Impacts of sea level rise and climate change on coastal plant species in the central California coast

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ABSTRACT

Local increases in sea level caused by global climate change pose a significant threat to the persistence of many coastal plant species through exacerbating inundation, flooding, and erosion. In addition to sea level rise (SLR), climate changes in the form of air temperature and precipitation regimes will also alter habitats of coastal plant species. Although numerous studies have analyzed the effect of climate change on future habitats through species distribution models (SDMs), none have incorporated the threat of exposure to SLR. We developed a model that quantified the effect of both SLR and climate change on habitat for 88 rare coastal plant species in San Luis Obispo, Santa Barbara, and Ventura Counties, California, USA. Our SLR model projects that by the year 2100, 60 of the 88 species will be threatened by SLR. We found that the probability of being threatened by SLR strongly correlates with a species' area, elevation, and distance from the coast, and that ten species could lose their entire current habitat in the study region. We modeled the habitat suitability of these 10 species under future climate using a species distribution model (SDM). Our SDM projects that 4 of the 10 species will lose all suitable current habitats in the region as a result of climate change. While SLR accounts for up to 9.2 km^2 loss in habitat, climate change accounts for habitat suitability changes ranging from a loss of 1439 km^2 for one species to a gain of 9795 km^2 for another species. For three species, SLR is projected to reduce future suitable area by as much as 28% of total area. This suggests that while SLR poses a higher risk, climate changes in precipitation and air temperature represents a lesser known but potentially larger risk and a small cumulative effect from both.

INTRODUCTION

The average global sea level is rising, with evidence to suggest that the rate is accelerating (IPCC, 2007; Titus *et al.*, 2009; Nicholls & Cazenave, 2010). As increasing atmospheric concentrations of greenhouse gases warm the atmosphere and oceans, sea level is rising due to thermal expansion of waters and the melting of glaciers and ice sheets (Nicholls & Cazenave, 2010). While global mean sea level has been gradually increasing for at least 20,000 years, this trend has accelerated in the last 15 to 20 years in response to climate change (IPCC, 2007). According to recent projections, global mean sea level could rise as much as 32 cm in the next 40 years and rise 75 to 190 cm over the next century (Pfeffer *et al*., 2008; Vermeer & Rahmstorf, 2009; Nicholls & Cazenave, 2010; Rignot *et al*., 2011; Slangen *et al*., 2012). Rising sea level and the potential for stronger storms pose an increasing threat to coastal communities, infrastructure, beaches, and ecosystems.

Given the dynamic nature of the coastal zone, the response of coastal areas to SLR is more complex than simple inundation. In addition to inundating low-lying areas, rising sea levels can increase flooding events, coastal erosion, wetland loss, and saltwater intrusion into estuaries and freshwater aquifers. Moreover, climate change will likely result in altered patterns of precipitation and warmer temperatures in some coastal areas along with increasing the risk of extreme high sea level events. This is expected to be especially common during high tides, particularly when exacerbated by winter storms and El Niño events (Cayan *et al*., 2008a). The combined effects of SLR and other climate change factors, including changes in fog, may cause rapid and irreversible coastal changes that will have significant effects on coastal habitats and species.

In the United States, climate-related changes are already being observed in the form of rising temperature and sea level, storms, early snowmelt, lengthening of growing seasons, and alterations in river flows, among others (Karl *et al*., 2009). Furthermore, these changes are projected to intensify over the coming century (Karl *et al*., 2009). Climate change in the form of increasing air temperature and varying precipitation will also affect coastal plant species in California (Hayhoe *et al*., 2004). Climatic factors are known to be important drivers of species' distributions (Woodward & Williams, 1987); climate change could alter the current distribution of a species by shrinking or enlarging and ranges shifting its climatic envelope (Jones *et al*., 2013; Smale & Wernberg, 2013). Many coastal species are also adapted to specific temperature ranges, and an increase in temperatures will likely change the distribution of these species (Titus *et al*., 2009). Rare and threatened native plants are more susceptible to extinction caused by climate change due principally to their small population sizes and specific habitat requirements. Gradual migration to new habitats can be especially difficult for rare plant species with small populations, since they may be constrained by low dispersal ability, genetic diversity, and limited habitat (Maschinski *et al*., 2011). Furthermore, unlike more mobile species, plant migration depends on a variety of dispersal agents (Howe, 1982) that also may also be negatively affected by climate change. Some studies estimate that endemic plant species' ranges may shift up to 90 miles under drastic climate change; however, the rate of movement over that distance would be far slower than the rate of climate change (Loarie *et al*., 2008).

Numerous studies have analyzed the effect of climate change on future habitats through species distribution modeling (SDM) (Guisan & Zimmermann, 2000; Bakkenes *et al*., 2002; Thomas *et* *al*., 2004; Guisan & Thuiller, 2005; Thuiller *et al*., 2005), which statistically relates multiple abiotic habitat characteristics with observed occurrences of a species (Kearney & Porter, 2004; Guisan & Thuiller, 2005; Araújo & Guisan, 2006). In California, Loarie *et al*. (2008) estimated that approximately 66% of California's endemic plant species may experience decreases of up to 80% in the size of their ranges within the next 100 years as a result of climate change. Although numerous studies have been published evaluating climate change effects on species distributions, to our knowledge no studies have incorporated the threat of exposure to SLR with species distribution under climate change. There is a pressing need to identify the existence of interacting effects between climate change and habitat loss and, if so, to quantify the magnitude of their impact (Mantyka-pringle *et al*., 2011).

Conceptually, the combined influence of climate change and SLR may result in three distinct patterns (Figure 1). In the first case, climate change could shift species inland and thus away from the threat of SLR (Figure 1A). Second, climate change could shift species toward the coast, thus threatening species that would not have otherwise been affected by SLR (Figure 1B). In the third case, climate change could shift species habitats along the coast, which depending on the coastline could result in no net change in the threat of SLR to the species (Figure 1C) (Loarie *et al*., 2008).

Our study evaluated the effect of SLR on 88 rare, largely endemic, coastal plant species within California's Tri-County Area (San Luis Obispo, Santa Barbara, and Ventura Counties) by the end of this century. We then developed an SLR risk analysis model to evaluate the relationship between a plant's characteristics and its likelihood of exposure to SLR in the future. We used

MaxEnt (Phillips *et al*., 2006) to project species' distributions under current and future climate and then compared that to the relative impact of SLR.

We addressed the following questions: (1) What is the extent of the impact of SLR on rare plant species along the central California coast; (2) Which plant characteristics are the best predictors of exposure to SLR; (3) To what extent will climate change shift the current habitat of rare coastal plant species in the future; (4) What is the relative impact of climate change compared to SLR on the habitat of species?

MATERIALS AND METHODS

Species Occurrence Data

Using the CalFlora Plant Database available from The CalFlora Database (http://www.calflora.org), we selected 88 species in the Tri-County Area that were likely candidates for exposure to SLR, given their occurrence at low elevations (0-30 meters). The selected 88 species represent 31 different taxonomic families; 6 habitat types including coastal fresh and brackish marshes, coastal dunes, scrub, coastal bluffs, and meadows and grasslands; multiple life histories including annuals, herbs, succulents, woody, and deciduous shrubs; a variety of elevation ranges; and a mix of state and federally listed species, as well as unlisted but rare species (Table S-1).

Species occurrence data were extracted from the 'RareFind' dataset of the California Natural Diversity Database (CNDDB) (http://www.dfg.ca.gov/biogeodata/cnddb/). CNDDB maintains information about the natural history and locations of rare, threatened, endangered, and special status species and natural communities of California and has been used for a variety of species distribution models (Hernandez *et al*., 2006; Williams *et al*., 2009; Regan *et al*., 2012). In CNDDB, location data for a species takes the form of polygonal occurrences, which are a rough proxy for populations. An occurrence is defined as the area of a cluster of individuals within ¼ mile of one another and separated by at least that distance from other occurrences. We excluded all occurrences recorded before 1970 and any that were greater than 4 km in diameter in order to minimize outdated and uncertain values. Due to incomplete and unknown data on a number of individuals present within each occurrence, we assumed that populations were distributed evenly across occurrences. Thus, we included occurrences regardless of the number of individuals or

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clusters of populations known to be extant within them. The 88 species accounted for a total of 1091 occurrences used in our analyses.

SLR Projections

The SLR scenarios in this study were generated as part of the California Climate Impact Assessments which were produced from a downscaled global climate model (GCM) analyzed by the Scripps Institution of Oceanography (Cayan *et al*. 2009). The "high scenario" was a 1.4 m rise by 2100, while the "low" scenario was a 1.0 m rise by 2100 (Cayan *et al*. 2009). The coastal hazards of erosion and flooding associated with the impacts of the GCM outputs were projected for a variety of planning horizons using a total water level (tides + wave run-up) methodology (Revell *et al*. 2011). Coastal erosion model projections mapped all of San Luis Obispo County and most of Santa Barbara County, while the coastal flood extents were projected and mapped for the entire state of California. These projections of future coastal hazards were made available by the Pacific Institute, which conducted an initial statewide vulnerability assessment identifying critical infrastructure, habitats, and social demographics at risk from SLR (Heberger *et al*. 2011).

For coastal flooding, the mapped hazard extent was extrapolated from existing FEMA 100-year coastal Base Flood Elevations (BFEs), escalated by the projected amount of sea level rise. A 100-year flood is defined as a flood extent that has a 1% chance of being equaled or exceeded in a given year (FEMA, 2005). These BFEs, which calculated a maximum elevation of wave run-up at the shoreline, were mapped inland using a simple bathtub approach (FEMA, 2005). This approach likely overestimates the inland extent of coastal flooding, but in areas of combined fluvial and coastal flooding, may suitably represent the joint probability of a combined fluvial and coastal storm event (Revell, *et al*. 2011). The coastal erosion hazards contained 3 components in the projected outputs: the effects of shoreline transgression from SLR, historic trends in shoreline change which provided an indirect accounting of sediment budget considerations, and the impact on erosion of a 100-year storm wave event (Revell *et al*. 2011). Inundation was mapped as the current extent of Mean High Water elevated by the SLR scenario over time by using a bathtub approach and ignoring hydraulic connectivity (Heberger *et al*. 2011).

SLR Threat Analysis

In order to analyze the threat of SLR to each species, the occurrences for the 88 species were combined with the above SLR threat layers for the year 2100, including inundation, flooding, and cliff and dune erosion in the Tri-County Area. We compared the geographic area of the occurrence data with the geographic area of the SLR threat layers to determine the area of overlap. We used the area of overlap to calculate the percent of each occurrence exposed to SLR for each species. We examined the area of exposure by aggregating the geographic areas of the four SLR-related threats to determine where any threat might occur.

SLR Risk Analysis

In order to determine the best predictors of exposure to SLR for our 88 species, we gathered several physical, spatial, and biological characteristics related to each species, including life history, federal and California listing status, as well as each occurrence's area, elevation, and distance from the coast (See Table S-1). These variables included both continuous (e.g. elevation, distance) and categorical (e.g. life history, listing status) data. The continuous variables all had occurrence-level specificity, whereas the categorical variables only had species-level specificity. We ran multiple logistic regressions using R 2.15.1 (R Core Development Team, 2012), to determine which variables (including interactions) resulted in the best predictive models for exposure to SLR. We selected the best model based on two measures: the lowest Akaike Information Criterion (AIC) value (Akaike, 1973; Bozdogan, 1987) and statistically significant coefficients.

Species Distribution Modeling

We modeled current and future habitat suitability using MaxEnt version 3.3.3k (Phillips *et al*., 2006), a machine-learning technique often used to model the spatial distribution of a species using environmental variables and species' occurrence data (Gogol-Prokurat, 2011). Species provides presence only data. Although many SDMs require both presence and absence data to predict distributions, MaxEnt has been recognized to be particularly effective with presence only data (Phillips *et al*. 2006; Regan *et al*., 2012). Moreover, MaxEnt can partially compensate for incomplete and small data sets on species occurrence and perform with nearly maximal accuracy level under these conditions (Hernandez *et al*., 2006). This is ideal for rare species that typically have small populations.

Based on the results of the SLR Risk Analysis, we identified the 10 species that were most likely to be substantially impacted by SLR in the Tri-County Area. These were *Centromadia parryi* ssp. *australis, Chloropyron maritimum* ssp. *maritimum, Cirsium rhothophilum, Dithyrea maritima, Erigeron blochmaniae, Lasthenia glabrata* ssp. *coulteri, Monardella crispa, Monardella frutescens, Scrophularia atrata,* and *Suaeda californica.* We examined the effect of climate change on each species by modeling current and future habitat suitability in MaxEnt, based on current location data calculated from centroid of species occurrence polygons in California and six environmental inputs consisting of four bioclimatic and two edaphic variables (i.e. Mean Diurnal Range; Annual Precipitation; Precipitation in the Wettest Quarter; Growing degree days above 5 C; Soil pH; and Available Water Holding Capacity). These environmental inputs have been used previously to model plant species distributions (Fitzpatrick *et al*., 2008; Riordan & Rundel, 2009; O'Donnell *et al*., 2012; Sheppard, 2013) because these variables were general factors influencing the distribution of a wide range of plant taxa (Woodward, 1987). The inclusion of soil characteristics has also been known to improve SDM performance when assessing climate change impacts (Austin & Van Niel, 2011) and has been used in various SDM studies (Syphard & Franklin, 2009; Regan *et al*., 2012; Belgacem & Louhaichi, 2013; Conlisk *et al*., 2013).

Historical climate was obtained from the Parameter-Elevation Regressions on Independent Slopes Model (PRISM) at Oregon State University, a method for extrapolating the measured historical data (Daly *et al*., 2002). Due to the large variability in long-range climatic predictions for 2100, we selected two GCMs: the Parallel Climate Model (PCM) (Washington *et al*., 2000) and the Geophysical Fluid Dynamics Lab (GFDL) (Delworth *et al*., 2006; Knutson *et al*., 2006) model, both used by the State of California for assessing climate change impacts because they produce accurate simulations of California's recent historical climate but show different levels of sensitivity to greenhouse gas forcing (Cayan *et al*., 2008b). As all GCMs, GFDL and PCM project warmer conditions for southern California by the end of the 21st century, but PCM projects a more modest annual temperature increase (2.5 °C for PCM vs. 4.4 °C for GFDL) and winter precipitation change (+8% for PCM vs. −26% for GFDL) while the GFDL projects a generally drier future based on the IPCC's A2 emissions scenario (i.e. business-as-usual) (Regan *et al*., 2012). We used downscaled monthly climate data from the two GCMs and PRISM (historical climate) at a grid size of 90-meter resolution (Flint & Flint, 2012), and then calculated bioclimatic parameters based on the methods described in Sork *et al*. (2010) for Growing Degree Days and used the WORLDCLIM database (www.worldclim.org) for other bioclimatic parameters. The time horizon for this data is centered on 2085, as opposed to 2100, though it represents an end-of-century 30-year average with 2085 being the median (Flint & Flint, 2012).

We calibrated the MaxEnt model using the default value settings suggested by Philips *et al*. (2006). We set the random test percentage to 33%, which retains a percentage of the occurrences at random in order to evaluate the model and the rest of the occurrences were used to build the final models. We ran 10 replicate runs and averaged the results. We evaluated our models under the current climate by using the area underneath the receiver operating curve statistic (AUC) (Philips *et al*., 2006). The AUC produces a single number between 0 and 1, where a higher AUC indicates a better model fit (Fielding & Bell, 1997; Giannini *et al*., 2012).

MaxEnt outputs are continuous probability layers for species occurrence under: (i) the historical climate with the PRISM climate model; and (ii) the two future projected climates with PCM and GFDL climate models. We converted the continuous probability maps from MaxEnt into binary presence/absence layers using a threshold value that minimizes the sum of sensitivity and specificity of the model (Jiménez-Valverde & Lobo, 2006). After removing current urban areas, which we deemed as unsuitable, from each of the three binary layers, we calculated the area of presence data to compare the relative gain or loss in habitat between the current and future scenarios. This then allowed us to quantitatively compare the habitat change from impacts of climate change with SLR.

Evaluating relative impacts of SLR and climate change

We quantified the relative impact of SLR on suitable habitat by overlapping the suitable habitat layers with the SLR threat layers to determine how much future suitable habitat will be lost to SLR. We calculated the total change in habitat area (*H*), the change in habitat area due to climate changes in air temperature and precipitation (*C*), the change in area due to SLR (*S*), and the interaction between them (*I*):

$$H = F_S - P \qquad \text{eq. 1}$$

$$C = F - P \qquad \text{eq. 2}$$

$$S = P - P_S \qquad \text{eq. 3}$$

$$I = H - (C - S) \qquad \text{eq. 4}$$

P (PRISM) is the present projected habitat layer based on the historical climate; F (Future, either GFDL or PCM) is the area of the future projected habitat layer; F_s (SLR) is the area of the future projected habitat layer after loss from SLR; and P_s is the area of the present projected habitat layer including the theoretical future loss from SLR. *C* and *S* are the direct effects of climate change and SLR, respectively. The difference between them and the total change in habitat area (Eq. 4) is the interaction between them, which can be positive (Figure 1A), negative (Figure 1B) or zero (Figure 1C).

We also calculated the proportional impact of SLR on habitat area under the future climate, *A*:

$$A = 1 - \left(\frac{F_S}{F}\right) \qquad \text{eq. 5}$$

RESULTS

SLR effects on current occurrences

We found that under the SLR projections for the year 2100, 17% of the 1091 occurrences of all species in our analysis would be affected by SLR, with a total of 10.6% threatened by routine inundation, 15.6% by a 100-year coastal flood, 5.9% by dune erosion, and 4.6% by cliff erosion. On the species level, we found that 65% of the 88 studied species are projected to have at least one occurrence impacted by SLR, with 12% of species having all of their occurrences within the SLR hazard zones (Figure 2). However, nearly two thirds (63%) of the species are projected to have less than 20% of their occurrences at risk. The risk profile of the remaining species is fairly uniformly distributed between 20% and 100% (Figure 2). Among all SLR threats, the threat profile from flooding alone closely mirrors the aggregate SLR threat profile. By contrast, inundation, dune erosion, and cliff erosion, are projected to affect almost 50% of species, with less than 5% of the species having all occurrences in the hazard zone (Figure 3).

SLR risk as a function of elevation and distance

The best-fitted logistic regression model to explain the SLR exposure of species occurrences incorporated occurrence area, elevation, and distance from the coast (Table 1). None of the species-level variables (life history and listing status) were significant predictors of exposure to SLR (Table S-1). Adding interaction terms did not improve the model. SLR threat to a species occurrence increases with occurrence area but decreases with elevation and distance from the coast (Table 1, Figure 4). Occurrences that are within 0.25 km of the coast and below 100 m in elevation are predicted to have a 100% chance of exposure to SLR.

The probability of exposure to inundation and flooding is qualitatively similar to that for the aggregate threat, with risk from flooding extending further inland than inundation (Table 2, Figure 5). In contrast, exposure to dune and cliff erosion depends only on distance from coast and occurrence area, but not elevation (Table 2, Figure 5).

Effects of Climate Change and SLR on Habitat (Species Distribution Modeling)

All runs for our 10 species consistently produced high AUC values greater than 0.95, indicating that MaxEnt modeled and predicted the current distribution of species effectively. Four species (*Cirsium rhothophilium, Erigeron blochmaniae, Monardella crispa, and Monardella frutescens*) were projected to have no habitat left in the study region under both the PCM and GFDL future climate models.

Under the GFDL climate model, four species (*C. maritimum* ssp. *maritimum, C. parryi* ssp. *parryi, D. maritimum, and L. glabrata* ssp. *coulteri*) are projected to significantly expand habitats with minimal loss to current modeled habitat (Figure 6). With SLR, only *C. maritimum* ssp. *maritimum* loses as much as 40% of the current habitat. *S. atrata* is projected to have only a very small amount of future suitable habitat, and this habitat does not overlap with the current habitat projected for this species. *S. californica* is projected to maintain about 25% of its current habitat under the GFDL model, with a very modest habitat expansion into new areas and no significant losses to SLR.

The PCM climate model primarily projects a contraction in future habitat (Figure 7). Only two species are projected to gain significant habitat under the PCM climate model; *L. glabrata* ssp.

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coulteri will gain extensive suitable habitat (+339% habitat relative to current habitat) and *C. parryi* ssp. *parryi* will gain some new suitable habitat (+65% habitat relative to current habitat) All species, except *L. glabrata* ssp. *coulteri,* maintain less than 45% of their current habitat under the PCM future climate model, with notable losses from SLR for *C. maritiumum* ssp. *maritimum* (Figure 7).

The total loss of current habitat due to SLR is projected to be similar across species (Table 3). In contrast, the projected changes in habitat resulting from climate change are much more variable across species and climate models. In terms of the area of habitat lost, the impact of SLR can be as much as half the magnitude of the projected impact of climate change (*C. maritimum* under PCM), but is generally a much smaller component of future habitat change (as little as 0.1%). Comparing the percent area lost due to SLR for the current and future climate models reveals that the proportional impact of SLR is generally less in the future than at present (the exceptions are *D. maritima* and *S. californica* under the PCM climate model). Additionally, the interaction between SLR and climate change is insignificant statistically, but it is also small in absolute terms because it only encompasses a fraction of the total habitat change (Table 3).

DISCUSSION

Using the most recent projections of SLR-related threats to the Tri-County Area for 2100, we have identified rare and endangered species that could be at risk from inundation, flooding, cliff and dune erosion. Our results indicate that SLR alone could cause the regional extinction of more than 12% of the species considered in this study (Figure 2). Model simulations by Nicholls *et al*. (1999) predicted that by 2080, SLR alone could cause the loss of up to 22% of the world's coastal wetlands. Another study, using the IPCC estimates of SLR for 2100, suggests that salt marshes could decline in area by 20% - 45%, and that tidal freshwater marshes could either increase by 2% or decrease by 39% (Craft *et al*., 2009). Our results align with these predictions in which some species will either gain or lose suitable habitat depending on the future climate scenario and the effects of SLR.

Although we used plant characteristics along with geographical parameters in our model to predict the SLR risks on each species, we found that area, elevation, and distance from the coast were the best predictors of a species' exposure to SLR. Thus, plant species that are closer to the coast, lower in elevation, and smaller in terms of their area of occurrence would be most likely to face exposure to SLR independent from species characteristics. In particular, species found at very low elevations are very likely to be exposed to SLR (Figure 2, 3). These species may face a high extinction risk without active management to improve their resilience.

Our results also suggest that climate change may cause a substantial shift in suitable habitat for many rare coastal plant species by the end of the century (Figure 4). However, there is a high degree of uncertainty in this outcome, as the habitat of species generally expanded under the

GFDL model, whereas the PCM model predicted a contraction in most species' habitats. However, for 4 of the 10 species analyzed, both climate models identified no future habitat in the Tri-County Area. This result suggests that regardless of how climate may change in California, some rare species will be lost without appropriate preventative action.

Our results are consistent with research on the impacts of climate change on terrestrial plants, which has found a wide range in the extent of predicted habitat loss. A number of European studies have found habitat loss ranging from as high as 32% - 83% under the A1F1, high emissions scenario, to as low as 2.3-28.6% under the B2, low emissions scenario (Bakkenes *et al*., 2002; Randin *et al*., 2009), and response of individual plant species to the forecasted climate change was diverse (Bakkenes *et al*., 2002). A small-scale study in the Austrian Alps, for example, found that 40-50% of plant species could go extinct as a result of climate change (Dirnböck *et al*., 2003). A similar study in the European Alps found that while 60% of plant species experienced low rates of habitat loss (2-5%), the other 40% of species would lose more than 90% of their suitable habitat (Theurillat & Guisan, 2001).

When comparing the relative impact of climate change and SLR on species' habitat, it is important to acknowledge that SLR is a direct effect of climate change, but our analysis treats them as two separate events. SLR is a more certain and predictable threat than climate change impacts on species distributions because the effect of climate change on habitat suitability depends on climate predictions/models (Figure 6 and 7). We found that while SLR poses a threat, range shifting due to climate change presents a much larger and more immediate threat. Therefore, the relative impact of SLR could vary substantially depending in part on future habitat predictions of each species (Table 3). If future habitat is predicted to shrink or shift towards the coast, the relative impact of SLR will be larger (Figure 1A) than if future habitat expands or shifts inland (Figure 1B). Our study did not find a significant interaction between SLR and climate change (Table 3). Thus we expect that there will be no cumulative effect on the loss of habitat from both. However, under a plausible worst-case scenario, the combination of SLR and climate change could eliminate all suitable habitats for some species. For example, the only suitable habitat for *S. atrata*, a primarily coastal species, was found near the inland edge of Santa Barbara County with no remaining coastal habitat.

As in most cases, our study includes a number of critical assumptions. First, the SLR projections did not capture other abiotic interactions that may prove important factors in influencing future species distributions, such as fluvial flooding and in particular, salt-water intrusion into coastal aquifers and wetlands. While many coastal species have some degree of tolerance to saltwater, SLR will likely increase inundation rates, allowing saltwater to contaminate fresh ground and surface water stores, which could alter vegetation drastically (Heberger *et al*. 2009). Saltwater intrusion would likely expand the extent of our SLR models farther inland than predicted at an accelerating rate over time (Heberger *et al*., 2009).

In projecting future habitat ranges of species, SDMs have a number of limitations. SDMs do not typically account for limits to a species' dispersal; they simply aim to predict the potential range of a species under a new climate. The ability of a species to migrate at a sufficient rate to keep pace with changing climate depends on the dispersal characteristics of that species (Collingham & Huntley, 2000). Plant species are far more limited in their dispersal capability that motile species, and rare plant species tend to be further limited (Graham & Grimm, 1990; Collingham *et* *al*., 1996). Given the limited rate of dispersal for most plants, and the discontinuities in suitable habitat (Figure 6 and 7), the actual future range of most of our species will be far smaller than the projected future range.

As with any SDM, MaxEnt assumes that species will not exhibit phenotypic adaptation to new environmental conditions (Hoagland *et al*., 2011) or rapid evolutionary change in response to shifting climate conditions (Wiens *et al*., 2009). Given that we are studying rare and frequently sensitive species, these are valid assumptions. Further, MaxEnt assumes that the current distribution of a species encompasses its entire climatic range, which may not be the case for rare species with only a handful of occurrences. Lastly, MaxEnt does not account for certain inter-specific interactions, such as dependence on pollinators, competition with invasive species, and herbivory (Fitzpatrick *et al*., 2008). For example, the geographic and ecological distribution of *C. maritimum* is largely dependent on the distribution of its host plant and pollinators such as bees and flies (USFWS, 2009).

Our SDM random sampling area (background) included the entire state of California, which may have led to our model overestimating available suitable habitat, largely because dispersal to far-flung areas is unlikely. Our model also may not have captured local adaptations or the effect of microhabitats. Along with abiotic environmental variables, other factors such as inter-species interactions, ecosystem dynamics, and land use changes could influence whether species could survive in what would otherwise appear to be suitable habitat. For example, promising research has begun to evaluate the ability of salt marsh species to migrate upslope, which could improve any future modeling efforts (Feagin *et al*., 2010; Wasson *et al*., 2013).

For most rare species, we do not know which climatic and edaphic variables are most important for predicting suitable habitat (USFWS, 2009; USFWS, 2010). As such, there is a high level of uncertainty about which environmental inputs are appropriate for use in MaxEnt. It was not feasible to model the distributions of our 10 species using more tailored, species-specific sets of environmental variables, as data on habitat preferences for many rare species are not available. Future modeling efforts that select more species-specific environmental variables may yield more accurate results. It would also be useful to expand our selection to the 88 species as well as to currently non-coastal species that could become coastal as sea levels rise.

This research represents an important first step in assessing the emerging threats to coastal plant species by addressing the factors relating to SLR and climate change. Our research implies that there is a need for human-assisted migration or similar management approached to preserve species that are unlikely to survive the effects of SLR and climate change. Further study and proactive management are required to ensure the survival of coastal plant species against both the short- and long-term threats of SLR and climate change.

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Figure 1. Conceptual Model of Suitable Habitat Shifts as a Result of Climate Change and the Resulting Impact of SLR on that Habitat. In Panel A, climate change shifts species range away from the coast, thus decreasing the threat of SLR. In Panel B, climate change shifts species range towards the coast, thus increasing the threat of SLR. In Panel C, climate change shifts species range up the coast (North), thus having no significant change to the threat of SLR.

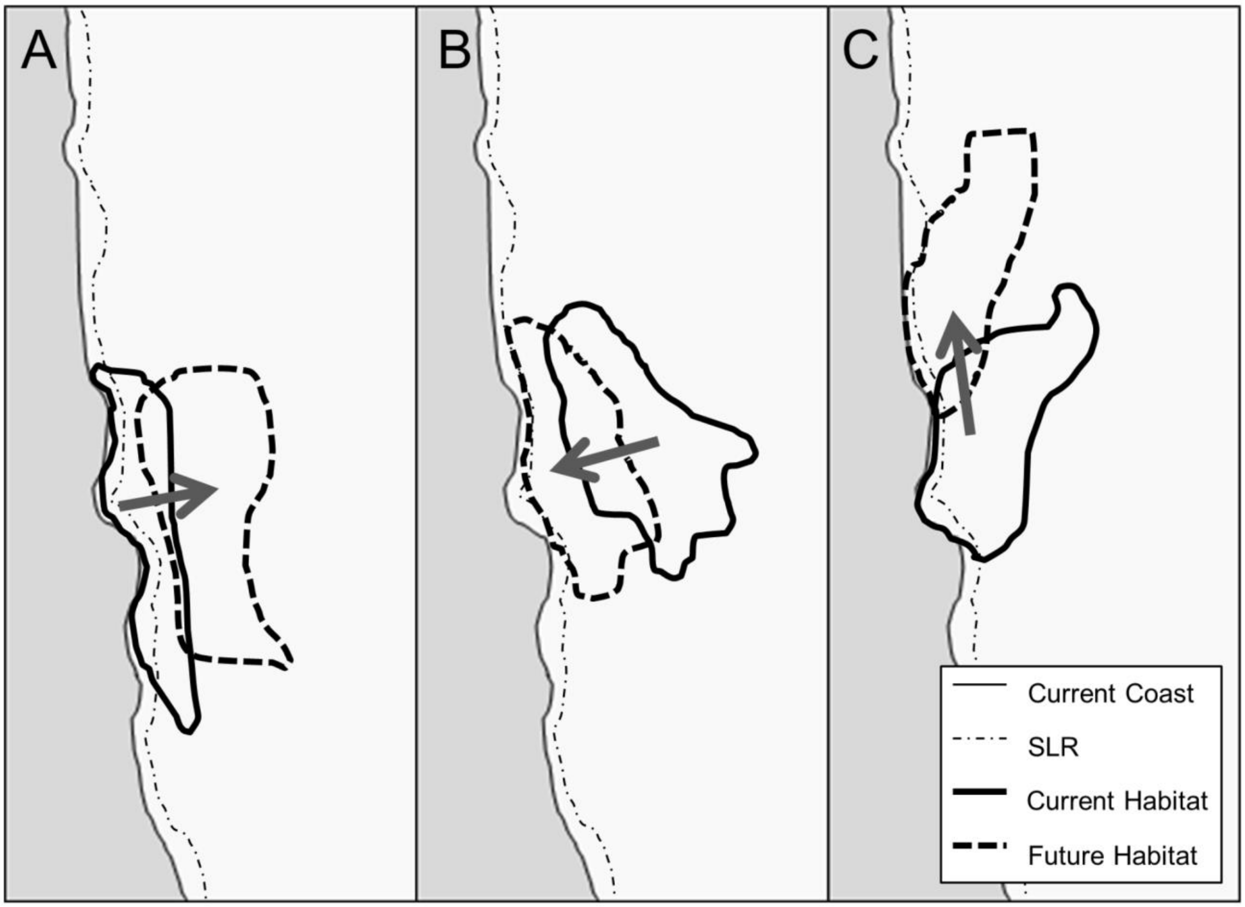

Figure 2. Histogram of percent of the 1091 species' occurrences threatened by sea level rise by percent of species. This indicates the extent of threat for each species and the cumulative threat to all species.

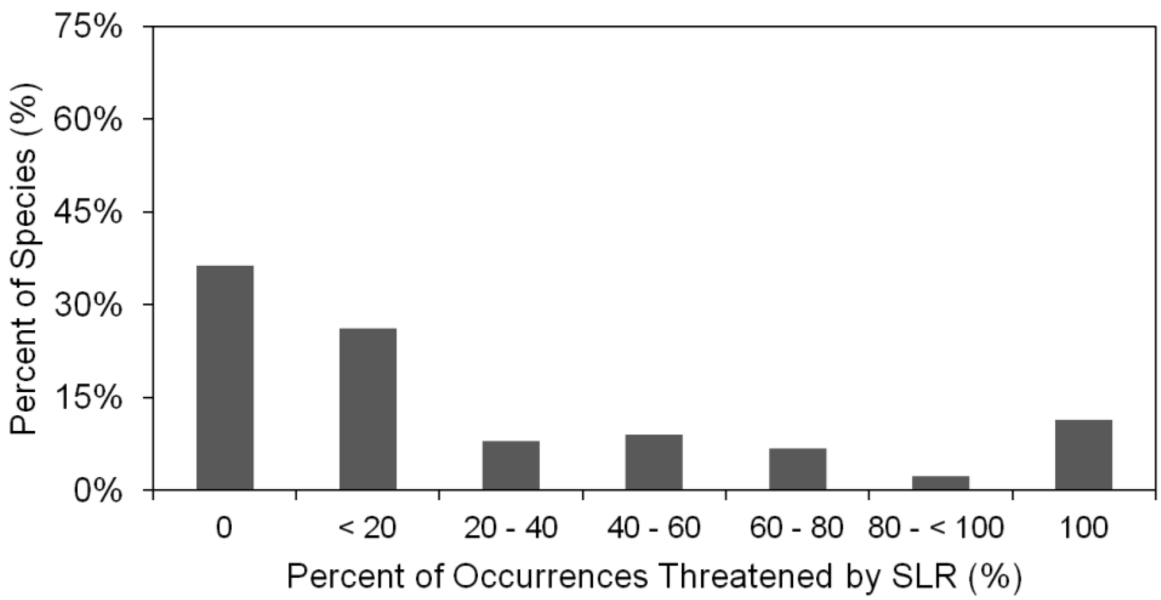

Figure 3. Histograms of percent of 1091 occurrences threatened by sea level rise threats: (a) inundation, (b) flooding, (c) dune erosion, and (d) cliff erosion by percent of species.

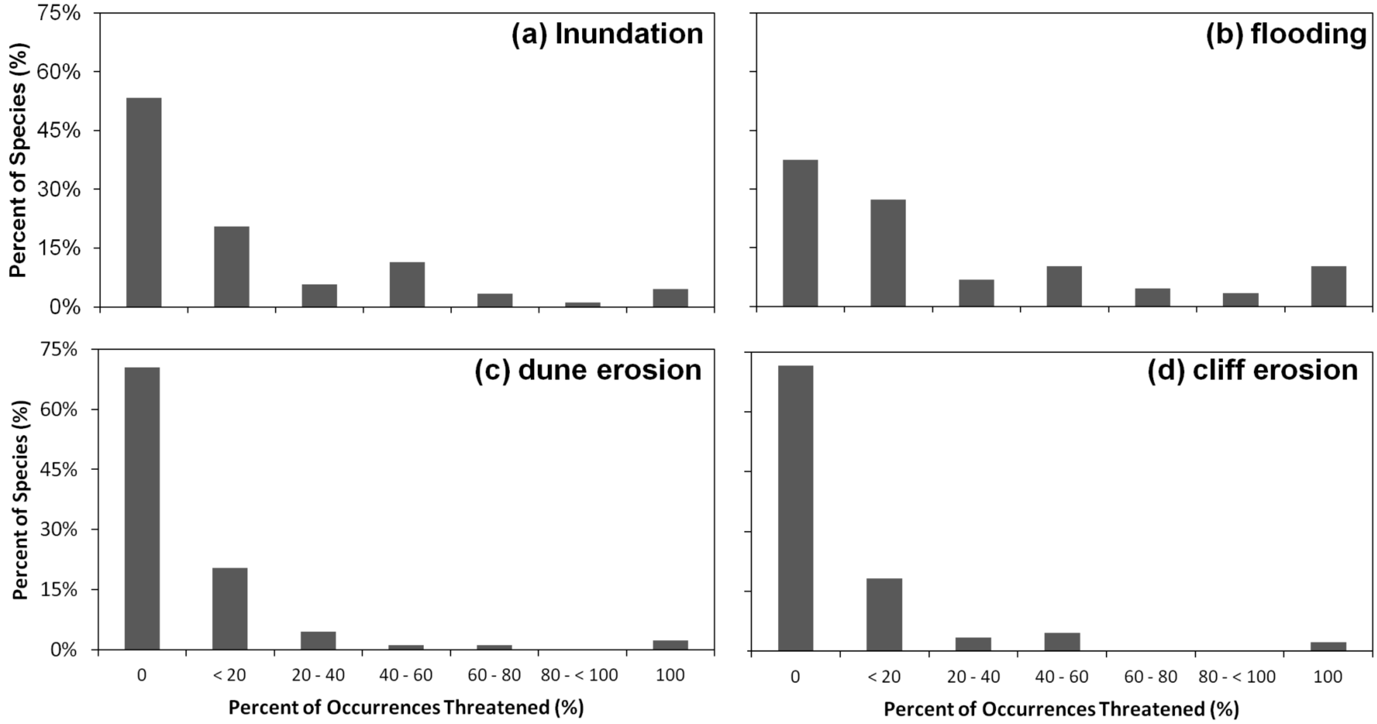

Figure 4. Contour plot showing probability of exposure to aggregated sea level rise threats for any combination of elevation and distance from the coast using the mean occurrence area.

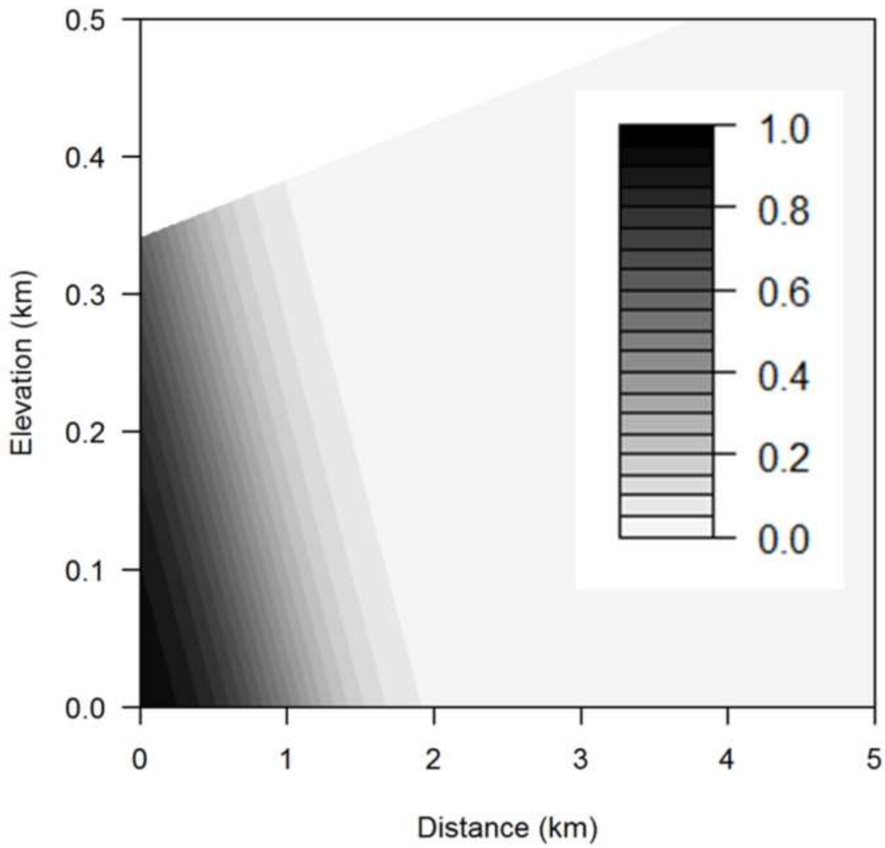

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Figure 5. Contour plot showing probability of exposure to sea level rise threats (a) inundation, (b) flooding, (c) dune erosion, and (d) cliff erosion for any combination of elevation and distance from the coast using a mean occurrence area. The darker the area, the greater the probability of threat.

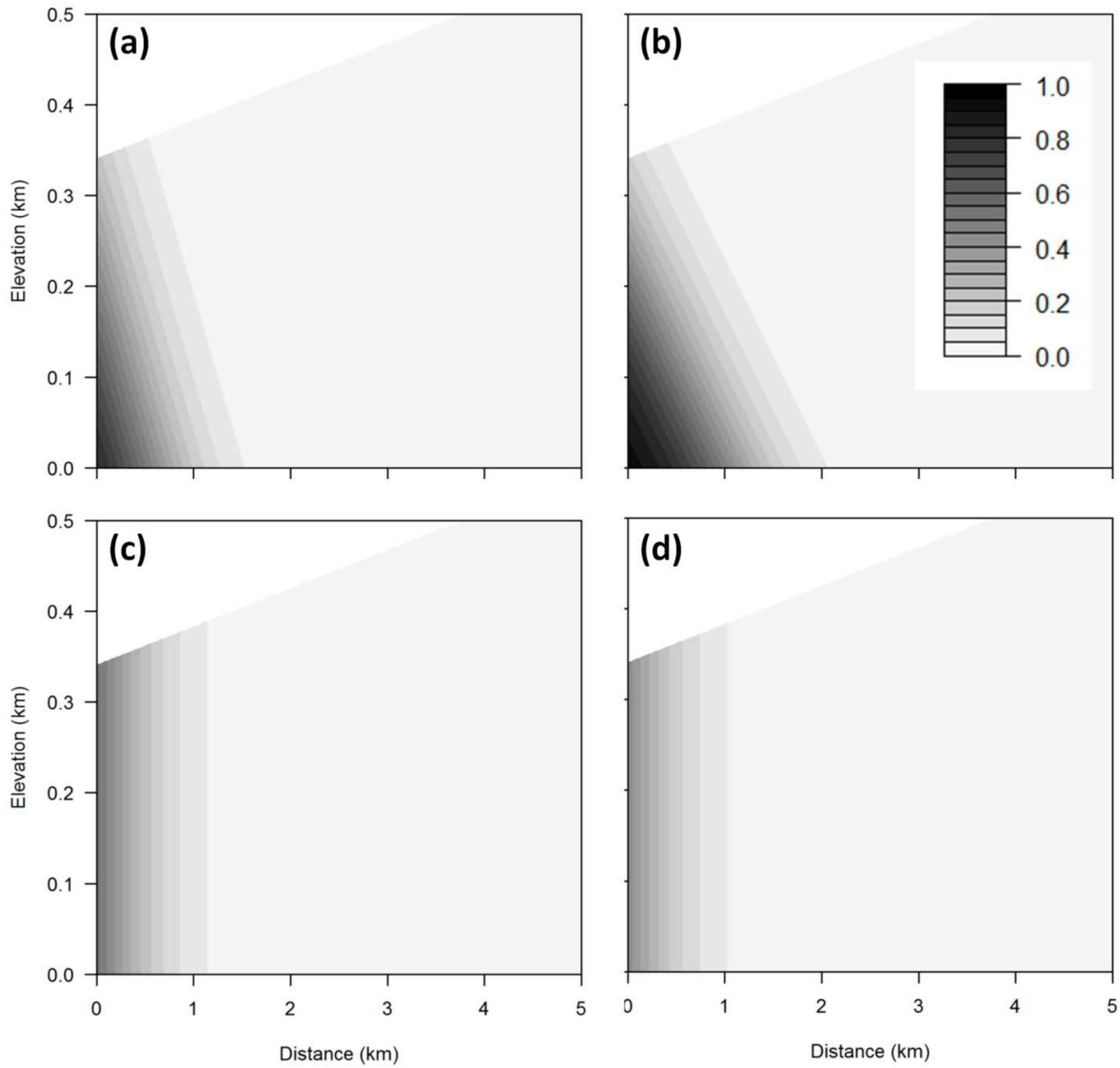

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Figure 6. Current and future habitat projected by the GFDL climate model within the Tri-County Area, expressed as percent of current habitat. The first set of columns for each species indicates all areas within the Tri-County, so current habitat is 100%. The second set of columns for each species indicates all areas within the Tri-County Area after loss to sea level rise. Current habitat is represented by everything above the x-axis. Unsuitable habitat is habitat that will become unsuitable in the future due to climate change. Suitable habitat is current habitat that will remain suitable even with climate change. New habitat is future habitat that will be created as a result of climate change and is represented by everything below the x-axis.

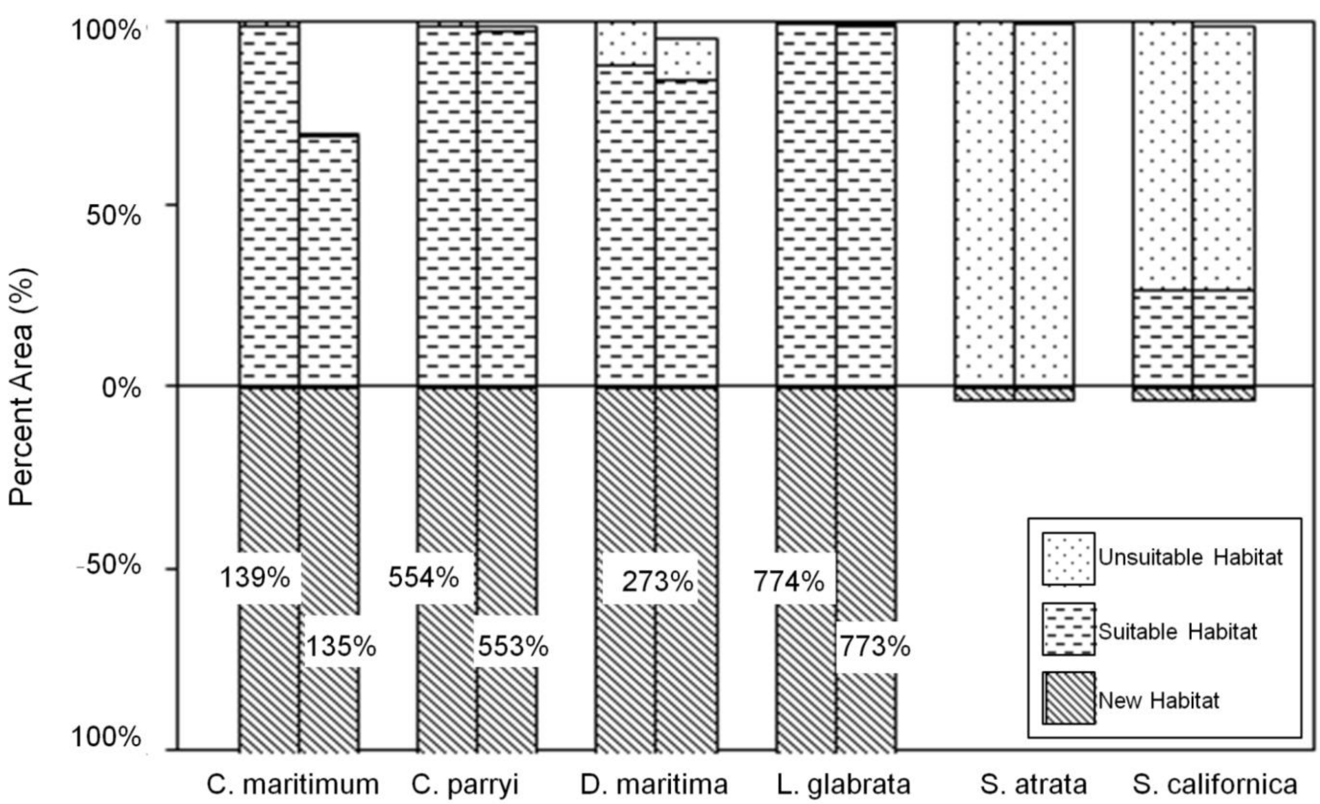

Figure 7. Current and future habitat projected by the PCM climate model within the Tri-County Area. The first set of columns for each species indicates all area within the Tri-County. The second set of columns for each species indicates all area within the Tri-County Area after loss to sea level rise. Current habitat is represented by everything above the x-axis. Unsuitable habitat is habitat that will become unsuitable in the future due to climate change. Suitable habitat is current habitat that will remain suitable even with climate change. New habitat is future habitat that will be created as a result of climate change and is represented by everything below the x-axis.

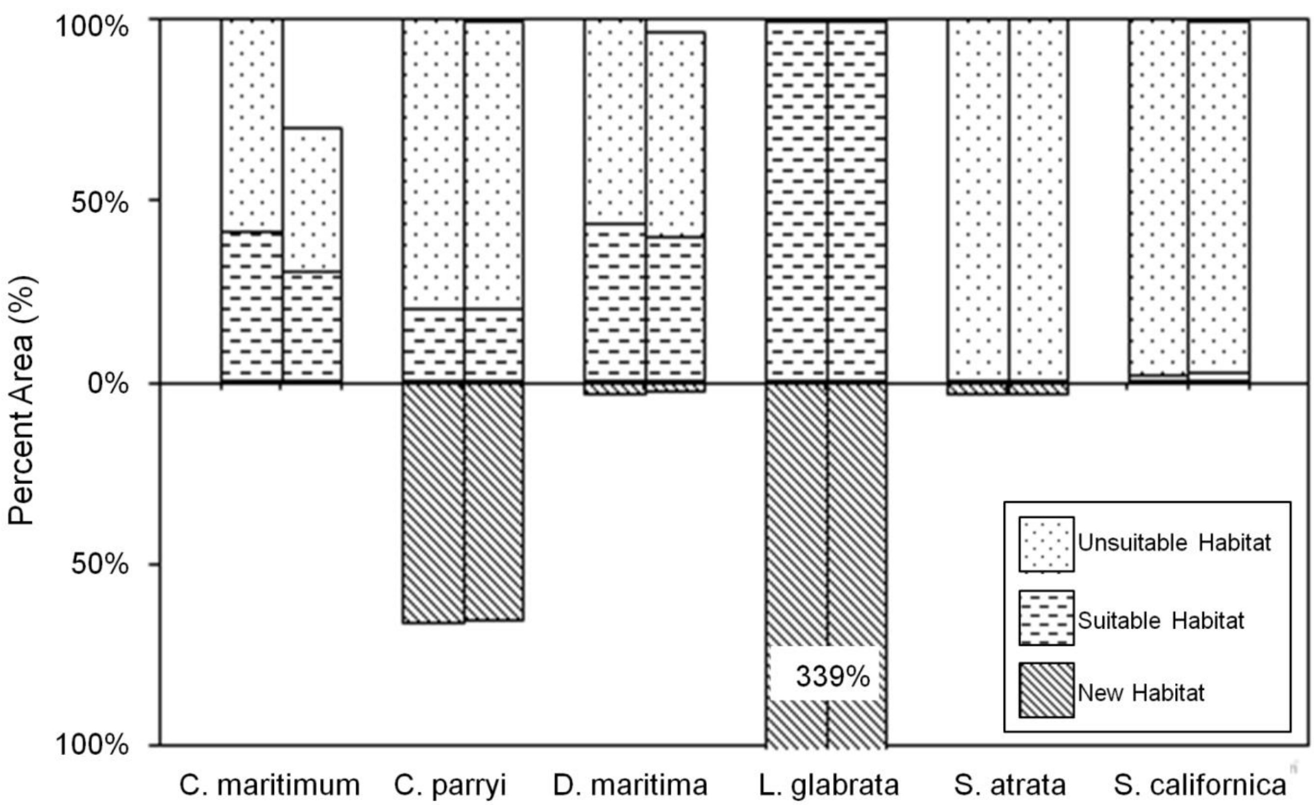

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Table 1. Coefficients table for Aggregate SLR risk model

	Estimate	Std. Error	Z value	Pr(>|z|)
(Intercept)	1.8792	0.2443	7.692	1.44e-14
Area (km2)	0.8787	0.1201	7.317	2.54e-13
Elevation (km)	-7.5795	3.2419	-2.388	0.0194
Distance (km)	-3.0909	0.3844	-8.041	8.88e-16

Table 2. Parameter Estimates for Inundation Risk Model

Parameter	Inundation	Flooding	Dune Erosion	Cliff Erosion
(Intercept)	0.5871*	1.5221***	-0.52014*	-0.88882**
Area (km2)	0.7189***	0.8693***	0.48797***	0.48498***
Elevation (km)	-7.9667*	-12.4263**		
Distance (km)	-2.9035***	-2.6919***	-2.65244***	-2.58650 ***

* <0.05, ** <0.001, ***<0.0001

Table 3. Changes in modeled habitat areas under climate change scenarios and projected SLR. Negative values indicate habitat contraction, whereas positive values indicate habitat expansion. Present habitat (P) is the total current habitat projected under the historical climate (PRISM). Total habitat change (H) is calculated as the present projected habitat subtracted from the future projected habitat under SLR. Habitat change due to climate change (C) was calculated as the present projected habitat subtracted from the future projected habitat without accounting for SLR. Habitat change due to SLR (S) was calculated as present projected habitat under SLR subtracted from present projected habitat. The percent area lost to SLR (A) is the percent of total suitable habitat that will be exposed to SLR.

Species	Present Habitat (P) (sq km)	Total Habitat Change (H) (sq km)		Habitat Change due to Climate Change (C) (sq km)		Habitat Change due to SLR (S) (sq km)	Interaction (I) (sq km)		Percent Area Lost to SLR (A) (%)		
	PRISM	PCM	GFDL	PCM	GFDL	PRISM	PCM	GFDL	PRISM	PCM	GFDL
C. maritimum	212.3	-14.7	+22.0	-12.2	+29.3	-6.5	4.0	-0.8	30.63	27.78	14.52
C. parryi	585.3	-83.0	+3,222.2	-80.3	+3,236.8	-7.1	4.3	-7.5	1.21	0.55	0.38
D. maritime	214.9	-123.9	+552.0	-114.9	+562.0	-9.2	0.2	-0.8	4.30	9.01	1.29
L. glabrata	1,265.5	+4,271.8	+9,777.7	+4,283.4	+9,795.5	-9.2	-2.3	-8.6	0.73	0.21	0.16
S. atrata	1,499.2	-1,439.2	-1,436.9	-1,439.2	-1,436.9	-6.1	6.1	6.1	0.40	0.00	0.00
S. californica	1,032.1	-1,008.7	-726.5	-1,007.3	-725.3	-8.7	7.4	7.6	0.85	5.31	0.37