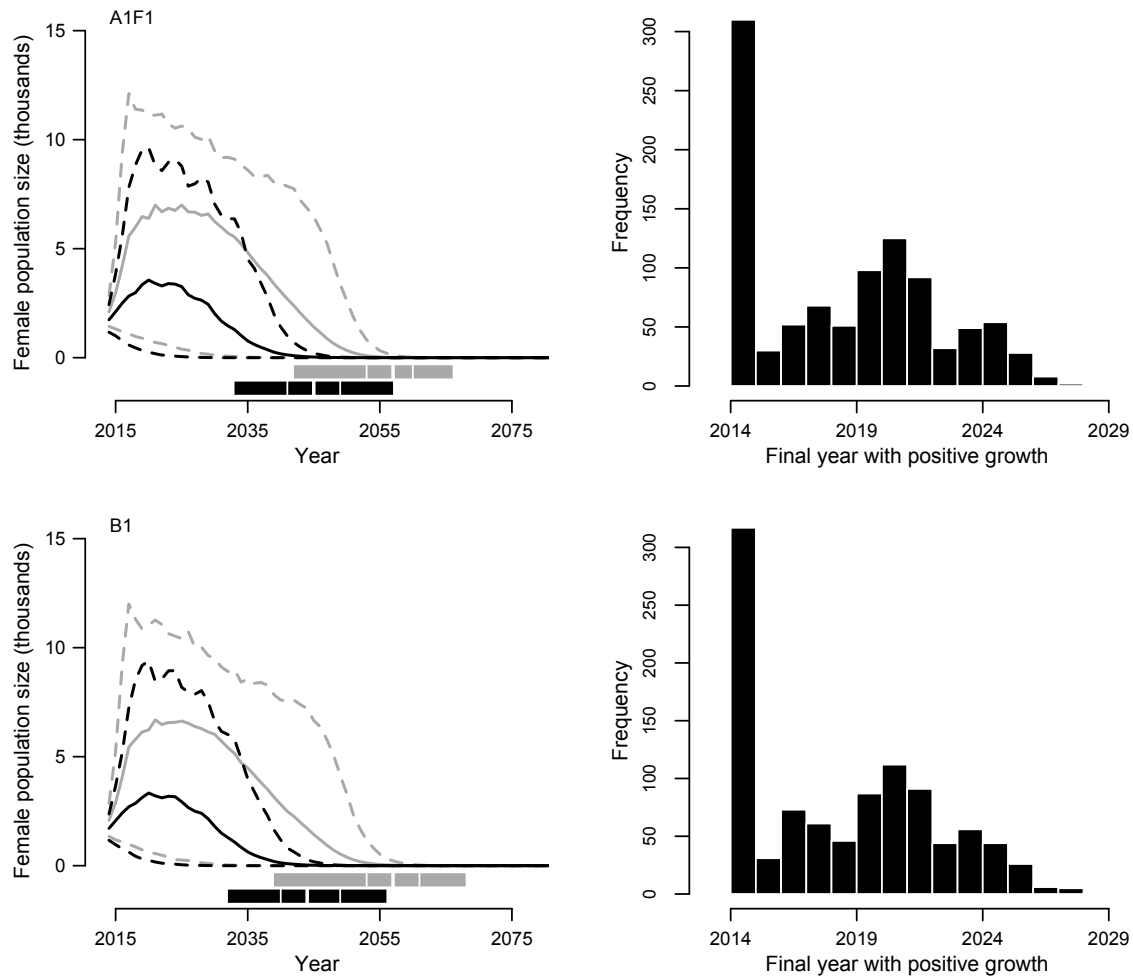


Fig. 5. Left panels: Projected population sizes over time for the A1F1 (top; black lines) and B1 (bottom; black lines) SLR scenarios, with the 5th and 95th percentiles (dotted lines). The same SLR scenario, but with tides ordered so that the highest tides occur consecutively at the end of the season to represent a best case (yet unrealistic) scenario, is shown in gray. Horizontal bars at bottom of these graphs are the 5th to 95th percentiles of extinction date; breaks in the bar show the median and quartiles. The right panels show, for each model iteration, the final year of positive population growth rate for the A1F1 (top) and B1 (bottom) scenarios. The first bar (2014) is the frequency of model iterations that never had positive growth rates.

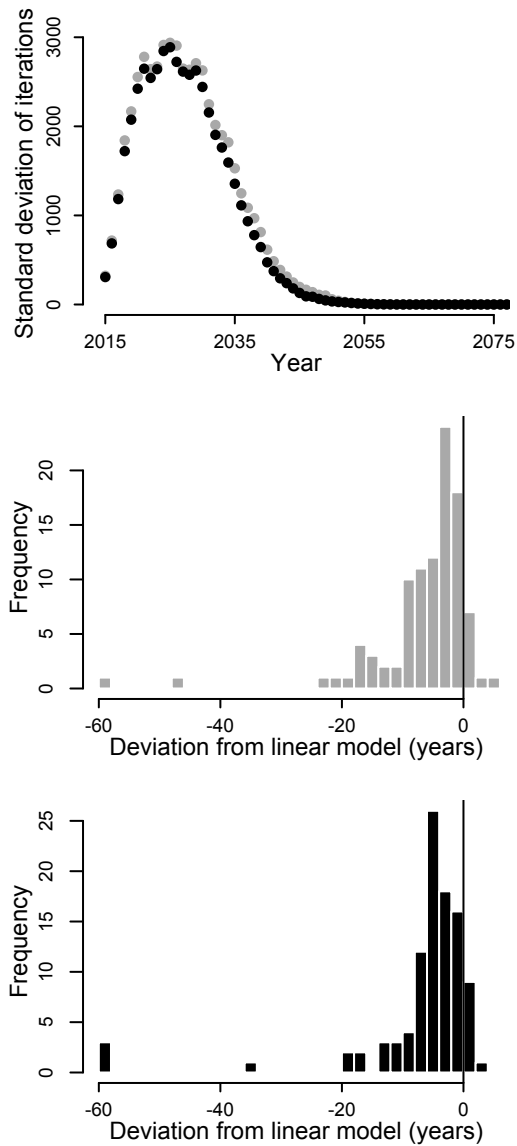


Figure 6. Top panel: The standard deviation, across model iterations, of the predicted population sizes in each year; shown for the A1F1 (gray) and B1 (black) SLR scenarios. Middle and bottom panels: Visualizations of the effect of non-linear responses of saltmarsh sparrow fecundity to sea level on extinction risk. We estimated the potential linear response by fitting a model to the first 25 years of the fecundity projections (females/female) from the population simulation. We used the coefficients of this linear trend to estimate the date when reproduction stops (the first year in which fecundity equals zero), assuming the change in fecundity continues to be linear. We then,

for each model iteration, calculated the difference between that prediction and when the population simulations estimate that reproduction stops; shown for A1F1 (gray) and B1 (black) scenarios. A vertical line at zero is shown for reference.

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## Supplementary Information

JAGS code for hierarchical model:

```
#for 33 years
for(i in 1:33){
  #the baseline varies stochastically around the mean (int_mu), which varies according to
  a linear equation with a parameter for trend over time (beta_year)
  alpha[i] ~ dnorm(int_mu[i], tau_year)
  int_mu[i] <- S + beta_year*i
  #the trend over the saltmarsh sparrow breeding season for a given year (beta[i]) varies
  stochastically around the mean (beta_mu)
  beta[i] ~ dnorm(beta_mu, tau_slope)
}

#priors
#first-order autoregressive parameter
gamma ~ dnorm(0, 0.0001)
#intercept for baseline (year = 0)
S ~ dnorm(0, 0.0001)
#trend in baseline over time
beta_year ~ dnorm(0, 0.001)
#mean trend in over saltmarsh sparrow breeding season
beta_mu ~ dnorm(0, 0.0001)
#variance parameter for height at high tide
sd ~ dunif(0, 100)
tau <- 1/(sd*sd)
#variance parameter for beta[]
sd_slope ~ dunif(0, 100)
tau_slope <- 1/(sd_slope*sd_slope)
#variance parameter for alpha[]
sd_year ~ dunif(0, 100)
tau_year <- 1/(sd_year*sd_year)

#for 33 years
for(y in 1:33){
  #for the length of the saltmarsh sparrow breeding season (in number of high tides)
  #the first high tide is separated to accommodate the first-order autoregressive component
  for(i in 1:length(storm_surge[,y])){
    # height at high tide i
    storm_surge[i, y] ~ dnorm(theta[i, y], tau)
    #mean at the beginning of the saltmarsh sparrow breeding season
    mu[i, y] <- alpha[y]+ beta[y]*(hightidenumber[i, y]-1)
  }
  theta[1, y] <- mu[1, y]
  for(e in 2:length(storm_surge[,y])){
```

```

#starting from the second high tide of the season, is influenced by an autoregressive
term and the previous high tide
theta[e, y] <- mu[e, y] + gamma*(storm_surge[e-1, y] - mu[e-1, y])
}
}

```

JAGS code for the influence of tide height on egg/nestling survival:

```

#priors
#intercept of offspring survival through tide
S ~ dnorm(0, 0.001)
#effect of tide height on offspring survival
slope ~ dnorm(0, 0.001)
#variance parameter for random nest effect
sd ~ dunif(0, 1000)
tau <- 1/(sd*sd)

#random nest effect to account for within-nest autocorrelation
for(e in 1:674){
  Nest[e] ~ dnorm(0, tau)
}

#for each visit to a nest
for(i in 1:length(survival_matrix[,1])){
  #for each day between visits, up to 12 days
  for(t in 1:12){
    logit(p[i, t]) <- S + Nest[nestID[i]] + slope*tide_height[i, t]
  }
  q[i] <- (p[i, 1]+((1-p[i,1])*index4BUGS[i, 1]))*(p[i, 2]+((1-p[i,2])*index4BUGS[i, 2]))*(p[i, 3]+((1-
  p[i,3])*index4BUGS[i, 3]))*(p[i, 4]+((1-p[i,4])*index4BUGS[i, 4]))*(p[i, 5]+((1-
  p[i,5])*index4BUGS[i, 5]))*(p[i, 6]+((1-p[i,6])*index4BUGS[i, 6]))*(p[i, 7]+((1-
  p[i,7])*index4BUGS[i, 7]))*(p[i, 8]+((1-p[i,8])*index4BUGS[i, 8]))*(p[i, 9]+((1-
  p[i,9])*index4BUGS[i, 9]))*(p[i, 10]+((1-p[i,10])*index4BUGS[i, 10]))*(p[i, 11]+((1-
  p[i,11])*index4BUGS[i, 11]))*(p[i, 12]+((1-p[i,12])*index4BUGS[i, 12]))
  survival_matrix[i, 2] ~ dbin(q[i], survival_matrix[i, 1])
}
}

```



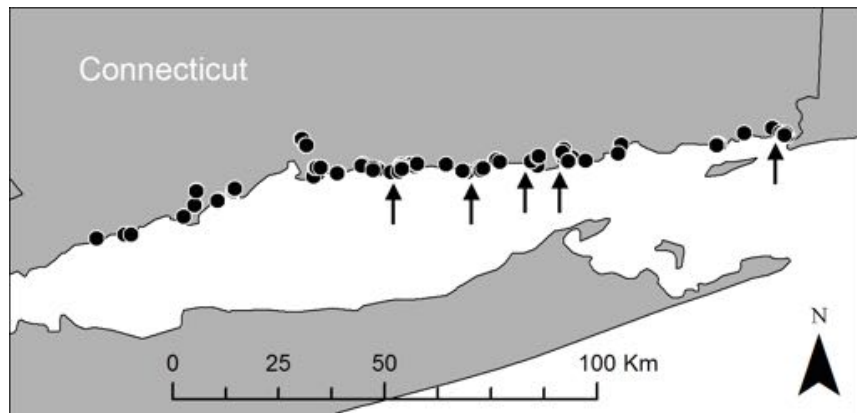


Fig. S1. The distribution of 119 demographic plots (dots) surveyed between 2002 and 2010. Plots from 2010, shown with arrows, were larger (ranging from three to 23 ha), but were surveyed using the same protocols.

Table S1. Harmonic constituents for the New London, CT, USA tide station

(<http://tidesandcurrents.noaa.gov>).

<b>Name</b>	<b>Amplitude (ft)</b>	<b>Phase (degrees)</b>	<b>Speed (degrees/hr)</b>
M2	1.22	58.3	28.9841042
S2	0.223	69.9	30
N2	0.285	34.6	28.4397295
K1	0.244	178.5	15.0410686
M4	0.085	343.7	57.9682084
O1	0.174	209	13.9430356
M6	0.039	206.1	86.9523127
MK3	0.017	28.9	44.0251729
S4	0.012	344.1	60
MN4	0.046	313.3	57.4238337
NU2	0.056	44.8	28.5125831
S6	0	0	90
MU2	0.045	347.7	27.9682084
2N2	0.041	13.4	27.8953548
OO1	0.011	209.8	16.1391017
LAM2	0.022	145.5	15
S1	0.019	215.6	15.5854433
MM	0	0	0.5443747
SSA	0.059	69.4	0.0821373
SA	0.181	135.3	0.0410686
MSF	0	0	1.0158958
MF	0	0	1.0980331
RHO	0.006	222	13.4715145
Q1	0.05	193.4	13.3986609
T2	0.022	52.4	29.9589333
R2	0.002	70.4	30.0410667
2Q1	0.01	233.8	12.8542862
P1	0.074	189.8	14.9589314
2SM2	0	0	31.0158958
M3	0.012	66.4	43.4761563
L2	0.036	127.1	29.5284789
K2	0.06	70.8	30.0821373
M8	0	0	115.9364166
MS4	0.012	5.7	58.9841042

Table S2. Posterior means and credible intervals for the non-tidal fluctuation model parameters.

Parameter names reference the model code.

<b>Description</b>	<b>Parameter</b>	<b>Mean (cm)</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>
Intercept	S	-14	-16	-13
Yearly trend	beta_year	0.45	0.36	0.54
Mean of year-specific parameters for within-season trends	beta_mu	0.063	0.057	0.069
Strength of autocorrelation	gamma	19	18	19
Residual variation	sd	6.1	6.0	6.2
Variation of <b>beta</b>	sd_slope	0.0049	0.00042	0.011
Yearly variation	sd_year	2.1	1.5	2.9

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

## 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 habitat transgression across three scales in adjacent coastal forest in southern New England. We found widespread shifts in tidal marsh vegetation toward a greater extent of flood-tolerant species (e.g. a 5.4% annual increase in *Spartina alterniflora*; credible interval: 2.3, 8.5), but no evidence that coastal forest is changing in a compensatory manner (e.g., annual change in canopy extent was 0.00046 ha; credible interval: 0.000045 – 0.00087). We found low mortality and high growth rates for trees at the forest edge, suggesting that transgression is unlikely in the short term. This apparent temporal mismatch in the timing of ecosystem change could have important implications for ecosystem migration, with severe consequences for the conservation of tidal marsh species.

## 1. Introduction

Global shifts in vegetation are expected in response to climate change (Gonzalez *et al.* 2010), but there is considerable uncertainty in 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.* 2013).

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 & 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 & Megonigal 2013; Schile *et al.* 2014). There are three major impediments to marsh transgression: elevation, human-built coastal protection, and biotic interactions with upland ecosystems at the marsh edge.

Better understanding the potential impediments to transgression 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 transgression 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 & 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).

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](http://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 & Niering 1993; Donnelly & 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.

Perhaps even more uncertain is how biotic interactions will influence the rate of marsh transgression, 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 & Midgley 2001). It has been suggested that trees might even 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 transgression process.

Studies that quantify rates of change at the marsh-upland ecotone are few, but are a powerful tool for understanding whether marsh transgression will keep pace with SLR (Smith *et al.* 2013; Wasson *et al.* 2013). Tidal marsh vegetation responds rapidly and predictably to increased inundation (Orson *et al.* 1998; Warren & Niering 1993; Donnelly & 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 transgression. 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. 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 (the distribution of sampling locations for all datasets in this paper is shown in Fig. A1). Marshes included several of the largest in the state, and span a range of land-ownership types. Plots were randomly selected from within these 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. Each 1-ha plot was surveyed by estimating the percent cover of all dominant marsh plants within 1-

m<sup>2</sup> quadrats, the locations for which were chosen by simple random sampling. We excluded from analyses any of the original 1-m<sup>2</sup> 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 covers. For the analyses in the paper, we collapsed the percent cover data into presence (greater than 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<sup>2</sup> 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 2026 quadrats in 2013 and 895 in 2002-2004. We conducted analyses for the four dominant species: *Juncus gerardii* and *Spartina patens*, which dominant higher elevations with *J. gerardii* typically present in the highest and driest areas; *Spartina alterniflora*, which is found in the lower, more frequently flooded areas (Niering & 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 2002-2004 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 a variable for the frequency of occurrence of *J. gerardii* during the original 2002-2004 survey to test whether gains in other species were compensatory with losses in *J. gerardii*. (code is provided in the Appendix).

We examined the potential influence of the 18.6-year lunar cycle (Baart *et al.* 2011) on the change in marsh plant occurrence by comparing the contribution to sea levels of the lunar cycle to the contribution of the general trend in MHW over time. We downloaded 2002-2013 sea level data from the New London, CT, USA tide station (the station most central and closest to most of the vegetation plots) from the National Oceanic and Atmospheric Administration's (NOAA) Tides and Currents web site (<http://tidesandcurrents.noaa.gov>). We calculated the magnitude of the 18.6-year lunar cycle's effect on sea level by calculating the astronomical component of tide with and without *f*, the contribution of the cycle:

$$\text{tide height}_t = \sum_{i=1}^{34} C_{\text{amplitude}_i} * f_{it} * \cos(C_{\text{speed}_i} * t + ((V_{it} - u_{it}) - C_{\text{phase}_i}))$$

where tide height at time *t* depends on the amplitude, phase, and speed (the *C* parameters) of the 34 harmonic constituents, *i*, for the New London tide station. We used the 'oce' package (Kelley *et al.* 2015) for R (R Development Core Team, 2015) to obtain, for each harmonic constituent, the astronomical phase, *V*, the lunar cycle phase modulation, *u*, and the lunar cycle amplitude correction, *f* (Parker 2005). We calculated the difference between astronomical tide with and without the lunar cycle contribution for every high tide during the approximate growing season (May 1 through August 31). We took the mean of each year to determine the contribution of the lunar cycle to MHW. We then subtracted the lunar cycle contribution in each year from the observed MHW over the same time period to get MHW without the influence of the lunar cycle.

## 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 (CLEAR 2016) 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 less than 0.5 m, which was assessed using the Orthorectify tool in ArcGIS (ESRI 2011). In addition to plots that had a georeferencing error of greater than 0.5 m RMSE, we discarded 1) any plots in which development that bisects marsh completely 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. 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 & Field 2014). We randomly placed 68 transects, across all land ownership types, in areas most likely to be experiencing marine transgression: i.e., slopes at the forest-to-marsh boundary that are less than  $3.5^\circ$  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 transect 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). 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, 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 and therefore the marsh edge fell in the part of the transect with coarser sampling (1-m<sup>2</sup> quadrats every 10 m instead of every 1 m; see Elphick & Field 2014), creating uncertainty in the exact distance to the marsh edge of trees from those transects. The 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* greater than 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 ½ 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 (U. S. National Institutes of Health). During training, technicians measured the same cores repeatedly until the correlation between measurements was greater than 0.95.

We created a master chronology using the 20 highest quality cores from each genus. For 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), 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 1994-2013.

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 shown 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 & 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 & Rubin 1992). Code for 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 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 originally had more *J. gerardii*, suggesting that losses in *J. gerardii* were compensatory with increases of species associated with lower elevations (Fig. 1). Back-transformed values for change (calculated using the mean species occurrence observed in 2002-2004) were: *J. gerardii* -16%

per decade (credible interval: -21 – -12); *S. patens* -0.28% per decade (-0.97 – 1.6); *S. alterniflora* 5.4% per decade (2.3 – 8.5); and *D. spicata* 5.1% per decade (3.3 – 7.0).

The magnitude of the increase in sea level over the survey period explained by the 18.6-year lunar cycle (Baart *et al.* 2012) was small (13.5%) relative to the observed increase in MHW (Fig. A3).

### 3.2. Canopy extent from aerial photos

Only nine of the 37 plot-level credible intervals for annual change in forest cover (in hectares) did not overlap zero, and all but one of these showed increases in total forest cover (Fig. 2). The overall mean change over time was positive with narrow credible intervals (4.6 ha/year; credible interval: 0.5 – 8.7; Fig. 2).

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

The estimated interaction effect between diameter at breast height (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). The effect of distance to marsh overlapped zero (0.0086; -0.0026 – 0.0200), suggesting that there was not strong evidence of declining mortality toward the marsh edge. We did not find strong evidence that mortality at targeted-site transects differ from 68 randomly-located transects, as the posterior distribution of the standard deviation for the site random effect was close to zero (Fig. A4). Only 12 of the 85 trees observed less than 1 m from



the marsh edge were dead; all were less than 38 cm DBH. This degree of mortality at the immediate edge of the marsh is within the sampling variation of the Bernoulli distribution predicted by our logistic model, suggesting that there is not strong evidence for an abrupt increase in mortality at the immediate marsh edge that would not be accounted for by the logistic curve.

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

At both of our focal sites, *Quercus* spp. individuals were growing faster at the marsh edge (within 1 m of marsh plants) than farther into the forest (Fig. 4a; 95% credible intervals for edge and interior individuals do not overlap). *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 transgression. We observed large declines in the occurrence of *J. gerardii*, an

indicator of the direct areas of marsh, and widespread increases in *S. alterniflora*, a flood-tolerant species, over just 11 years. This result extends the geographic scope of inferences from Warren and Niering (1993), Donnelly and Bertness (2001), and Smith (2014), elucidating a regional pattern of vegetation shifts toward a greater extent of flood-tolerant species. We did not measure SLR directly at our study sites, but there has been a strongly increasing trend in MHW in our study area during the growing season, likely driven by locally high SLR and changes to meteorological forcing (J. O'Donnell unpublished data). As a result of this trend, tidal marshes are likely being inundated for longer periods of time than the change 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 MHW 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 largely 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 and low elevation marsh plants (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 (average diameter at breast height  $\sim 10$  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. Smith (2013) found evidence for substantial marsh transgression 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. Regardless of the cause, however, this discrepancy highlights the challenges ahead for southern New England’s tidal marshes.

Our results demonstrate that it is important to start considering marsh and coastal forest ecosystems together to make realistic predictions of future marsh extent. 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). The future extent of tidal marsh ecosystems

globally is likely to depend in large part on the responses of the ecosystems they 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 persistence in the face of future stresses. Additional data on rates of ecosystem change at ecotones would allow for a better understanding of the potential for losses in the extent of graminoid-dominated biomes that are bounded on either side by competition with forests and physiogeographic limits. This phenomenon is already being observed at high elevations and latitudes (e.g. Walker et al. 2006) and coastal areas in other parts of the world, such as at the ecotone of mangroves and tidal marsh (e.g. Saintilan and Williams 1999).

The timing of marsh transgression 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 event. 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 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 the mechanisms by which marsh plants are excluded from the forest understory.

Over timescales relevant to conservation, biotic factors, especially competition, might be dominant in determining the extent of tidal marshes. It is not clear whether transgression can occur rapidly enough to prevent the extinction of tidal marsh endemics, like 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.

## Figures and tables

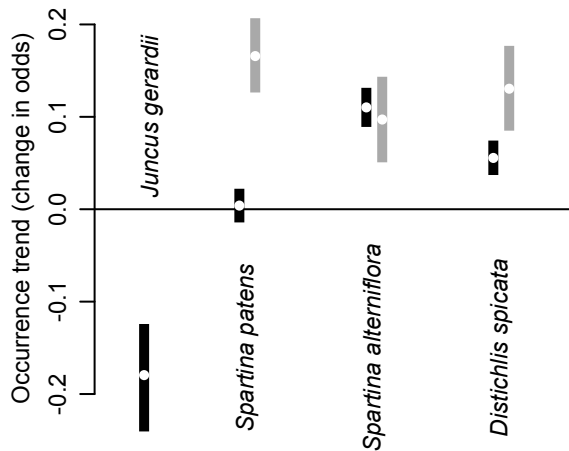


Fig. 1. Parameter estimates for statewide change in occurrence (change in the odds per year) of *J. gerardii*, *S. patens*, *S. alterniflora*, and *D. spicata* between 2002-2004 and 2013. Black bars are 95% credible intervals and the white dots are the means. Gray bars are the parameter estimates for the effect of *J. gerardii* occurrence on the parameter for annual change in frequency of occurrence. If the gray interval is completely above zero, there were greater gains in occurrence in areas that had more *J. gerardii* in 2002 or 2004. Data represented 2921 1-m<sup>2</sup> quadrats from 55 1-ha plots across 12 marsh complexes.

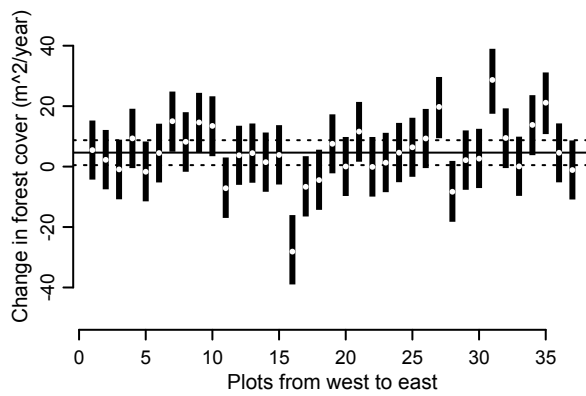


Fig. 2. Change in forest cover ( $\text{m}^2/\text{year}$ ) at 37 plots in Connecticut for 1974-2010, organized from west to east. Black bars are plot-level 95% credible intervals and white dots are the mean estimates. The horizontal solid and dotted lines are the mean and 95% credible intervals of the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

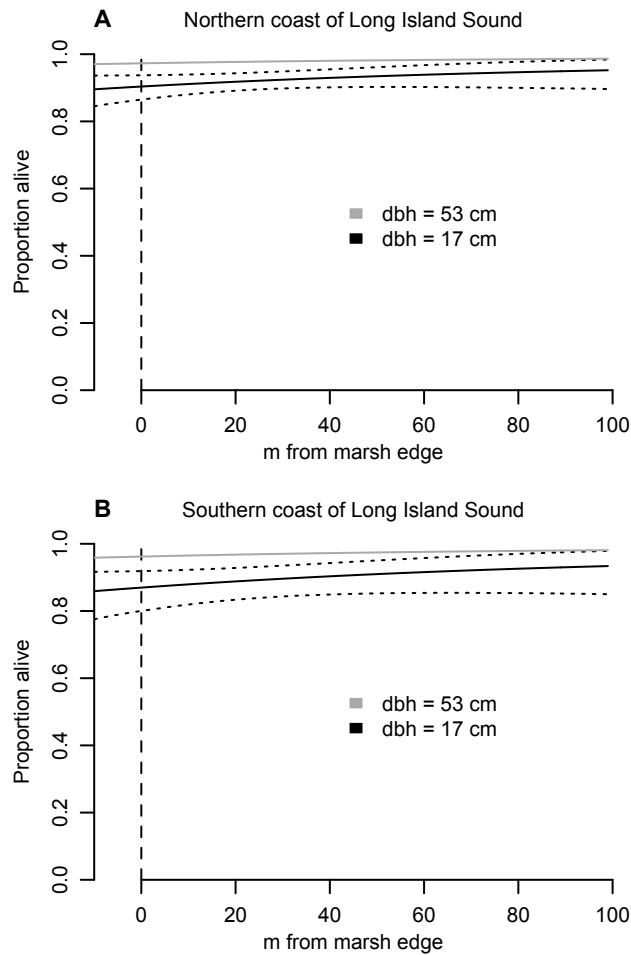


Fig. 3. Recent tree mortality over the first 100 m of the marsh-to-forest boundary on the northern (A) and southern (B) coasts of Long Island Sound (LIS), shown for two sizes: the observed mean DBH (17 cm) and upper 0.95 percentile (53 cm). Dotted lines are 95% credible intervals, which are shown only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



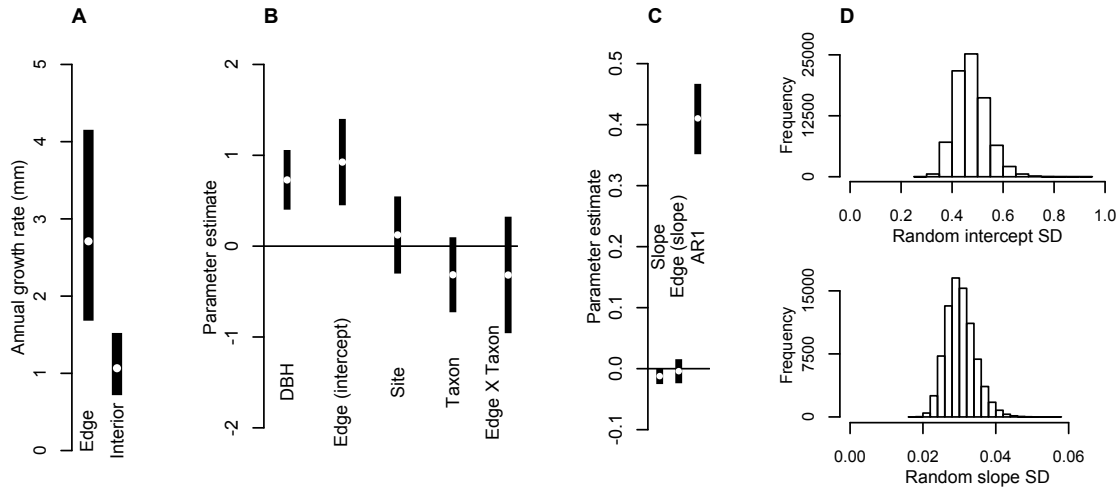


Fig. 4. *Quercus* spp. growth rates from 1993-2013. A) Estimates of mean annual growth at the marsh edge and in the forest interior (estimated from 43 trees). Black bars are 95% credible intervals and white dots are means. B) and C) Effect sizes of the fixed effects (note different scales). D) Posterior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

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## Appendix

The online Appendix contains the decision rules for tracing canopy extent, code for statistical analyses, and supplementary figures (A1-A7).

### *Decision rules for tracing canopy extent*

- Ignore any natural non-marsh areas, rocks, development, or small bodies of water behind the tree line or within coastal forest – i.e. they are treated as part of the forest.
- Natural un-vegetated areas (usually mud flats or salt pannes) surrounded by marsh are treated as part of the marsh.
- If rocks or boulders interrupt the boundary between marsh and forest, trace around their edge to create an uninterrupted forest border.
- When development appears at the edge of coastal forest, but in an area that is not adjacent to marsh, trace so that the new development does not change the total area of coastal forest between time steps.

### *JAGS code*

#### ***Tidal marsh vegetation change***

Code for the model that incorporates just 2002-2004 data is specified in black; the expanded model components for change between survey periods are specified in gray:

```
#priors for the precision parameters of the marsh and plot-level random effects
sd1 ~ dunif(0, 1000)
tau1 <- 1/(sd1*sd1)
sd2 ~ dunif(0, 1000)
tau2 <- 1/(sd2*sd2)
```

```
#intercept for occurrence in 2002
mu ~ dnorm(0, 0.001)
```

```
#intercept for change parameter
change_int ~ dnorm(0, 0.001)
```

```
#effect of J. gerardii extent on change in occurrence  
theta ~ dnorm(0, 0.001)
```

```
#zero inflation parameter (only for J. gerardii model)  
psi ~ dunif(0, 1)
```

```
#marsh-level random effect  
for(i in 1:12){  
  T[i] ~ dnorm(0, tau1)  
}
```

```
#plot-level random effect (log-normally distributed)  
for(i in 1:55){  
  Y[i] ~ dnorm(0, tau2)  
  X[i] <- exp(Y[i])  
}
```

```
#logistic model for 2921 quadrats across 55 plots and 12 marsh complexes
```

```
for(i in 1:2921){  
  logit(p[i]) <- mu + X[plot[i]] + T[marsh[i]] + change[i]*year[i]  
  #change between 2002-04 and 2013 depends on extent of Juncus in 2002-04  
  change[i] <- change_int + theta*Juncus[i]  
  occurrence[i] ~ dbin(p[i], 1)  
  #zero-inflation parameter (only for J. gerardii model): replace p[i] above with q[i]  
  inflate[i] ~ dbern(psi)  
  q[i] <- p[i]*inflate[plot[i]]  
}
```

### ***Canopy change from aerial photos***

```
#priors for the precision parameters  
sd ~ dunif(0, 1000)  
tau <- 1/(sd*sd)  
#precision of measurement error  
sd2 ~ dunif(0, 1000)  
tau2 <- 1/(sd2*sd2)  
#precision of random intercept  
sd3 ~ dunif(0, 1000)  
tau3 <- 1/(sd3*sd3)  
#precision of random slope  
sd4 ~ dunif(0, 1000)  
tau4 <- 1/(sd4*sd4)
```

```
#prior for mean intercept and mean slope
```

```

mu_int ~ dnorm(0, 0.001)
mu_slope ~ dnorm(0, 0.001)

#random intercept and slope for 37 plots
for(i in 1:37){
  intercept[i] ~ dnorm(0, tau3)
  slope[i] ~ dnorm(mu_slope, tau4)
}

#observation process for 1974
for(i in 1:37){
  mu74[i] <- mu_int + intercept[i] + slope[i]*1
  change74[i] ~ dnorm(mu74[i], tau)
  #measurement error component
  for(j in 1:10){
    1974[i, j] ~ dnorm(change74[i], tau2)
  }
}

#observation process for 1990
for(i in 1:37){
  mu90[i] <- mu_int + intercept[i] + slope[i]*17
  change90[i] ~ dnorm(mu90[i], tau)
  #measurement error component
  for(j in 1:10){
    1990[i, j] ~ dnorm(change90[i], tau2)
  }
}

#observation process for 2010
for(i in 1:37){
  mu10[i] <- mu_int + intercept[i] + slope[i]*37
  change10[i] ~ dnorm(mu10[i], tau)
  #measurement error component
  for(j in 1:10){
    2010[i, j] ~ dnorm(change10[i], tau2)
  }
}

```

***Recent tree mortality at the marsh-to-upland boundary***

```

#priors for the precision parameter of site-level random effect
sd ~ dunif(0, 1000)
tau <- 1/(sd*sd)

```

```

#prior for the Long Island Sound-wide effect of distance from marsh edge
beta_distance ~ dnorm(0, 0.001)

#prior for diameter at breast height
beta_dbh ~ dnorm(0, 0.001)

#prior for distance from marsh edge*diameter at breast height interaction
beta_interaction ~ dnorm(0, 0.001)

#coast-specific intercept
for(i in 1:2){
  mu_int[i] ~ dnorm(0, 0.001)
}

#prior for random intercept for non-random transects
for(i in 1:8){
  random_int[i] ~ dnorm(0, tau)
}

for(i in 1:1098){
  #distance_max and distance_min are read in as data to account for uncertainty in
  distance from marsh edge for transects in which marsh plants occurred more than 20 m
  from the start
  distance[i] ~ dunif(distance_max[i], distance_min[i])

  #logistic regression model for the probability a tree along the transect is alive
  #the site-level random effect (random_int) is hierarchically centered on the coast-
  specific intercept (mu_int)
  logit(p[i]) <- mu_int[coast[i]] + random_int[site[i]] + beta_distance*distance[i] +
  beta_dbh*DBH[i] + beta_interaction*DBH[i]*distance[i]
  alive[i] ~ dbern(p[i])
}

```

***Tree growth rates at the marsh-to-upland boundary***

```

#prior for mean of random slope
slope_int ~ dnorm(0, 0.001)
#prior for mean of random intercept
mu_int ~ dnorm(0, 0.001)
#prior for autoregressive term
lambda ~ dnorm(0, 0.001)

#prior for precision parameter of annual variation in growth
sd ~ dunif(0, 1000)

```

```

tau <- 1/(sd*sd)
#prior for precision parameter of random slope
sd2 ~ dunif(0, 1000)
tau2 <- 1/(sd2*sd2)
#prior for precision parameter of random intercept
sd3 ~ dunif(0, 1000)
tau3 <- 1/(sd3*sd3)

#priors for regression coefficients
for(i in 1:5){
  #for variables that influence slope
  beta_slope[i] ~ dnorm(0, 0.001)
  #for variables that influence the intercept
  beta_int[i] ~ dnorm(0, 0.001)
}

#regression model for annual growth rates of N trees
for(i in 1:N){
  random_slope[i] ~ dnorm(0, tau2)
  random_int[i] ~ dnorm(0, tau3)
  slope[i] <- slope_int + random_slope[i] + beta_slope[1]*edge[i]
  int[i] <- mu_int + random_int[i] + beta_int[1]*dbh[i] + beta_int[2]*edge[i] +
  beta_int[3]*site[i] + beta_int[4]*taxon[i] + beta_int[5]*taxon[i]*edge[i]

  #observation process is split into t = 1 and t = 2:20 to accommodate autoregressive
  component
  #for t = 1
  log_rings[i, 1] ~ dnorm(mu[i, 1], tau)
  mu[i, 1] <- int[i] + slope[i]*1
  resids[i, 1] <- log_rings[i, 1] - mu[i, 1]
  #for year t = 2:20, with first-order autoregressive term
  for(t in 2:20){
    log_rings[i, t] ~ dnorm(mu[i, t], tau)
    mu[i, t] <- int[i] + slope[i]*t + lambda*(log_rings[i, t-1] - mu[i, t-1])
  }
}

```

*Supplementary Figures*

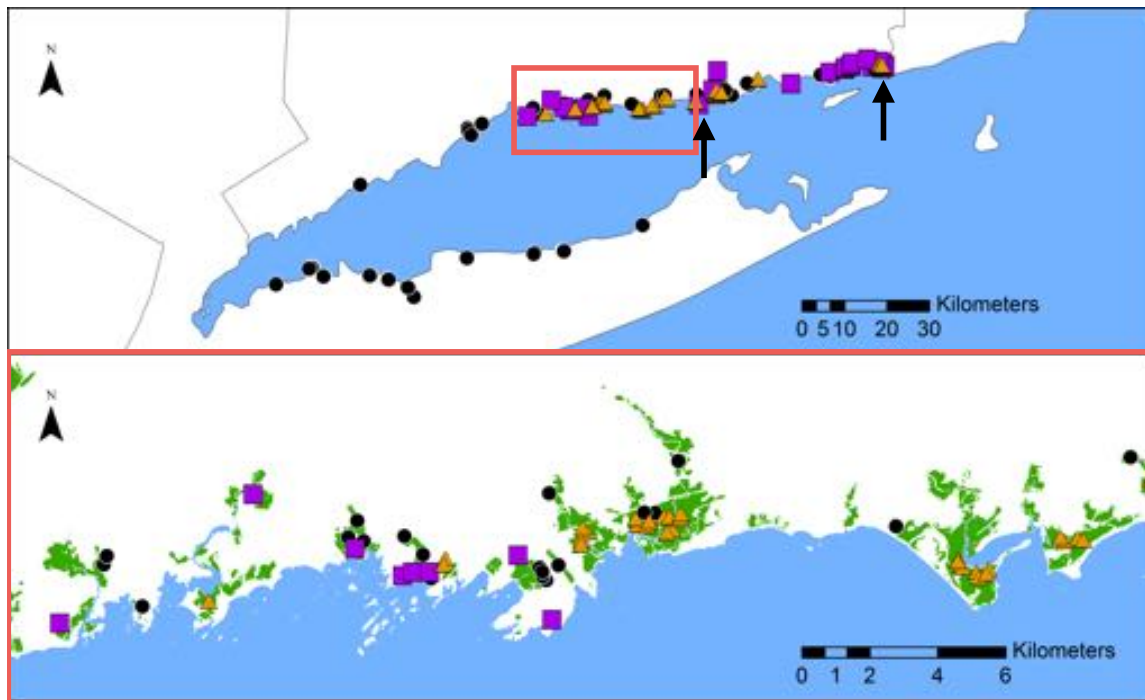


Fig. A1. The spatial distribution of plots for analyses of tidal marsh vegetation change (triangles; 55 plots), canopy extent from aerial photos (squares; 37 plots), recent tree mortality at the marsh-to-forest boundary (circles; 171 plots), and tree coring (arrows; 2 sites). Red outline shows the location of the inset in the bottom panel. Tidal marsh is shown in green.



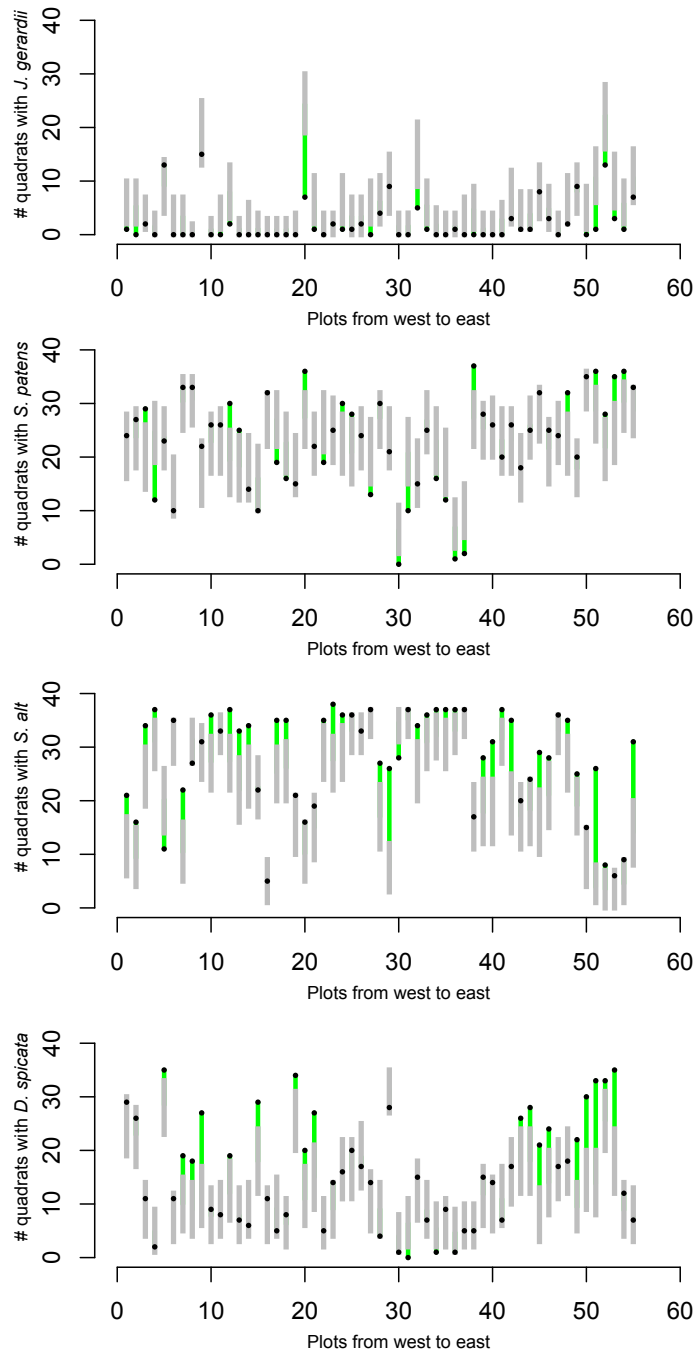


Figure A2. Posterior predictions of the expected number of quadrats within each of 55 1-ha plots that contained *J. gerardii*, *S. patens*, *S. alterniflora* (abbreviated *S. alt*), and *D. spicata*. 95% credible intervals for the hypothesis of no change between 2002-04 and 2013 are shown in gray;

black dots are the observed number of occupied quadrats in 2013. Green bars show the difference between the upper or lower credible interval and the observed data.

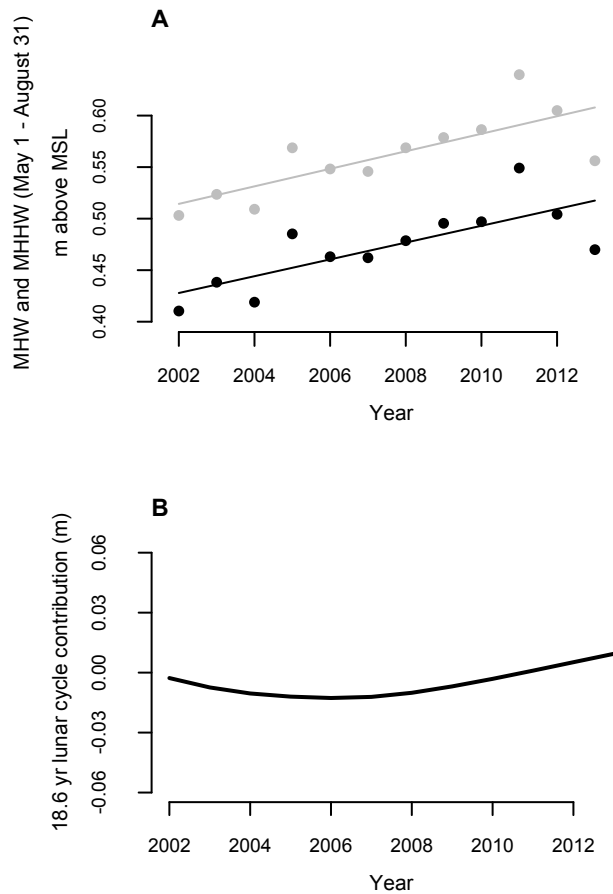


Figure A3. A) Observed Mean High Water (MHW; black) and Mean Higher High Water (MHHW; gray) during the growing season from 2002 to 2013. The contribution of the 18.6-year lunar cycle has been removed. Lines show the linear least squares fit. B) The magnitude of the 18.6-year lunar cycle that was removed from A.

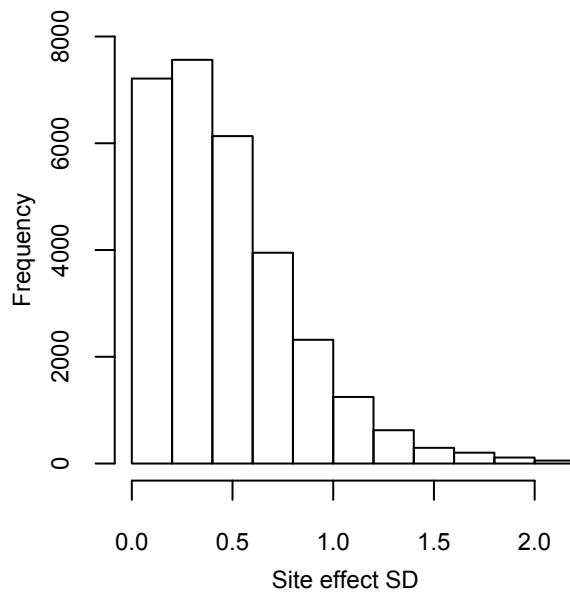


Figure A4. The posterior distribution of the standard deviation of the random site effect, which is a measure of site-level variation in the odds of finding dead trees at the marsh edge. The bulk of the density of the distribution is close to zero, suggesting little variation across sites.

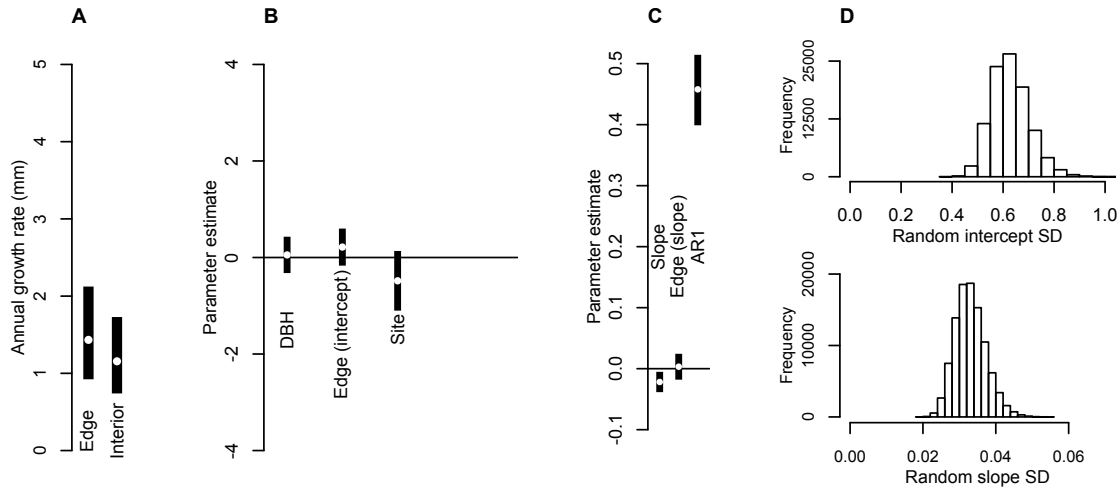


Figure A5. *A. rubrum* growth rates from 1993-2013. A) Estimates of mean annual growth at the marsh edge and in the forest interior (estimated from 49 trees). Black bars are 95% credible intervals and white dots are means. B) and C) Effect sizes of the fixed and random effects. D) Posterior distributions of the random intercept and slope.

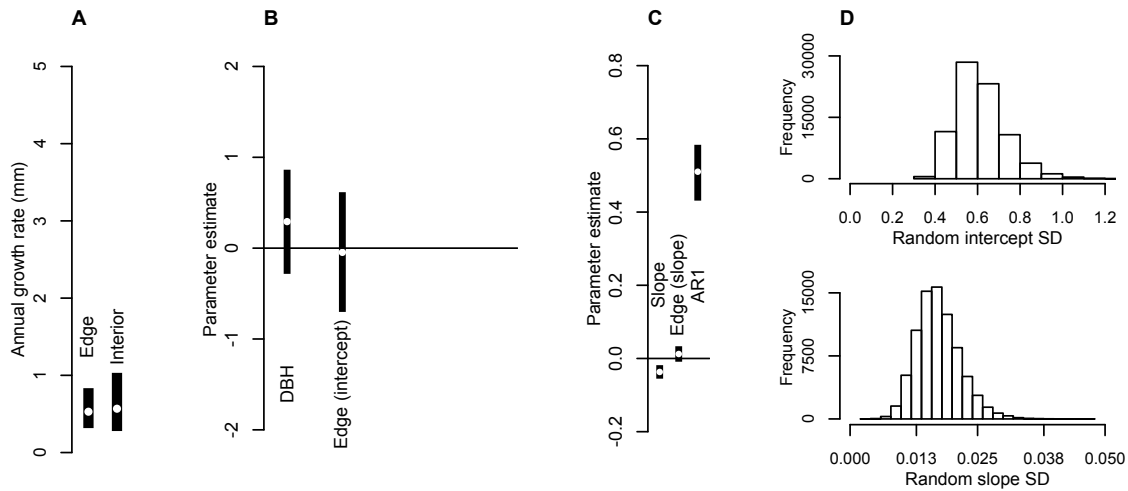


Figure A6. *N. sylvatica* growth rates growth rates from 1993-2013. A) Estimates of mean annual growth at the marsh edge and in the forest interior (estimated from 21 trees). Black bars are 95% credible intervals and white dots are means. B) and C) Effect sizes of the fixed effects. There is not site effect because *N. sylvatica* was only found at Barn Island WMA. D) Posterior distributions of the random intercept and slope.

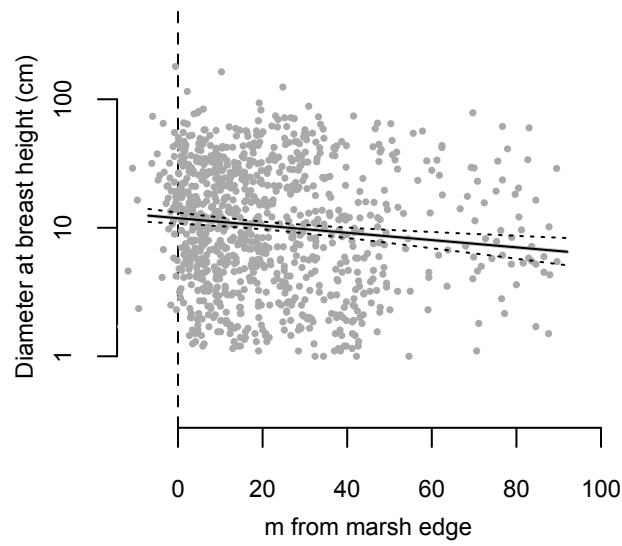


Figure A7. Diameter at breast height of living trees ( $n = 979$ ) decreases with distance from marsh edge. The solid and dotted black lines show the mean and 95% credible intervals of the trend.

## **How will social factors influence the effectiveness of common conservation strategies for facilitating ecosystem migration?**

### **Abstract**

The human aspects of conservation are often overlooked, but will be critical for identifying strategies for biological conservation in the face of climate change. We surveyed the behavioral intentions of coastal landowners with respect to a range of conservation strategies aimed at facilitating ecosystem migration. We found that several popular strategies, including conservation easements and increasing awareness of ecosystem services, are unlikely to mitigate losses from sea-level rise. Less common approaches to land protection are more likely to be effective, but may also be more expensive. Our research highlights the importance of incorporating human dimensions into ecosystem modeling and conservation planning, and shows that failure to do so has the potential to lead to the use of ineffective strategies and an overly optimistic view of the potential for ecosystem migration.

### **Main text**

Conserving biodiversity in the face of a changing climate is one of humanity's greatest challenges (Cowling 2015), but it is uncertain which strategies will be most effective in confronting this challenge. There is growing consensus that any strategy must integrate knowledge from the natural and social sciences (Hagerman et al. 2010a, Whitehead 2014), yet progress toward widespread integration has been slow (Cowling 2015). While research on how people will respond to climate change is a rapidly growing field (Hornsey et al. 2016), it is still largely focused on beliefs, attitudes, and the general actions people are likely to support rather



than specific actions they would take to achieve biological conservation (Tam and McDaniels 2013). Illustrating this lack of research, less than 2% of the studies identified in a recent systematic review of the determinants and outcomes of climate change beliefs (Hornsey et al. 2016) addressed human behavior with respect to biological conservation. In addition to the challenges to understanding human behavior toward conservation in general, climate change is likely to introduce a host of specific challenges, including the invisibility of causes, lack of direct experience with the consequences, and the distance of impacts in time and space (Weber 2010, Myers et al. 2012).

Much of the nascent literature on the human dimensions of biodiversity conservation under climate change is focused on the beliefs of scientists and protected areas managers (e.g. Schliep et al. 2008, Hagerman et al. 2010b, Rudd 2011, Lemieux and Scott 2011). While this research is important for understanding conservation in protected areas, such areas constitute only 15.4% of the globe's land area and 3.4% of ocean area (Juffe-Bignoli et al. 2015), and conservation strategies outside of already-protected areas are necessary for meeting global conservation goals (Rodrigues et al. 2004). Whether these strategies are based on adding to protected areas networks or actions outside of protected areas, the behaviors of people, especially private landowners, are likely to be among the most important determinants of success (Guerrero et al. 2010, Knight et al. 2010).

Here we show how the behavioral intentions of landowners could determine the effectiveness of a leading strategy for conservation under climate change: facilitating the migration of species and ecosystems (Williams et al. 2005, Hannah et al. 2007). We focused on tidal marshes because they provide a disproportionate share of global ecosystem services (Costanza et al. 2014) and are already experiencing ecosystem shifts in response to climate-

driven sea-level rise (Warren and Niering 1993, Donnelly and Bertness 2001, Field et al. 2016).

The success of mitigation strategies for preventing marsh losses will be determined by the behavior of millions of individual landowners (Strauss 2015) who might decide to build shoreline protection that would prevent marsh migration. In our study area alone (coastal Connecticut, USA; Fig. S1), there are over 30,000 landowners in the zone projected to become tidal marsh by 2100 (Hoover 2009, Connecticut Environmental Conditions Online 2014).

First, we report results from a systematic mail survey of the behavioral intentions of landowners with respect to building shoreline protection or participating in alternative conservation agreements aimed at protecting corridors for marsh migration. We then quantify the effects on behavioral intentions of a set of beliefs, attitudes, and group membership attributes that would be natural targets for intervention aimed at encouraging conservation behavior. Finally, we integrate social data and ecosystem projections to quantify the effect that behavioral intentions, and the factors that influence them, are likely to have on the extent of the marsh migration zone that is available for protection.

#### *Behavioral intentions with respect to conservation strategies*

Conservation easements are one of the most commonly used land protection strategies because they are flexible and often many times cheaper than purchasing land outright (Gustanski et al. 2000). We found, however, that conservation easements were by far the least preferred conservation agreement of the options presented to coastal landowners (Fig. 1; n = 1003). Only 6.9% of landowners reported being likely or strongly likely to participate in an easement in the next ten years, and only 3.2% (95% credible interval: 2.1-4.4%) chose easements as their first choice, compared to 17% (15-20%) for outright purchase (Fig. 1). Landowners also showed

greater preferences for two less common conservation agreements. Restrictive covenants, which are binding agreements to forgo shoreline protection that are entered into mutually by a neighborhood, were the most preferred option of 8.2% (6.5-10%) of landowners. Future interest agreements, in which ownership of a property reverts to a conservation organization in the event of a flood that reduces the total property value by more than 50% of its value, were the most preferred option of 27% (24-30%) of landowners (Fig. 1; see SI for more details about the agreements). Forty-five percent (42-48%) of respondents preferred to not participate in any of the agreements presented, and 22% of respondents reported being likely or strongly likely to build shoreline protection within the next 20 years. These results suggest that conservation easements, though popular with conservation practitioners, might not be as effective in the face of climate change as alternatives. It is notable that more landowners preferred restrictive covenants compared to easements, even though covenants do not offer a monetary incentive. Strategies that offer better incentives to landowners, such as outright purchase and future interest agreements, are more expensive for conservation organizations but might be required to achieve high participation rates. These low reported participation rates might be even lower in practice because intentions do not always translate into actions (Webb and Sheeran 2006), although it is possible that concerted outreach efforts could increase participation.

### *Strengthening beliefs in sea-level rise and coastal flooding*

One strategy for encouraging conservation is to strengthen peoples' beliefs in climate science and the impacts of climate change through public awareness campaigns and education (Maibach et al. 2011, Wendling et al. 2013). Strengthening beliefs that climate change is real has been shown to encourage conservation behaviors (Wendling et al. 2013), but the effect size is often

small to moderate (Boyes and Stanisstreet 2012, Hornsey et al. 2016) and stronger effects are often related to low-stakes activities, such as recycling and planting trees (Boyes and Stanisstreet 2012). Much less is known about the influence of climate change beliefs on high-stakes behaviors that have the potential to affect personal wealth and wellbeing.

We found that stronger beliefs about coastal flooding were related to stronger stated intentions for both pro- and anti-conservation behavior, although the effect sizes were moderate compared to other factors that influence intentions (Fig. 2). People with stronger beliefs that sea-level rise is real or that marsh migration would happen on their properties reported being more likely to participate in conservation agreements (Figs. 2, 3). Landowners with these beliefs, however, also reported being more likely to build shoreline protection (Figs. 2, 3). We set up a hypothetical scenario that quantifies the expected effect size (based on coefficients from our regression analysis; see **Methods**) of a successful intervention such that all coastal landowners believed that it was likely or strongly likely that water levels would rise on their properties. While there is currently mixed evidence for whether public awareness campaigns focused on climate change could achieve such a scenario (Maibach et al. 2008), it sets a clear benchmark for how much of a shift in attitudes one could expect under a best-case scenario. The magnitude of this shift depends on both the effect size in question (from Fig. 2) and the current distribution of beliefs and attitudes (Fig. 3) because there is potential for a larger shift if the current distribution is far from the hypothetical scenario. Under this hypothetical best-case scenario, our models predict an 11% increase in the number of landowners who would intend to build shoreline protection but only a 6% increase in the number who would participate in easement programs (Fig. 3). This result opens the door to the possibility that increasing awareness might do more harm than good when it comes to conservation.

Recent evidence suggests that climate awareness and education efforts might be most effective immediately after target populations experience extreme weather events (Myers et al. 2013, Howe et al. 2014). Because 12% of our respondents' homes were flooded during 2012's Hurricane Sandy, we quantified whether such events also have potential to influence behavioral intentions and thus the effectiveness of conservation strategies. Landowners whose homes flooded reported stronger intentions to sell outright as well as a greater likelihood of participating in at least one conservation agreement (Fig. 2). This direct relationship between experience with extreme weather and behavioral intentions suggests that conservation strategies are likely to be most effective after extreme weather events, although it is unclear how long after extreme weather this effect is likely to last.

#### *Attitudes toward ecosystem services*

Another strategy for encouraging pro-conservation behavior is making the links between ecosystem functions and their benefits to humans (ecosystem services; World Resources Institute 2011) more central to research, policy, and communication. This strategy has received considerable attention over the last decade and proponents of the ecosystem services approach have used powerful language to describe its potential to spur a conservation renaissance by changing peoples' attitudes and behaviors (Daily and Matson 2008). There has been little empirical research, however, on the attitudes of the public toward this approach, especially compared to more traditional concepts such as nature's inherent benefits (e.g. Metz and Weigel 2010). Empirical evidence is especially lacking on whether attitudes about ecosystem services have the potential to influence conservation behaviors.

Tidal marshes protect coastlines from damaging storm tides, which are becoming more frequent and extreme because of climate-driven sea-level rise (Möller et al. 2014). As such, raising awareness of the ecosystem services provided by tidal marshes is a common strategy of ongoing education efforts in our study area and other coastal areas around the world (e.g. Schuyt and Brander 2004). The capacity for marshes to protect coastal areas from storm tides is ideal for testing the potential for ecosystem services to influence behavior, as this phenomenon has a direct, well-established, and easily-communicated link to the wealth and wellbeing of coastal landowners (Lane et al. 2013, Hinkel et al. 2014). Despite its perceived potential, however, we found that landowners who placed greater importance on marshes' protection of coastal areas did not report being more likely to participate in conservation agreements, nor did they report being less likely to use shoreline protection (Figs. 2, 3). In contrast, landowners who placed greater importance on the value of marshes to wildlife were less likely to use shoreline protection and more likely to participate in both conservation easements and restrictive covenants (Figs. 2, 3). Our results highlight the need for additional research on the attitudes, beliefs, and behavioral intentions of key stakeholders in relation to ecosystem services to better quantify their power to help meet global conservation goals. Importantly, our results show that the ecosystem services concept is not a panacea, and it would be bad decision-making, in the excitement over its potential, to write off nature's inherent benefits as a potential driver of conservation behavior.

#### *Membership in environmental organizations*

A third strategy for encouraging pro-conservation behavior is to increase membership in environmental groups such as national and local land trusts, wildlife conservation organizations, and hunting groups. Membership in environmental groups is one of the most common forms of

political group membership, and is increasing (Dalton 2005), yet little is known about how this trend affects the prevalence of conservation behavior. Information on the behaviors of environmental group members will be important, however, if they are to be a key demographic in supporting conservation strategies in the face of climate change. Environmental groups generally have a direct line to their members via mail, email, or social media, which increases opportunities to inform members about key conservation issues and encourage specific behaviors. As a result, members presumably are better informed about key issues than the general population, and it has been shown that people who already have strong beliefs about climate science can be more likely to support immediate action (Wendling et al. 2013). Moreover, members' experience with the environmental groups would potentially alleviate concern about being treated fairly (e.g. being adequately compensated) when entering into conservation agreements. We found that environmental group members tended to have stronger beliefs that coastal flooding and sea-level rise are real (Fig. S2), but membership *per se* did not consistently influence intentions once climate change and flooding beliefs were accounted for (Fig. 2). Members of local or national wildlife conservation organizations did not report being more likely than non-members to participate in any of the conservation agreements or less likely to build shoreline protection (Fig. 2). Members of either national or local land trusts reported being more likely than non-members to participate in easements and restrictive covenants, but did not report being more likely to forgo shoreline protection (Fig. 2). Members of hunting organizations reported being less likely than non-members to participate in future interest agreements, purchases, or restrictive covenants (Fig. 2).

Members of environmental groups did not report being more likely than non-members to believe that they would be offered a monetary incentive to participate in one of the conservation

agreements, and only members of local land trusts were less likely than average to be worried about receiving a fair price (Fig. S2). Concern about receiving a fair price and disbelief about being offered an incentive both reduced landowner intentions to participate in conservation agreements (Fig. 2). This result, coupled with the low proportion of positive beliefs toward incentives (Fig. 3), suggests that landowners have concerns that environmental groups might not act fairly or transparently in their efforts to encourage tidal marsh migration. Reducing these concerns could have a strong effect on the proportion of landowners who are likely or strongly likely to forgo shoreline protection or participate in easements. Indeed alleviating concern about getting a fair price is predicted to have a larger effect than any of the other issues we examined (Fig. 3). Even if concern about receiving a fair incentive can be eliminated, our results suggest that relatively few landowners would be likely to participate in easements (13%, 95% credible interval: 11-15%; Fig. 3), further raising doubt about the effectiveness of this popular conservation strategy as a means to effect widespread land-ownership shifts in the face of climate change. Our results also suggest that while environmental group members may ultimately support conservation actions, for example through private donations, there is little evidence that they differ from the general population when it comes to higher stakes decisions.

### *Synthesis*

Quantifying behavioral intentions in relation to strategies for facilitating ecosystem migration uncovered surprising correlations that can help guide conservation practitioners to avoid strategies that would be ineffective for, or even detrimental to, meeting conservation goals in the face of climate change. We found 1) that strengthening beliefs in climate change can have both negative and positive outcomes, 2) little evidence that a focus on the ecosystem services of



marshes will lead to greater participation in conservation, and 3) that members of environmental groups are not likely to act differently than the general population when faced with high stakes decisions about adaptation. These results, coupled with landowners' low intentions for participating in conservation easements, suggest that some of the most widely-used conservation strategies might not be up to the challenge of biodiversity conservation in a changing climate. We did find evidence that emerging approaches could be more effective, although these approaches might also be more expensive, and some of the challenges we have identified, such as the likelihood and fairness of incentives, could be straightforward to address. Addressing these roadblocks to conservation is critical for coastal areas in the short-term, where the impacts of climate change are already being directly felt (Strauss et al. 2016) and half of the world's population (Nganyi et al. 2010) is adapting to climate change alongside imperiled species and ecosystems.

Our results raise questions about the assumption that coastal ecosystems in human-dominated landscapes can survive sea-level rise by migrating landward. The mean development rate for coastal towns in our study area is currently 14% of land area per decade (standard error: 8.9%; CLEAR 2016). Moreover, we found that 22% of landowners reported being likely or strongly likely to build shoreline protection, and that people closer to existing marsh (who have the potential to block corridors for migration behind them) reported being more likely to protect (Fig. 2). To quantify how spatial correlations between behavioral intentions and the extent of the marsh migration zone influences how much of this zone is currently available for protection, we overlaid our analysis of spatial variation in behavioral intentions with projections of marsh distribution in 2100 (Hoover 2009). These projections of marsh show the maximum potential for migration under 1.2 m of sea-level rise and assume no additional human barriers to marsh

migration (i.e. rolling easements as water levels rise). We estimate that only 7.1% (95% credible interval: 5.4 – 8.9%) of the marsh migration zone is owned by landowners who are currently likely or strongly likely to participate in conservation easements. This figure, however, would be increased to 20.3% (16.8 – 24.3%) if concern about the likelihood of receiving a fair incentive could be eliminated (Fig. 4).

The best case scenario is a mixed-strategy to land protection that assumes that 1) behavioral intentions translate into behaviors, 2) each landowner could be offered their most preferred agreement of those presented here, and 3) it would be possible to implement a large proportion of future interest agreements and restrictive covenants, which have not yet been widely implemented in practice. Under this scenario, 55.4% (51.6 – 59.1%) of the migration zone is owned by landowners who are currently likely or strongly likely to participate in conservation agreements that would prevent shoreline protection. This figure would increase to 70.4% (59.9 – 79.8%) if concern about the likelihood of receiving a fair incentive could be eliminated (Fig. S3).

As we have shown, failing to incorporate human dimensions into projections for tidal marshes is likely to greatly overestimate the ability of ecosystems to respond to climate change greatly. The potential for this bias to be widespread warrants greater integration of human dimensions into ecosystem modeling. Projections of species and ecosystems under climate change scenarios are ubiquitous in the ecological literature and many of these projections implicitly assume that human land use decisions will not influence ecosystem shifts. Our results suggest that better incorporating the constraints imposed by human behavior into these models would go a long way towards making their use in conservation planning and policy development more realistic.

## Methods

### *Survey development*

We defined our study population as people who own land along the Connecticut coastline within the zone that is projected to become tidal marsh by 2100 (Figure 1), assuming that no new barriers to marsh migration are constructed (Hoover 2009). We randomly selected streets from within the marsh migration zone and for each looked up associated non-commercial properties from town tax assessor's databases. For 3050 properties, we recorded the assessed value, name and address, and property size. We obtained approximate coordinates for each property, in WGS 84 decimal degrees, from <http://www.gpsvisualizer.com/geocoder/> and calculated the distance of each property to current tidal marsh (from Hoover 2009) in ArcGIS (ESRI 2014).

We developed agreement scenarios for conservation easements, purchase, and restrictive covenants based on the options discussed in Titus (2011), which we adapted to be consistent with the laws concerning land protection by non-profit organizations in our study area. We based the value of the incentive for easements on the median value per acre of easements enacted in our study area from 1998 - 2016 (The Trust for Public Land 2016). The scenario for future interest agreements was based on land protection strategies currently being explored by land trusts and town conservation commissions in our study area (H. Crawford, Town of Madison Conservation Commission, *personal communication*). The full terms of the agreements can be found in questions 15A-D of the questionnaire (SI). We also solicited input from a conservation practitioner who works with landowners in our study area (A. Sullivan, the Trust for Public Land, *personal communication*) to identify potential practical concerns that could influence landowner intentions.

We measured stated behavioral intentions with respect to the conservation agreements and constructing shoreline protection within the next 20 years (Q6C) using 5-point Likert scales (Colman et al. 1997, Lozano et al. 2008). We also used 5-point Likert scales (strongly unlikely to strongly likely, or very bad to very good, as appropriate) to quantify climate change beliefs, attitudes about ecosystem services and wildlife, and concerns about incentives. We measured landowners' preferred agreement, including the option of not participating in any agreement, as a choice. The interview script and question bank are in the SI.

We quantified the effects of variables that potentially influence behavioral intentions and would also be natural targets for interventions aimed at increasing conservation behavior: climate change beliefs, whether landowners were affected by Hurricane Sandy in 2012, attitudes towards tidal marsh ecosystem services and wildlife, membership in environmental groups, and concerns about receiving a fair incentive. We also included variables that might need to be accounted for to recover unbiased estimates of the effects of interest listed above: political party membership, property size, distance to current marsh, whether properties already contained shoreline protection, and demographic factors (see Table S1 and questionnaire in SI). We ruled out the presence of problematic correlation between independent variables by calculating variance inflation factors, which were less than three for all variables (Table S1). The full list of variables and an index to the associated question in the survey is given in Table S1. Climate change belief questions were presented after we stated that landowners were selected to participate in our survey because research suggested that water levels would rise on their property (the questionnaire included a link to this research). We adapted questions from public opinion surveys of climate change beliefs and attitudes (Leiserowitz et al. 2014) to solicit beliefs about sea-level rise and coastal flooding specifically. We coded beliefs about sea-level rise as a 10-part

scale from very sure that sea-level rise is not happening to very sure that it is happening (see Q14 of questionnaire).

We recruited coastal landowners for pre-test interviews via local meetings, LISTSERVS, and web pages for three environmental groups in our study area. We conducted interviews with six coastal landowners (who were then removed from the survey sample) by phone and in person to discuss their understanding of draft questions and relevant terminology, as well as social psychological variables that are beyond the scope of this paper.

We randomly assigned landowners to one of three survey versions that differed only by a one-page education message that came after all questions about behavioral intentions, attitudes, norms, or perceived control, but before questions about the importance of tidal marsh attributes (see SI for the three alternative questionnaires). Analysis of the education messages will be addressed elsewhere. We conducted a four-wave mail survey following the Tailored Design Method (Dillman et al. 2008): 1) between February 13, 2015 and March 13, 2015 we sent out the initial cover letter and a 5.5”-by-8.5”, color questionnaire, 2) one week later we sent a reminder postcard, 3) one week later we sent a reminder letter with a second copy of the questionnaire, and 4) two weeks later we sent the final reminder postcard (see SI for all letters and postcards). Each postcard or letter informed participants that by returning their questionnaire they would be entered into a raffle to win one of two \$250 Amazon.com gift cards. Approximately one week after the final postcard was sent, we called non-respondents who were listed in public records (n = 2185) to encourage them to return the questionnaire. We made all calls between 09:00 and 21:00, making as many as possible after 17:00 or on weekends. We were able to reach 612 landowners via phone and leave messages with 645. Cornell Survey Research Institute administered the survey and conducted non-response phone calls.

We received 1003 completed surveys (33% response rate) before we closed the survey period on June 15, 2016. We conducted independent sample t-tests to quantify any non-response bias by property size and distance to current marsh, the variables that we considered most likely to be affected. The difference between the means of respondents and non-respondents was small for both variables (property size: 0.04 ha; distance to marsh: 6.5 m). Only the effect of distance to marsh on response rate was positive and statistically significant (using  $\alpha = 0.05$ ), but the effect size was too small to warrant non-response weighting ( $\eta = 0.06$ ; Vaske 2008).

### *Statistical methods*

We quantified behavioral intentions and the effects of independent variables using a hierarchical Bayesian approach for combined variable estimation and selection in a generalized linear modeling framework (Gelman et al. 2004, Curtis and Gosh 2011). By specifying that a group of three or more related independent variables (e.g. climate change beliefs) arise from a common distribution that is centered on zero, we represented the prior knowledge that most independent variables are likely to have a small effect on the response variables, but that some might have moderate to large effects. This prior specification pulls estimates toward each other, which leads to better estimates of the vector of regression coefficients, avoids over-fitting, and estimates the uncertainty of each variable while accounting for the uncertainty of every other variable in the model (Gelman et al. 2004). We represented the relationship between variable groups using a normal distribution centered on zero with unknown variance. To ensure the independent variables were on comparable scales, we divided all variables that were not already Likert or indicator-scale by two standard deviations (Gelman 2008).

We accounted for any missing responses to questions using a data augmentation structure that allows for uncertainty in independent variables by specifying a parent distribution for each (see Schofield et al. 2007, Royle 2008, Reed et al. 2014). The percent of missing responses for each variable is shown in Table S1. We used a Bernoulli distribution as the parent distribution for indicator variables (using a uniform prior on the Bernoulli parameter), a normal distribution for continuous variables (using a normal prior on its mean and a uniform prior on its variance), and a categorical distribution for Likert items (using a Dirichlet prior). See SI for model code.

We used a Bernoulli distribution to describe variation in the landowner intentions to participate in any conservation agreement and multinomial distribution with ordered logistic regression for Likert-scale responses (see model code in SI). We coded Likert scale responses as one through five, representing strongly unlikely, unlikely, neutral, likely, and strongly likely, respectively. We also modeled respondents' first choice of conservation agreement, including the option of not participating in any of the given agreements, using a multinomial distribution.

To estimate the effects of interventions aimed at factors that influence behavioral intentions, we obtained posterior predictions of intentions for strengthening the target factor while holding all other independent variables constant at their sample means. We strengthened factors by specifying that half of the population would respond with strongly likely, very important, or strongly agree, as appropriate, and the other half of the population would respond with likely, important, or agree.

We quantified spatial variation in behavioral intentions across a hexagonal grid of planning units from the Environmental Protection Agency's Environmental Monitoring and Assessment Program (<https://archive.epa.gov/emap/archive-emap/web/html/>). The hexagons in this grid are similar in size to the marsh complexes in our study area and have previously been

used to design sampling for studies of tidal marsh birds (Wiest et al. 2016). The spatial model included a hexagon-level random effect and fixed effects for concern about receiving a fair price and the likelihood of receiving an incentive (see code in SI). We included these variables to allow simulating the effect of interventions aimed at alleviating concerns about incentives. As above, we simulated interventions by specifying that half of the population would respond with strongly likely, very important, or strongly agree, as appropriate, and the other half of the population would respond with likely, important, or agree. We corrected hexagon-specific projections of the extent of the marsh migration zone by the proportion of landowners in those hexagons who would be likely or strongly likely to participate in conservation agreements, propagating uncertainty from estimating behavioral intentions.

We fit models using JAGS (Plummer 2016) in R (R Core Development Team 2015) with the R2jags package (Su and Yajima 2015). Besides the priors described above, we use uninformative priors for all variables (see model code in SI). We ran three chains for 100,000 iterations after a 25,000-iteration burn-in; the potential scale reduction factors (Brooks and Gelman 1998) for all parameters were less than 1.01.



## Figures and tables

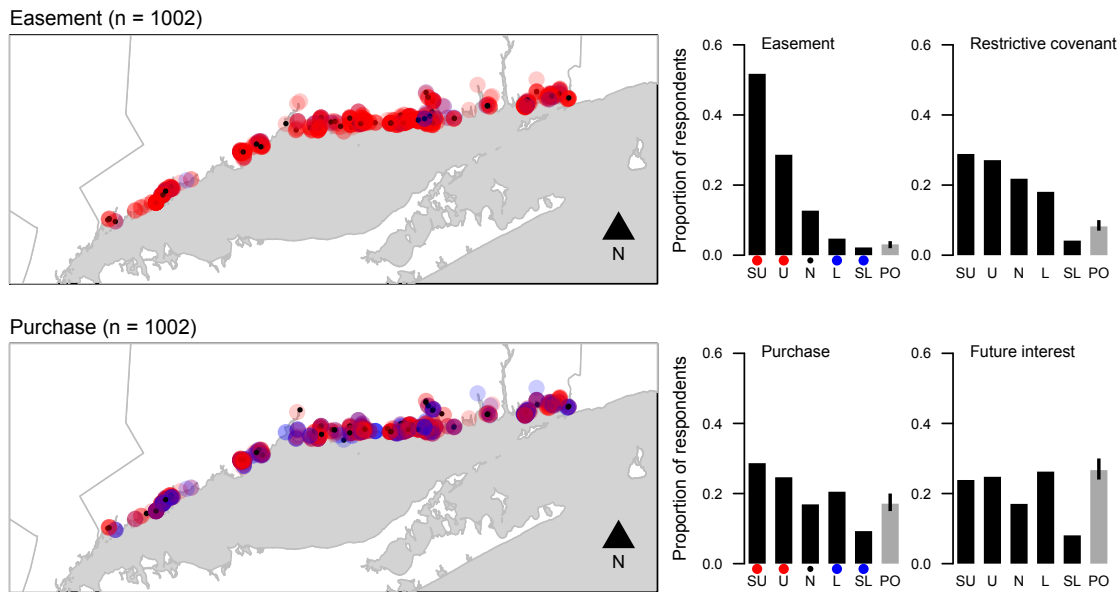


Figure 1. The stated behavioral intentions of landowners with respect to conservation easements, outright purchases, restrictive covenants, and future interest agreements. Responses are on a Likert scale and the spatial distribution of intentions is shown for easement and purchase: strongly unlikely (SU; red circle), unlikely (U; red circle), neutral (N; small black circle), Likely (L; blue circle), strongly likely (SL; blue circle). The gray bars show landowners' most preferred option (PO) and the associated 95% credible intervals (black whiskers).

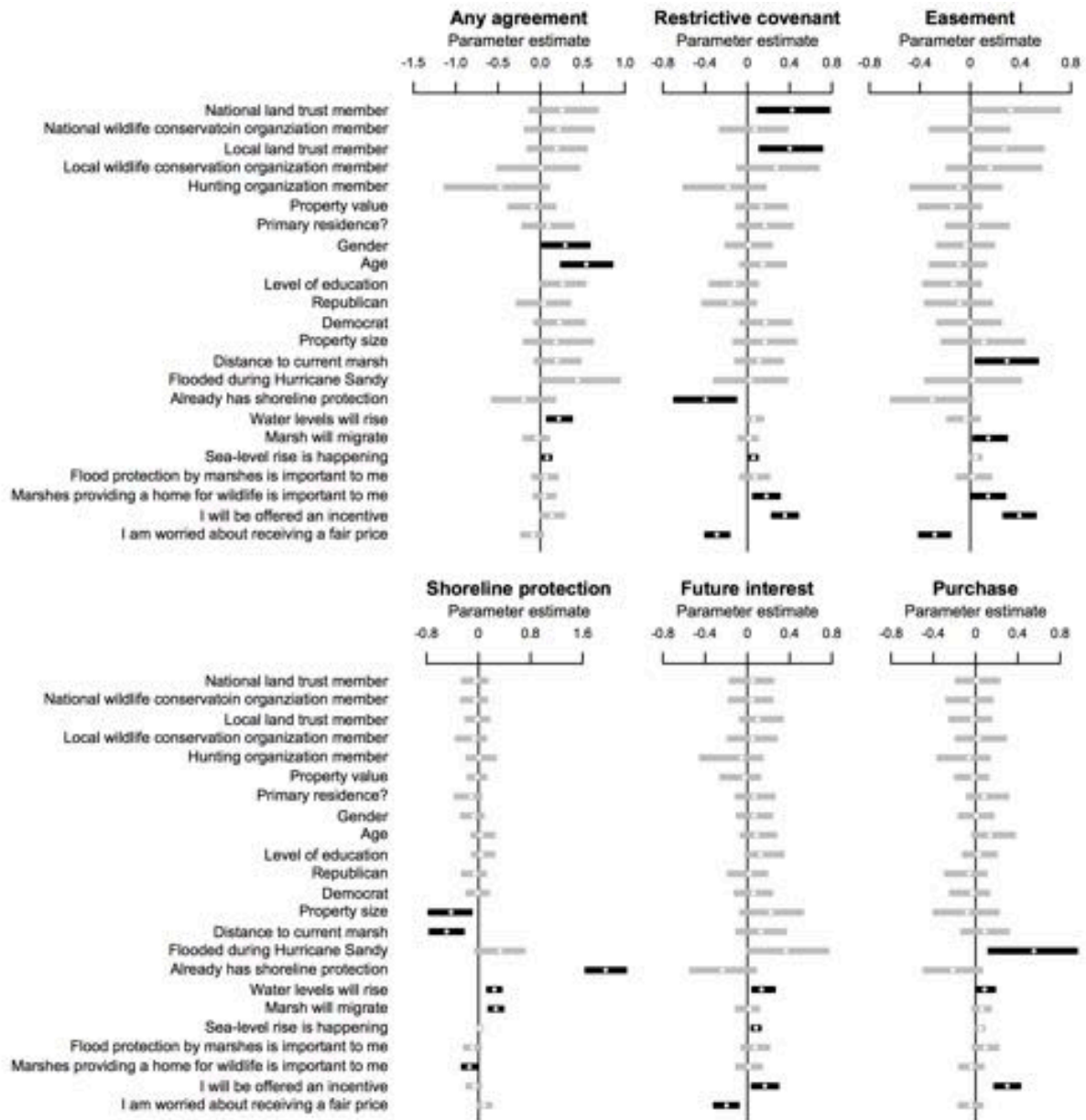


Figure 2. Parameter estimates for variables that potentially influence behavioral intentions with respect to four conservation agreements (restrictive covenants, easements, future interest agreements, purchase) and to the likelihood of constructing shoreline protection (shoreline protection). Bars are 95% credible intervals and white dots are posterior means. Credible intervals that do not overlap zero are shown in black.

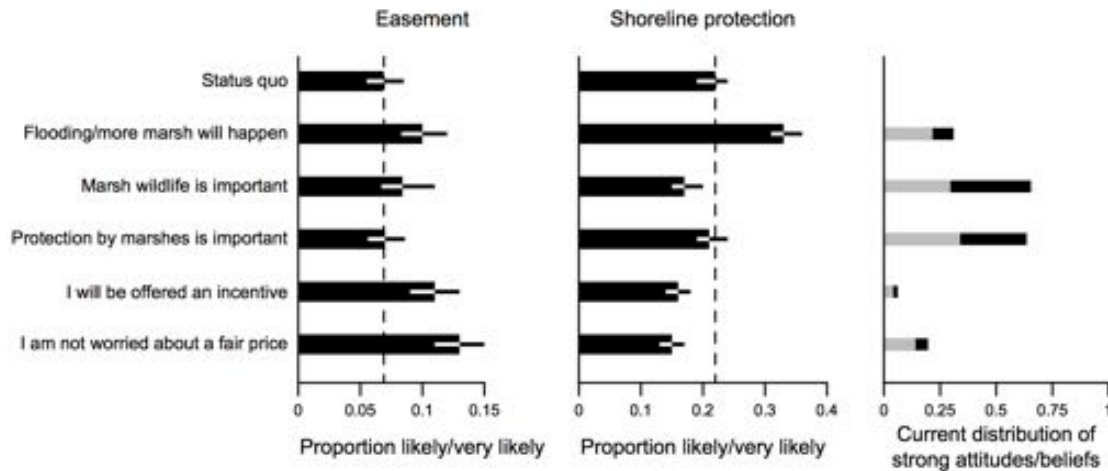


Figure 3. The predicted effect of changing the beliefs and attitudes that influence behavioral intentions. Bars show the posterior prediction with 95% credible intervals (whiskers) for the proportion of landowners who are likely or strongly likely to participate in easements or to build shoreline protection given different beliefs and attitudes. The predicted participation rates under status quo conditions (top bars) closely match the observed proportion of respondents from the survey (dotted line). The other bars show the predicted participation rates after a hypothetical awareness campaign that could strengthen each of the beliefs and attitudes listed on the y-axis such that half of the population would respond with strongly likely, very important, or strongly agree, as appropriate, and the other half of the population would respond with likely, important, or agree. Each belief or attitude on the y-axis was considered individually, while holding all other variables constant at their sample means. The right panel shows the current proportion of the population that reported strong beliefs or attitudes, and the relative contribution to this proportion by people who responded with likely/important/agree (gray) or strongly likely/very important/strongly agree (black).

Available for conservation easement

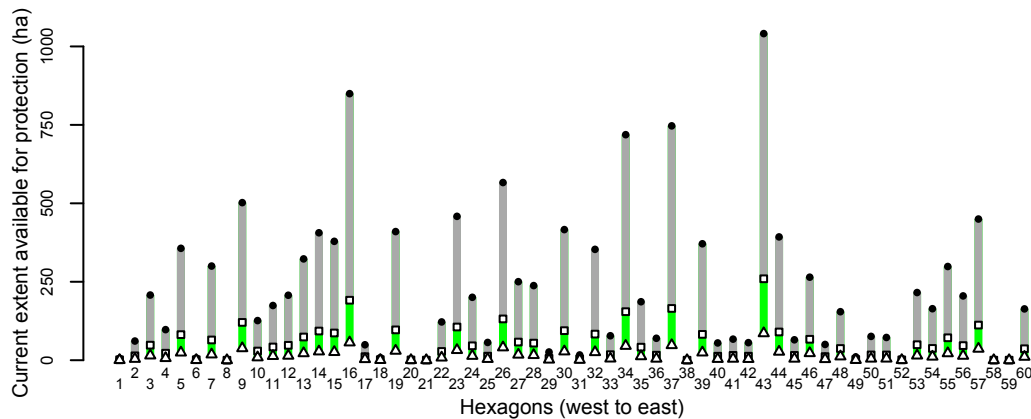
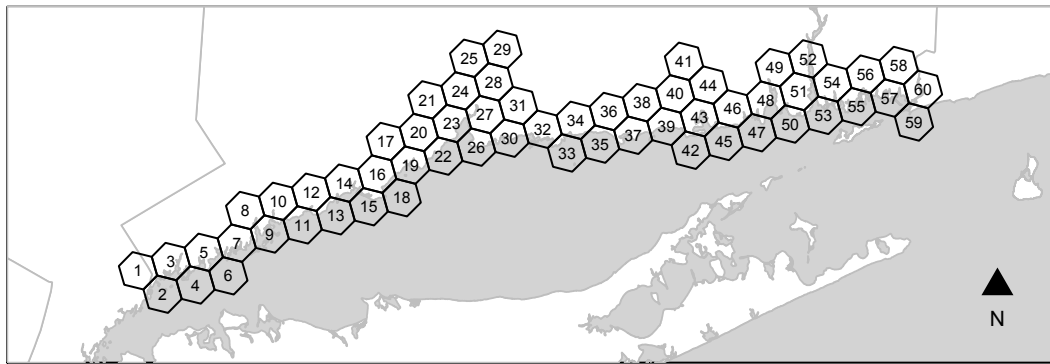


Figure 4. The estimated effect of behavioral intentions on the extent of the marsh migration zone that is available for conservation easements. Top: The locations of hexagonal planning units that were used to summarize the spatial extent of the marsh transgression zone and spatial variation in behavioral intentions. Numbers reference the bars in the bottom figure. Bottom: The estimated extent of the marsh migration zone that is available for conservation easements. Closed circles show the hexagon-specific extent of the marsh migration zone. Open triangles show the extent after accounting for the proportion of landowners who would be likely or very likely to participate in conservation easements, assuming no outreach to eliminate concerns about incentives. Closed squares show the extent if concern about incentives could be eliminated. These three scenarios are connected by colored bars to aid in visualizing the differences between them. Numbers below points refer to the hexagon numbers in the top figure.

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## Supplementary Information

*JAGS code for estimating the effects of variables that influence behavioral intentions*

#priors for the standard deviations of independent variable groups

sdA ~ dunif(0, 1000)

sdB ~ dunif(0, 1000)

sdC ~ dunif(0, 1000)

sdD ~ dunif(0, 1000)

sdE ~ dunif(0, 1000)

#priors for the precisions of independent variable groups

tauA <- 1/(sdA\*sdA)

tauB <- 1/(sdB\*sdB)

tauC <- 1/(sdC\*sdC)

tauD <- 1/(sdD\*sdD)

tauE <- 1/(sdE\*sdE)

#prior distribution for the effects of 12 landowner characteristics

for(i in 1:12){

A[i] ~ dnorm(0, tauA)

}

#prior distribution for the effects of 4 geographic characteristics

for(i in 1:4){

B[i] ~ dnorm(0, tauB)

}

#prior distribution for the effects of 3 climate change/sea-level rise beliefs

for(i in 1:3){

C[i] ~ dnorm(0, tauC)

}

#priors for the effects of 2 variables related to incentives

for(i in 1:2){

D[i] ~ dnorm(0, tauD)

}

#priors for the effects of 2 attitudes toward marsh attributes

for(i in 1:2){

E[i] ~ dnorm(0, tauD)

}

#prior for the regression equation intercept

#four intercepts are required for ordered logistic regression with five groups

for(i in 1:4){

```

Int4sort[i] ~ dnorm(0, 0.001)
}
Int[1:4] <- sort(Int4sort[])

#prior for Dirichlet distribution used to describe the priors for Likert scale variables
for(j in 1:5){
  alpha[j] <- 1/5
}

#parameters for the distributions of independent variables (used for data augmentation)
#indicator variables are distributed according to Bernoulli, Likert scale items are
categorical, and continuous variables are normal
#landowners characteristics
sdAcov[1] ~ dunif(0, 1000)
tauAcov[1] <- 1/(sdAcov[1]*sdAcov[1])
psiA[1] ~ dunif(0, 1)
psiA[2] ~ dunif(0, 1)
sdAcov[2] ~ dunif(0, 1000)
tauAcov[2] <- 1/(sdAcov[2]*sdAcov[2])
sdAcov[3] ~ dunif(0, 1000)
tauAcov[3] <- 1/(sdAcov[3]*sdAcov[3])
psiA[3] ~ dunif(0, 1)
psiA[4] ~ dunif(0, 1)

#geographic characteristics
sdBcov[1] ~ dunif(0, 1000)
tauBcov[1] <- 1/(sdBcov[1]*sdBcov[1])
sdBcov[2] ~ dunif(0, 1000)
tauBcov[2] <- 1/(sdBcov[2]*sdBcov[2])
psiB[1] ~ dunif(0, 1)
psiB[2] ~ dunif(0, 1)

#climate change/sea-level rise beliefs
pC[1:5, 1] ~ ddirch(alpha[])
pC[1:5, 2] ~ ddirch(alpha[])
sdCcov[1] ~ dunif(0, 1000)
tauCcov[1] <- 1/(sdCcov[1]*sdCcov[1])

#variables related to incentives
pD[1:5, 1] ~ ddirch(alpha[])
pD[1:5, 2] ~ ddirch(alpha[])

#attitudes toward marsh attributes
pE[1:5, 1] ~ ddirch(alpha[])

```

```

pE[1:5, 2] ~ ddirch(alpha[])

#for 1003 respondents
for(i in 1:1003){
#distributions of independent variables (used for data augmentation)
#landowner characteristics
assval[i] ~ dnorm(0, tauAcov[1])
primres[i] ~ dbern(psiA[1])
gend[i] ~ dbern(psiA[2])
age[i] ~ dnorm(0, tauAcov[2])
edu[i] ~ dnorm(0, tauAcov[3])
repub[i] ~ dbern(psiA[3])
dem[i] ~ dbern(psiA[4])

#geographic characteristics
acresGIS[i] ~ dnorm(0, tauBcov[1])
marshdist[i] ~ dnorm(0, tauBcov[2])
sandy[i] ~ dbern(psiB[1])
protected[i] ~ dbern(psiB[2])

#climate change/sea-level rise beliefs
floodbelief[i] ~ dcat(pC[1:5, 1])
newmarshbelief[i] ~ dcat(pC[1:5, 2])
SLRisreal[i] ~ dnorm(0, tauCcov[1])

#incentives
incent[i] ~ dcat(pD[1:5, 1])
fairprice[i] ~ dcat(pD[1:5, 2])

#attitudes towards marsh attributes
floodprotect[i] ~ dcat(pE[1:5, 1])
wildlifehome[i] ~ dcat(pE[1:5, 2])

#covariate vector for landowner characteristics
Amat[i] <- A[1]*natland[i] + A[2]*natwild[i] + A[3]*localland[i] + A[4]*localwild[i] + A[5]*hunt[i] +
A[6]*assval[i] + A[7]*primres[i] + A[8]*gend[i] + A[9]*age[i] + A[10]*edu[i] + A[11]*repub[i] +
A[12]*dem[i]

#covariate vector for geographic characteristics
Bmat[i] <- B[1]*acresGIS[i] + B[2]*marshdist[i] + B[3]*sandy[i] + B[4]*protected[i]

#covariate vector for climate change/sea-level rise beliefs
Cmat[i] <- C[1]*floodbelief[i] + C[2]*newmarshbelief[i] + C[3]*SLRisreal[i]

```



```
#covariate vector for variables related to incentives
```

```
Dmat[i] <- D[1]*incent[i] + D[2]*fairprice[i]
```

```
#covariate vector for attitudes toward marsh attributes
```

```
Emat[i] <- E[1]*floodprotect[i] + E[2]*wildlifehome[i]
```

```
#regression equation for ordered logistic regression incorporates all covariate vectors from above
```

```
log(mu[i]) <- Int - (Amat[i] + Bmat[i] + Cmat[i] + Dmat[i] + Emat[i])
```

```
p[1, i] <- mu[1, i]
```

```
for(j in 2:4){
```

```
logit(mu[j, i]) <- Int[j] - (Amat[i] + Bmat[i] + Cmat[i] + Dmat[i] + Emat[i])
```

```
p[j, i] <- mu[j, i] - mu[j-1, i]
```

```
}
```

```
p[5, i] <- 1 - mu[4, i]
```

```
#the response variable multinomial distributed (1-5, strongly unlikely - strongly likely)
```

```
easement[,i] ~ dmulti(p[1:5, i], 1)
```

```
}
```

```
JAGS code for estimating spatial variation in behavioral intentions
```

```
#prior for the intercept of the regression equation
```

```
Int ~ dnorm(0, 0.001)
```

```
#prior for the variance term of the hexagon-level random effect
```

```
sdHEX ~ dunif(0, 1000)
```

```
tauHEX <- 1/(sdHEX*sdHEX)
```

```
#hexagon random effect, for 60 hexagons
```

```
for(i in 1:60){
```

```
hexRE[i] ~ dnorm(0, tauHEX)
```

```
}
```

```
for(i in 1:length(LikelyorStronglyLikely)){
```

```
#regression equation; HEX is a vector that indexes hexagon for respondent i
```

```
logit(mu[i]) <- Int + hexRE[HEX[i]]
```

```
#response variable is 1 if landowner reported being likely or strongly likely to sell their land, 0 otherwise
```

```
LikelyorStronglyLikely[i] ~ dbern(mu[i])
```

```
}
```

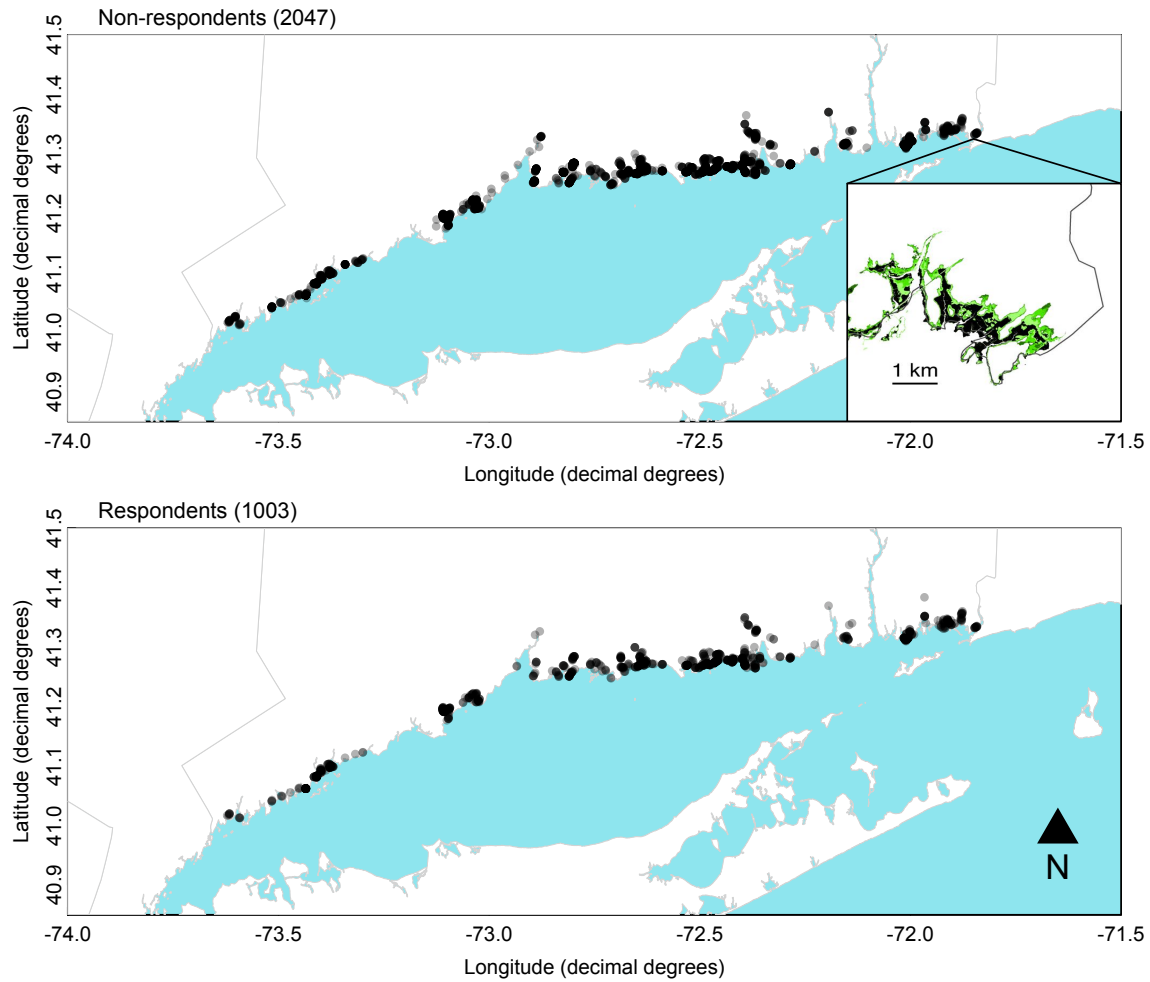


Figure S1. Locations of the coastal properties of survey respondents (bottom) and non-respondents (top). Each property is shown as a transparent black dot so that darker areas show greater concentrations of properties. The inset shows an example of the marsh migration zone; the projected extent of tidal marsh in 2100 is shown in green and current marsh is shown in black.

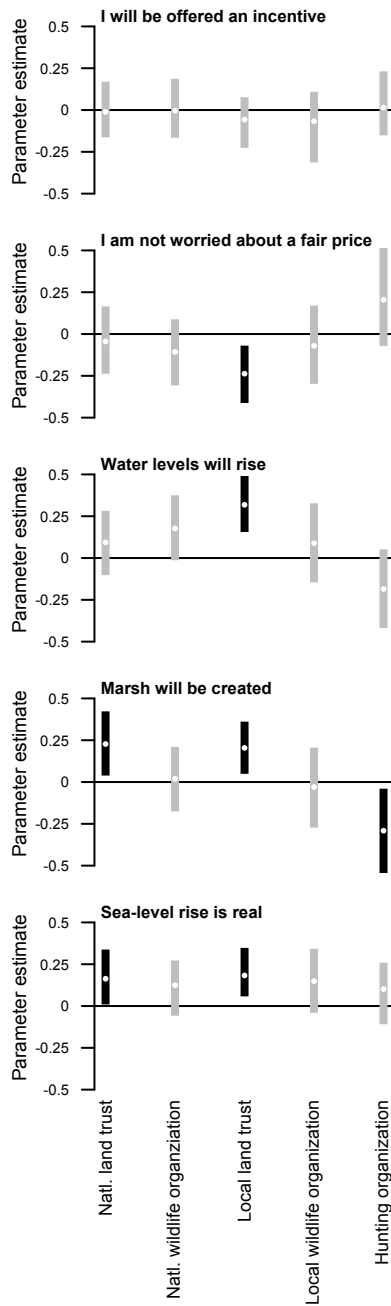


Figure S2. The influence of environmental group membership on (from top to bottom) landowners' perceived likelihood of receiving an incentive, concern about receiving a fair price, belief that water levels will rise on their properties, belief that marsh will be created on their property, and belief that sea-level rise is real. Bars are 95% credible intervals and white dots are

posterior means. Credible intervals that do not overlap zero indicate an effect of group membership and are shown in black.

Mixed strategy for land protection

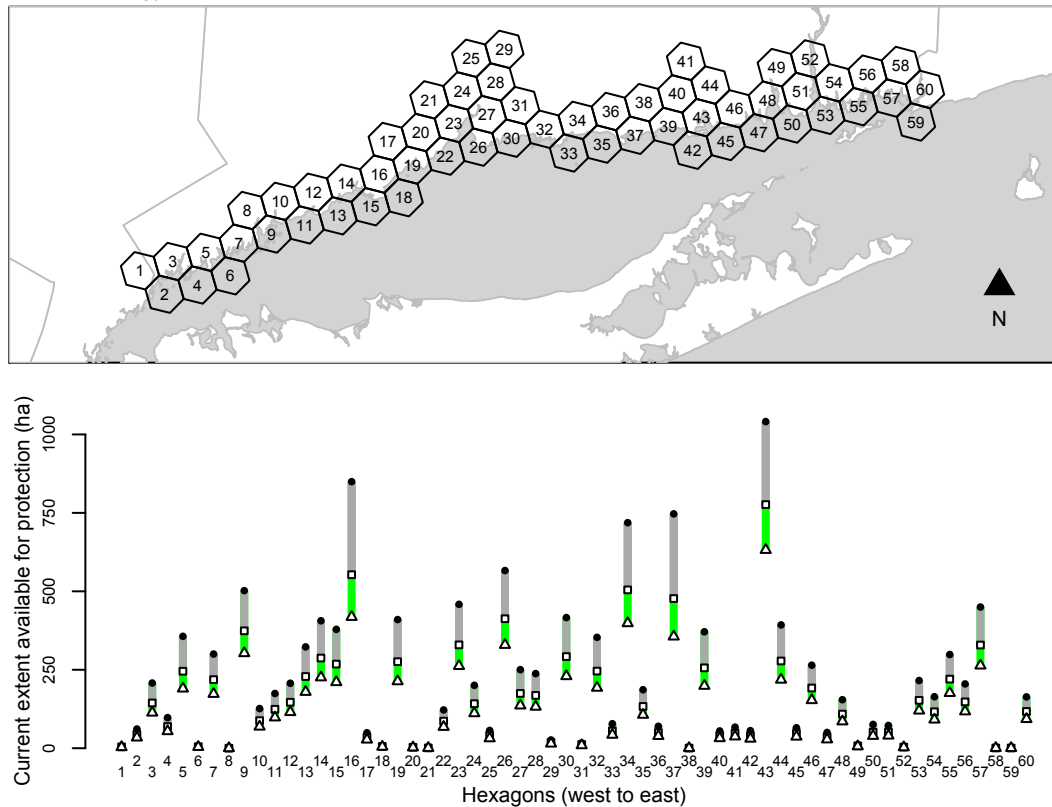


Figure S3. The estimated effect of behavioral intentions on the extent of the marsh migration zone that is available using a mixed strategy in which every landowner is offered their most preferred agreement. Top: The locations of hexagonal planning units that were used to summarize the spatial extent of the marsh transgression zone and spatial variation in behavioral intentions. Numbers reference the bars in the bottom figure. Bottom: The estimated extent of the marsh migration zone that is available for conservation easements. Closed circles show the hexagon-specific extent of the marsh migration zone. Open triangles show the extent after accounting for the proportion of landowners who would be likely or very likely to participate in one agreement, assuming no outreach to eliminate concerns about incentives. Closed squares show the extent if concern about incentives could be eliminated. These three scenarios are

connected by colored bars to aid in visualizing the differences between them. Numbers below points refer to the hexagon numbers in the top figure.

Table S1. List of independent variables showing, from left to right, the associated survey question number, the type of scale used to measure the variable, the name used to refer to the variable in the model code, variance inflation factors (VIF), and the percent of respondents who did not answer the question. Complete questions are given in the questionnaire, below.

<b>Question</b>	<b>Variable scale</b>	<b>Variable name</b>	<b>VIF</b>	<b>Proportion missing</b>
Q24A	Indicator	natland	1.46	0.00
Q24B	Indicator	natwild	1.32	0.00
Q24C	Indicator	localland	1.35	0.00
Q24D	Indicator	localwild	1.18	0.00
Q24E	Indicator	hunt	1.13	0.00
A	Continuous	assval	1.15	0.04
Q1	Yes/No	primres	1.15	0.07
Q21	Indicator	gend	1.24	0.08
Q22	Continuous	age	1.23	0.10
Q23	Ordinal	edu	1.25	0.04
Q25A	Indicator	repub	1.28	0.08
Q25B	Indicator	dem	1.36	0.08
Q6A	SU-SL (1-5)	floodbelief	2.26	0.07
Q6B	SU-SL (1-5)	newmarshbelief	2.13	0.08
Q14B	SU – SS (1-10)	SLRisreal	1.16	0.03
Q10A	SA-SD (1-5)	incent	1.11	0.10
Q17	SA-SD (1-5)	fairprice	1.14	0.13
B	Continuous	acresGIS	1.27	0.43
C	Continuous	marshdist	1.27	0.00
Q4	Indicator	sandy	1.22	0.08
Q12	Yes/No	protected	1.54	0.08
Q20F	EU - EI (1-5)	wildlifehome	1.69	0.09
Q20A	EU - EI (1-5)	floodprotect	1.45	0.09

*Mail survey questionnaire*

## **Coastal Flooding and Salt Marshes in Connecticut: A Survey of Landowners**



**A study conducted by:**

# **UConn**

**UNIVERSITY OF CONNECTICUT**

**This survey is for all coastal landowners in Connecticut. All opinions matter and are valuable, even if this is a new topic for you.**



The purpose of this survey is to learn about your opinions on increased coastal flooding and salt marshes in your community. You were chosen as part of a random sample of people who own land in areas that will likely convert naturally to salt marsh in the future. Our report on this research will be shared with state and local officials so that the opinions of people like you are considered when developing coastal management policies and programs that could benefit landowners in your area. Even if you aren't very interested in these topics or live far from existing salt marshes, we still would like you to answer the questions and return the questionnaire. Please be assured that your identity will be kept strictly confidential and your responses will never be associated with your name or address.

In this questionnaire, a **salt marsh** is a coastal wetland that is flooded by salt water brought in by the tides at least twice each month. As increased coastal flooding continues, salt marsh will likely move inland into areas that are **not currently marsh**, as shown below. We are interested in your thoughts on this process and how it might affect you.



Please complete this questionnaire as soon as you can, place it in the envelope provided, and drop it in any mailbox; return postage has been paid. Your participation in this survey is voluntary and you may stop at any time, but we encourage you to respond to all questions.

**THANK YOU FOR YOUR HELP!**

**This survey is an effort of the University of Connecticut and will contribute to a graduate student's dissertation research, as well as inform coastal management policies and programs that could benefit landowners in your area.**

### What are the characteristics of your coastal property in Connecticut?

Coastal property includes land within one mile of the coast.

1. Is your coastal property your primary residence? *(Check one)*

☐ Yes      ☐ No

2. Approximately how many acres is your coastal property? *(Fill in the blank)*

\_\_\_\_\_ number of acres

3. How many times has the first floor of the house on your coastal property flooded in the last 10 years? *(Fill in the blank)*

\_\_\_\_\_ number of times the first floor of my house has flooded

4. Did the first floor of your house flood as a result of Hurricane Sandy (October 2012)? *(Check one)*

☐ Yes      ☐ No

5. What percent of your property is currently salt marsh (coastal wetland that is flooded by salt water brought in by the tides)? *(Fill in the blank with a whole number from 0-100)*

\_\_\_\_\_ percent of my property is salt marsh

**The next several questions concern your thoughts about increased coastal flooding, whether it will impact your coastal property, and what actions you will take on your property.** Shoreline protection is any construction designed to prevent water levels from rising on your property. Common examples include bulkheads, revetments, and concrete sea walls.

6. Research by The Nature Conservancy (<http://coastalresilience.org>) suggests that part of your property is likely to convert naturally to salt marsh in the future as a result of increased coastal flooding. What are your thoughts about the likelihood of water level rising on your property and your potential response? *(Check one box for each row)*

Within the next twenty years, how likely is it that...	Strongly Unlikely	Unlikely	Neither	Likely	Strongly Likely
...water levels will rise naturally on any part of your coastal property?	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...rising water levels would create salt marsh in new locations on your coastal property?	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...you will use shoreline protection (such as bulkheads, revetments, and/or concrete sea walls) to prevent water levels from rising?	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

...you will allow water levels to rise naturally? ☐ ☐ ☐ ☐ ☐

7. Assuming that water levels may rise on your coastal property in the next 20 years, what are your thoughts about allowing water levels to rise naturally (not using shoreline protection) on your coastal property? (Check one box for each row)

	Strongly Disagree	Disagree	Neither	Agree	Strongly Agree
Allowing water levels to rise on my property would be bad.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Most people who are important to me think I should allow water levels to rise.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Most people who are like me will allow water levels to rise on their coastal property.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Allowing water levels to rise naturally on any part of my coastal property is up to me (as opposed to other people).	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

8. If water levels are allowed to rise naturally on your coastal property in the next 20 years, how likely are each of the following outcomes for your coastal property? (Check one box for each row)

Allowing water levels to rise naturally on my coastal property will result in ...	Strongly Unlikely	Unlikely	Neither	Likely	Strongly Likely
...losing my land to the sea.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...more habitat for saltmarsh wildlife.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...more salt marsh for storm protection.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...others thinking I am neglecting to care for my property.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...more mosquitos.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...more expensive insurance.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...reduced property value.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...increased risk of my house flooding.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

9. How good or bad would each of the following outcomes be for your coastal property? (Check one box for each row)

Outcomes	Very Bad	Bad	Neither	Good	Very Good
Losing my land to the sea	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
More habitat for saltmarsh wildlife	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
More salt marsh for storm protection	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Others thinking I am neglecting to care for my property	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

More mosquitos	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
More expensive insurance	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Reduced property value	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Increased risk of my house flooding	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

10. In the next twenty years, do you think the following situation will occur? How will it influence your ability to allow water levels to rise on any part of your coastal property?  
(Check one box for each row)

	Strongly Disagree	Disagree	Neither	Agree	Strongly Agree
I will be offered a <u>monetary incentive</u> to allow water levels to rise on my coastal property.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Being offered a <u>monetary incentive</u> would enable me to allow water levels to rise on any part of my property.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

11. How important are the thoughts of others when it comes to your coastal property?  
(Check one box for each row)

	Strongly Disagree	Disagree	Neither	Agree	Strongly Agree
When it comes to my property, I want to do what people important to me think I should do.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
When it comes to my property, I want to be like people important to me.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

12. Is there currently shoreline protection on your coastal property? (Check one)

☐ Yes, I built it.   ☐ Yes, it was on my property when I bought it.   ☐ No   ☐ I don't know

13. In the **past**, have you allowed water levels to rise on any part of your coastal property?  
(Check one)

☐ Yes   ☐ No   ☐ Not applicable (water levels have not risen on any part of my property)

14. Do you think that sea level rise is happening? (Check one)

☐ Yes   ☐ No

How sure are you? (*Check one*)

Very Unsure	Unsure	Neither	Sure	Very Sure
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

15. To address some people's concerns about coastal flooding in Connecticut, non-profit organizations that focus on land conservation are offering a variety of voluntary agreements to interested landowners. We are interested in whether the following agreements might be of interest to you.

**A. A conservation easement** is a binding agreement with a conservation organization that prevents shoreline protection from taking place on the land in perpetuity. The landowner retains ownership of their property, with the remainder of their private property rights intact. Because use is permanently restricted, a property subject to a conservation easement may be worth less on the open market than comparable unrestricted parcels. How likely are you to sign a conservation easement within the next ten years if a conservation organization offered to pay you a one-time sum of \$4,000 for each undeveloped acre? (*Check one*)

Strongly Unlikely	Unlikely	Neither	Likely	Strongly Likely
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**B. How likely are you to sell your property (including your house)** to a conservation organization for fair market value within the next ten years, if the conservation organization made you an offer? (*Check one*)

Strongly Unlikely	Unlikely	Neither	Likely	Strongly Likely
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**C. A restrictive covenant** is a mutual agreement among neighbors that requires everyone in the neighborhood to allow water levels to rise naturally, creating salt marsh in new locations on your property. Such an agreement could prevent the unintended consequences of additional shoreline protection on nearby properties, such as increased erosion or unplanned flooding on your property. How likely are you to sign such an agreement within the next ten years, if your neighbors also participated? (*Check one*)

Strongly Unlikely	Unlikely	Neither	Likely	Strongly Likely
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**D.** You may have the option of signing an agreement that would transfer ownership of your property (including your house) to a conservation organization in the event of a flood that reduces the total property value by more than 50% of its current value. Under this agreement, the conservation organization would be required to pay you the pre-flood property value at the time of transfer. How **likely** are you to sign such an agreement within the next ten years? *(Check one)*

Strongly Unlikely	Unlikely	Neither	Likely	Strongly Likely
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

16. Which of the agreements shown in A-D above are you most likely to participate in? *(Check one)*

☐ A   ☐ B   ☐ C   ☐ D   ☐ I am not likely to participate in any agreements

17. Do you agree or disagree with the following statement? *(Check one)*

If I sold my property to a conservation organization for fair market value, I would be worried about receiving a fair price. *(Check one)*

Strongly Disagree	Disagree	Neutral	Agree	Strongly Agree
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

# BELLWETHER BIRD

Saltmarsh Sparrows are the only bird species in the world found only in salt marshes.



1 in 3 Saltmarsh Sparrow nests in Long Island Sound are washed away during high tides.



**If salt marshes can migrate into new areas, Saltmarsh Sparrows can survive in the face of sea level rise.**

# **SALT MARSHES**

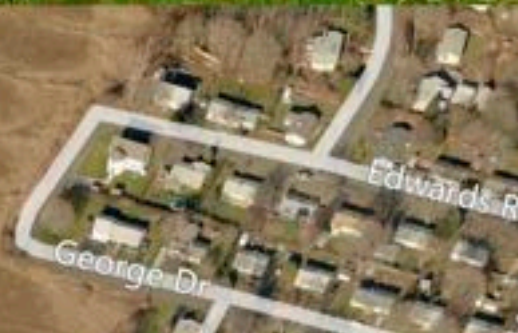
## **UNSUNG HEROES OF OUR COASTS**

**Salt marshes store more carbon per acre than tropical forests.**

**Long Island Sound's marshes can survive sea level rise if they can migrate into new areas.**



**Salt marshes keep communities safe by reducing wave height and coastal erosion.**

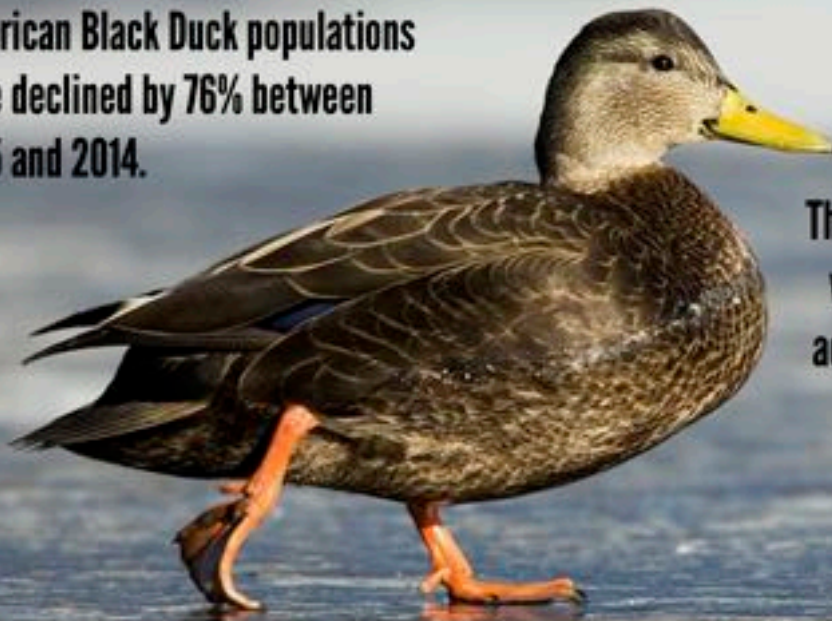




# NEW ENGLAND'S DUCK

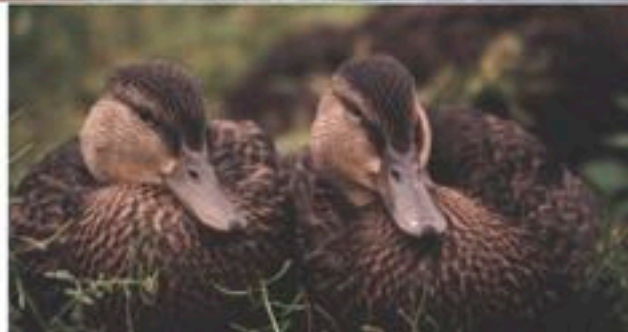
**The American Black Duck is the iconic and native duck species of the Northeast.**

**American Black Duck populations have declined by 76% between 1955 and 2014.**



**The Atlantic Flyway, which includes CT, accounts for 91% of the wintering American Black Duck population.**

**American Black Ducks rely on healthy coastal salt marshes from Newfoundland to North Carolina to survive the winter.**



18. How interesting did you find the information on the previous page? (Check one)

Very Uninteresting	Uninteresting	Neither	Interesting	Very Interesting
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

19. After reading the information on the previous page, we would like to know your thoughts about increased coastal flooding, whether it will impact your coastal property, and what actions you will take on your property. (Check one box for each row)

Within the next twenty years, how likely is it that...	Strongly Unlikely	Unlikely	Neither	Likely	Strongly Likely
...you will use shoreline protection (such as bulkheads, revetments, and/or concrete sea walls) to prevent water levels from rising?	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
...you will allow water levels to rise naturally?	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

	Strongly Disagree	Disagree	Neither	Agree	Strongly Agree
Allowing water levels to rise on my property would be bad.	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

20. How important to you are the following attributes of salt marshes? (Check one box for each row)

Outcomes	Not at all important	Slightly important	Moderately important	Very important	Extremely important
A. Flooding protection	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
B. Erosion protection	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
C. Wildlife viewing	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
D. Hunting opportunities	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
E. Carbon storage	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
F. Providing a home for wildlife	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

Which of the attributes shown in A-F above is most important to you? (Check one)

☐ A   ☐ B   ☐ C   ☐ D   ☐ E   ☐ F

## Background Information

21. Are you male or female? (*Check one*)      ☐ Male      ☐ Female

22. In what year were you born? (*Fill in*) 19\_\_\_\_

23. What is the highest level of formal education you have completed? (*Check one*)

- ☐ Less than high school
- ☐ High school diploma/G.E.D.
- ☐ Some college or technical school
- ☐ Associate's degree
- ☐ College undergraduate degree (e.g. B.A., B.S.)
- ☐ Graduate or professional degree (e.g. M.S., Ph.D., M.D.)

24. Which conservation organizations, if any, are you a member of? (*Check all that apply*)

- ☐ National land conservation organization (e.g. Trust for Public Land, The Nature Conservancy)
- ☐ National bird or wildlife conservation organization (e.g. Audubon, Ducks Unlimited)
- ☐ Local land conservation organization or land trust
- ☐ Local/state bird or wildlife organization society
- ☐ Hunting or fishing organization
- ☐ None

25. Do you consider yourself a Republican, a Democrat, an Independent, or a Libertarian? (*Check one*)

- ☐ Republican
- ☐ Democrat
- ☐ Independent
- ☐ Libertarian

## Thank you for your time and effort!

To return this questionnaire, place it in the envelope provided, and drop it in the mail.  
(Return postage has been covered).

*Mail survey letters*  
***First cover letter***

DATE  
NAME  
ADDRESS

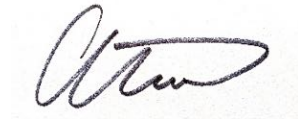
Dear NAME or current owner,

Increased coastal flooding is a critical issue affecting communities across Connecticut. I am writing to ask for your help in improving our understanding of landowners' views on increased coastal flooding and salt marshes in their community. The best way we know how to do this is by asking people who live by the coast to share their thoughts and opinions with us. Your address is one of only a small number that have been randomly selected to help with this study by completing the enclosed survey.

Please be assured that your identity will be kept strictly confidential and **your responses will never be associated with your name or address.**

This brief survey should take less than 15 minutes. Please complete the enclosed questionnaire as soon as you can and drop it in any mailbox; return postage has been paid. Your participation in this survey is voluntary and you may stop at any time. As an added incentive to participate, landowners who complete and return this survey will be automatically entered into a raffle to win one of two Amazon gift cards, worth \$250 each. If selected, the gift card will be sent to you by mail within five weeks of completing the survey. **Your name and address will still never be associated with your responses.**

The UConn Institutional Review Board approval number for this study is H14-086.  
Many thanks,



Chris Field  
PhD Student



Dr. Chris Elphick  
Associate Professor

***Second Cover Letter***

DATE  
NAME  
ADDRESS

Dear NAME or current owner,

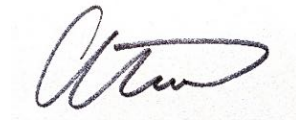
About three weeks ago, we sent you a survey request asking for your opinions on coastal flooding and salt marshes in your community. To the best of our knowledge, we have not received your responses.

We are writing again because of the importance that your responses have for helping to get accurate results. It is only by hearing from nearly everyone in the sample that we can be sure that the results truly represent coastal landowners like you.

Please complete the enclosed questionnaire as soon as you can and drop it in any mailbox; return postage has been paid. Your participation in this survey is voluntary and you may stop at any time. As an added incentive to participate, landowners who complete this survey will be automatically entered into a raffle to win one of two Amazon gift cards, worth \$250 each. If selected, the gift card will be sent to you by mail within five weeks of completing the survey. **Your name and address will still never be associated with your responses.**

The UConn Institutional Review Board approval number for this study is H14-086.

Many thanks,



Chris Field  
PhD Student



Dr. Chris Elphick  
Associate Professor

*Mail survey postcards*

DATE

Dear NAME,

Last week, we mailed you a letter asking for your help with a study about coastal flooding and salt marshes in your community. The next several years will be critical for influencing the development of policies and programs that help communities prepare for increased coastal flooding. It is important that your views are heard.

If you or someone in your household has already completed the questionnaire, please accept our sincere thanks. If not, please complete and return the questionnaire as soon as possible. We are especially grateful for your help with this important study. As an added incentive to participate, landowners who complete this survey will be entered into a raffle to win one of two Amazon gift cards, worth \$250 each.

For your convenience, a second copy of the questionnaire will be sent to you soon.

Many thanks,

Chris Field

A handwritten signature in black ink, appearing to read 'Chris Field', with a stylized, cursive script.

PhD Student

Dr. Chris Elphick

A handwritten signature in purple ink, appearing to read 'Chris Elphick', with a stylized, cursive script.

Associate Professor

DATE

Dear NAME,

In recent weeks, our research team has asked you, as part of a random selection of coastal landowners in Connecticut, to let us know your opinions on increased coastal flooding and salt marshes in your community. We plan to start summarizing results in the coming weeks, so we hope that all questionnaires will be completed by then.

You can help us by filling out the questionnaire we mailed to your household last week and returning it (postage has been provided). As an added incentive to participate, landowners who complete this survey will be entered into a raffle to win one of two Amazon gift cards, worth \$250 each.

By responding you are ensuring that your opinions are heard as policies and programs are developed to address the important issue of increased coastal flooding in Connecticut. Many thanks for considering our request.

Respectfully and with appreciation,

Chris Field

A handwritten signature in black ink, appearing to read 'Chris Field', with a stylized, flowing script.

PhD Student

Dr. Chris Elphick

A handwritten signature in purple ink, appearing to read 'Chris Elphick', with a stylized, flowing script.

Associate Professor

### *Interview script*

Welcome participants and thank them for participating.

Good afternoon. My name is Chris Field. I am a graduate student at UConn. Assisting me is (insert name) who is also from UConn. Thanks for coming to our session today. We are preparing for a survey of coastal landowners to understand how they will respond to sea level change. Our discussion today will inform our survey. We are asking you to take part because you are a coastal landowner in Long Island Sound, and you can help us ensure that our survey is relevant to other landowners like you.

We will talk about issues related to sea level rise and programs that landowners can take advantage of in the face of sea level rise. We will also ask for your help in defining words and phrases in a way that makes sense to landowners. Finally, we will run some of our survey questions by you to get your thoughts on them. We need your help to improve our questions so that they are as clear as possible to other coastal landowners.

[Read cover letter]

Participation in this interview is voluntary and anonymous. We will not be collecting personal information or linking your names with your comments. We would like to use an audio recorder, so that we can listen to the discussion and transcribe it later, but it is your right to opt out of being recorded. Is anyone concerned about audio recording?

If you would like a copy of the final study report, we would be pleased to send it to you. Please let me know at the end of our session.

The session will last for about an hour and 30 minutes. Before we begin, let's discuss our approach for the session:

- There are no right or wrong answers. We want to know your opinions. This is not a quiz.
- I'll ask a question, and then we will go around the circle so that each person can give their response.
- Please feel free to share any ideas you have and be honest.
- Please be respectful of the thoughts and opinions of others.
- Please turn off your cell phones.
- We do hope that all of you will be able to stay for the entire session.

Does anyone have any questions?

Let's begin our discussion.

#### **Reasoned Action Approach questions**

In your opinion, what are some of the advantages and disadvantages of allowing water levels to rise naturally on the edges of your coastal property?

What would make it easier for you to avoid taking measures to prevent water levels rising naturally?

Do you think your neighbors would approve or disapprove of allowing water levels to rise naturally? What type of people do you think will allow this to happen on their own property?



If a non-profit organization offered to pay you for putting a conservation easement on your land, would you consider that a “voluntary program” or a “voluntary agreement”?

What benefits do you think salt marshes provide coastal landowners? Do you prefer the term “ecosystem services” or “nature’s benefits to society” to describe these benefits? Or do you have another term that you like better?

**List of questions to cover for each question:**

[Pass out list of questions and go through them one at a time.]

Is the question clear?

Think about how, hypothetically, you would answer the question. How did you arrive at your answer?

Do you have any suggestions for making the questions clearer?

**Wrap-up**

[Highlight key points of the discussion and answer any final questions.]

[Have participants, on their own, write their definitions of the **Keywords and phrases**]

*Interview topics*

**Keywords and phrases**

Coastal resilience

Salt marsh

Mean-High-Water

High-tide line

Ecosystem

Ecosystem services

Conservation easement

Land trust

Non-profit land-conservation organization

Tax incentive

Restrictive covenant

Habitat

Endangered species

**Survey questions**

- . How **likely** are you to allow water levels to rise naturally on the edges of your property over the next twenty years, creating salt marsh where it is not currently?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

2. How **likely** are you to sell your property to a land trust for fair market value within the next ten years?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

3. You may have the option of signing an agreement with a land trust that would require you to allow water levels to rise naturally on the edges of your property, creating salt marsh where it is not currently. This agreement would result in a Federal tax deduction of 30% of your gross adjusted income over the next six years. How **likely** are you to sign such an agreement within the next ten years?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

4. If your neighbors also participate, you may have the option of signing an agreement that would mutually require landowners in your neighborhood to allow water levels to rise naturally, creating salt marsh where it is not currently. How **likely** are you to sign such an agreement within the next ten years, assuming your neighbors also participated?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

5. You may have the option of signing an agreement that would transfer ownership of your property to a land trust once the Mean High Water line reaches the center of your property. Under this agreement, the land trust would be required to pay you the current fair market value of the property at the time of transfer. How **likely** are you to sign such an agreement within the next ten years?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

6. You may have the option of signing an agreement that would transfer ownership of your property to a land trust in the event of a flood that reduces the total property value by more than 50% of its current value. Under this agreement, the land trust would be required to pay you the post-flood property value at the time of transfer. How **likely** are you to sign such an agreement within the next ten years?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

7. How **likely** are you to sign an agreement with a land trust that would require you to allow water levels to rise naturally on the edges of your property, creating salt marsh where it is not currently, if the land trust paid you a one-time sum of \$4,000 for each acre?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

**Please briefly describe how you would define the following words or phrases:**

Mean-High-Water

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Ecosystem services

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Land trust

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Conservation Easement

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High-tide line

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### Example question 1

How **likely** are you to allow water levels to rise naturally on the edges of your property over the next twenty years, which will create salt marsh where it is not currently?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

- 1) Is the question clear? Yes/No
- 2) Please circle any words or phrases in the above question that you did not understand.
- 3) Please answer the question hypothetically. Briefly describe how you arrived at your answer:

- 4) Do you have any suggestions for making the question clearer?

### Example question 2

If your neighbors also participate, you may have the option of signing an agreement that would mutually require landowners in your neighborhood to allow water levels to rise naturally, which will create salt marsh where it is not currently. How **likely** are you to sign such an agreement within the next ten years, assuming your neighbors also participated?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

- 1) Is the question clear? Yes/No
- 2) Please circle any words or phrases in the above question that you did not understand.
- 3) Please answer the question hypothetically. Briefly describe how you arrived at your answer:

- 4) Do you have any suggestions for making the question clearer?

### Example question 3

You may have the option of signing an agreement that would transfer ownership of your property to a land trust in the event of a flood that reduces the total property value by more than 50% of its current value. Under this agreement, the land trust would be required to pay you the post-flood property value at the time of transfer. How **likely** are you to sign such an agreement within the next ten years?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

- 1) Is the question clear? Yes/No
- 2) Please circle any words or phrases in the above question that you did not understand.
- 3) Please answer the question hypothetically. Briefly describe how you arrived at your answer:

- 4) Do you have any suggestions for making the question clearer?

### Pre-test interview question bank

#1a#

How **likely** are you to allow water levels to rise naturally on the edges of your property over the next twenty years, creating salt marsh where it is not currently?

Strongly Unlikely	Unlikely	Slightly Unlikely	Neither	Slightly Likely	Likely	Strongly Likely
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#1b#

How **likely** are you to allow water levels to rise naturally on the edges of your property over the next twenty years, which will create salt marsh where it is not currently?

Strongly Unlikely	Unlikely	Slightly Unlikely	Neither	Slightly Likely	Likely	Strongly Likely
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#2#

How **likely** are you to sell your property to a conservation organization for fair market value within the next ten years?

Strongly Unlikely	Unlikely	Slightly Unlikely	Neither	Slightly Likely	Likely	Strongly Likely
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#3a#

You may have the option of signing an agreement with a conservation organization that would require you to allow water levels to rise naturally on the edges of your property, which will create salt marsh where it is not currently. Voluntarily signing this agreement would result in a Federal tax deduction of 30% of your gross adjusted income over the next six years. How **likely** are you to sign such an agreement within the next ten years?



<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#3b#

You may have the option of signing an agreement with a conservation organization that would require you to allow water levels to rise naturally on the edges of your property, creating salt marsh where it is not currently. Voluntarily signing this agreement (without receiving monetary compensation from the conservation organization) would result in a Federal tax deduction of 30% of your gross adjusted income over the next six years. How **likely** are you to sign such an agreement within the next ten years?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#4a#

If your neighbors also participate, you may have the option of signing an agreement that would mutually require landowners in your neighborhood to allow water levels to rise naturally, which will create salt marsh where it is not currently. How **likely** are you to sign such an agreement within the next ten years, assuming your neighbors also participated?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#4b#

If your neighbors also participate, you may have the option of signing an agreement that would mutually require landowners in your neighborhood to allow water levels to rise naturally, creating salt marsh where it is not currently. How **likely** are you to sign such an agreement within the next ten years, assuming your neighbors also participated?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#4c#

If your neighbors also participate, you may have the option of signing an agreement that would mutually require landowners in your neighborhood to allow water levels to rise naturally, which will create salt marsh where it is not currently. Entering into such an agreement could prevent the unintended consequences of shoreline hardening, such as increased erosion or flooding on your property. How **likely** are you to sign such an agreement within the next ten years, assuming your neighbors also participated?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#5a#

You may have the option of signing an agreement today that would transfer ownership of your property to a conservation organization in the future, once the Mean High Water line reaches the center of your property. Under this agreement, the conservation organization would be required to pay you the current fair market value of the property at the time of transfer. How **likely** are you to sign such an agreement within the next ten years?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#5b#

You may have the option of signing an agreement today that would transfer ownership of your property to a conservation organization in the future, once the Mean High Water line reaches the center of your property. Under this agreement, at the time of transfer the conservation organization would be required to pay you the fair market from the date of signing. How **likely** are you to sign such an agreement within the next ten years?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#6#

You may have the option of signing an agreement today that would transfer ownership of your property to a conservation organization in the event of a flood that reduces the total property value by more than 50% of its current value. Under this agreement, the conservation organization would be required to pay you the post-flood property value at the time of transfer. How **likely** are you to sign such an agreement within the next ten years?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#7a#

How **likely** are you to sign an agreement with a conservation organization that would require you to allow water levels to rise naturally on the edges of your property, which will create salt marsh where it is not currently, if the conservation organization paid you a one-time sum of \$4,000 for each undeveloped acre?

<b>Strongly Unlikely</b>	<b>Unlikely</b>	<b>Slightly Unlikely</b>	<b>Neither</b>	<b>Slightly Likely</b>	<b>Likely</b>	<b>Strongly Likely</b>
<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#8#

Please rank the following attributes of tidal marshes according to how important they are to you. Place a “1” next to the attribute that is most important, a “2” next to the attribute that is the next most important, and so on. Please be sure that no two attributes have the same ranking.

- \_\_\_ Flooding protection
- \_\_\_ Erosion prevention
- \_\_\_ Wildlife viewing
- \_\_\_ Hunting opportunities
- \_\_\_ Carbon storage
- \_\_\_ Protection of wildlife

#9#

Considering the items above, please select one:

- All of these are important to me
- Some of these are important to me
- None of these are important to me

## **Estimating the return on investment of alternative data sources for spatial planning**

### **Abstract**

Compared to the development of methods and tools for spatial conservation planning, relatively little attention has been paid to the costs and benefits of obtaining additional sources of data and incorporating them into planning efforts. In particular, little is known about the relative importance of ecological vs. non-ecological data for identifying spatial priorities or the likely return on investment of incorporating better data. We present a simple approach for quantifying the sensitivity of spatial planning results to different ecological and non-ecological data layers, and estimating the potential gains in efficiency from incorporating additional data. Using a case study of spatial planning for tidal marshes and a threatened endemic species in the face of sea-level rise, we show that better data on the costs of conservation actions have the greatest potential to improve the efficiency of spatial planning. Incorporating spatial data on landowners' likelihood of selling had little effect on identifying relative priorities but drastically changed the outlook for whether conservation goals could be achieved. Our framework could be applied to other systems to guide the development of spatial planning and to identify general rules of thumb for the importance of alternative data sources for conservation problems in different socio-ecological contexts.

### **Introduction**

Systematic conservation planning is fundamental to making the best use of the limited resources available for conservation (Margules and Pressey 2002, McCarthy et al. 2012). Approaches to spatial systematic planning are well established and the tools for implementing them are

becoming increasingly more sophisticated (e.g. Marxan; Watts et al. 2009), but less is known about which types of data are most important to ensure that these tools lead to cost-effective decision-making. Ecological data are the foundation of most spatial planning because they are often necessary for measuring progress toward conservation goals and easier to obtain by conservation planners (who are typically trained as ecologists) than social or economic data (Cowling 2015). Accordingly, much of the research on better understanding the sensitivity of spatial planning to the underlying data, and potential trade-offs associated with obtaining better data, is focused on different types of ecological data (e.g. Grantham et al. 2008, Brooks et al. 2004, Rondinini et al. 2006).

It is becoming more widely recognized, however, that ecological data are just one component of effective spatial planning. In particular, economic costs and other social data, such as willingness to participate in conservation, can lead to more efficient planning. Despite this potential for better planning, it is not yet common practice to incorporate a wide range of non-ecological data sources into planning efforts (Naidoo et al. 2006, Naidoo and Ricketts 2006, Guerrero et al. 2010, Knight et al. 2010). One potential cause of this lag is that allocating greater effort toward non-ecological data sources is associated with trade-offs, including the potential to shift focus away from the biology of conservation (Arponen et al. 2010), the cost of data collection, delaying action while waiting for better data (Grantham et al. 2009), and the expertise needed to obtain and interpret additional data types. Adding additional layers, each of which has its own uncertainty, also results in a greater degree of uncertainty in the planning process. The potential costs of greater uncertainty include the need for more sophisticated, and potentially less accessible, planning tools that are capable of incorporating uncertainty, and less interpretable results, especially for non-specialist stakeholders.

There is little guidance in the literature for navigating the costs and benefits of incorporating different types of data into spatial planning. To address this need, we present a framework for generating evidence that can be used to weigh the relative importance of different data sources for spatial planning and to determine how detailed data layers need to be. This framework could be used for pilot analyses to determine which data are likely to be most important within a given system or to accumulate evidence for better understanding the relative importance of ecological, cost, and other social data for spatial planning in general. Our approach has three components designed to help planners navigate the tradeoffs associated with choosing appropriate data types: 1) quantifying the sensitivity of conservation planning results to the types of data that are incorporated, 2) quantifying how much uncertainty is added from each data layer to visualize the trade-offs between greater uncertainty and greater efficiency, and 3) estimating the efficiency gains produced by each planning solution.

We illustrate this framework using a conservation planning problem for a system that is rich in ecological data: the protection of tidal marshes and an endemic tidal marsh bird across the north shore of Long Island Sound (LIS), USA. Approximately 5% of the US human population lives within 80 km of LIS, and the tidal marshes in this region lie in the core of the range of the saltmarsh sparrow (*Ammodramus caudacutus*; Wiest et al. 2016). Saltmarsh sparrows breed only in northwest Atlantic tidal marshes (Greenlaw and Rising 1994) and are the focus of on-going conservation efforts from local to national conservation organizations. A primary strategy of these efforts, and thus the one considered here, is protecting land to protect corridors for tidal marshes that would allow marshes to migrate landward to mitigate losses from sea-level rise.

Here we integrate three types of data – ecological, economic cost, and human behavior – to address two common spatial planning goals: estimating and ranking the conservation value of

planning units, and identifying a minimum set of planning units to meet conservation goals for the least cost. We used our approach to determine the relative importance of these data types and the consequences of using coarser data layers that required less effort to obtain, but are more typical of data used in spatial planning. These datasets include remote sensing of habitat layers, count surveys, and county-level median cost data.

## **Methods**

### *Data sources, conservation planning approach, and planning units*

Our spatial planning objective was to identify areas for the least cost that could provide migration corridors for marshes in planning units and that provide the greatest protection to current saltmarsh sparrow nesting habitat. Accordingly, we measured conservation value in relation to two targets: the projected extent of tidal marsh in 2100 assuming no additional barriers to marsh migration are constructed (Hoover 2009), and the current extent of saltmarsh sparrow nesting occurrence (Meiman and Elphick 2012). We also considered two less effort-intensive data sources that are potential proxies for saltmarsh sparrow nesting: saltmarsh sparrow abundance, estimated from count surveys (Wiest et al. 2016), and the current extent of tidal marsh, estimated from remote sensing (Hoover 2009). We considered three goals that span the minimum and maximum extent likely to be set by practitioners: 33%, 66%, and 95% of each target's extent (or population when using abundance estimates as a proxy for nesting extent). Estimating conservation value in relation to a set of alternative goals allowed us to quantify the effect on our results of setting conservative vs. ambitious goals. If for a given scenario the goal for the projected migration zone could not be met because there was not enough land area owned

by willing sellers, we adjusted the goal to be the percentage of the migration zone that is owned by landowners who reported being likely to sell.

We estimated the costs of properties within the migration zone using a Bayesian regression analysis of randomly selected properties from town assessor's databases (see SI for methods). We also incorporated a freely available, but less precise, proxy for land costs: county-scale, median values for agricultural land from the US Census Bureau (2016). We analyzed information on the spatial variation in behavioral intention data (Field et al. 2016) to estimate the proportion of landowners in each town who would be likely to sell their properties to a conservation organization for fair market value (see SI for methods).

We defined planning units as cells (approximately 23 km<sup>2</sup>) in the hexagonal grid from the Environmental Protection Agency's Environmental Monitoring and Assessment Program (<https://archive.epa.gov/emap/archive-emap/web/html/>). The planning units in this grid are similar in size to the larger marsh complexes in our study area and have previously been used to design sampling for estimating the abundance of saltmarsh sparrows (Wiest et al. 2016). For each planning unit, we used the data listed above to calculate the "fraction-of-the-spares" index (FOS; Phillips et al. 2010), which takes a value between zero and one, with a value of one indicating that the planning unit is necessary for meeting conservation goals. We divided the FOS index by the cost of land to obtain a benefit/cost ratio (Phillips et al. 2010), which we used as our measure of conservation value. The FOS estimates conservation value in relation to multiple targets, performs well compared to other conservation indices, is straightforward to calculate and recalculate as necessary, and can be used to estimate conservation value for prioritization or identifying a minimum set to meet conservation goals (Phillips et al. 2010).



The ease with which the FOS index can be calculated lends itself to propagating uncertainty in the true conservation value by calculating the index across the entire range of uncertainty for all data layers. Accordingly, we recalculated the FOS index for each planning unit 10,000 times, each time using independent draws from the uncertainty distributions for each data layer. The resulting confidence bounds represent the entire range of uncertainty contributed by the data layers that were used to calculate the index.

### *Sensitivity*

Our “best scenario” incorporated the best available data: projections of marsh migration, modeled saltmarsh sparrow nesting occurrence, land cost data from within the migration zone, and spatial data on likelihood of selling (1, 2, 5, and 7 in Table 1). We estimated conservation value for each planning unit for five alternative scenarios in which we either excluded a data layer (likelihood of selling) or replaced it with a less accurate proxy (land cost, nest occurrence; see Fig. 2 for the scenarios). For each reduced effort scenario, we compared the conservation value of planning units to that obtained using the best scenario to quantify how sensitive these values were to the excluded data layer. First, we compared reduced effort scenarios to the best scenario using Spearman’s rank correlations to estimate the similarity of the rankings produced by the FOS. We then calculated the number of planning units shared by each reduced effort scenario and the best scenario using a 10-planning unit moving window across the ranking from lowest to highest conservation priorities. This analysis gave a measure of similarity across the entire ranking and made it possible to determine whether, for example, there was high agreement between scenarios for the highest ranked planning units, but low agreement for the lowest ranked planning units, or vice versa. We propagated the uncertainty of the FOS index for both analyses

by calculating correlations for each of 10,000 independent draws of the index's uncertainty distribution. Together, these analyses quantify how successfully the reduced effort scenarios can approximate the ranking of conservation value produced by the best scenario.

### *Contribution to uncertainty*

The uncertainty within data layers, which can arise from estimation uncertainty (Wilson et al. 2005, Rondinini et al. 2006) or stochastic biological processes (Game et al. 2008), is rarely incorporated into spatial planning (Lechner et al. 2014). Uncertainty in conservation is ubiquitous and often substantial, however, and methods that explicitly aim to make the best decisions under uncertainty can lead to better outcomes (Game et al. 2008). Quantifying how much uncertainty is added from each data layer can enable one to visualize the trade-offs between greater uncertainty and greater efficiency. To achieve this for each reduced effort scenario, we quantified the proportion of the uncertainty that is contributed by the excluded data layer as:

$$\frac{1}{N} * \sum_{i=1}^N [1 - CV(\text{reduced effort scenario } PU_i) / CV(\text{best available data } PU_i)],$$

where  $N$  is the number of planning units,  $i$ , and  $CV$  is the coefficient of variation.

### *Return on investment through more efficient networks*

Spatial planning with data that are more precise, accurate, or directly related to the target of interest presumably results in more efficient solutions for identifying the minimum set of land purchases required to meet a conservation goal. Given that conservation benefits are fixed, the

difference in cost between solutions identified by the best available data vs. reduced effort data is an intuitive and practically relevant index of the ROI of obtaining better data. We calculated this measure by identifying, for each scenario, the minimum set of planning units that meets conservation targets for a the least cost.

We identified minimum sets by sequentially choosing the planning unit with the highest conservation value until both conservation goals were met, recalculating the FOS after each step. We then estimated potential gains in efficiency from using the best available data compared to each reduced effort scenario as follows:

$$Cost/ha \text{ using } BEST = \frac{Total \text{ cost of } MinSet_{BEST}}{Targets_{BEST} \text{ contained within } MinSet_{BEST}}$$

$$Cost/ha \text{ using } RES = \frac{Total \text{ cost of } MinSet_{RES}}{Targets_{BEST} \text{ contained within } MinSet_{RES}}$$

$$Cost \text{ savings of } BEST = Cost/ha \text{ using } RES - Cost/ha \text{ using } BEST,$$

where *BEST* is the best scenario, *RES* is the reduced effort scenario, *MinSet*<sub>*BEST*</sub> is the minimum set identified using the best scenario, *MinSet*<sub>*RES*</sub> is the minimum set identified by the reduced effort scenario, and *Targets*<sub>*BEST*</sub> is the total extent of the targets, as estimated by the best scenario, that is contained within *MinSet*<sub>*RES*</sub> or *MinSet*<sub>*BEST*</sub>. We multiplied the cost to benefit ratios by 100 to obtain estimates in terms of cost/100 ha, since this is a more intuitive scale for planning than single hectares.

## Results

Estimates of the conservation value of different planning units using the best scenario had wide, but often still largely non-overlapping uncertainty bars (Fig. 1). Incorporating landowner likelihood of selling added the most estimation uncertainty (a mean of 22% of uncertainty in the conservation value estimates) and ignoring these data did not substantially affect rankings of conservation value or the efficiency of the minimum set of planning units needed to meet goals (Figs. 2, 3). Accordingly, we found a trivially small cost savings when incorporating data on a landowner's likelihood of selling (Fig. 2). When likelihood of selling was ignored, which assumes that all land is available for protection, the minimum number of planning units needed to meet conservation goals varied from 18 to 54, depending on the goal (Fig 2). In contrast, for every other scenario, not even protecting all land with likely sellers in every planning unit would be enough to meet goals (Fig. 2).

Incorporating high-resolution land cost data added substantial estimation uncertainty (11%), but also had the largest influence on conservation value rankings (Fig. 2). Ignoring costs altogether resulted in poor approximations of ranked conservation values (Fig. 2). Using the median value of agricultural land as a proxy produced ranked conservation values that were better than those when ignoring costs, but rankings were still only about 70-75% similar to those produced by the best scenario (Fig. 2). The agricultural land cost data tended to rank planning units similarly to the better cost data for the highest value planning units, but dissimilarly for the lower value sites (Fig. 3). Ignoring land costs altogether resulted in dissimilar rankings across the entire range of conservation values (Fig. 3). Adding high-resolution land cost data also produced the greatest cost savings among the alternative scenarios: as much as \$13 million/100 ha compared to using agricultural value and \$10 million/100 ha compared to ignoring costs for the 95% goal (Fig. 2). Compared to ignoring costs altogether, using agricultural value improved

conservation rankings, but produced less efficient minimum sets for the 66% and 95% conservation goals (Fig. 2). As expected, cost savings were generally higher for more ambitious conservation goals, as there was greater potential for increased efficiency in identifying minimum sets (Fig. 2).

Incorporating nest occurrence data added little estimation uncertainty (4.5%) compared to high-resolution land costs or data on likelihood of selling. Using remotely-sensed habitat layers or individual abundance as proxies for nesting occurrence produced rankings that were only approximately 75% similar to those from the best scenario. The planning units identified as having the highest conservation value by these ecological data proxies were not the same as those produced by the best scenario, although all ecological data sets identified similar planning units as being of lowest conservation value (Fig. 3). The use of nesting occurrence data produced a greater cost savings (\$6 million/100 ha) than high-resolution land cost data (\$5 million/100 ha) for the 33% goal, but otherwise the savings from better ecological data were small compared to costs. This high savings from using nest occurrence data for the least ambitious conservation goal suggests that data on bird abundance alone do a poor job of identifying the highest priorities. This result is supported by low similarity between this scenario and the best scenario for the highest value planning units (Fig 3).

## **Discussion**

Application of the general framework presented here would encourage efficient use of resources by allowing planners to quantify the likely consequences of proceeding with less than ideal data. For example, by focusing on a specific region, we were able to obtain ecological, cost, and human behavior data that would have been time consuming and costly to obtain over a larger

area. Results from these smaller regions can then be used to quantify the likely payoff of investments in obtaining these data across larger areas.

Perhaps more importantly, applying this framework to other systems would facilitate the accumulation of evidence that could be used to find generalities about which types of data are likely to be most important for spatial planning in different social and ecological contexts. For example, it was perhaps not surprising that in our planning region both costs and ecological data provided cost savings that were substantial compared to the cost of collecting the data. Land in coastal areas is costly, so even small improvements in efficiency have the potential to lead to significant cost savings. For instance, although exact comparisons are hard to make, each of our more detailed data sets was produced for ~US\$200,000-300,000 and with substantial other information gains not used here. In contrast, estimated cost savings are in the millions of dollars, suggesting substantial return on investment.

Previous research also has shown that saltmarsh sparrow nesting is often weakly correlated with the number of individuals in an area and that large areas of saltmarsh habitat are not used for nesting (Meiman and Elphick 2012). Consequently, we would expect habitat area and individual abundance to be less effective proxies than they might be for other species. Still, for our planning scenarios, the cost savings for better land cost data were more than an order of magnitude greater than those for ecological data for the more ambitious conservation goals. This discrepancy suggests that if there are limited resources for data collection or if threats are so immediate that delaying conservation action could substantially worsen outcomes, as is true for our planning region (Field et al. 2016), obtaining better land cost data is likely to be the smarter investment.

We found strong evidence for spatial variation in the likelihood that coastal landowners would be willing to sell their land to a conservation organization (Fig S2), but the pattern and strength of this variation was not large enough to influence conservation priorities as much as variation in ecological data or costs. The overwhelming importance of costs, driven by spatial variation, has been found previously (Naidoo and Ricketts 2006, Zhu et al. 2015). Incorporating information on land availability did not alter spatial priorities, it drastically changed the outlook for whether it is possible to meet conservation goals in our planning region. This critically important result raises questions about whether the action considered is likely to be a smart use of limited resources, and highlights the need to investigate the trade-offs between conserving tidal marshes versus other ecosystems.

For the analyses presented here, we compared reduced effort data against the best available data, which themselves are imperfect. Importantly, though, each data layer that we considered in the best scenario had robust uncertainty estimates, which we propagated by estimating conservation value across the full posterior distributions. By doing this we also addressed the inherently uncertain nature of cost data, which is a common source of criticism in conservation planning (Arponen et al. 2010).

For this analysis, we used the FOS index because it is well suited for both site prioritization and identifying minimum set solutions, and encourages a focus on ROI, which is a powerful framework for determining conservation priorities (Naidoo and Ricketts 2006, Withey et al. 2012). The framework presented here is not dependent on the spatial planning method used, however. For example, the approach for estimating the cost savings of data layers could easily be replicated using popular tools such as Marxan (Watts et al. 2009).

Our results highlight the potential for large efficiency gains when using high quality cost data. We combined intensive data collection and a spatial regression model to estimate costs, an approach that is similar to hedonic pricing (e.g. Tyrväinen 1997). Other approaches to estimating costs might also be appropriate, including those that are quite different from our method (e.g. Withey et al. 2012). Consequently, an emphasis on understanding and predicting spatial variation in conservation costs, akin to recent improvements in estimating species distributions (e.g. Guisan and Thuiller 2005), could improve the effectiveness of spatial conservation planning greatly.

In our example, the large savings provided by better cost data arose in part because the spatial resolution of the proxy for cost was low compared to the spatial resolution of the ecological proxies. This discrepancy in spatial resolution is likely to be representative of typical spatial planning problems. High-resolution, remotely-sensed habitat layers are freely available for many parts of the world, and the development of cost layers typically does not receive the same degree of attention as the development of ecological layers. As more sophisticated cost models become commonplace, however, the approach we present here would be useful for improving our understanding of what level of sophistication is likely to result in the most efficient use of conservation resources.



## Figures and tables

Table 1. The types and sources for data layers used for spatial planning.

Index	Type of data	Data layer	Source
1	Ecological target: marsh migration	Projections of tidal marsh migration	Hoover 2009
2	Ecological target: saltmarsh sparrow nesting habitat	Saltmarsh sparrow nesting occurrence	Meiman and Elphick 2012
3	Ecological target: saltmarsh sparrow nesting habitat	Saltmarsh sparrow abundance	Wiest et al. 2016
4	Ecological target: saltmarsh sparrow nesting habitat	Extent of current tidal marsh	Hoover 2009
5	Economic cost	The cost of land purchase adjacent to tidal marsh	Bayesian regression using tax assessors data
6	Economic cost	Median cost of land purchase in coastal counties	US Census
7	Human behavior	Behavioral intentions of coastal landowners with respect to land purchase	Analysis of data from Field et al. 2016

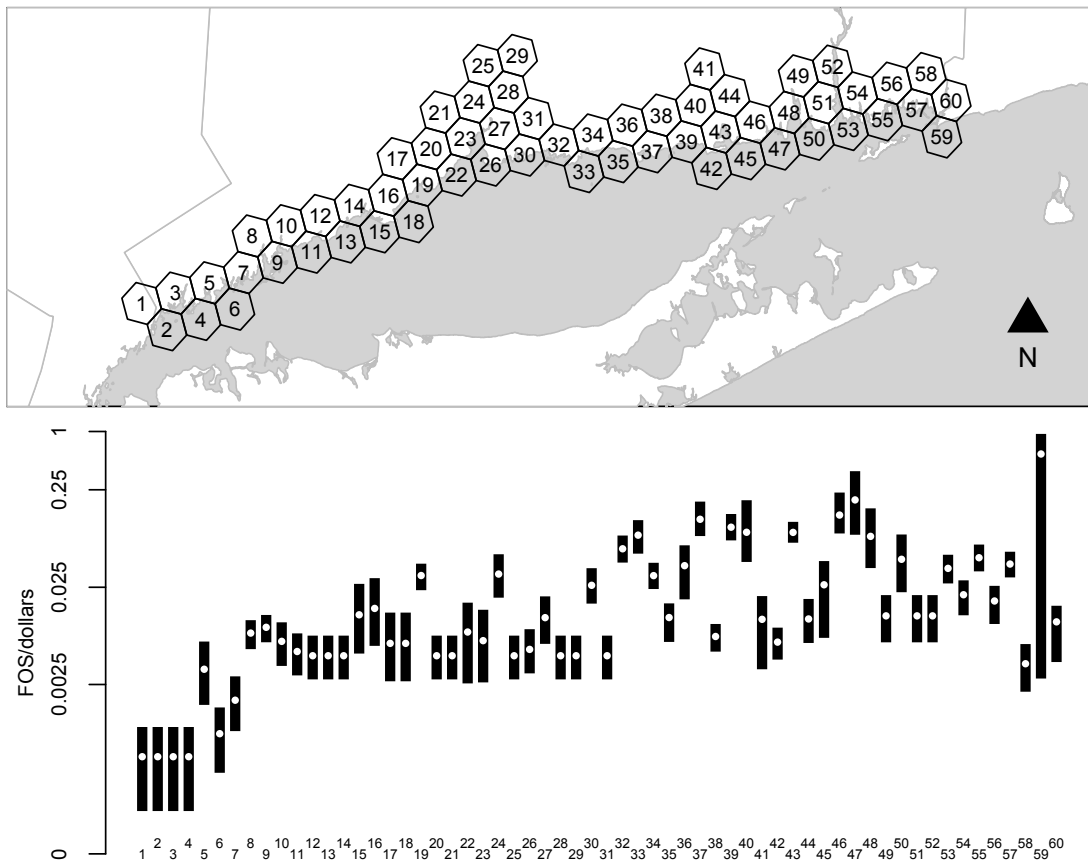


Figure 1. Estimates of conservation value for planning units across the north shore of Long Island Sound, USA, using the best available data. Top: The hexagonal planning units with numerical indices that correspond to the bottom graph. Bottom: For each planning unit, conservation value is measured using the fraction-of-the-spares (FOS) index divided by the total value of land available for purchase. Black bars show the 95% confidence bounds; white dots show means.

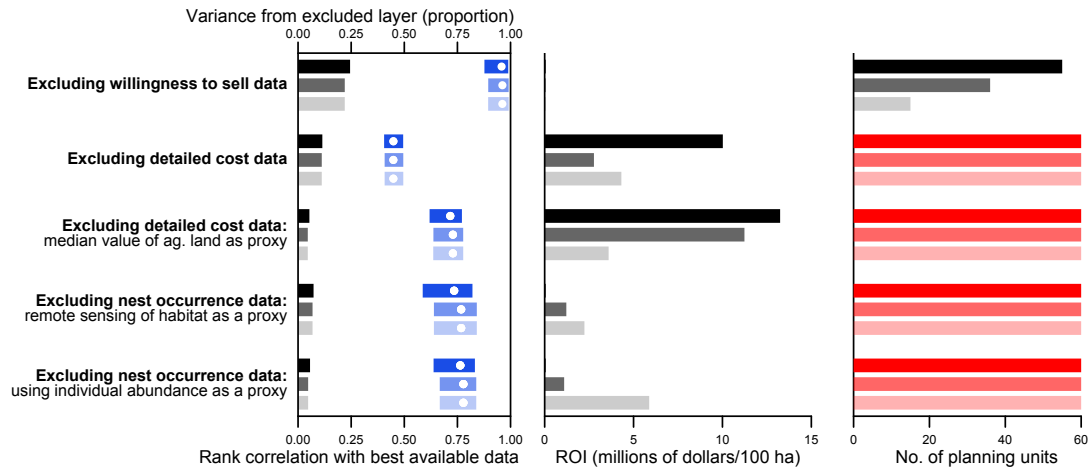


Figure 2. Comparisons between the scenario using the best available data and five scenarios that use reduced effort data. For all plots, lighter to darker colors correspond to the 33%, 66%, and 95% conservation goals, respectively. Left: Blue bars show the 95% confidence bounds for the correlations between the conservation value rankings produced by the best available data and the corresponding reduced effort scenarios listed on the left; white dots show means. For each reduced effort scenario, the proportion of the uncertainty in estimating conservation value that is contributed by the excluded data layer is shown by grayscale bars. Middle: The cost savings in terms of solution efficiency, of using data on nesting occurrence, high-resolution land cost, and likelihood of selling compared to the associated reduced effort scenarios listed on the left. Right: The minimum number of planning units needed to meet conservation goals for each scenario listed on the left. Solutions that did not meet conservation goals, despite incorporating all planning units in our planning region, are shown in red.

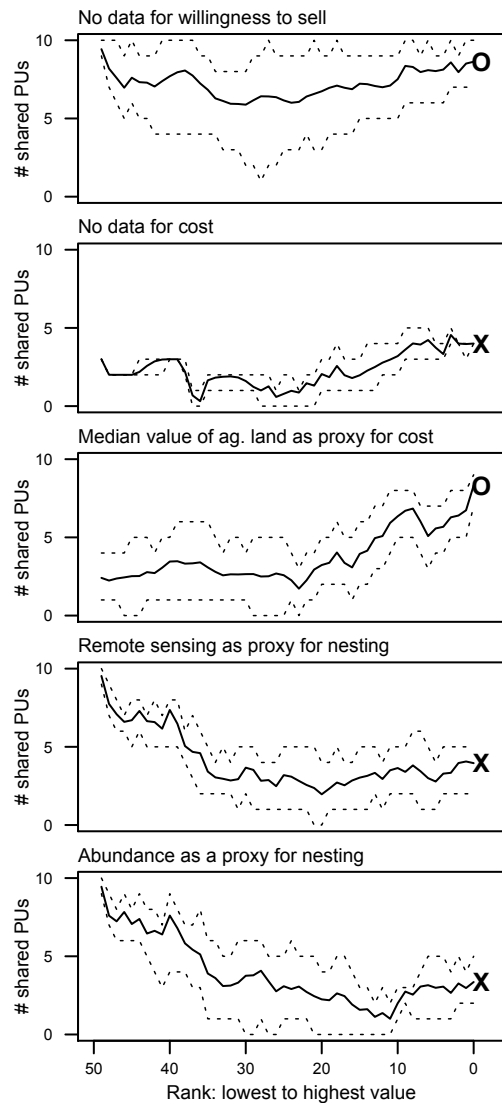


Figure 3. The number of planning units, in a 10-unit window, that co-occur in matched windows for the rankings produced by the scenario using the best available data and each reduced effort scenario (shown for the 66% goal; results were not sensitive to how ambitious goals were). Solid lines show the mean number of shared planning units for the 10-unit moving window, and dotted lines show 95% confidence bounds. The highest ranked planning unit is marked with an O if it is the same for the reduced effort scenario and the best available data scenario, and marked with an X otherwise.

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## Supplementary Information

### *Analysis of cost data*

We randomly selected 2,848 parcels from within the marsh migration zone and looked up their assessed value from individual town tax assessors' databases. For each parcel, we divided the assessed value by 0.7, as properties in our planning region are assessed at 70% of market value. We modeled the value of parcels using Bayesian lognormal regression with an effect for parcel size and a random effect for town. We used uninformative priors for all parameters (see model code). The posterior distributions for the effect of parcel size and the town-level random effect were both well above zero, suggesting that their inclusion in the model was warranted (Fig. S1). We predicted the total cost of unprotected land in the marsh transgression zone for each planning unit by 1) matching each planning unit to the town that contains the majority of its extent, 2) drawing from the posterior predictions of median cost/ha of land in the migration zone for that town, and 3) multiplying posterior draws by the extent of unprotected land in each planning unit that is likely available for purchase (see *Analysis of Likelihood of Selling*). We repeated this process for 10,000 draws of the posterior predictions so that the resulting posterior predictions for the cost of land in the migration zone included uncertainty from parameter estimation. For towns that by chance were not represented in the random sample (because they had a very small extent of marsh migration), we used the posterior prediction for a new town, which includes the uncertainty described by the variance parameter of the town random effect (see Fig. S1). We fit models using JAGS (Plummer 2016) in R (R Core Development Team 2015) with the R2jags package (Su and Yajima 2015). We used uninformative priors for all variables (see model code). We ran three chains for 100,000 iterations after a 25,000-iteration burn-in; the potential scale reduction factors (Brooks and Gelman 1998) for all parameters were less than 1.01.

### *Analysis of Likelihood of Selling*

We estimated landowners' likelihood of selling their land to a conservation organization using data from Field et al. (2016). We used logistic regression to model the probability that a landowner would respond that they were likely or very likely to sell, as opposed to one of the other Likert-scale responses: strongly unlikely, unlikely, or neutral. We included a random effect for town, the standard deviation for which was well above zero, suggesting strong evidence for spatial variation in intentions (Fig. S2). We tested whether a random effect by planning unit better explained the spatial variation in our dataset by comparing WAIC values (Gelman et al. 2013b) between models with random effects by town (WAIC: -593.9; pD: 2.2; lppd: -591.7) and planning unit (-595.7; 2.2; -593.5), as well as a model with no random effect (-603.6; 0.2; -603.4). Because the WAIC values for models with town and planning unit random effects were similar, and both were smaller than the model with no random effect, we chose the town random effect so that all socio-economic data were estimated at the same spatial scale. For 10,000 draws of the posterior predictions of intentions for each town, we multiplied the proportion of landowners who would be likely or strongly likely to sell their land by the extent of the migration zone to estimate how much of this extent is likely available for purchase, with confidence bounds for the estimation uncertainty of the statistical model.

### *Propagating the uncertainty of nest occurrence data*

We obtained and propagated uncertainty for both parameter estimation and sampling variance of the binomial model used to estimate nesting occurrence. To do this, for each of 10,000 draws from the posterior distributions of the model parameters, we estimated the total hectares within

each planning unit that contained saltmarsh sparrow nesting as the sum of Bernoulli random variables:

$$\sum_{i=1}^{C_y} rBernoulli(p_i),$$

where for planning unit  $y$ ,  $p_i$  is the probability of nesting in cell  $i$ , and  $C_y$  is the total number of cells (cells are from Meiman and Elphick 2012).

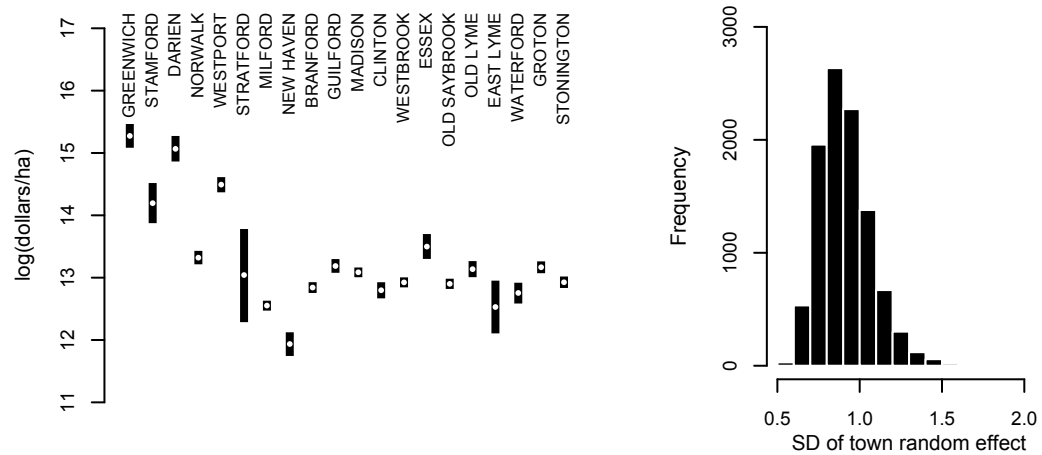


Figure S1. The median cost of land/ha for towns in our planning region. Left: Black bars are 95% credible intervals from the posterior predictions; white dots are the posterior means. Right: The posterior distribution for the standard deviation of the random effect for town is largely non-zero, providing evidence for spatial variation in land cost.

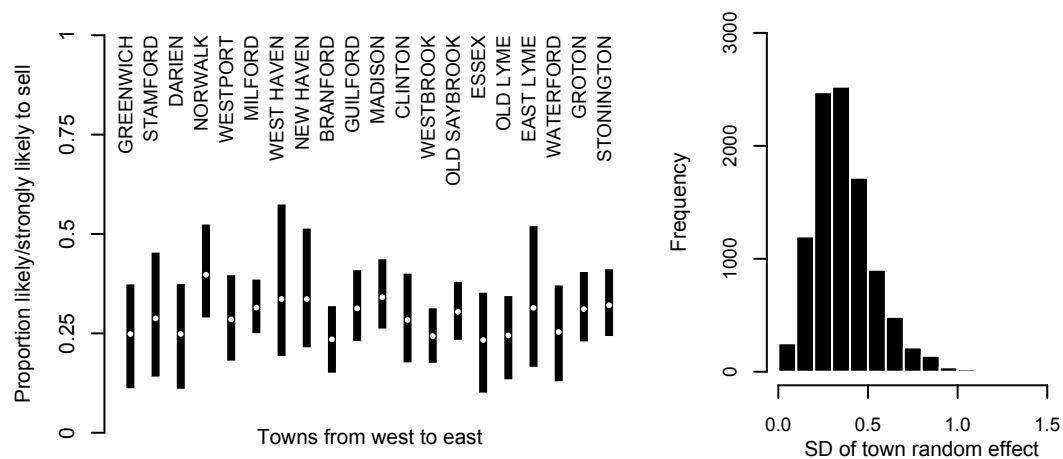


Figure S2. The proportion of landowners who would report being likely or strongly likely to sell their land to a conservation organization, by town. Left: Black bars are the 95% credible intervals for posterior predictions; white dots are posterior means. Right: The posterior distribution for the standard deviation of the town random effect was largely non-zero, providing evidence for spatial variation in likelihood of selling.

*JAGS code for estimating land value*

```
#prior for residual variation
sd ~ dunif(0, 1000)
tau <- 1/(sd*sd)
#prior for variance term of town-level random effect
sd2 ~ dunif(0, 1000)
tau2 <- 1/(sd2*sd2)
#prior for intercept of regression equation
Int ~ dnorm(0, 0.001)
#prior for regression coefficient for property size
B ~ dnorm(0, 0.001)

#town random effect, for 20 towns
for(i in 1:20){
  townRE[i] ~ dnorm(0, tau2)
}
for(i in 1:length(logvalue)){
  #regression equation; town is a vector that indexes the town of property i
  mu[i] <- Int + B*hectares[i] + townRE[town[i]]
  #land value is log-normally distributed, so the log of the response variable is normally
  distributed
  logvalue[i] ~ dnorm(mu[i], tau)
}
```

*JAGS code for estimating the proportion of likely sellers*

```
#prior for intercept
Int ~ dnorm(0, 0.001)
#prior for variance term of the town-level random effect
sdtowns ~ dunif(0, 1000)
tautowns <- 1/(sdtowns*sdtowns)

#town random effect, for 20 towns
for(i in 1:20){
  townRE[i] ~ dnorm(0, tautowns)
}

for(i in 1:length(LikelyorStronglyLikely)){
  #regression equation; town is a vector that indexes town for respondent i
  logit(mu[i]) <- Int + townRE[town[i]]
  #response variable is 1 if landowner reported being likely or strongly likely to sell their land, 0
  otherwise
  LikelyorStronglyLikely[i] ~ dbern(mu[i])
}
```

## **How does choice of statistical method to adjust counts for imperfect detection affect inferences about animal abundance?**

### **Abstract**

1. There is ongoing debate about the value of increasing model complexity in ecology, especially as it relates to models that correct occupancy or abundance estimates for imperfect detection. While both arguments for and against increasing complexity have merit, there is a need for greater clarity on how to determine what level of complexity is necessary. We present a general approach and case study for comparing alternative detection methods that vary in their complexity. Our approach puts emphasis on the logistical costs of methods, which are often overlooked in the debate about method complexity, and developing models that address common sources of error in ecological datasets while avoiding unwarranted complexity.
2. We used point counts of saltmarsh sparrows (*Ammodramus caudacutus*) to compare estimates of abundance from three alternative protocols that vary by logistical costs: single observer, multiple observers, and multiple visits. We also compare results from counts to those from captures and nest searches from the same populations to provide much needed broader context for the evaluation of point count methods.
3. We found that parameter estimates derived from alternative count protocols were similar and that predictions of point-level abundance were highly correlated ( $r = 0.96$ ). We found little correlation between pairwise comparisons of abundance estimated from point count data, the number of individuals captured, and the number of nests (all comparisons  $r = 0.5$

or less).

4. Choosing point counts over more direct measures may have a greater effect on inferences than choosing among specific count protocols. For saltmarsh sparrows, there is likely little added benefit to adopting count protocols that require additional logistical costs. Determining the frequency of cases like this has broad implications for the appropriate design of studies that rely on estimates of abundance, especially when resources are limited. The general approach we present can be used to assess whether general rules of thumb can be developed to benefit people charged with implementing field studies and allocating limited resources.

## **Introduction**

The increasing sophistication of analysis methods to better handle the noise and sources of bias in ecological datasets has lead to greater confidence in inferences and made it possible to investigate a wider range of questions in ecology (Gimenez et al. 2014). Greater sophistication, however, often comes with the cost of increased complexity, which can hamper implementation in various ways, including the need for additional statistical expertise, reduced accessibility of results to other ecologists and to land managers (LaDeau 2010), increased probability of making a mistake when implementing a complex model (Gimenez et al. 2014), increased potential for overlooking the information contained in historical datasets that cannot support modern methods, and problems with parameter identifiability (Welsh et al. 2013). Determining the best ways for ecologists to navigate this trade-off has resulted in a debate between those who, correctly, see the benefits of more sophisticated analytical methods and those who, also correctly, have concerns about the increased difficulty, relative to the benefits, of implementing more complex methods.



The debate over model complexity has been especially prevalent in discussions about occupancy and detection models (as shown by debate on the Dynamic Ecology blog; McGill 2013), which use additional model components to correct estimates of abundance or occupancy for imperfect detection. Failing to account for imperfect detection can substantially bias inference about species abundance and occupancy (Kéry & Schmidt 2008), but correcting this bias often requires that ecologists design studies that incorporate additional field methods, which have associated costs, in order to provide information on detection. It is important to note, however, that detection is often considered to be simply a nuisance parameter that must be accounted for in order to get unbiased estimates of abundance or occupancy, which are usually the true objects of inference (Royle and Dorazio 2006).

Logistical costs are often overlooked in evaluations of alternative analytical methods, but in practice both analytical and logistical costs are likely to influence the implicit cost-benefit analysis field ecologists use when choosing methods. Recent studies using occupancy and abundance surveys have demonstrated how framing method comparisons in the context of logistical constraints can provide ecologists with guidance for balancing field costs with statistical rigor (e.g. Field et al. 2005; Bornand et al. 2014; Banks-Leite et al. 2014). The logistical costs for detection models primarily depend on how information on detection rates is obtained. Most often, there is replication in the survey design in one or more dimensions, usually over time and/or by having multiple individuals conduct surveys simultaneously. Replication over time can be either short-term (e.g. using time intervals to track individual detections temporally; Farnsworth et al. 2002; Alldredge et al. 2007a) or long-term (e.g. visiting the same plot multiple times; Royle 2004a). Single-observer/single-visit designs typically require little to no additional costs compared to methods that do not account for detection. Multiple visit

methods take more time and require more frequent travel between study sites. Multiple observer methods require hiring and training more individuals than might otherwise be needed.

While there have been many studies comparing the relative performance of alternative detection methods (e.g. Moore 2004; Alldredge et al. 2007b; Reidy et al. 2011), there has been comparatively little research on how results from these methods, which often use count data, compare to more direct measures of abundance (e.g. marking and recapturing individuals) or measures that are more directly related to population dynamics (e.g. total number of reproducing individuals; see DeSante 1981). Such comparisons would provide important context for framing the debate about whether effort is better spent correcting count data for detection or collecting more direct or intensive data that may be less subject to biases that require analytical correction (freeing analysts to focus directly on the parameters of interest).

To resolve the debate surrounding method complexity, especially for detection methods, it would be helpful to have a framework for comparing methods and systematically assessing when additional analytical complexity is needed. Such a framework for generating relevant evidence would facilitate the transition from debate into evidence-based inquiry. Our paper presents a generalizable case study, in which we: 1) designed a field protocol that enables us to compare alternative methods as well as make 1:1 comparisons to more direct measures of abundance, 2) use logistical costs to inform which comparisons are likely to be the most informative and increase the relevance of the results to real-world decision making, 3) conduct comparisons within a single modeling framework to make it possible to combine methods and make the relationship between methods more apparent, and 4) build models guided by posterior predictive checks whenever models are expanded to avoid unwarranted model complexity.

We focus on avian point counts, which have seen a proliferation of methods to account for imperfect detection. Some widely used examples include distance sampling (Buckland 2001), time-of-detection (Farnsworth et al. 2002; Alldredge et al. 2007a), double-observer (Nichols et al. 2000), and multiple-visit (Royle 2004a) methods. These methods vary greatly in their analytical and logistical complexity. For example, relatively inexpensive time-of-detection methods require only one observer while other proposed methods, which have the potential to produce better estimates of detection, can require up to five or more observers (e.g. Alldredge et al. 2006).

We combined point count, capture, and nest density datasets collected simultaneously on the same populations of saltmarsh sparrows (*Ammodramus caudacutus*) to 1) compare different methods of collecting count data to determine whether they produce substantially different conclusions, and 2) determine how well results from counts correlate with population sizes obtained by more intensive methods. Saltmarsh sparrows represent a good case for applying detection models: First, their habitat (mainly low-growing herbaceous grasses, such as *Spartina alterniflora* and *S. patens*) is structurally simple and homogenous, reducing the effect of habitat heterogeneity on detection rates. Second, because tidal marshes are open and saltmarsh sparrows are non-territorial and sing both infrequently and quietly, observers detect both sexes primarily by sight. These features make it more likely that abundance estimates are based on the entire population, unlike many bird species, for which it is primarily singing males that are sampled. Finally, in our survey area, saltmarsh sparrows were the most numerous bird species and there were rarely more than three species detected, both reducing the risk of identification errors and the possibility that observers would be distracted by the activities of non-focal species (cf. Alldredge et al. 2007b).

We compare the results from a point count survey design that allows comparisons of results based (i) on a single observer (using time-of-detection), (ii) two observers, and (iii) multiple visits. We included an effect of distance from observer within each of these three methods rather than distance sampling (*sensu* Buckland 2001) because the assumption of perfect detection at the location of the observer cannot be met for tidal marshes, which are dominated by short, dense vegetation. In keeping with the focus on logistical costs, the two-observer models that we consider also included a time-of-detection component (because these methods impose little additional logistical costs; see Figure 1). All point count methods are then compared to more direct, but much more time intensive, measures of abundance – capturing individuals and nest searches. Both methods require sampling periods on the order of hours, rather than minutes as with point counts.

## **Methods**

### *Data collection*

We surveyed 120 1-ha plots in salt marshes along the Connecticut, USA, coast during 2002-2008. We visited each plot 3-5 times between 30 May and 31 August. Most plots were randomly located by simple random sampling within marsh complexes. For additional details on plot selection, see Gjerdrum et al. (2008). Three types of abundance data were collected at each plot: point count detections, capture events, and nest totals. All three types of data were collected at each plot during the same time frame each day, making a direct comparison possible using simple correlations.

Point count data were collected on all bird species found within the marsh or at the marsh edge; here we use only information from saltmarsh sparrows, one of the most frequently detected species. Our count protocol included (removal-based) time-of-detection (Farnsworth et al. 2002), dependent double-observer (Nichols et al. 2000), distance-based (Buckland 2001), and multiple-visit (Royle 2004a) methods. For the time-of-detection protocol, we used a five-minute count divided into one-minute intervals. For the double-observer protocol, the primary observer called out detections (following the time-of-detection protocol) to the secondary observer, who also recorded any detections missed by the primary. We recorded the distance to the observer for each detection using bands at 0-25 m, 25-50 m, and > 50 m; we only use data from 0-50 m here. We conducted all point counts before 11:00, with more than half conducted before 07:00. In total, 16 different observers conducted counts.

We mist-netted and banded sparrows during 3-hour banding sessions for each visit, all of which were completed by 11:00. For each session, we used an array of six, 12-m mist-nets, placed along a different side of the plot during each visit. We drove birds into the net arrays by systematically walking through the plot toward the nets at regular intervals during each visit. For each session, we summed the number of unique individuals captured, excluding hatch-year birds, for the analysis. We searched for nests by systematically walking the plots and flushing females from nests and by carefully searching suitable nesting areas. Previous analyses have shown that over 85% of nests were found prior to hatching, suggesting that we missed few active nests (Gjerdrum et al. 2008; Bayard and Elphick 2011). In the following analysis, we used the total number of active nests found over all visits.

## *Statistical methods*

We modeled count data using hierarchical models of detection and abundance, which allowed us to construct models that were appropriate for our sampling design of small count areas sparsely distributed over a large landscape (Royle 2004b; Royle and Dorazio 2006). We developed the specific structure of models by starting with a simple observation process and adding complexity using continuous model expansion guided by posterior checks at each step to determine whether the additional model complexity was warranted (cf. Gelman et al. 2004; Gelman and Shalizi 2013). Specifically, we devised expanded models, within which the simpler models were nested, based on our knowledge of the system and commonly recognized sources of variation in point count data. We then checked the posterior distribution of the additional parameter of the expanded model to determine whether the 95% credible interval did not overlap zero, which would suggest that the expanded model is warranted (Kruschke 2013).

We started with a single-observer model for which information on detection was collected using removal-based time-of-detection (Farnsworth et al. 2002) with a five-minute count divided into one-minute intervals. Plots of detections over time showed evidence of double-counting individuals in the last minute with more detections in minute five than minute four. The probability that a removal process without double counting would produce this pattern is  $< 0.0003$  using parameters that could produce totals similar to our observed data (5 observation intervals; total abundance = 800; per-minute detection = 0.25). Accordingly, only minutes one through four were used for analysis. The observation process was represented, following Royle (2004b), using a multinomial distribution with cell probabilities:

$$\text{eqn 1} \quad \pi_1 = p$$

$$\pi_2 = (1 - p)p$$

$$\pi_3 = (1 - p)^2 p$$

$$\pi_4 = (1 - p)^3 p$$

where  $p$  is the constant, per-minute probability of detecting an individual, and  $\pi_j$  is the probability of first detecting an individual in minute  $j$ . The focus of the first steps of model building was on variables that potentially affect the observation component of detection: the probability that an observer detects an individual given that it makes itself available for detection during the count. To isolate the availability component of detection for this initial stage of model building, we used the conditional multinomial likelihood:

$$\text{eqn 2} \quad f(Y_{obs_i} | N_i, p) = \frac{Y_{obs_i}!}{Y_{obs_{i1}}!Y_{obs_{i2}}!Y_{obs_{i3}}!Y_{obs_{i4}}!} \left( \frac{\pi_1}{1 - \pi_0} \right)^{Y_{obs_{i1}}} \left( \frac{\pi_2}{1 - \pi_0} \right)^{Y_{obs_{i2}}} \left( \frac{\pi_3}{1 - \pi_0} \right)^{Y_{obs_{i3}}} \left( \frac{\pi_4}{1 - \pi_0} \right)^{Y_{obs_{i4}}}$$

where  $\pi_0$  is the probability of not observing an individual during a four-minute count,  $(1 - p)^4$ , and  $Y_{obs_{ij}}$  is the total number of individuals observed during minute  $j$  at point  $i$ . We modeled variation in  $p$  using a linear equation:

$$\text{eqn 3} \quad \text{logit}(p_i) = \alpha + \beta_{observer} * \text{observerID}_i$$

where  $\alpha$  is an intercept term,  $\beta_{observer}$  is a vector of regression coefficients describing the observer effects, and  $\text{observerID}_i$  is a vector that indexes which observer conducted the count at point  $i$  (e.g. [0, 0, 1, 0, 0, ... 0, 0] indexes observer three). The observer effects,  $\beta_{observer}$ , were treated as a normally-distributed random effect (eqn 5). Doing so reduced the number of parameters to

estimate and made it possible to use borrowing strength (cf. Schaub & Kéry 2008) from observers who conducted many counts to get better estimates for observers who conducted few.

$$\text{eqn 5 } \beta_{\text{observer}} \sim \text{normal}(0, \tau_{\text{observer}})$$

The variance parameter,  $\tau_{\text{observer}}$ , gives an estimate of the magnitude of variation in  $p$  due to observer differences, which will be close to zero if variation among observers is small.

Double-observer models were built from the single-observer model outlined in eqns 1-5 by adding a uniquely-defined detection parameter for the second observer,  $p_2$ , to the multinomial cell probabilities in eqn 1:

$$\text{eqn 6 } \pi_{11} = p_1$$

$$\pi_{12} = (1 - p_1)p_1$$

$$\pi_{13} = (1 - p_1)^2 p_1$$

$$\pi_{14} = (1 - p_1)^3 p_1$$

$$\pi_{21} = (1 - p_1)^4 p_2$$

$$\pi_{22} = (1 - p_1)^4 (1 - p_2)p_2$$

$$\pi_{23} = (1 - p_1)^4 (1 - p_2)^2 p_2$$

$$\pi_{24} = (1 - p_1)^4 (1 - p_2)^3 p_2$$

$$\pi_{00} = (1 - p_1)^4 (1 - p_2)^4$$



where  $\pi_{kj}$  is the probability of an individual being observed by observer  $k$  in minute  $j$ , and  $\pi_{00}$  is the probability of an individual being missed during the survey by both observers. To test whether the act of recording data influenced the second observer's detection probability (e.g. by distracting them), we built a model that included an effect of observer role on detection rate:

$$\text{eqn 7 } \text{logit}(p_i) = \alpha + \beta_{\text{observer}} * \text{observerID}_i + \beta_{\text{role}_i} * \text{role}_i$$

where  $\text{role}_i$  is 1 if the observer is recording the data, 0 otherwise.

To test whether adding model complexity was warranted to account for any potential decline in detection with increasing distance from the observer, we fit a model with a distance effect (eqn 8). Because distance is an individual-level covariate, including it requires changing the model replicates,  $i$ , from point locations to individuals.

$$\text{eqn 8 } \text{logit}(p_i) = \alpha + \beta_{\text{observer}} * \text{observerID}_i + \beta_{\text{distance}} * \text{distance}_i$$

Finally, we conducted posterior checks to test whether time of year when the survey was conducted (days elapsed since 1 May) influenced detection.

$$\text{eqn 9 } \text{logit}(p_i) = \alpha + \beta_{\text{observer}} * \text{observerID}_i + \beta_{\text{date}} * \text{date}_i$$

The models described so far only address the probability that an observer detects an individual given that it makes itself available for detection during the count. To incorporate into the model the probability that an individual makes itself available, as well as abundance ( $N_i$ ), the parameter of inferential interest, we added to each detection model the component of the full multinomial likelihood that is missing from the conditional likelihood in eqn 2:

$$\text{eqn 10 } Y_{\text{obs}_i} \sim \text{binomial}(1 - \pi_0, N_i)$$

Fitting a model that includes both eqn 10 and eqn 2 simultaneously is equivalent to using the complete multinomial likelihood. At this point, it is possible to incorporate a multiple-visit component to the model (Royle 2004a), which could provide additional information that would aid in estimating detection. The typical home range size of both male and female saltmarsh sparrows is larger than the size of our 1 ha plots (Shriver et al. 2010), however, so we had an *a priori* belief that plots were not closed populations over the course of the sampling period. Closed populations are a key assumption of multiple-visit methods. Before incorporating this information into the models, therefore, we used simulations with a simple multiple-visit model to quantify the magnitude of the potential bias from violating the closure assumption (see *Supporting Information* for model code; Figure 3). The true abundance used in our simulations was three individuals per 1-ha plot, which is typical of the abundances observed in our dataset. We tested a design with three visits and the same number of plots as our dataset ( $n = 120$ ). We simulated the violation of the closure assumption by giving each plot an equal probability of (a) immigration of an individual from a different plot, (b) emigration of one individual, or (c) no immigration or emigration with respect to the plot boundaries between survey visits. We also simulated a scenario in which the abundance between visits was Poisson-distributed around the plot-level mean. Because violating the closure assumption was likely to bias our abundance estimates (see **Results**), instead of incorporating a multiple-visit component that assumes that the plot-level populations are closed over the sampling period, we allowed plot-level abundance  $N_{iv}$  to vary by location and visit,  $v$ , according to a Poisson distribution with a plot-specific mean and variance,  $\lambda_i$ :

$$\text{eqn 11 } N_i \sim \text{poisson}(\lambda_i)$$

With this structure we are in effect modeling a mean abundance over time for each plot,  $\lambda_i$ , so that the plot-level abundances across visits are Poisson random variables. Variation in  $\lambda_i$  is modeled as:

$$\text{eqn 12 } \log(\lambda_i) = \mu + \varepsilon_i$$

where  $\mu$  is an intercept term and  $\varepsilon_i$  describes variation in mean abundance among locations using a normally-distributed random effect with variance  $\tau_{plot}$ :

$$\text{eqn 13 } \varepsilon_i \sim \text{normal}(0, \tau_{plot})$$

For single and double-observer models, we used the posterior predictions of plot-level abundances to enable comparisons to total individuals captured and nest totals at each plot. We estimated Pearson's correlation coefficients between these totals and (i) unadjusted counts, (ii) mean posterior predictions from the single-observer model, and (iii) mean posterior predictions from the double-observer model.

All models were fit in a Bayesian mode of analysis using the software JAGS (version 3.2.0, Plummer 2003) in R (R Development Core Team 2013) using the R2jags package (Su and Yajima 2012). We standardized the covariate vector for survey date by subtracting the mean and dividing by two standard deviations (Gelman 2008). We used uninformative distributions for all priors. We ran three chains for each model with a burn-in period of 50,000 iterations. The three chains were run for 100,000 iterations; the potential scale reduction factors (Brooks and Gelman 1998) for all parameters were less than 1.01.

## Results

### *Model building*

For the single-observer model, the 95% credible interval of the distance effect overlapped zero (mean: 0.23; credible interval: -0.53 – 1.3), and was therefore not retained in the model. We then included a date effect, which was retained (0.62; 0.0020 – 1.3). Including a normal distribution to account for overdispersion was warranted, as the standard deviation was largely non-zero (1.2; 0.97 – 1.5). The four-minute, individual detection rate (mean among observers) of the final single-observer model was 0.61 (0.45 – 0.74) and the mean abundance was 1.1 birds/1-ha plot (0.73 – 1.4).

For the double-observer model, the standard deviation of the observer random effect was largely above zero (0.33; 0.14 – 0.60), indicating heterogeneity among observers, and the 95% credible interval of the role effect did not overlap zero (-1.9; -2.5 – -1.4), so both variables were considered important and retained. We then considered a distance effect (-0.12; -0.78 – .75), which was not retained, followed by a date effect (0.97; 0.21 – 2.0), which was retained. The inclusion of overdispersion was warranted, as the standard deviation of the normally-distributed variation was largely non-zero (1.3; 1.0 – 1.5). The four-minute, individual detection rate (mean among observers) of the final double-observer model was 0.63 (0.51 – 0.75) and the mean abundance was 1.0 birds/1-ha plot (0.73 – 1.4), almost identical to that for the single-observer model.

Simulations of the basic multiple-visit model show that abundance estimates are sensitive to violations of the closure assumption when plot-level abundance is very low, as is the case for our study design of widely-distributed sparse counts (Figure 3a,b; Figure S2). Regardless of detection rate, the model overestimated the number of birds in a plot when the closure

assumption was violated, with especially large uncertainty bounds and bias at low detection rates (Figure 3b; Figure S2). The model did not perform well when detection rates were low because of large uncertainty and/or unidentifiable parameters (Figure 3a).

### *Correlations of counts, captures, and nests*

We found only weak correlations between capture totals and unadjusted counts ( $r = 0.44$ ; 95% confidence interval:  $0.36 - 0.50$ ; Figure 4a), counts adjusted using the one-observer model ( $r = 0.48$ ;  $0.42 - 0.55$ ; Figure 4b), or counts adjusted using the two-observer model ( $r = 0.50$ ;  $0.44 - 0.56$ ; Figure 4c). Additionally, both models underestimated the total population size of the sampled area of our study (the posterior distributions of the sum of plot-level abundances using count data divided by the sum using capture data are shown in Figures 4b and 4c). We also found weak correlations between nest totals and unadjusted counts ( $r = 0.43$ ;  $0.28 - 0.57$ ; Figure 5a), counts adjusted using the one-observer model ( $r = 0.43$ ;  $0.28 - 0.57$ ; Figure 5b), or counts adjusted using the two-observer model ( $r = 0.50$ ;  $0.36 - 0.63$ , Figure 5c). In contrast, there was a high correlation between the estimates from one-observer and two-observer models ( $r = 0.96$ ;  $0.96 - 0.97$ ; Figure 6), both of which were also highly correlated with unadjusted counts (one observer:  $r = 0.95$ ;  $0.94 - 0.95$ ; two observers:  $r = 0.98$ ;  $0.98 - 0.99$ ).

## **Discussion**

Our results suggest that more complex survey methods, which often impose additional logistical costs, do not necessarily result in a better (or even substantially different) measure of abundance,

highlighting the need for comparisons of methods in other systems and with other types of ecological data to provide better guidance to field ecologists. While the best approach will need to be determined on a study-by-study basis (Banks-Leite et al. 2014), clearer patterns about when certain corrections are warranted may emerge as careful evaluations of alternative methods accumulate (Elphick 2008). Identifying such generalities would have enormous value in several respects. For example, unwarranted dependence on complex field methods could detract from biological understanding if it prevents the publication of analyses that use historical datasets initiated before accounting for detection became commonplace. Similarly, if biological inferences are not improved, the limited resources available for ecological and conservation studies could be wasted because of the perceived rigor of designs that account for detection. In this paper we are not suggesting that complex models should be shunned. But, we do believe that we need a more systematic approach to assessing when they are necessary and when they are not (Elphick 2008), and that our case study provides a useful framework for conducting the studies needed for such an assessment.

The flexibility of hierarchical models makes them well-suited to deal with less-than-perfect datasets, and gets directly to the parameter of interest, abundance (Royle & Dorazio 2006). However, model complexity comes with costs that even for widely implemented model structures are only beginning to be fully understood, such as the potential for higher Mean Squared Error as a result of reduced precision or non-identifiable parameters (see Welsh et al. 2013, Guillera-Arroita et al. 2014). The precision of abundance estimates was similar for single and double-observer models, but still fairly low, despite taking advantage of the borrowing strength of random effects, and lower than it would be for comparable models that do not incorporate a detection component. Moreover, complex models often require additional

assumptions that could introduce other biases when not met. For our system, for example, we had an *a priori* reason to suspect that a key assumption of multiple-visit methods (that survey areas are closed populations over the course of sampling) was not being met and would therefore introduce bias if a multiple-visit component was included. Our concern was validated using a simple simulation. Given the relatively small area and typically low density of point counts, even small violations such as a single bird moving in or out of the area can represent a large proportion of the population, making the multiple-visit method challenging to implement in these situations. It is possible that including a time-of-detection component to the double-observer model, while providing more information with which to estimate detection, also introduced bias. However, the only assumption of the time-of-detection method that we thought *a priori* was likely to be violated was double counting, which we minimized by reducing the count length. Removing the time-of-detection component from the double-observer model reduced abundance estimates, but not substantially (mean plot-level abundance was 0.76; 0.55 – 1.1; Figure S1).

The choice between point count correction methods was largely inconsequential for saltmarsh sparrows compared to the decision to use point counts versus collecting some other type of abundance data. Furthermore, ignoring detection would not have substantially biased measures of relative abundance between points, as the correlations between adjusted and unadjusted counts were quite high. However, ignoring detection would have resulted in biased estimates if one were interested in absolute abundance, as the detection estimates from both count methods were significantly less than one. Still, even corrected count data were biased low compared to banding data, demonstrating that biases in count data are not always adequately corrected by detection methods. In such cases, imperfect detection may not be the largest source

of bias, which is important context that is often overlooked in the debate surrounding detection bias in ecological data.

Nest searching and capture totals are both subject to their own biases. In the case of capture totals, one large source of bias is likely to be detection rate. Correcting for detection in our capture data, however, would have further increased the difference in total population size between point counts and total captures. Detection is potentially a problem with the nest data as well, although our previous works suggests that relatively few nests go undetected in the 1-ha plots that this study is based upon (Gjerdrum et al. 2008). More important, however, is that re-nesting could weaken the correlation by causing an overestimate in the number of breeding females in a plot, especially if plot-specific factors cause variation in re-nesting rates. We expect this bias to be low in this system because the primary source of nest failure and subsequent re-nesting is tidal flooding, which affects plots synchronously and consistently during spring tides (Bayard & Elphick 2011). Nonetheless, nest density, while likely to be a good index of breeding activity, is unlikely to provide complete estimates of population size without detailed information on re-nesting rates. This problem is exacerbated in species without a simple monogamous breeding system or with skewed and variable sex ratios, both of which apply to saltmarsh sparrows (Hill et al. 2010; Hill et al. 2013).

The methodological approach we have demonstrated here could be applied to additional case studies, which would aid in the development of general rules of thumb for choosing detection methods, as well as better understanding the role of model complexity in ecology in general. Such general guidelines would also benefit people charged with implementing field studies and allocating limited resources, especially if future studies emphasize the logistical costs of alternative methods. Explicitly incorporating monetary, or time, costs in future studies would



allow the relative merits of each approach to be cast in a more formal cost/benefit framework. Better understanding the costs and benefits of alternative methods would facilitate addressing questions of practical relevance, such as whether biases in estimates or choosing a particular way to measure abundance are likely to lead to incorrect inferences about ecological questions or bad decision-making when used as the basis for conservation or policy (Elphick 2008; Banks-Leite et al. 2014).

## Figure and tables

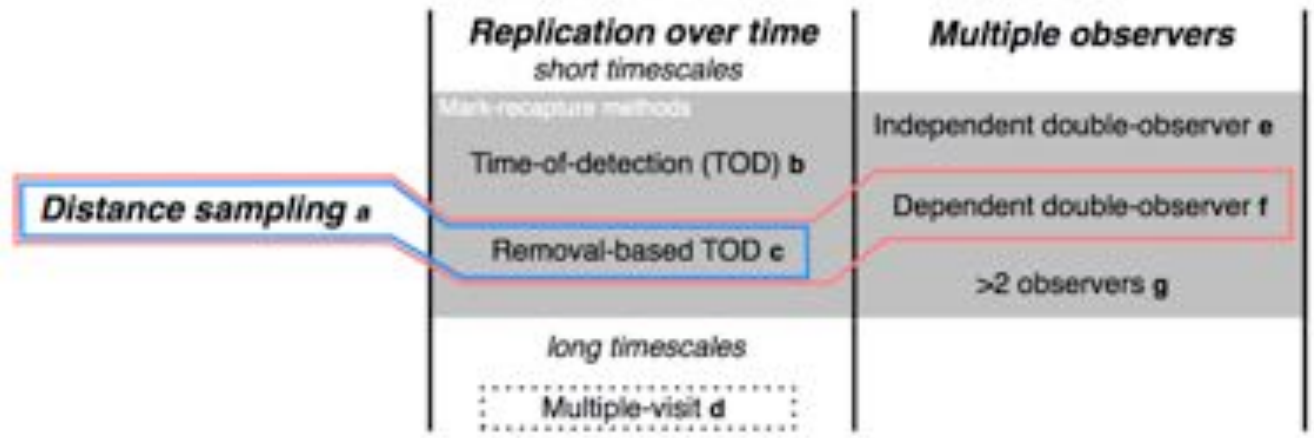


Figure 1. Commonly used methods for accounting for imperfect detection, grouped by how information on detection rates is obtained. The two models we compared in this paper are outlined in blue (a model that uses information from only one observer and has a distance component and removal process) and pink (a model that requires a distance component, removal process, and a dependent double-observer component). The line around the multiple-visit method is dotted because we consider it here, but were not able to use it in our final analysis (see **Results**). Examples of each method include: a) Buckland 2001, b) Alldredge et al. 2007a, c) Farnsworth et al. 2002, d) Royle 2004a, e) Forcey et al. 2006, f) Nichols et al. 2000, g) Alldredge et al. 2006.

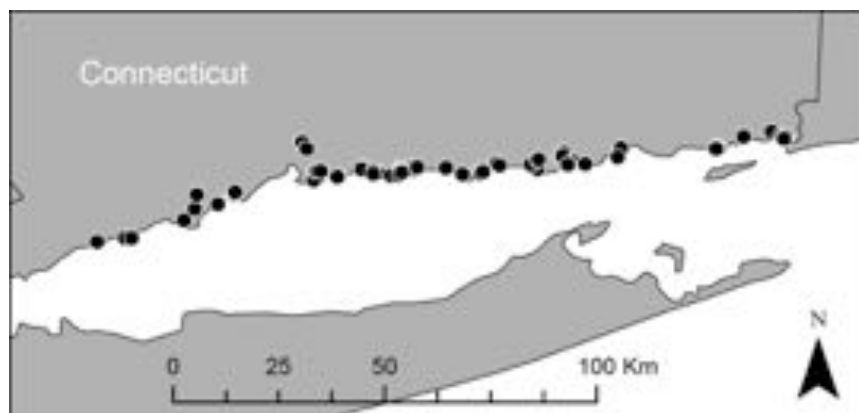


Figure 2. The distribution of 120 plots across coastal Connecticut.

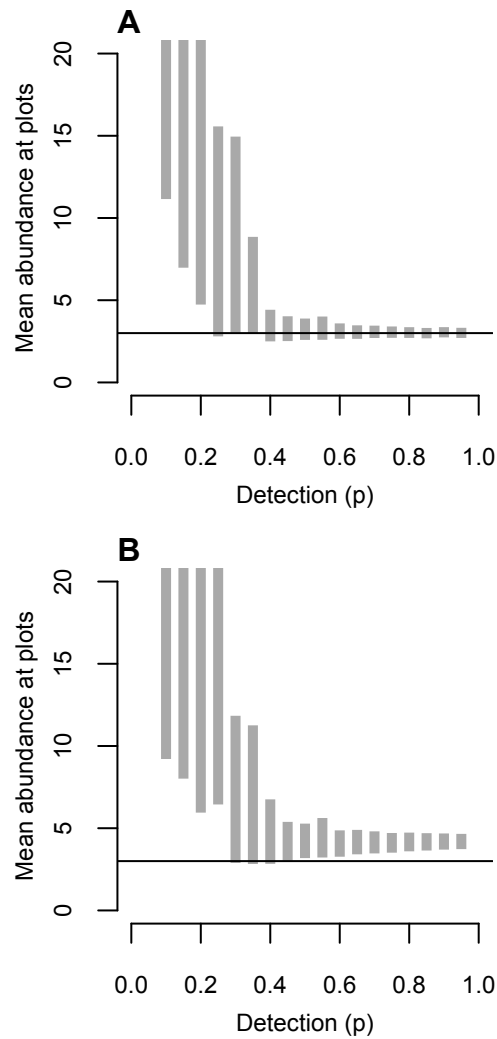


Figure 3. Tests of violation of the closure assumption for the multiple-visit method. A) No violation. Gray bars are the 95% credible intervals of the abundance estimate. B) Random temporary emigration: equal probability of a single individual moving in, a single individual moving out, or no movement. True abundance (three individuals) is marked by the horizontal black line. The horizontal axis shows the range of simulated detection rates.

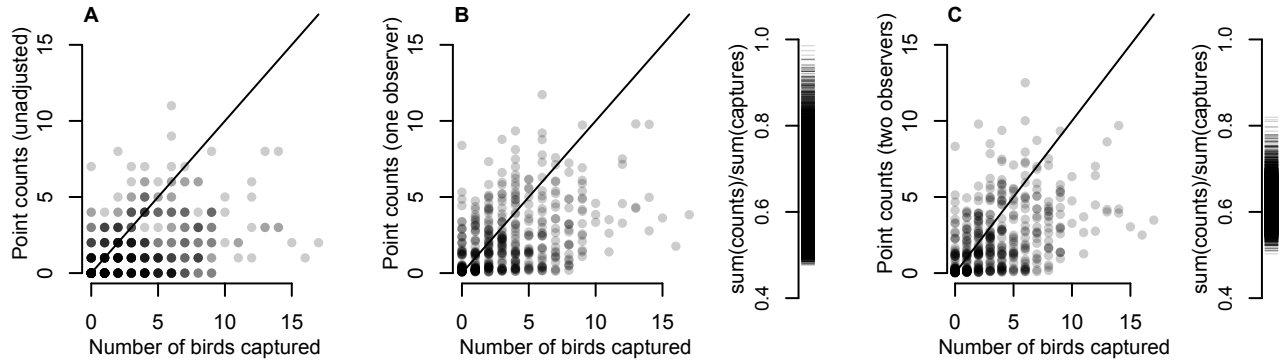


Figure 4. Correlations between estimates from count data and total number of captures. The total number of individuals captured during that visit's session vs. A) unadjusted counts ( $r = 0.44$ ), B) one observer ( $r = 0.48$ ), and c) two observers ( $r = 0.50$ ). Black lines show the 1:1 expectation and dotted lines show the linear least squares fit. For B) and C), draws from the posterior distribution of the sum of counts divided by the sum of captures are shown as tick marks to the right of the main plot. Uncertainty arises from estimating the plot-level abundance (using the count data).

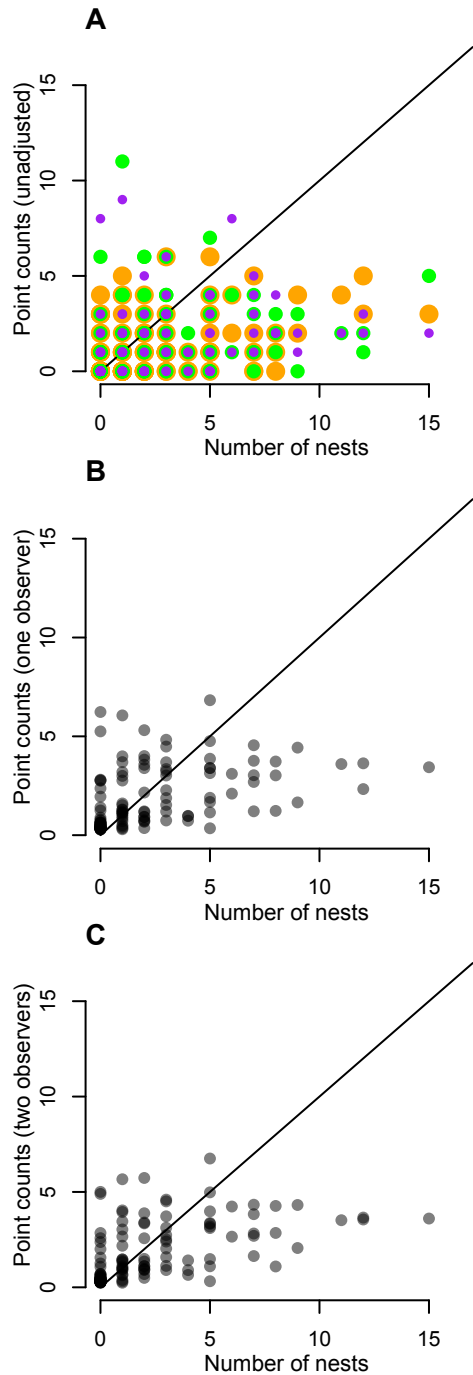


Figure 5. Correlations between count data and nest totals. A) The total number of unique nests found over the season in each plot vs. the unadjusted counts are colored by visit (orange=1<sup>st</sup> visit, green=2<sup>nd</sup> visit, purple=3<sup>rd</sup> visit;  $r = 0.43$ ). For plots with more than three visits, only the first

three are shown for consistency across plots. B) Nest totals vs. one observer counts ( $r = 0.43$ ). C) Nest totals vs. two observer counts ( $r = 0.50$ ). The 1:1 line is shown.

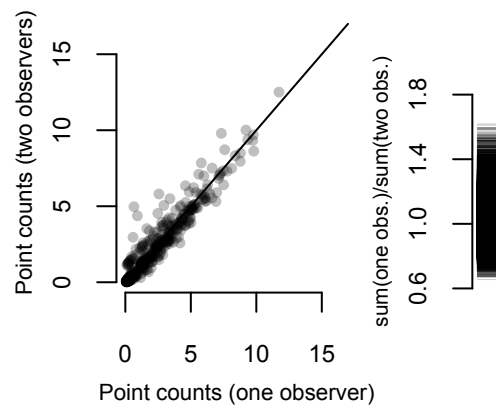


Figure 6. Plot-level abundance estimates from the one-observer model vs. the two-observer model ( $r = 0.96$ ). The black line shows the 1:1 expectation. Draws from the posterior distribution of the sum of the single-observer estimates divided by the sum of the double-observer estimates are shown as tick marks to the right of the main plot.



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### Supporting Information

R code to simulate plot-level abundances after violation of the closure assumption:

```
#create a vector of values for p, from 0.1 to 0.95
p = seq(0.1, 0.95, by=0.05)

#create a empty vector for the abundance at each of 3 visits to 121 plots
Count = mat.or.vec(121, 3)
#create a empty vector for the abundance at each of 3 visits to 121 plots after the
violation
CountViolated = mat.or.vec(121, 3)
#create a vector from which to sample one bird moving out of the plot, no movement, or
one bird moving into the plot with equal probability
violation = c(-1, 0, 1)
#create a vector for plot-level abundance
N = mat.or.vec(121, 1)

for (z in 1:length(p)){
  for(e in 1:121){
    #average plot-level density is 3
    N[e] = rpois(1, 3)
    for(t in 1:3){
      #choose one of the two violation scenarios below
      #abundance between visits is Poisson-distributed
      Nviolated[e,t] <- rpois(1, N[e])
      #one bird moving out of the plot, no movement, or one bird moving into the plot with
      equal probability between visits
      Nviolated[e,t] <- max((N[e] + sample(violation, 1, replace=TRUE)), 0)
      #simulate the detection process using p and N
      CountObs[e, t] <- rbinom(1, Nviolated[e], p[z])
    }
  }
}
```

JAGS code to estimate plot-level abundance from data that do not meet the assumption of closure over the sampling period:

```
#prior for mean abundance
lambda ~ dunif(0, 1000)

#prior for detection rate
p ~ dunif(0, 1)

for(e in 1:121){
  #plot-level abundance is Poisson-distributed
```

```
N[e] ~ dpois(lambda)
for(t in 1:3){
#observed count is a binomial process with parameters p and N
CountAdj[e, t] ~ dbin(p, N[e])
}
}
```

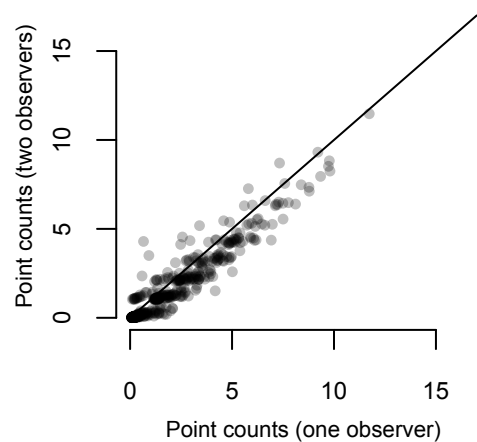


Figure S1. Plot-level abundance estimates from the one-observer model vs. the two-observer model with the time-to-detection component removed. The black line shows the 1:1 expectation



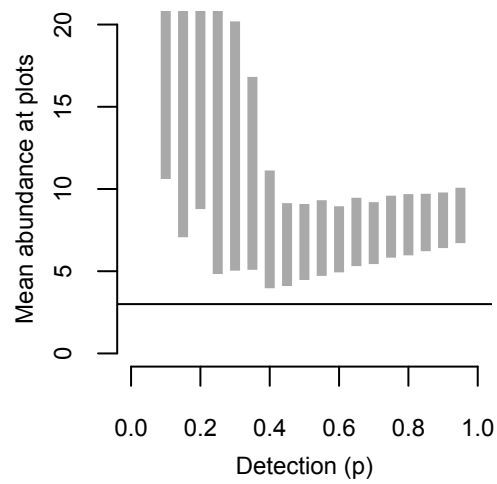


Figure S2. Tests of violation of the closure assumption for the multiple-visit method when abundance between visits is Poisson-distributed. Gray bars are the 95% credible intervals of the abundance estimate. True abundance (three individuals) is marked by the horizontal black line.