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Modeling climate change impacts on tidal marsh birds: Restoration and conservation planning in the face of uncertainty

Samuel D. Veloz,† Nadav Nur, Leonardo Salas, Dennis Jongsomjit, Julian Wood,
Diana Stralberg,[1] and Grant Ballard

PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, California 94954 USA

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Abstract. The large uncertainty surrounding the future effects of sea-level rise and other aspects of climate change on tidal marsh ecosystems exacerbates the difficulty in planning effective conservation and restoration actions. We addressed these difficulties in the context of large-scale wetland restoration activities underway in the San Francisco Estuary (Suisun, San Pablo and San Francisco Bays). We used a boosted regression tree approach to project the future distribution and abundance of five marsh bird species (through 2110) in response to changes in habitat availability and suitability as a result of projected sea-level rise, salinity, and sediment availability in the Estuary. To bracket the uncertainty, we considered four future scenarios based on two sediment availability scenarios (high or low), which varied regionally, and two rates of sea-level rise (0.52 or 1.65 m/100 yr). We evaluated three approaches for using model results to inform the selection of potential restoration projects: (1) Use current conditions only to prioritize restoration. (2) Use a single future scenario (among the four referred to above) in combination with current conditions to select priority restoration projects. (3) Combine current conditions with all four future scenarios, while incorporating uncertainty among future scenarios into the selection of restoration projects. We found that simply using current conditions resulted in the poorest performing restoration projects selected in terms of providing habitat for tidal marsh birds in light of possible future scenarios. The most robust method for selecting restoration projects, the "combined" strategy, used projections from all future scenarios with a discounting of areas with high levels of variability among future scenarios. We show that uncertainty about future conditions can be incorporated in site prioritization algorithms and should motivate the selection of adaptation measures that are robust to uncertain future conditions. These results and data have been made available via an interactive decision support tool at www.prbo.org/sfbayslr.

Key words: Black Rail (*Laterallus jamaicensis*); boosted regression trees; Clapper Rail (*Rallus longirostris*); conservation prioritization; habitat suitability; Marsh Wren (*Cistothorus palustris*); salt-marsh Common Yellowthroat (*Geothlypis trichas*); sea-level rise; tidal marsh Song Sparrow (*Melospiza melodia*); zonation.

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[1] Present address: Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2R3 Canada.

† **E-mail:** sveloz@prbo.org

INTRODUCTION

The prospect of accelerating global change requires resource managers and decision makers to adjust their management strategies and to develop adaptation plans that anticipate novel environmental conditions (Williams and Jackson 2007). Ideally, adaptation plans for future climate changes would incorporate both models of future environmental conditions and knowledge and/or models of how ecosystems will respond. Unfortunately, models of future climate conditions are often highly uncertain (Meehl et al. 2007) and we generally lack precise knowledge of how ecosystems or species will respond to the changes the models project (Walther 2010). Effective planning for climate change must contend with substantial uncertainty (Polasky et al. 2011).

Uncertainty in future environmental conditions can be partitioned into several broad classes. For example, although our knowledge of the global climate systems has grown considerably, crucial gaps in our understanding of key processes in the atmospheric cycle still exist (Meehl et al. 2007), resulting in variation in projections from various general circulation models (GCMs). Further, because of a lack of understanding concerning the dynamics of glaciers and ice sheets, the sea-level rise projections reported in the most recent Intergovernmental Panel on Climate Change (IPCC) report did not include these dynamics (Meehl et al. 2007). Other sources of uncertainty include effects from potential policy decisions or assumptions of CO_2 emissions reductions, which can have large impacts on ecosystem processes. For instance, water policy such as the amount and timing of water released from dams or the removal or construction of dams can have large impacts on downstream ecosystems. Scientific advances can reduce the uncertainty for questions which fall within the first broad class but will not help for questions in the second. Therefore managers cannot count on science alone to reduce uncertainties in projections of future conditions and they must develop strategies for planning amidst this uncertainty.

The degree of uncertainty in future projections dictates which approaches should be used when incorporating models into management decisions. When our knowledge of a system is relatively high, we may be able to provide probabilistic estimates of the uncertainty in our future projections, in which case formal decision theory is an appropriate approach for informing management decisions (McDonald-Madden et al. 2010). However, when uncertainties in key model parameters are too high to infer probabilities, scenario planning (Peterson et al. 2003) or robust decision making (Dessai and Hulme 2007) can serve as important alternative approaches to use available science to guide decision making (Polasky et al. 2011).

Tidal marsh habitat is one of the most threatened ecosystems globally and at regional scales (Greenberg et al. 2006) mainly due to the conversion of habitat for urbanization or other land uses (Takekawa et al. 2006). This narrow intertidal vegetation zone supports an array of plant and animal species, and in, North America, several endemic species or subspecies that have evolved specialized adaptations to this harsh saline environment (Greenberg et al. 2006). Many of these tidal marsh endemic taxa are listed as threatened, endangered or of special concern primarily because of habitat loss.

Recently, global efforts have been initiated to restore tidal marsh habitat in part to support the recovery of threatened and endangered species but also to promote the array of ecosystem services tidal marshes provide such as flood protection (Gedan et al. 2010), carbon sequestration (Hopkinson et al. 2012), and recreation (Zedler and Leach 1998). However, the sustainability of ongoing and planned restoration projects may be in jeopardy because tidal marsh habitat is particularly vulnerable to sea-level rise (Craft et al. 2009, Stralberg et al. 2011) and other climate-change effects such as changes in salinity (Callaway et al. 2007, Parker et al. 2011).

One of the critical decisions faced by managers in the San Francisco Estuary pertains to where to restore tidal marsh ecosystems and whether tidal marsh restoration efforts will likely succeed with future climate change. Here we focus on the prioritization of potential marsh restoration projects and ask the question: which marshes are more likely to succeed in providing high quality wildlife habitat into the future?

Unfortunately our understanding of tidal marsh response to climate change over the next century is still largely incomplete (Fagherazzi et al. 2012). In the San Francisco Estuary, where over 14,000 hectares of wetlands have been restored or are planned for restoration, recent modeling studies found that the ability of tidal marsh habitat to keep pace with sea-level rise is highly dependent upon the assumed rate of sea-level rise and availability of suspended sediment ("sediment" used throughout for convenience) (Stralberg et al. 2011). For example, models project the amount of "mid-marsh habitat" (defined as −0.2 m to +0.1 m relative to mean higher high water [MHHW]) in 2110 to either increase by almost 250%, given high sediment supply, and low sea-level rise or decrease by almost 91%, given low sediment supply and high rates of sea-level rise (Stralberg et al. 2011). This uncertainty is partly due to our limited understanding of how sea level will respond to rising global temperatures (Vermeer and Rahmstorf 2009, Price et al. 2011) and also to our lack of understanding of both current and future sediment dynamics within the estuary (Cloern et al. 2011). Some of this uncertainty will decrease as our knowledge of the global climate system and estuarine ecosystems improves, but some of the uncertainty is also due to highly unpredictable public policy decisions and other human behaviors. Therefore, decisions about the prioritization of tidal marsh restoration projects will need to be made with a highly uncertain estimate of whether these projects will continue to provide the ecosystem functions they were designed to sustain.

Here we explore alternative methods for prioritizing tidal restoration projects given high uncertainty in projections of future environmental conditions (marsh elevation and salinity) in the San Francisco Estuary. We use projections of abundance and distribution of five tidal marsh bird species as a metric of ecological function to prioritize potential restoration projects and evaluate how well the projects perform under future scenarios designed to represent our uncertainty in future conditions. Although there are many sources of uncertainty that could influence tidal marsh restoration management decisions (e.g., upstream watershed management, land use decisions) our scenarios only account for the uncertainty in several specific aspects of future environmental conditions (i.e., with regard to marsh elevation and salinity). We are not attempting to account for all sources of uncertainty in our exercise, but the scenarios we have chosen represent plausible extreme differences in projections of tidal marsh ecosystem response to climate change. Therefore, these scenarios provide a good test of our approach for prioritizing restoration decisions based on models with high uncertainty.

Tidal marsh bird species were chosen as indicators of tidal marsh ecosystem function because they are higher trophic-level organisms and as such, can serve as indicators of tidal marsh structure and function. More pragmatically, quantitative data were lacking at sufficient scales for the modeling of other tidal marsh-dependent taxa (Carrigan and Villard 2002). Furthermore, increasing bird abundance and bird species diversity is a major goal for most of the restoration projects we examined here. The five chosen bird species depend on tidal marsh habitat during all stages of their life cycles but occupy different niches such that these species combined can be related to multiple components of the tidal marsh ecosystem (Spautz et al. 2006, Nordby et al. 2009, Stralberg et al. 2010).

We use results from four scenarios (each combination of high and low sediment and high and low sea-level rise) to simulate habitat suitability for five species of tidal marsh birds as measures of restoration project success. We hypothesize that, given the high uncertainty in our knowledge of future conditions, a systematic prioritization of tidal marsh restoration projects that considers results from current conditions and all four future scenarios will result in the selection of restoration projects that is most robust with respect to the high uncertainty in future environmental conditions. We compare this method to prioritization approaches that select restoration priorities on the basis of a single future scenario combined with current conditions or only current conditions.

METHODS

Study area

Our modeling efforts spanned the saline and brackish portions of the San Francisco Estuary (Suisun, San Pablo, and San Francisco Bays, hereafter "Estuary") and focused on portions that are either currently at an elevation that supports tidal marsh habitat (−0.5 m to +0.3 m relative to MHHW), or projected to achieve such elevations in the future under sea-level rise (Fig. 1). Modeling was restricted exclusively to tidal marsh habitat as we did not have equivalent marsh bird survey data from mudflats or upland areas. Study sites were initially established to monitor bird populations using locations that were visited several times each year over multiple years (Spautz et al. 2006). These sites (i.e., marshes) were located in tidal marsh habitat throughout the region and were selected to sample the range of environmental conditions that occur throughout the Estuary in this habitat type.

Study species

We modeled the distribution and abundance of Black Rail (*Laterallus jamaicensis*), Clapper Rail (*Rallus longirostris*), Common Yellowthroat (*Geothlypis trichas*), Marsh Wren (*Cistothorus palustris*) and Song Sparrow (*Melospiza melodia*). In the San Francisco Estuary, four of these species are represented by one or more subspecies that are entirely or mainly confined to tidal marsh habitats in this region: California Black Rail (*L. j. coturniculus*), which is a California Threatened species, California Clapper Rail (*R. l. obsoletus*), which is a Federally Endangered species, Saltmarsh Common Yellowthroat (*G. t. sinuosa*), a California Species of Special Concern, and three tidal marsh subspecies of Song Sparrow, all of which are California Species of Special Concern: Alameda (*M. m. pusillula*), Samuel's (also referred to as "San Pablo"; *M. m. samuelis*), and Suisun (*M. m. maxillaris*) (Shuford and Gardali 2008).

Survey methods

Surveys for Clapper Rails required specialized survey methods (Liu et al. 2009); these data were available from 2005 to 2010. All six years of survey data were used in the bird modeling for this species to provide a long-term average for the "current" (2010) distribution. An average of 9 survey stations were established at 212 marsh sites. Survey stations were located on the edge and/or interior of each marsh site and were surveyed at least 3, and up to 5 times per year between 15 January and 15 April. Biologists recorded the estimated distance and bearing to individual Clapper Rails detected by sight or sound for 10 minutes at each survey station. Generally, detections that overlapped or were within 5 degrees were considered to be the same bird(s) previously detected. If no Clapper Rails were detected within 200 m of a survey station after the first 2 passive survey visits, call-broadcast surveys were used on the 3rd visit to elicit a response. The call-broadcast surveys consisted of an initial 5 minutes of passive listening, and if no Clapper Rails were detected, then 1 minute of call-broadcast followed by 4 minutes of passive listening. Detections were plotted on a map and summarized by the observer to determine unique individuals.

We used passive point-count surveys of five minute duration (Ralph et al.1993) for surveys for Black Rail, Common Yellowthroat, Marsh Wren and Song Sparrow (Spautz et al. 2006, Stralberg et al. 2010). For these species, we used the most recent 10 years of survey data, i.e., 2000 to 2009, to provide a long-term average reflecting "current" (2010) distribution. Counts were conducted within the breeding season (mid-March to end of May) and excluded juveniles. Only observations within 50 m radius of the point-count center were used. All point count survey stations were located approximately 200 m apart. Additional details on the analysis of bird survey observations can be found in Appendix A, Spautz et al. (2006) and Stralberg et al. (2010).

Physical parameters

Physical variables were initially selected for inclusion in the models based on previous work modeling tidal marsh habitat characteristics in relation to bird abundance in tidal marshes (Stralberg et al. 2010) and other published studies (Watson and Byrne 2009) (Table 1). All variables were calculated at a 50-m by 50-m grid-cell resolution. For Clapper Rail, the variables were summarized using a 100-m radius from the center of each grid cell, for all other species we used a 50-m radius, areas which approximate the home ranges of the five tidal marsh species (Goals Project 2000). We were limited to variables for which data were available throughout the Estuary and that would also be available for projecting future scenarios. Elevation and tidal range variables and data sources are described in Stralberg et al. (2011). Channel metrics were based on a map of current tidal channels derived

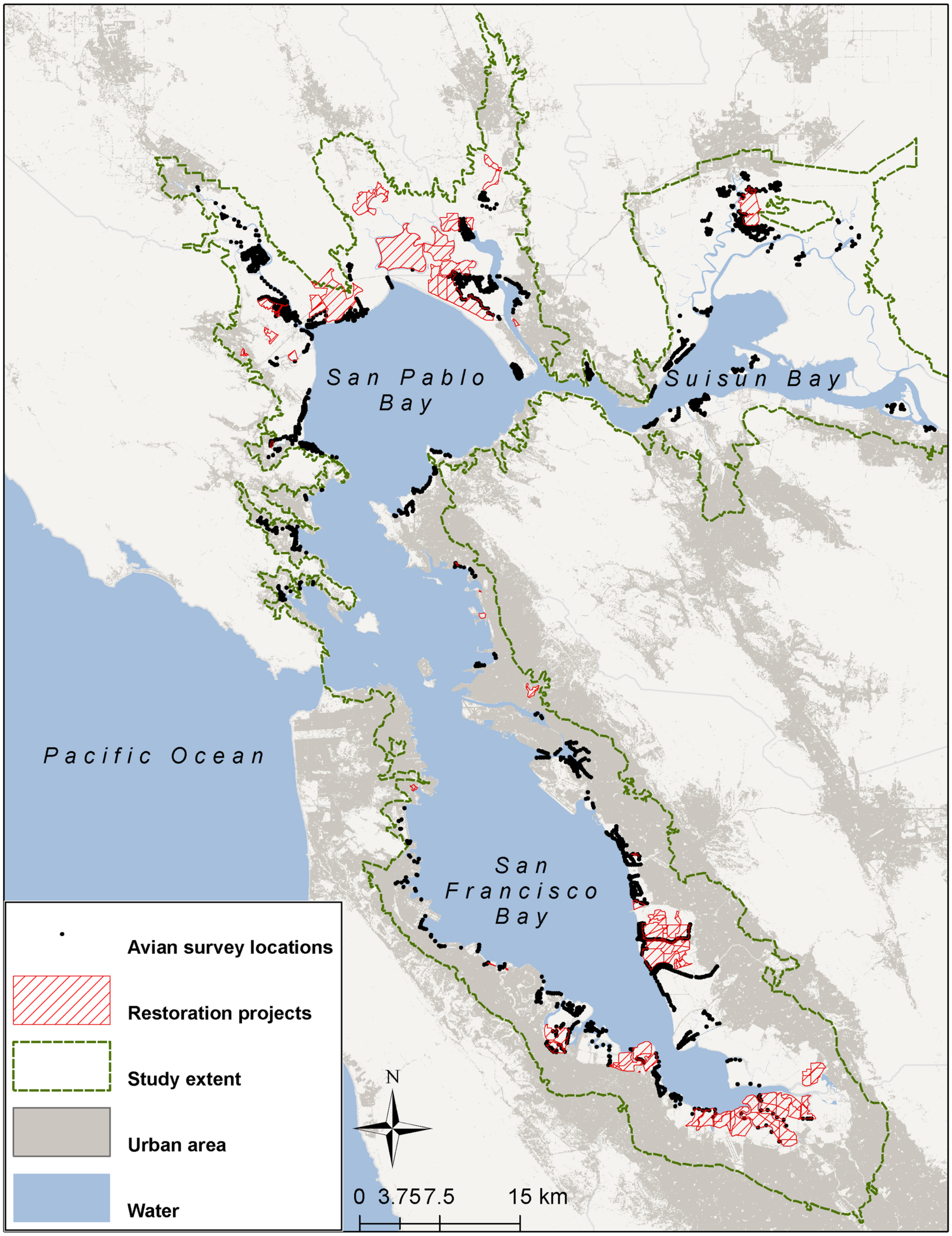

Fig. 1. San Francisco Estuary tidal marsh regions (Suisun, San Pablo, and San Francisco Bays) and avian survey sites used in the analysis. The footprints of 97 proposed or in progress restoration sites are also displayed.

Table 1. Units of measurement for physical parameters included in models. Also indicated (static) is whether the parameter was allowed to vary by time interval in future projections.

Variable	Units	Static variable
Mean spring salinity	Practical salinity units (PSU)	No
Mean summer salinity	Practical salinity units (PSU)	No
Mean marsh elevation (relative to MHHW)	m	No
Most frequent marsh elevation (relative to MHHW)	m	No
Standard deviation of marsh elevation (relative to MHHW)	m	No
Tidal range (difference between MHHW and MLLW)	m	Yes
High-marsh (0.2 to 0.3 m) proportion	Proportion	No
Mid-marsh (−0.2 to 0.1 m) proportion	Proportion	No
Low-marsh (−0.5 to −0.3 m) proportion	Proportion	No
Mean slope	Percent rise	No
Percent of area that is channels	Percent	Yes
Distance to edge of bay	m	Yes
Distance to nearest channel	m	Yes
Distance to nearest levee	m	Yes
Distance to nearest urban area	m	Yes

from current elevation and slope characteristics from a digital elevation model with a 5-m by 5-m spatial resolution. Distance values were calculated using Euclidean distance in ArcGIS 9.3.1 (ESRI 2009) and based on layers found in San Francisco Bay Area EcoAtlas (http://www.sfei.org/ecoatlas).

Estimates of current mean summer (June, July, August) and spring (March, April, May) salinity were calculated based on a spatial interpolation of salinity observations throughout the bay (Appendix B). Observations at point locations were averaged across time and then spatially interpolated to a 50 m × 50 m grid using local polynomial interpolation in ArcGIS 9.3.1.

The effect of salinity on bird distributions was hypothesized to be most extreme during the late spring and summer seasons, when run-off from precipitation is minimal. Therefore, only these two seasons were included in our models. Spring and summer salinity were highly correlated (Pearson's $r = 0.91$); thus we only included one of the seasons in our final models. We initially considered both salinity variables; whichever salinity variable had greater relative influence in initial exploratory models was retained for final models. Additionally, bird models included bay region and observation year modeled as factors. Clapper Rail models included a factor for whether a tape playback was used during the survey. We assume that the physical variables we use for predicting bird abundance, particularly salinity and elevation, serve as proxies for the vegetation composition and structure that tidal marsh birds depend upon.

Some variables were static across future scenarios; locations of levees and urban areas and the distance to levee or urban areas variables remained constant. Because we have no projections for how tidal channels will change in the future and because at least one published model indicated no change in tidal range in the future (Cayan et al. 2008) we made the simplifying assumption that distance to nearest channel, channel percent and tidal range would not change in the future.

Distribution and abundance models

Tidal marsh birds were modeled using boosted regression trees (BRT) (Elith et al. 2008). BRTs have been shown to be less prone to over-fitting to training data sets than standard classification and regression trees and have better predictive performance than other statistical algorithms (Elith and Graham 2009). They also have the benefit of implicitly incorporating interactions and non-linear responses into predictions.

For each species, we tested all possible combinations of models with tree complexities (number of splits in each tree) of 1 to 5 and learning rates (how quickly the model finds a solution) of 0.01, 0.005, and 0.001. The number of trees was chosen based on an optimization routine described in Elith et al. (2008). The optimal combination of parameters was selected based on the predictive deviance using a 10 fold cross-validation of the models and the final number of trees fit. We chose models with moderate learning rates that resulted in the lowest deviance with fewest trees. However, where differences among models in predictive deviance (based on cross-validation) were negligible, the final model was selected using the parameters that resulted in the simplest models (fewer trees, smaller tree complexity, larger learning rate) since simpler models have been shown to generally have superior predictive performance (Elith et al. 2010).

We used a two-step process to predict abundance for each species: first we modeled presence/absence and then we modeled abundance conditional on the species' predicted presence. We modeled presence/absence for each species in the surveyed area using BRTs with a binomial link function fit to the entire dataset (i.e., all marsh sites). We then used a threshold value to assign either 0 (species absent) or 1 (species present) to each cell if its estimated probability of occurrence (from the binomial BRT) was below or above the threshold value, respectively. Except for Clapper Rail, the threshold used was the overall species prevalence in the survey dataset after correcting for probability of detection. The prevalence was estimated by fitting an imperfect-detection occupancy model to the survey data which considered variation in probability of detection throughout the landscape (Appendix B; Liu et al. 2005). There is uncertainty around the estimate of probability of detection and therefore around the threshold (prevalence), but we did not quantify this.

The number of detections per survey per ha was used as a measure of relative abundance (Nur et al. 1999). For the second phase, we used another BRT model for each bird species to estimate abundance from the physical variables' values. However, the abundance BRT models were constructed from datasets filtered to exclude marsh sites where the species was never found (no individual detected at that site across all years). Thus, the abundance models are conditional on the species' being present. We then used the predicted presence/absence layer as a mask, such that abundance was predicted only for cells for which presence was also predicted (i.e., above the threshold value). For Clapper Rail, we set the presence threshold at a relatively low value of 0.1, to ensure that predicted abundance (presence probability × abundance conditional on presence) equaled observed abundance, consistent with recommendations by Freeman and Moisen (2008) for species with low observed prevalence. The total abundance of a species across the Estuary was estimated by summing the predicted abundance across all tidal marsh cells in the San Francisco Estuary.

All statistical analyses and BRT models were conducted using the R statistical software (R Development Core Team 2012), package "gbm" (Ridgeway 2010) with modifications by Elith et al. (2008), package "pscl" (Zeileis 2008), and package "unmarked" (Fiske and Chandler 2011).

Current (2010) abundance predictions were based on the same 50-m grid layers used to develop the models, constrained to potentially vegetated tidal marsh regions of the bay (i.e., between −0.5 m and 0.3 m with respect to MHHW). We assessed the accuracy of our probability of occurrence models using a cross-validated area under the receiver operating characteristic curve (AUC, Hanley and Mcneil 1982). AUC assesses how well predictions discriminate observed presences from observed absences. AUC values can vary between 0 and 1, with 1 being perfect discrimination between presence and absence and values of 0.5 indicating discrimination no better than random. We evaluated the predictive accuracy of our abundance models using the Pearson correlation coefficient (COR), between predicted and observed abundance (Potts and Elith 2006).

Future scenarios

Subregion-specific SLR and sediment scenarios were taken from Stralberg et al. (2011) (Appendix C). We used two nonlinear sea-level rise scenarios based on functions proposed by the National Research Council to extrapolate intermediate (0.52 m) and high (1.65 m) scenarios of sea-level rise by 2110 ("NRC-I" and "NRC-III", respectively). We used only the "low" scenario of organic accumulation rates (1–2 mm/yr, depending on the subregion) from Stralberg et al. (2011), given that marsh accretion rates were found to be relatively insensitive to organic accumulation across the range of SLR and sediment scenarios evaluated (Stralberg et al. 2011).

For estimating the future salinity of the Estuary we used 100-year (2000–2099) salinity projections for 50 bay segments and delta outflow values obtained from the Computational Assessments of Scenarios of Change for the Delta Ecosystem project (Cloern et al. 2011) which consisted of daily salinity projections based on the Geophysical Fluid Dynamics Laboratory (GFDL) general circulation model for two carbon dioxide emissions scenarios: B1 and A2. The B1 scenario assumes that global greenhouse-gas emissions will level off throughout the next century while the A2 scenario assumes accelerating increases of greenhouse-gases throughout this century and beyond. Because the sea-level rise assumptions used in the salinity simulations were based on IPCC projections (Meehl et al. 2007), they did not match our more recent estimates from the NRC. Thus we had to adjust the salinity projections to match the NRC sea-level rise projections (NRC-I and NRC-III). To accomplish this, separate regression models were developed for each bay segment and for each emission scenario (B1 and A2), in order to separate the effects of sea-level rise (SLR) and delta outflows (a function of precipitation) on daily salinity values. Linear regression models were specified as:

$$\begin{aligned}\text{Salinity} = \beta_1 \times \text{SLR} + \beta_2 \times \text{Season}\\ + \beta_3 \times \text{net delta outflow}.\end{aligned}$$

Seasons were defined as consecutive three month periods, with spring defined as March, April, and May and summer defined as June, July, and August. Daily values were averaged over seasons and 20-year time periods to match our marsh elevation projections. The difference between current and future projections was added to the observed current salinity layer to obtain future salinity projections that retain the spatial patterns of current salinity in the Estuary.

Future projections of bird abundance were restricted to areas in which vegetated marsh was expected to occur (Stralberg et al. 2011), i.e., above −0.5 m with respect to MHHW. For mapping, we included areas that are currently protected from tidal flows by levees. However, in our population summaries, we only included potential marsh areas not currently affected by levees. Separate maps were made for each species and scenario in 20 year increments from 2010 to 2110.

Landscape prioritization

We used the conservation planning software Zonation 3.0 (Moilanen 2007) to prioritize all current and future potential tidal marsh habitat in the San Francisco Estuary. The Zonation algorithm creates a hierarchical ranking of the landscape by iteratively removing pixels from the landscape based on their biological value to all species under consideration. Here we used the "core area Zonation" removal rule for which at each iteration the algorithm minimizes the loss of for the species-equivalent with the smallest proportion of its distribution remaining thereby retaining core areas for all "species" (Moilanen 2007, Ballard et al. 2012). Maps of projected bird densities for each time period and scenario were included as separate "species" in the analysis (Thomson et al. 2009).

Restoration project prioritization

We used six different Zonation strategies for ranking restoration projects (Table 2). We first obtained a Zonation solution in which we only included the current projections of the five species to simulate a conservation prioritization that did not account for climate change ("Head in the sand").We also obtained one Zonation solution that corresponded to a single sediment and sea-level rise (SLR) scenario combination ("I feel lucky"), for a total of four such strategies. Each of the four "I feel lucky" strategies only relied on maps of projected tidal marsh bird abundance for the current conditions and the respective sediment and SLR scenario (five time periods 2030, 2050, 2070, 2090, 2110) in the Zonation solution.

Finally, we obtained a Zonation solution which was based on maps for the current distributions as well as the maps for all future scenarios ("Combined"). In this final solution we used the standard deviation of the predictions for each species for each cell across the four future scenarios for each time period to discount predictions and account for across-scenario uncertainty in future predictions (Moilanen et al. 2006). Zonation accounts for uncertainty by subtracting the standard deviation from the predicted abundance value at each pixel, so that predictions with higher degree of certainty (lower standard deviation) have greater weight in the prioritization than those cells that are less

Table 2. The six different strategies used to prioritize restoration projects for providing the best habitat for tidal marsh birds. The prioritization strategy lists which scenarios were included as inputs into the Zonation analysis to rank the landscape.

Prioritization strategy	Years included	Strategy name
Current tidal marsh bird abundance	2010	Head in the sand
Current and high sediment/high SLR	2010, 2030, 2050, 2070, 2090, 2110	I feel lucky a
Current and high sediment/low SLR	2010, 2030, 2050, 2070, 2090, 2110	I feel lucky b
Current and low sediment/high SLR	2010, 2030, 2050, 2070, 2090, 2110	I feel lucky c
Current and low sediment/low SLR	2010, 2030, 2050, 2070, 2090, 2110	I feel lucky d
Use all scenarios†	2010, 2030, 2050, 2070, 2090, 2110	Combined

† Variation in projections of tidal marsh bird abundance among future scenarios within each time period was used to down-weight pixels in the "Combined" strategy.

certain, all else being equal.

We estimated the relative value of 97 planned and ongoing tidal marsh restoration projects throughout the Estuary provided by the San Francisco Bay Joint Venture (SFBJV 2012) using Zonation. We summed the Zonation rankings within each restoration polygon and selected the polygons with the highest summed values. This process necessarily will tend to weight larger restoration projects higher but we felt this was appropriate as larger projects can potentially provide more habitat. We tested alternative methods in which the projects were evaluated by standardizing the Zonation results by area and by ranking the projects using replacement costs (Cabeza and Moilanen 2006) but the results were not qualitatively different than those obtained using the methods above, so we only present results based on summed rankings. We evaluated each restoration selection strategy by calculating the number of tidal marsh birds that could be supported by the habitat provided in the top 25% of restoration projects in each of the four future scenarios. Thus we expected that a selection strategy based on a single restoration scenario ("I feel lucky") would be optimal when that scenario was used for evaluation (i.e., when the correct future scenario is used for restoration planning) but we hypothesized that a single future scenario prioritization strategy would be sub-optimal when a different scenario was used for model projection (i.e., when an incorrect future scenario is used for restoration planning).

We tested for differences among selection strategies after accounting for effects of year (as linear trend) and future scenario (as a factor), and including species as a random effect, because generally we are not interested in estimating the effect of each species. We hypothesized that the "Combined" strategy would result in a selection of top restoration projects that would be comparatively robust to uncertainty regarding future scenarios. Therefore, we evaluated the significance of the contrast of each of five strategies vs. the "Combined" strategy in the linear mixed model by inspecting the posterior distribution of the parameter estimate for each contrast, profiled from 5000 Markov chain Monte Carlo samples. Support for our hypothesis would be evidenced in 95% credible intervals of the parameter estimates with regard to selection strategy that consisted entirely of negative values and thus excluded 0, indicating higher gains in bird numbers under the "Combined" strategy compared to each of the other strategies. Linear mixed model analyses were conducted using the lme4 package (Bates et al. 2012) in R.

RESULTS

Birds: current distributions and abundance

Year, tidal range and salinity were consistently influential in the models for the five tidal marsh species (Table 3). Distance to bay, distance to nearest channels, and mean elevation were also found to be highly influential in the models for some species (Table 3). The accuracy of bird distributional models varied considerably among the five species studied. Models for the two rail species had the lowest predictive accuracy of the five species modeled while the more common songbird species were modeled with higher accuracy (Table 3). Projections for all species modeled and tidal marsh habitat under current and future scenarios are available for viewing online and are available to download (www.prbo.org/sfbayslr).

Table 3. Estimates of predictive accuracy from species distribution (mean ± SE) and abundance models for five species of tidal marsh birds within the San Francisco Estuary; Black Rail (BLRA), Clapper Rail (CLRA), Common Yellowthroat (COYE), Marsh Wren (MAWR) and Song Sparrow (SOSP). COR is the Pearson correlation coefficient between the observed and predicted abundance from the models. The Relative influence columns indicate the top three most influential covariates in the abundance models for each species, + indicates a positive correlation between abundance and increasing values of the covariate, - indicates a negative correlation between abundance and increasing values of the coavariate, I indicates a unimodal optimal range of the covariate within which bird abundance is projected to be highest.

	Prediction accuracy		Relative influence of covariates		
Species	AUC	COR	Highest influence	Second highest influence	Third highest influence
BLRA	0.64 ± 0.10	0.18 ± 0.02	Year	Dist. to bay (+)	Dist. channel (+)
CLRA	0.73 ± 0.01	0.50 ± 0.05	Tidal range (−)	Year	Mean elev. (−)
COYE	0.93 ± 0.01	0.77 ± 0.01	Summer salinity (−)	Tidal range (−)	Dist. bay (+)
MAWR	0.94 ± 0.01	0.87 ± 0.01	Summer salinity (−)	Tidal range (I)	Year
SOSP	0.84 ± 0.02	0.73 ± 0.01	Spring salinity (I)	Year	Tidal range (I)

Projected future distributions and abundance

Projections for future estuary-wide tidal marsh bird populations were highly variable among the future scenarios we used, particularly towards 2110 (Fig. 2). Furthermore, responses to the scenarios we evaluated differed among the five species we modeled (Fig. 2). For example, estuary-wide abundances of Black Rail were projected to increase by 146% for the high sediment/low SLR scenario at 2110 but decrease by 84% for the low sediment/high SLR scenario (Fig. 2A). Additionally, we projected Black Rail and Song Sparrow to increase in abundance for the low sediment/low seal level rise scenario (Fig. 2A, E) while we projected Common Yellowthroat and Marsh Wren to remain relatively unchanged for the same scenario (Fig. 2C, D). Without the implementation of restoration projects, we projected that all species would experience abundance declines from 2010 for the low sediment/high SLR scenario (Fig. 2) except for Black Rail at 2030 and 2050 and Common Yellowthroat at 2030 (Fig. 2A, C).

The direction of abundance change varied among the five species (Fig. 2). For Common Yellowthroat (Fig. 2C) and Marsh Wren (Fig. 2D), we projected differences in abundances to be greater between the SLR scenarios than between the sediment scenarios. In the earlier years, Clapper Rail (Fig. 2B) and Song Sparrow (Fig. 2E) changes in abundance were closely tied to the sediment scenarios but projected responses to the scenarios diverged inconsistently in later years. Spatial projections of the abundances of Song Sparrow across the Estuary illustrate that although projections are highly variable among scenarios (Fig. 3A, B), relatively high abundance was projected in some locations for both of the most extreme scenarios (Fig. 3).

Landscape prioritization

The Zonation solutions based on the six selection strategies resulted in widely differing landscape rankings in space (Fig. 4) and large variation in the top restoration projects selected by each strategy. In addition, there were large differences in the abundance of tidal marsh birds supported by the restoration projects selected under the different restoration selection strategies (Fig. 5). The "Head in the sand" strategy consistently resulted in fewer birds than the other strategies (Fig. 5). There were significantly fewer birds added in the "Head in the sand" strategy than the "Combined" strategy (Table 4). The parameter estimates in our linear mixed model indicated that the low sediment/low SLR scenario strategy resulted in significantly fewer birds supported than the "Combined" scenario, that is, no overlap with zero (Table 4). For all other "I feel lucky" strategies, the 95% credible interval of the posterior distribution of the difference in parameter estimates overlapped with zero (Table 4), but the overlap was small in all three cases (Fig. 6) and modes were always negative, suggesting higher bird gains when using the "Combined" strategy. We found significant differences in the abundance of birds added depending on which future scenario was used

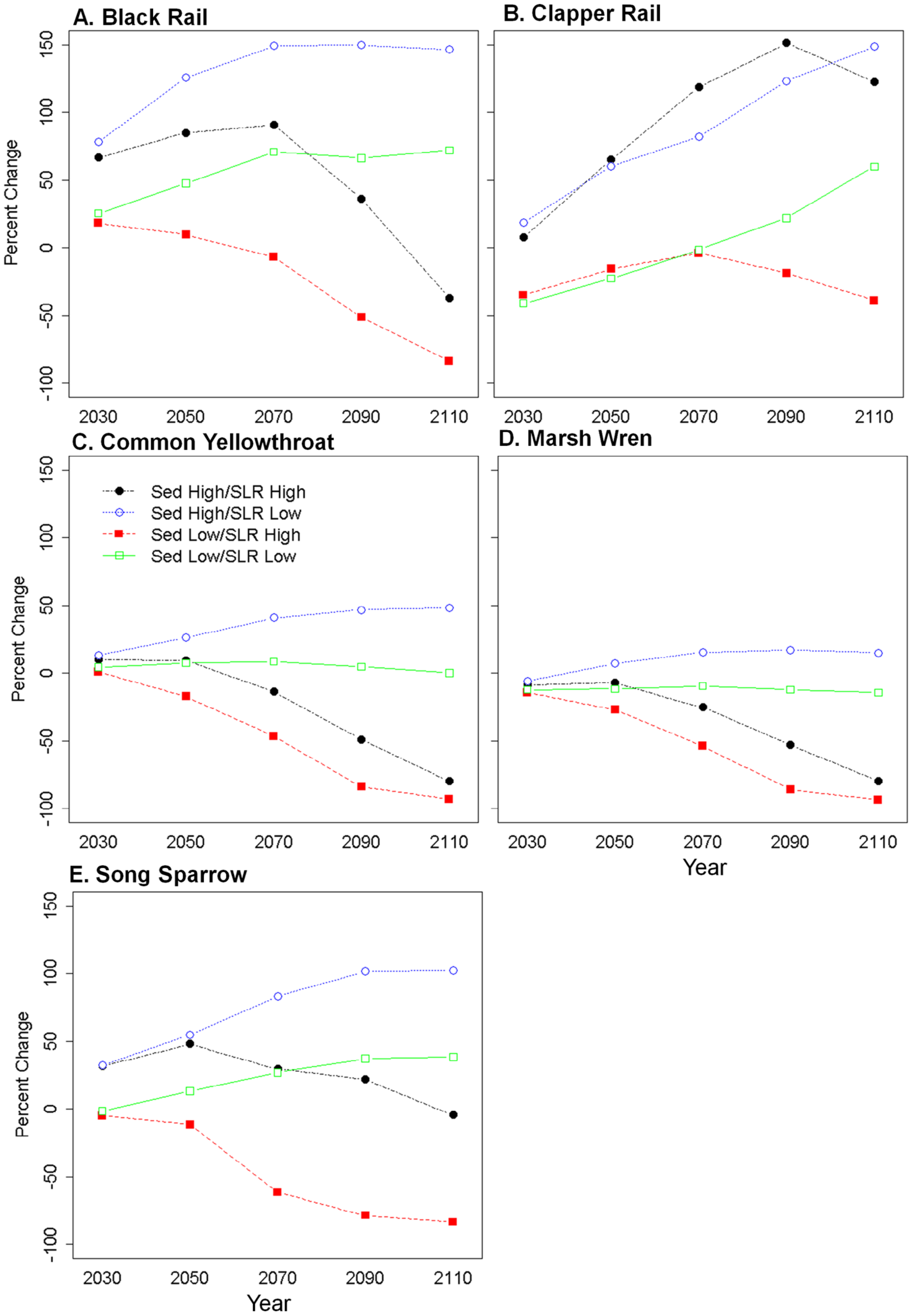

Fig. 2. The projected percent change from predicted 2010 abundance of Black Rail (A), Clapper Rail (B), Common Yellowthroat (C), Marsh Wren (D) and Song Sparrow (E) for each combination of the sediment/sea-level rise scenarios. For all species except Clapper Rail, year 2010 predictions are an average of predictions for years 2000–2009, for Clapper Rail the predictions are an average for years 2005–2010. Future projections are made for each 20 year period between 2030–2110.

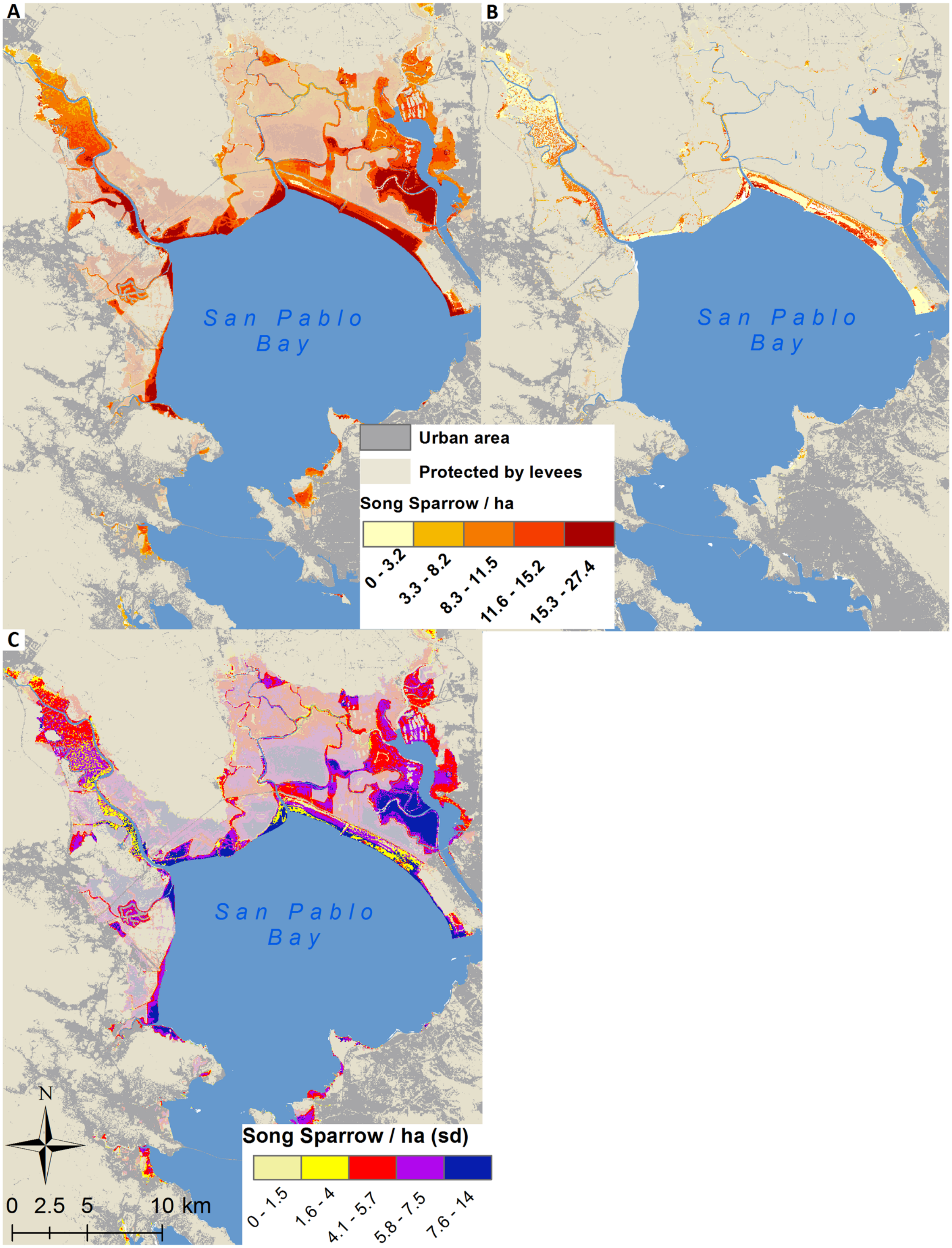

Fig. 3. Projected density (birds/ha) of Song Sparrow at 2110 for a high sediment low sea-level rise scenario (A) and a low sediment high sea-level rise scenario (B). The standard deviation of Song Sparrow density across the four scenarios at 2110 is also shown to illustrate uncertainty in future projections (C). For illustrative purposes, the figure is zoomed into the San Pablo Bay region. Areas currently protected by levees are partially visible to indicate restoration potential.

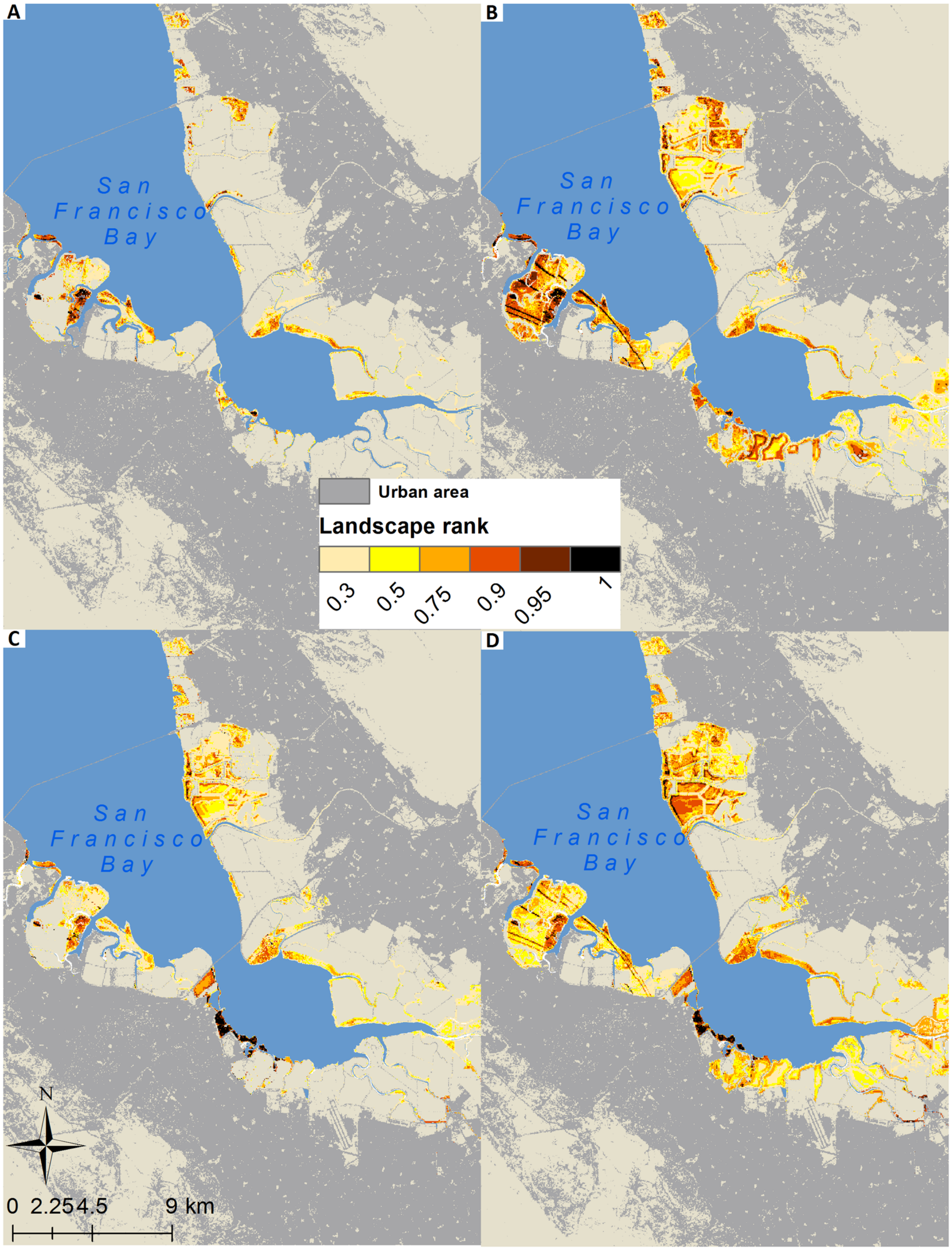

Fig. 4. Maps of Zonation landscape conservation prioritization based on projections of abundance of five tidal marsh bird species for current (2010) environmental conditions ("Head in the sand") (A), current and a future scenario of high sediment/low sea-level rise ("I feel lucky b") (B), current and a future scenario of low sediment/high sea-level rise ("I feel lucky c") (C), and the "Combined" selection strategy which includes the four future scenarios and current conditions (D). In all maps higher pixel values indicate greater habitat importance for tidal marsh birds. For illustrative purpose, the figure is zoomed into the southern portion of San Francisco Bay.

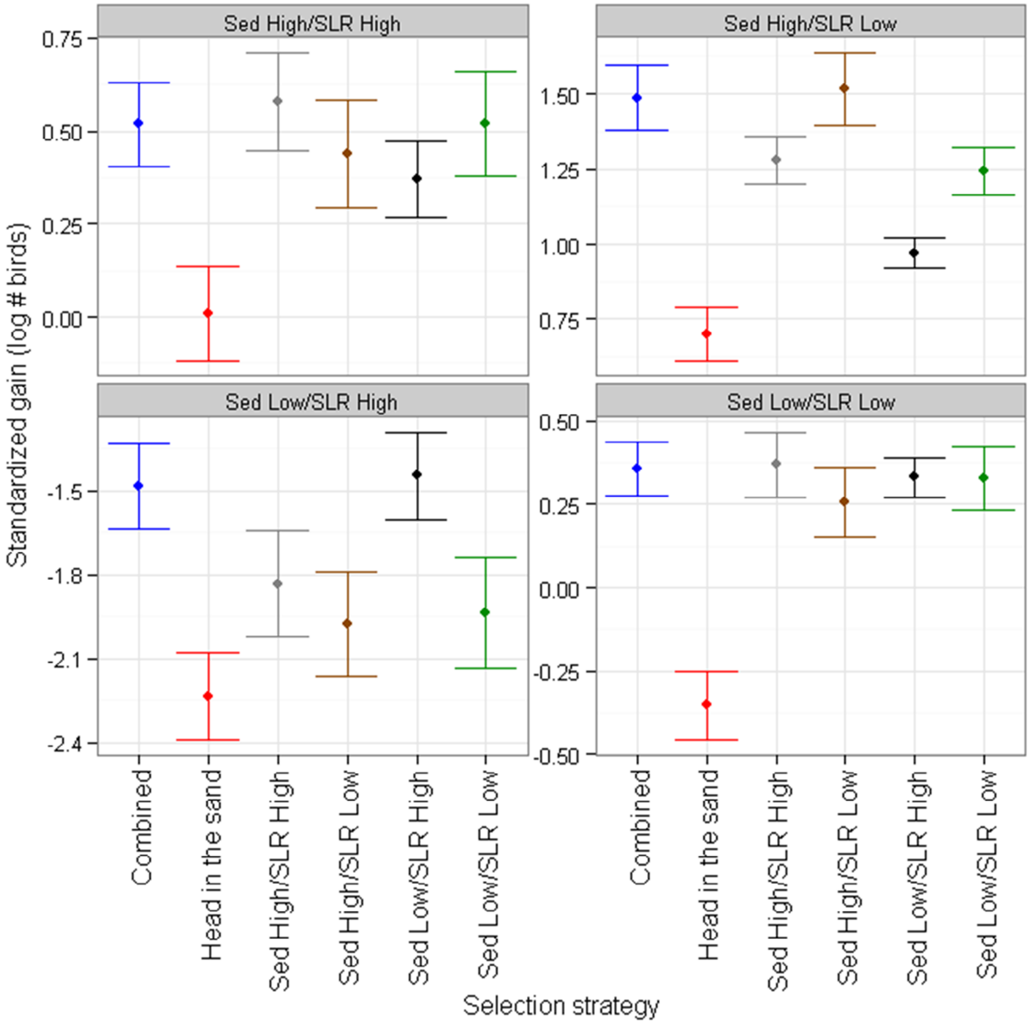

Fig. 5. The standardized gain in the number of tidal marsh birds in the San Francisco Estuary added by including restoration projects selected with the selection strategy along the X axis. Each future scenario is represented in individual panels and the performance of each restoration selection strategy was evaluated against each "actual" future scenario. The predicted gain for each species was first standardized by subtracting the log transformed mean gain for each species across time. We then plotted the mean standardized value across five tidal marsh bird species and five time periods. Error bars around the mean represent ±1 SE.

to evaluate the selection strategy and we also detected a significant negative linear trend with respect to year (Table 4).

We found that the difference in tidal marsh birds supported by restoration projects comparing the "Combined" strategy and other strategies was greatest in the future (Fig. 7) when the variation in future conditions across scenarios was greatest (Fig. 8). At 2030 and 2050 when the variation in bird response across scenarios was lowest (Fig. 8) restoration sites selected using either sediment scenario with the high SLR scenario resulted in as many or more birds than the "Combined" strategy (Fig. 7). In contrast, by 2110 when variation in bird response across scenarios was highest (Fig. 8), all "I feel lucky" prioritization strategies resulted in the selection of restoration projects that supported between 10% and 30% less birds than the "Combined" strategy (Fig. 7). Thus the superiority of the "Combined" strategy was most clearly manifest in the long-term (80 to 100 years in the future).

Table 4. Linear mixed effects model results comparing the log transformed abundance of tidal marsh birds added with respect to the selection of high priority restoration sites using different selection strategies. The factors included in the model included future scenarios (sediment concentration and sea-level rise, four levels), restoration selection strategy (six levels) and a linear trend for year. Species (five levels) was included as a random effect. Upper and lower 95% credible intervals were obtained for the model parameter estimates from 5000 Markov chain Monte Carlo simulations. Scenario parameter estimates refer to the comparison of three scenarios with Sed High/SLR High. Selection Strategy parameter estimates refer to the comparison of the five listed strategies with the Combined strategy.

Factor	Estimate	Lower	Upper	SE	t
Intercept	13.537	9.553	17.212	2.059	6.574
Scenario					
Sed High/SLR Low	0.794	0.652	0.946	0.073	10.866
Sed Low/SLR High	−2.225	−2.373	−2.076	0.073	−30.460
Sed Low/SLR Low	−0.191	−0.349	−0.049	0.073	−2.618
Selection strategy					
Head in the sand	−0.688	−0.881	−0.516	0.089	−7.695
I feel lucky a (Sed High/SLR High)	−0.120	−0.293	0.082	0.089	−1.342
I feel lucky b (Sed High/SLR Low)	−0.160	−0.338	0.012	0.089	−1.789
I feel lucky c (Sed Low/SLR High)	−0.163	−0.346	0.014	0.089	−1.818
I feel lucky d (Sed Low/SLR Low)	−0.180	−0.360	−0.001	0.089	−2.013
Year	−0.003	−0.005	−0.001	0.001	−3.169

DISCUSSION

Projecting the responses of species and ecosystems to future climate will always involve uncertainty. It is reasonable to assume that some land managers and other decision makers may choose to ignore future forecasts that have high levels of uncertainty. We sought to find an optimal prioritization of marshes based on their capacity to retain ecosystem function under four different future scenarios that together probably bracket the full range of possibilities. Our approach was to incorporate future projections into the prioritization, so as to account for possible future scenarios in the choices managers must make. Our results demonstrate that simply using current conditions as guidance can lead to an inefficient use of resources and to reduced biodiversity protection. This is because the future distributions and characteristics of marshes are projected to differ significantly from current conditions. If indeed one of the future scenarios we evaluated is realized, we show that prioritizing using any of the "I feel lucky" strategy would still be better than prioritizing based on current conditions alone.

We found that the high variation in ecosystem response to various SLR and sediment concentration scenarios translates into high variability in the response of tidal marsh bird populations (Fig. 2). Given the high variability in projections of physical forcings, in particular global sea-level rise (Vermeer and Rahmstorf 2009, Price et al. 2011), and our limited understanding of some processes, such as sediment transport, scientists may be unable to provide a probabilistic estimate of which future scenarios are more likely. Thus, decision makers may need to make choices based on model projections that have high uncertainty and could benefit from analyses that consider multiple alternative scenarios.

Our results suggest that the requirements of the five tidal marsh species we modeled reflect different aspects of marsh ecosystem quality. The different sediment supply and SLR scenarios together with changes in salinity influence the future distribution and composition of the marsh plant community (Veloz et al. 2012), which in turn strongly influences bird species distribution and abundance. The choice of sediment scenario was of greater importance during the first half of the 21st century for Black Rail and Song Sparrow, which are associated with marsh characteristics typical of mature mid and high-marsh habitat dominated by gumplant (*Grindelia stricta*) and channel cover (Spautz et al. 2006). For the other species the choice of sea-level rise scenario, which also influences salinity levels, was consistently more important. Species which were less sensitive to the sediment scenarios and more sensitive

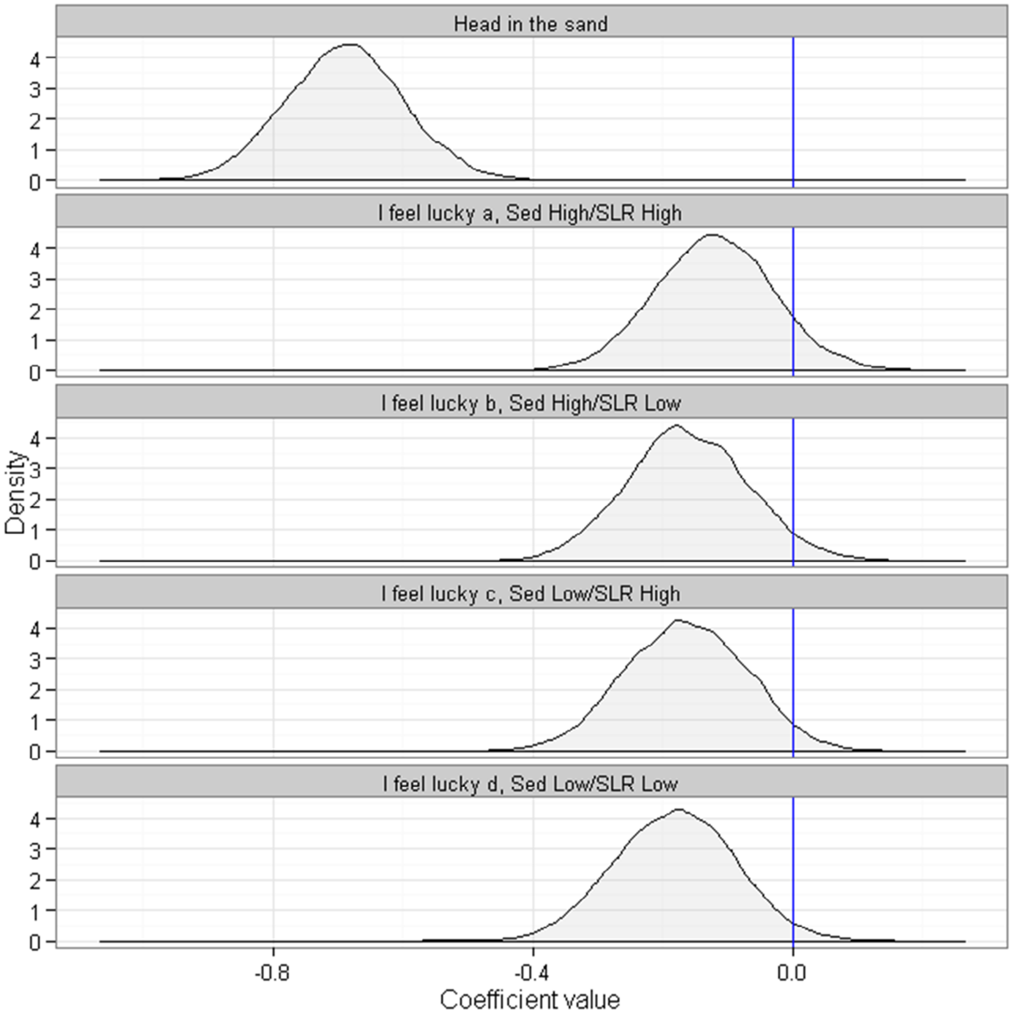

Fig. 6. Posterior distributions of parameter estimate from the linear mixed effects model assessing the gain in the log number of tidal marsh birds added from restoration projects using six different selection strategies. Results for five selection strategies were compared to the "Combined" selection strategy; distribution of parameter estimates for the difference in log number of tidal marsh birds is shown with a vertical blue line at 0. Negative estimates indicate fewer gains in bird numbers than the combined strategy.

to SLR scenarios are likely to be those species that are most constrained by habitat characteristics reflecting difference in salinity levels. Therefore, sensitivity to salinity should be most pronounced comparing the two SLR scenarios. The two species that we found to be most sensitive to salinity levels, Common Yellowthroat and Marsh Wren, were the least sensitive to the different sediment scenarios and occur at the highest densities in Suisun Bay, which currently has relatively low salinity levels compared to the rest of the Estuary. Both species are associated with taller vegetation that dominates low salinity marshes such as Alkali Bulrush (*Bolboschoenus maritumus*) (Spautz et al. 2006).

We found that projected differences in bird abundance due to sea-level rise scenario tended to increase through time, reflecting divergence in assumptions regarding the rates of sea-level rise, which are projected to be much greater in the second half of the 21st century, particularly for the high sea-level rise scenario. Our results indicate that tidal marsh birds in the San Francisco Estuary are especially vulnerable to

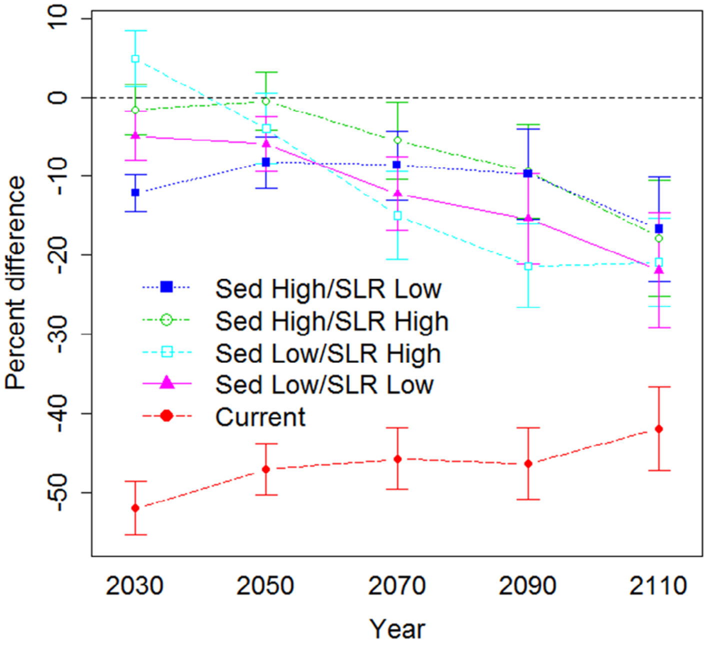

Fig. 7. The percent difference in the number of tidal marsh birds added for selected restoration projects using five different selection strategies (shown in different colors) in comparison to the number of birds added for restoration projects selected using the "Combined" strategy plotted through time. Points indicate the mean across the five tidal marsh species and the error bars indicate ±1 SE. The black dashed line indicates no difference between the number of birds added by restoration projects using the "Combined" strategy and the other strategies.

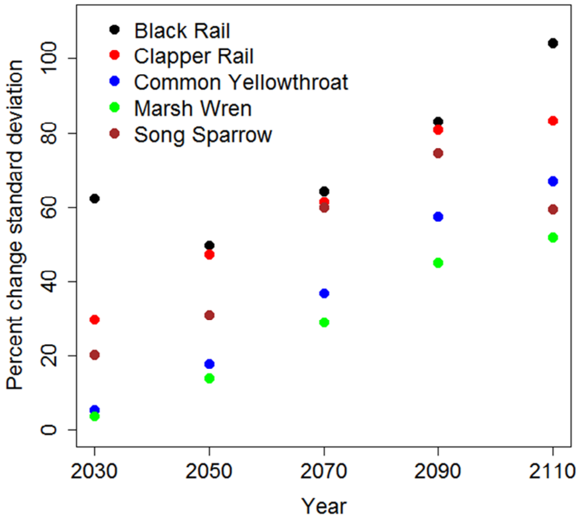

Fig. 8. The standard deviation of the percent change in the projected Estuary population of each tidal marsh bird species modeled across the four future scenarios for each future time period.

higher rates of sea-level rise, which can result in the loss of habitat due to marsh drowning (Stralberg et al. 2011), and other habitat changes due to increases in salinity (Cloern et al. 2011). For the Clapper Rail, which occurs primarily in areas with higher salinity and is associated with characteristics of low-marsh habitat such as Pacific cordgrass (*Spartina foliosa*; Goals Project 2000, USFWS 2009), three of the four scenarios project an increase in abundance and distribution. However, the models do not specifically account for potential changes in reproductive and survival rates that may occur with extensive transition from mid- to low-marsh habitat due to the loss of high-tide refugia from predators and increases in nest flooding (Nur et al. 2012).

The high variation in our predictions of bird abundance among scenarios exemplifies the uncertainty that decision makers face when planning for sea-level rise. In the face of this uncertainty, decision makers are forced to prioritize the allocation of resources for restoration projects and to make planning decisions now that may not be optimal in the future. By modeling a range of scenarios that bracket this uncertainty, we were able to assess the sensitivity of tidal marsh bird populations to changes in habitat caused by the factors we adjusted in each scenario. Although we are unable to determine the likelihood of one scenario vs. another, our models can be used by decision makers to assess the factors that contribute to the vulnerability of each species, so that appropriate management action can be taken. For example, the sensitivity to the sediment scenarios we found for several species indicates that the active management of sediment in tidal marsh ecosystems could promote the sustainability or restoration of tidal marsh bird habitat. If active sediment management is not an option, then our results indicate that restoration projects will provide a greater benefit to tidal marsh birds in regions of the Estuary that naturally contain higher concentrations of sediment and should be initiated as soon as possible so that restored marshes will reach higher elevations sooner and thus be more resilient to increasing rates of SLR during the second half of the century (Stralberg et al. 2011).

We argue that the uncertainty in the projections of future environmental conditions should be explicitly incorporated into models that will be used for informing management (Moilanen et al. 2006). In our study, the variability among the scenarios we tested increased through time in our experiment. By discounting pixels with high variability in our landscape prioritization exercise, we forced the "Combined" solution to conserve pixels that are consistently good across scenarios, particularly towards the end of our modeling time period when the differences between sea-level rise scenarios are projected to be the most extreme. Although modeling different future scenarios can be difficult and computationally intensive for landscape level studies, the added understanding of sensitivities to alternative future conditions may be especially valuable when uncertainty in future conditions is high as is the case with global SLR projections. However, our results also indicate that when uncertainty in future conditions is relatively low, the benefits of combining the results from different scenarios are less pronounced or nonexistent compared with picking a single future scenario (Fig. 6).

We should note that we did not attempt to account for all sources of uncertainty in our model projections nor did we attempt to explore the full range of the variables that defined our future scenarios. In our analysis the "Combined" scenario incorporates the variation in future model projections from four different future scenarios. However, a more comprehensive uncertainty analysis could also incorporate uncertainty in our estimates of the state of physical variables used to model tidal marsh bird abundance (e.g., elevation measurement uncertainty), as well as uncertainty due to missing variables that also constrain the distribution and abundance of species. Additionally, the future scenarios we tested represent bookend estimates of sediment and SLR rates. It is possible that more intermediate scenarios of these variables could be used in a prioritization that is equal to or better than the "Combined" strategy tested here. In any case, the wide range in future estimates of tidal marsh abundance that we found in our models provides a strong illustration for how considering variation in projections from different scenarios can inform management decisions.

The use of conservation prioritization algorithms to rank the landscape for conservation importance offers an objective method to select sites that offer the greatest benefits to the most species (Moilanen 2007). Our application of Zonation does rely upon statistical species distribution models, which have been found to be less accurate at predicting to novel environmental conditions than predicting to the same conditions where the model was calibrated (Veloz et al. 2012). However, the future conditions which were used as inputs into our distribution models do not represent novel conditions for the tidal marsh bird species we studied. Species distribution models also rely upon other assumptions that are frequently violated (Wiens et al. 2009). For example, the tolerances of species are assumed to be represented by their spatial distributions and these tolerances are also assumed to remain unchanged into the future. Both theory and empirical studies suggest that species may not fully exploit their fundamental niches because of dispersal limitations or species interactions (Soberón 2007), and that realized niches of species can shift through time (Veloz et al. 2012). However, a Zonation landscape prioritization based on species distribution models projected across the last glacial/interglacial transition more closely matched a landscape prioritization based on current distributions than other recently tested reserve-selection strategies (Williams et al. 2013). We argue that our models can be used to aid in decisions that are likely to be influenced by the rate of SLR and sediment availability, arguably the two most important factors determining the fate of the San Francisco Estuary marshes.

Beyond being used to rank potential restoration projects, our landscape prioritization maps can be used to identify areas that have the potential to substantially contribute to the habitat availability of tidal marsh species given our future sea-level rise scenarios. They may be used to evaluate the conservation costs of proposed developments that might permanently remove critical future tidal marsh habitat from the ecosystem, particularly in current upland areas that could support future marsh migration and that may be important to prioritize for protection, so as to not foreclose on future management options.

Our study only incorporates the habitat needs of tidal marsh songbirds and rails, ignoring other tidal marsh species such the federally endangered saltmarsh harvest mouse (*Reithrodontomys raviventris*), fish, and invertebrates. While we maintain that the five tidal marsh bird species that we selected are good indicators of tidal marsh ecosystem function due to their ecological diversity, it remains to be seen whether the species we modeled do a sufficient job of incorporating the resource needs of other tidal marsh taxa. Additionally, promoting habitat for tidal marsh species could lead to the loss of mudflat habitat which is important for shorebirds and other taxa (Stralberg et al. 2009). Future work should include projected responses of a wider variety of taxa to ensure that needs of the entire ecosystem are prioritized.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Analysis of bird survey observations

An important aspect of the Clapper Rail survey data was the large number of zeroes in the dataset due to absence of the species at a site or low probability of detection during a survey. The Clapper Rail is absent from some areas in the Estuary for reasons not captured by the set of covariates in our models. We excluded any marsh sites (multiple point count locations were sampled at each distinct marsh site) where no detections of Clapper Rail were ever recorded throughout the span of the study. Thus we did not make predictions for Suisun Bay. Filtered this way, the dataset still included points where the species was never detected, and numerous visits to points where no bird was recorded. The filtered dataset (Table A1) included 5,603 records of visits to points that were collapsed into 1,811 point-year records by taking the maximum number of detections at a point each year. We considered the maximum number detected to be a better index of true abundance than the mean number, due to the difficulty in detecting this secretive species (Liu et al. 2009). Current and projected indices were corrected with an estimate of probability of detection (see below).

Black Rails have not been found during our surveys within the San Francisco Bay (although they were present in San Pablo and Suisun Bays); they have been reported absent as breeders in San Francisco Bay (Evens and Nur 2002). Therefore we developed models without including the surveys in the San Francisco Bay and our models for this species are summarized without including projections for the San Francisco Bay. However, we include extrapolations in our maps to illustrate potentially suitable habitat for the species.

The prevalence and rate of detection of the other three tidal marsh species was adequate for including all records from all sites surveyed, regardless of the history of detections of the species at the site. The summaries of numbers of records and detections, number of points and sites surveyed for each species are shown in Table A1. As with Clapper Rail, data were collapsed into maximum number of detections per point per year and model outputs corrected for probability of detection.

In order to predict true, absolute abundance we needed to estimate the probability that a species was present during a survey but was not detected (Buckland et al. 1993, Royle et al. 2005, Thomas et al. 2009). To do so we discriminated between true zeroes (points where the species was never detected because it was absent) and apparent zeroes (points where the species was present but was not detected). To correct for apparent zeroes (i.e., to account for probability of detection) we developed a detection correction

Table A1. Sampling effort, summary of: point-year records, point-year detections and point-year absences; detection probability, and ratio of mean count to maximum count for surveys included in models.

Species	No. sites	No. points	No. point-year records	Sum of point-year detections/no. zeros	Detection probability	Mean count/ max count
Black Rail	36	455	1,424	366/1,150	0.06	NA
Clapper Rail	85	536	1,811	1,260/1,183	0.38	NA
Common Yellowthroat	41	447	2,238	1,131/1,579	0.31	0.76
Marsh Wren	51	560	2,238	3,397/1,140	0.30	0.66
Song Sparrow	66	627	2,238	9,705/95	0.29	0.79

factor. For Clapper Rail, we used the maximum counts per three visits to a point each year to fit a simple mixture model that includes a probability of detection parameter and a single count (Poisson) parameter (Zuur et al. 2009). The estimated probability of detection is with respect to three visits to a point, and all points in the dataset share the same probability of detection (i.e., it was not modeled to be marsh- or point-specific). For Marsh Wren, Song Sparrow, Black Rail and Common Yellowthroat, there were enough detections in single visits to fit a mixture model that estimated the probability of detection for a single visit for these species (Royle et al. 2005). We used the inverse of detection probability as our correction factor. We did not incorporate uncertainty around estimates of probability of detection into our estimates of total abundance, which could reduce the precision of our predictions but likely will not greatly affect our analysis of changes in abundance across scenarios. Finally, for the three songbird species, we adjusted maximum detections per visit to take into account over-counting because of double counting of individuals, and counting of transients. For Song Sparrow, Common Yellowthroat, and Marsh Wren, we determined the ratio of maximum counts per visit to mean counts per visit, and corrected the maximum count by the ratio of mean to maximum counts per visit (Table 1). Detections of the two rail species were rare, and so no adjustment was necessary.

APPENDIX B

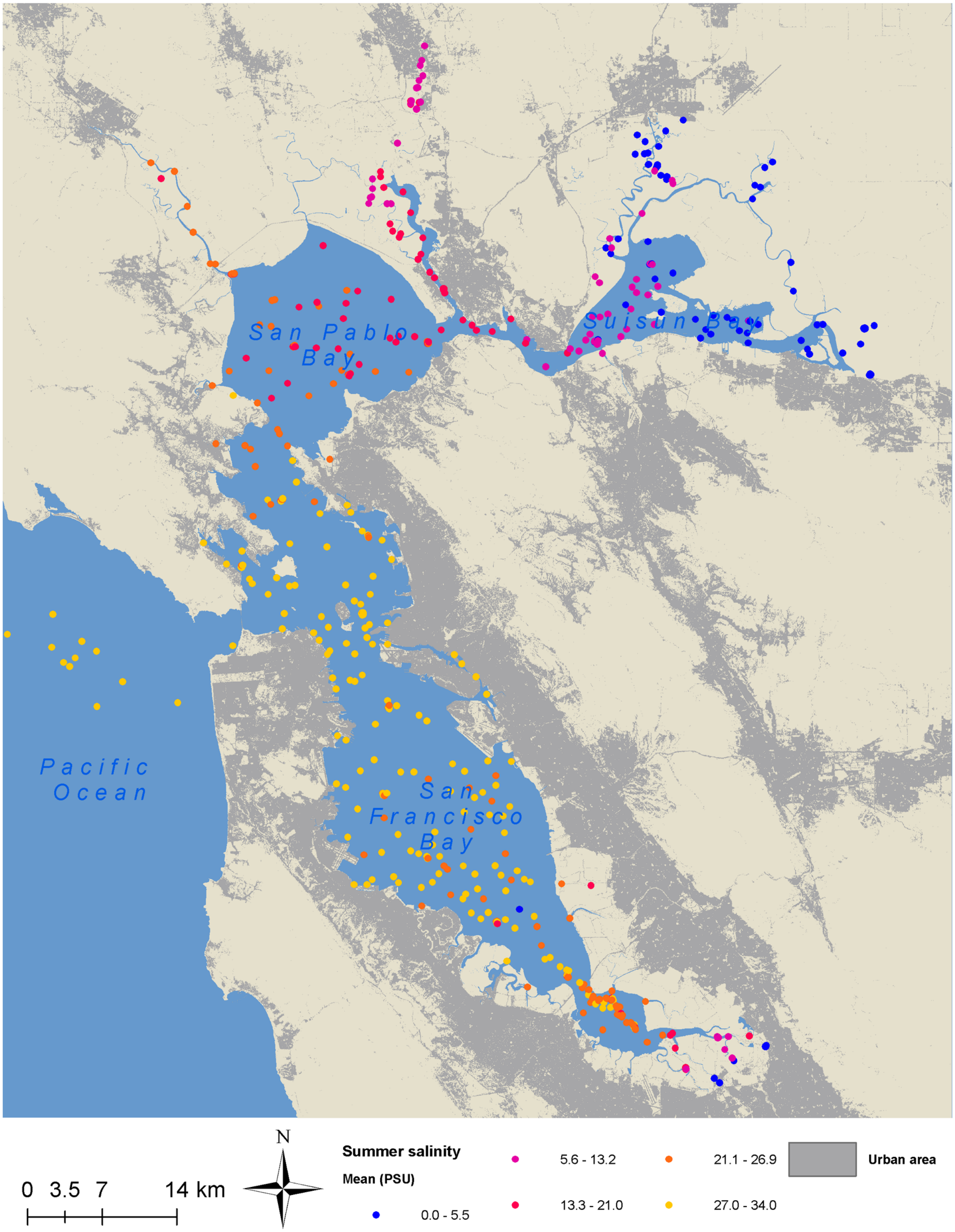

Fig. B1. Map of locations where salinity data were collected and used in the spatial interpolation to create summer salinity grids. The color ramp for sampling location indicates the salinity gradient within the Estuary and is expressed in practical salinity units (PSU).

APPENDIX C

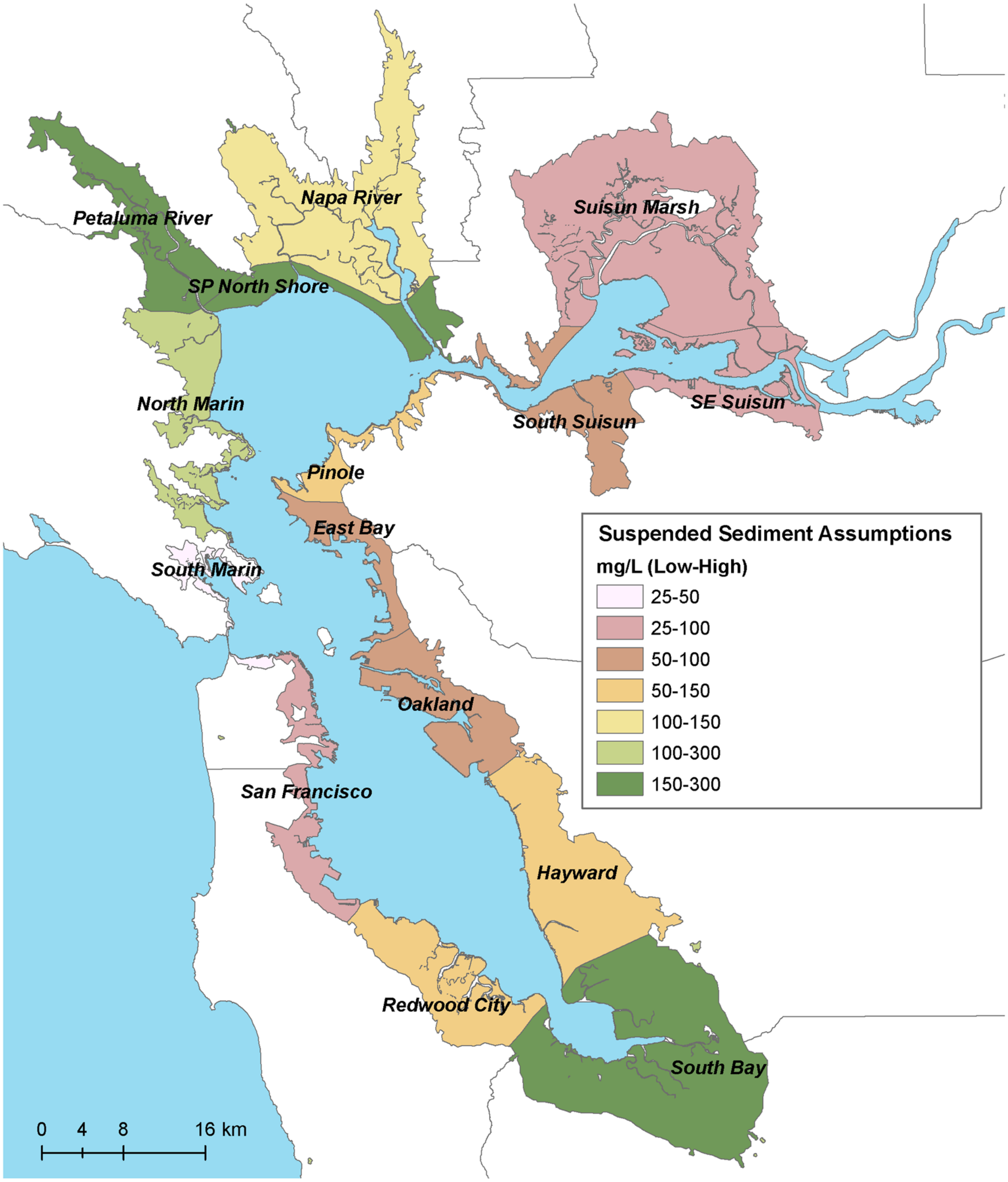

Fig. C1. Map of the study sub-regions. Different colored polygons show values for the high and low sediment assumptions used in the marsh accretion modeling. Sediment values assigned to each subregion were based on observations where avaliable and on expert opinion where data was unavailable.