

Will the California Current lose its nesting Tufted Puffins? (#21985)

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Will the California Current lose its nesting Tufted Puffins?

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Tufted Puffin (*Fratercula cirrhata*) populations have experienced dramatic declines since the mid-19th century along the southern portion of the species range, leading citizen groups to petition the United States Fish and Wildlife Service (USFWS) to list the species as endangered in the contiguous U.S. While there remains no consensus on the mechanisms driving these trends, decreases in the California Current Large Marine Ecosystem suggest climate-related factors, and in particular the indirect influence of sea-surface temperature on puffin prey. Here, we use three species distribution models (SDMs) to evaluate projected shifts in habitat suitability for Tufted Puffin nesting for the year 2050 under two future Intergovernmental Panel on Climate Change (IPCC) emission scenarios. Ensemble model results indicate warming marine and terrestrial temperatures play a key role in the loss of suitable Tufted Puffin nesting conditions in the California Current under both business-as-usual (RCP 8.5) and moderated (RCP 4.5) carbon emission scenarios. Under both emission scenarios, ensemble model results suggest that more than 93% of currently suitable nesting habitat in the California Current is likely to become unsuitable. Moreover, the models suggest a net loss of greater than 18% of suitable nesting sites throughout the entire North American range of the Tufted Puffin, regardless of emission-reduction strategies. These model results highlight continued Tufted Puffin declines — particularly among southern breeding colonies — and indicate a significant risk of near-term extirpation in the California Current.

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Abstract

Tufted Puffin (*Fratercula cirrhata*) populations have experienced dramatic declines since the mid-19th century along the southern portion of the species range, leading citizen groups to petition the United States Fish and Wildlife Service (USFWS) to list the species as endangered in the contiguous U.S. While there remains no consensus on the mechanisms driving these trends, decreases in the California Current Large Marine Ecosystem suggest climate-related factors, and in particular the indirect influence of sea-surface temperature on puffin prey. Here, we use three species distribution models (SDMs) to evaluate projected shifts in habitat suitable for Tufted Puffin nesting for the year 2050 under two future Intergovernmental Panel on Climate Change (IPCC) emission scenarios. Ensemble model results indicate warming marine and terrestrial temperatures play a key role in the loss of suitable Tufted Puffin nesting conditions in the California Current under both business-as-usual (RCP 8.5) and moderated (RCP 4.5) carbon emission scenarios. Under both emission scenarios, ensemble model results suggest that more than 93% of currently suitable nesting habitat in the California Current is likely to become unsuitable. Moreover, the models suggest a net loss of greater than 18% of suitable nesting sites throughout the entire North American range of the Tufted Puffin, regardless of emission-reduction strategies. These model results highlight continued Tufted Puffin declines — particularly among southern breeding colonies — and indicate a significant risk of near-term extirpation in the California Current.

Introduction

Worldwide, species are facing increasing challenges associated with rising sea and air surface temperatures (Thomas et al., 2004). Warming climates have resulted in species range shifts (Parmesan & Yohe, 2003), ecological responses (Walther et al., 2002) and changes in habitat quality (Hickling et al., 2006). Foden et al. (2013) found that 83% of birds, 66% of amphibians and 70% of corals that were identified as highly vulnerable to the impacts of climate change are not currently considered threatened with extinction on the IUCN Red List of Threatened Species, indicating that species' vulnerabilities are likely to be much greater than conservation status alone would suggest.

In recent years in the United States, the USFWS and the National Marine Fisheries Service (NMFS) have received several petitions to list species under the Endangered Species Act based on the impacts of climate change (Siegel, K., Cummings, B. 2005; Wolf, S., Cummings, B., Siegel, K., 2008). However, the link between climate change and risk to a species can be difficult to assess. One approach to examining these linkages is to model the interaction between climate and suitable habitat for a given species, given what is already known about the relationship between the species and its habitat. This approach has become an integral component of conservation planning in a world of changing environments (Hagen & Hodges, 2006; Richardson & Whittaker, 2010). Ultimately, understanding these linkages can help inform conservation assessments and species and ecosystem management strategies (Carnaval & Moritz, 2008; Ponce-Reyes et al., 2017), for example, by estimating the likelihood of losing (or gaining) particular suitable habitats of interest under future climate conditions.

Tufted Puffins as a Pertinent Example

The Tufted Puffin (*Fratercula cirrhata*) is an iconic species that is experiencing dramatic population declines across the southern portion of its geographic range (Piatt & Kitaysky, 2002). While Tufted Puffin populations in the Alaska Current have remained relatively stable (but see Goyert et al., 2017), populations in the California Current large marine ecosystem (area of the eastern Pacific Ocean spanning nearly 3,000 km from southern British Columbia, Canada to Baja California, Mexico) have declined by approximately 90% relative to early 20th century estimates, and are currently declining 9% annually (Hanson & Wiles, 2015). The number of occupied breeding colony sites in Washington State has declined by 60% relative to the 1886-1977 average, and 45% relative to the 1978-1984 average (Hanson & Wiles, 2015). Range contractions at the southern edge of the Tufted Puffin's habitat in both the eastern and western Pacific Ocean have led to preliminary conservation actions by state agencies such as the Washington Department of Fish and Wildlife and Japan Ministry of the Environment (MOE, 2011; Hanson & Wiles, 2015; WAC 232-12-014, 2016).

Tufted Puffin Biology and Ecology

Tufted Puffins are seabirds belonging to the family *Alcidae* and nest in colonies located on both sides of the North Pacific, ranging in North America from the Channel Islands in southern California (34° N) to coastal northern Alaska (68° N) (Piatt & Kitaysky, 2002) and in Asia from Hokkaido, Japan (43° N) through the Kamchatka Peninsula (63° N) (WDFW, 2015). They are central-place foragers during the nesting season, when they dig burrows or use crevices for nesting on nearshore rocks, islands and sea stacks (Piatt & Kitaysky, 2002). During the nesting season, puffins exhibit large foraging radii around their colonies (up to 40 km, e.g., Menza et al. (2016) Figure 12) and are able to carry more than twenty fish at a time while flying

back to the colony to feed their chicks (Piatt & Kitaysky, 2002; Hanson & Wiles, 2015). While little is known about the wintering distribution and ecology of Tufted Puffins, summer (May-September) breeding colonies are well documented and provide the most useful biological data for conservation management (Piatt & Kitaysky, 2002). Extensive breeding colony surveys dating back to the early 20th century allow us to examine any potential link between climate and species range extent.

Tufted Puffins are subject to multiple well-documented ecological stressors—such as increasing eagle predation, habitat degradation, declining prey availability, and fishing net entanglement (Baird, 1991; Degange, et al., 1991; Ricca, et al., 2008)—but several mechanisms associated with temperature stress may be important in driving puffin declines along their southern range boundary. Gjerdrum et al. (2003) found dramatically reduced growth rates and fledgling success in years with high Sea Surface Temperature (SST) anomalies. Other researchers cite the nutritional demands of puffin chicks and the prey availability and preferences correlating with fledgling success (Hipfner et al., 2007), suggesting a mechanism for the negative effects of high sea surface temperature on puffin chicks. These and other studies point to a link between temperature and demographic trends in the Tufted Puffin and help identify this species as a candidate for distribution modeling. Modeling outputs may help expose proposed interactions between high ocean temperatures, prey distribution in the water column and puffin breeding success.

As a result of these potential threats and documented population declines, the USFWS was petitioned to list the California Current population of the Tufted Puffin (*Fratercula cirrhata*) as endangered under the Endangered Species Act (Sewell, 2014). In order to respond to this

petition, the USFWS is currently examining Tufted Puffin status and trends, evaluating threats to its survival, the adequacy of existing regulatory mechanisms to conserve the species, the loss of its habitat, and other relevant factors. Given that climate—specifically, increasing sea-surface temperatures—may be a particularly important factor influencing puffin population dynamics and ultimately reducing puffin breeding range, and given the vast geographic extent of puffin nesting sites (34° of latitude and roughly 70° of longitude in North America) and historical data on the occupancy of these sites, the Tufted Puffin is an excellent candidate for species distribution modeling.

Species Distribution Models in Conservation Planning

Species distribution models (SDMs) are a powerful way to examine how climate variables relate to species geographic distribution and the distribution of suitable habitat (Guisan & Zimmermann, 2000; Guisan & Thullier, 2005). By associating species occurrence with climate variables, these models can 1) test for associations in space and time between putative environmental drivers and changes in species range and 2) project changes in suitable habitat under future climate change scenarios (Bellard et al., 2012). SDMs use a variety of underlying statistical models to capture the relationship between habitat and climate and create detailed outputs highly useful for wildlife management (Carvalho et al., 2011; Guisan et al., 2013). Recent Endangered Species Act listing decisions and management plans have drawn on SDM results to provide critical spatial and temporal conservation information. For example, climate envelope models were used to develop spatially explicit conservation strategies that account for climate change, notably in the case of the North America Wolverine (*Gulo gulo*), where the models were the basis of an ESA listing (81 FR 71670, 2016).

Here we use 50 years of species nesting habitat distribution information—ranging from the Bering Sea to California—to map Tufted Puffin nesting habitat. We use this colony occupancy data to model the relationship between nesting habitat and current environmental conditions to project future suitable breeding sites in the same geographic range. We present these results as an example of how this information can be used in a regulatory context (e.g., Endangered Species Act listing decisions) and in a conservation planning context.

Materials and Methods

Environmental Data

Environmental data for the current period, which we define here as the years 1950-2000, were downloaded from WorldClim, a set of global climate layers derived from interpolation of monthly climate observations (Hijmans et al., 2005, last accessed January 2017). After removing WorldClim bioclimatic variables displaying high collinearity and considering factors relevant to Tufted Puffin breeding phenology, we selected six environmental variables for analysis: annual temperature range (ATR), mean diurnal temperature range (MDR), mean temperature of the warmest quarter (MTWQ), annual precipitation (AP), precipitation of the warmest quarter (PWQ) and distance-to-distance (DIST), a variable we created to help models discern suitable nesting habitat as occurring only in rocky, coastal habitats within meters of the sea, a biological requirement of puffins (Piatt & Kitaysky, 2002); (see Table 1 for measurements and units). Each variable for the current period was scaled to a 5 arcmin grid cell size (ca 10 km x 10 km). After scaling, all environmental variables within the relevant geographic range were cropped to only

include locations within 200 kilometers of the ocean, given the Tufted Puffin's obligate nearshore nesting habitat.

The same 6 environmental variables above were averaged over the period of 1910-1950 to construct a 'past' climate regime used to project past Tufted Puffin range. Past climate variables were selected using gridded climate data obtained from monthly observations from the Climate Research Unit CRU TS v. 4.01 dataset (Harris et al., 2014 (crudata.uea.ac.uk), last accessed March 2017). Past environmental data were similarly scaled down to the same 5 arcmin grid cell size as the current data.

Future Climate

We selected emissions scenarios Radiative Concentration Pathways (RCP) 4.5 and 8.5 as defined by the IPCC 5th Assessment Report (IPCC, 2014) as future environmental projections against which to forecast changes in Tufted Puffin breeding distribution. Downscaled model output for environmental variables for both future RCP scenarios were averaged across the following general circulation models: Hadley Centre's HadGEM2-ES (Collins et al., 2011), NOAA's GDFL-CM3 (Griffies et al., 2011) and NASA's GISS-E2-R (Nazarenko et al., 2015) for the year 2050 (average of 2041-2060) (Hijmans et al., 2005, last accessed January 2017). Utilizing the average of multiple prominent U.S. climate model outputs helps incorporate variance in potential future climate projections within our model. The 2050 timeframe and these emissions scenarios (roughly speaking, a moderate-reduction scenario and business-as-usual scenario with no emission reductions) were selected as the most relevant to the conservation decisions presently surrounding the Tufted Puffin (IPCC, 2014).

Species Data

Species distribution data were obtained courtesy of USFWS, Washington Department of Fish and Wildlife and Environment Canada, and were derived from expansive U.S. and Canada breeding colony surveys conducted by groups including USFWS, Washington Department of Fish and Wildlife, Alaska Department of Fish and Game, Environment Canada, California Department of Fish and Wildlife, and others (Speich & Wall, 1989; Hodum et al., unpubl.; World Seabird Union (<https://seabirds.net>, last accessed March 2017); BCMCA (<http://bcmca.ca>, 2017, last accessed May 2017), see supplemental online materials). Count data consisted of estimates of numbers of breeding individuals present at known nesting colonies and the spatial coordinates of those observations. Biological data for the ‘current’ period of climate data (Table 2) represents the most recent survey data of known nesting sites from 1950-2009. While the climatological data runs until the year 2000, biological data from up to 2009 were included to incorporate recent detailed state-wide surveys in both Oregon and Washington, information critical to examining trends across the puffin’s southern range. We converted count data to presence/absence values, given the nature of our analysis, which asked whether breeding habitat was likely to be suitable (≥ 1 nesting birds) or not (0) under future conditions. Some observations were adjusted geographically up to one grid cell (ca 10 km) to fall within gridded terrestrial environmental variables. Observations further than 15km from terrestrial grids (e.g., remote islands) were removed from the analysis. The environmental variables described above were selected to model potential interactions between climate conditions and puffin range during the breeding season.

Given the low proportion of absence-to-presence observations for Tufted puffin surveys and potential bias in survey locations, we added pseudo-absence (PA) observations (i.e.,

generated absence observations existing within the range of the SDM) to all models. SDMs using both presence and absence have been shown to perform more accurately than models relying on presence-only observations (Elith et al., 2006, Barbet-Massin et al., 2012). PA generation methodology is also important in both model predictive accuracy and avoiding model over-fitting (Barbet-Massin, Thuiller, & Jiguet, 2010, Barbet-Massin et al., 2012). Adapting these recommendations in Barbet-Massin et al. (2012), 1000 PAs were randomly generated twice across the SDM a minimum of 30km from any presence or true absence point.

Model Parameterization

Because Tufted Puffins rely heavily on both terrestrial and marine environments for reproduction, we initially tested the correlation between sea-surface temperature and air-temperature data across puffin colony observations. Sea surface temperature (SST) data for this comparison comprised an average of mean monthly temperature for June, July and August, months aligning with Tufted Puffin breeding season obtained from the Hadley Centre, UK (Rayner et al., 2003 (metoffice.gov.uk/hadobs) last accessed March 2017) and the corresponding air temperature readings (MTWQ) (Hijmans et al., 2005). Both sets of environmental variables were scaled to a 5 arcmin grid cell size and represented means from the years 1950-2000. A high correlation coefficient ($r = 0.96$) allowed us to use air temperature—which is available in higher spatial resolution—than SST in the final analysis. This strong relationship between air- and sea-surface temperature has also been documented across several other marine and aquatic species distribution studies (Stefan & Preud'homme, 1993; Domisch et al., 2013). Additionally, within R software (R Core Team, 2013), a principal component analysis (PCA) (Pearson, 1901) was performed to compare variance in environmental variables between areas where colonies collapsed in recent years to those that persist. This technique has been shown to help identify

differences in environmental niches of species occurrence data (eg. Broennimann et al., 2012; Peña-Gómez et al., 2014); here, we use it to create an index of environmental variables to identify likely drivers of Tufted Puffin declines after accounting for the covariances among variables.

Species Distribution Modeling

Model Algorithms

SDMs were constructed with the R package BIOMOD2 (BIODiversity MODelling) (Thuiller et al., 2009; R Core Team, 2013). All SDMs were constructed for a spatial range larger than the current estimated U.S. Tufted Puffin distribution (180°W to 120°W longitude and 33°N to 69°N). Using a larger extent both increases the range of environmental gradients available for model construction and introduces novel climates useful for projecting potential migration (Thuiller et al., 2004; Fitzpatrick & Hargrove, 2009; Domisch et al., 2013). Models were also constructed using a subset of all biological and environmental data from 126°W to 120°W and 33°N to 48.5°N. This measure is intended to account for the spatial variance of puffin distribution and examine the temperature-habitat relationship in the California Current large marine ecosystem exclusively —the portion of the range that has experienced the greatest decline and has been petitioned for listing under the US Endangered Species Act.

To help acknowledge and estimate uncertainty, 3 different models using different statistical approaches were selected from the BIOMOD framework; generalized linear models (GLM) (McCullagh & Nelder 1989), generalized boosting models (GBM, also referred to as boosted regression trees) (Ridgeway 1999) and random forests (RF) (Breiman, 2001). The GLM models used a logit link between the response variable mean and combination of explanatory

variables (Guisan, Edwards, & Hastie, 2002) (i.e., logistic regression). GBMs incorporate regression and machine-learning techniques through boosting many decision-tree models to increase model performance (Elith et al., 2008). Decision models recursively partition sets of explanatory and outcome variables in a stagewise manner until subsets of data are explained by trees of bifurcating decisions (Elith et al., 2008). Boosting then sequentially fits decision trees to training data, selecting the trees that best fit the data (Elith et al., 2008). Finally, RF represents a machine-learning technique creating classification trees similar to those in GBMs, but instead uses random bootstrap samples of data and explanatory variables upon the construction of each tree (Breiman, 2001).

The significant differences in statistical and machine learning approaches across GLM, GBM and RF algorithms provides variance across which to test sensitivity between models as well as estimations of model uncertainty (Marmion et al., 2009; Rodríguez-Castañeda et al., 2012). Additionally, using models with relatively more ensemble (GBM and RF) and parsimonious (GLM) approaches to habitat selection as well as utilizing both parametric (GLM) and non-parametric (RF) techniques provides robust analysis of environmental drivers of range change (Marmion et al., 2009) and led to the selection of these three model algorithms.

Model Calibration

Having generated two variants of the dataset by generating distinct pseudo-absences, we then constructed twenty models for each algorithm (GLM, GBM, RF), for each dataset variant, for a total of 120 models. All models then utilized past environmental data as well as both future emission scenarios to project both past and future puffin range changes. Each model run

performed a random 70:30 split of the biological data using 70% for model calibration and 30% for model evaluation. This technique addresses spatial autocorrelation and is frequently utilized when faced with dependent biological sampling (surveying of species around only areas of known occurrence) (Araújo et al., 2005). Model selection and calibration parameters were kept constant between past and current models to maintain consistency and repeatability. For all models, the default modeling options of the BIOMOD package were utilized (Thuiller et al., 2009).

Ensemble Modeling and Evaluation

The area under the receiver operating characteristic curve (AUC) and the True Skill Statistic (TSS) were the two model metrics used to evaluate model performance. AUC maps sensitivity rate (true positive) against (1-specificity) values (= false-positive rate) and is a popular metric for species distribution model evaluations because it evaluates across all thresholds of probability conversion to binary presence or absence (Fielding & Bell, 1997; Guo et al., 2015). Higher AUC scores represent better model performance, with AUC scores between 0.7-0.8 classified as ‘fair’, 0.8-0.9 as ‘good’ and 0.9-1.0 as ‘excellent’ (Guo et al., 2015). TSS scores display (sensitivity + specificity – 1) with sensitivity quantifying omission errors and specificity quantifying commission errors (Allouche et al., 2006; Guo et al., 2015; Shabani et al., 2016). TSS scores of zero or less indicate model performance no better than random and scores of 1.0 indicating perfect performance. Both scores were emphasized in this analysis to provide strong measure of ordinal model performance and to prediction accuracy in threshold-dependent conservation planning (Allouche et al., 2006; Shabani et al., 2016).

Ensemble models were created using weighted averages of TSS scores both within and across algorithms. This technique captures uncertainty stemming from random sampling of the

dataset as well as variance across modeling techniques (Gallardo & Aldridge, 2013), thereby providing the user with a robust sense of model fit and sensitivity to particular parameters. TSS scores below 0.7 were excluded from the ensemble to remove influence from poor predictive models (Araújo et al., 2011). A proportional weight decay was used averaging model weights, resulting in weights proportional to TSS evaluation scores. Additionally, binary conversions, which maximized model TSS performance, were used in some range-change analyses. Range-change analyses were performed allowing future migration to potential suitable future habitat as well as with no potential migration. Ensemble binary thresholds and their impact on projections are noted below.

Results

Model Performance

Models from all three algorithms, and especially the ensemble model, scored very high in both model performance metrics (Table 3). GLM, GBM and RF algorithms displayed mean TSS scores and standard deviations of 0.854 ± 0.023 , 0.904 ± 0.017 and 0.915 ± 0.014 , respectively. Similarly, GLM, GBM and RF mean AUC scores were very high, indicating good model accuracy (Table 3). Techniques utilizing machine learning methods (RF & GBM) consistently displayed the highest performance by both AUC and TSS scores (Table 3), perhaps due to these machine-learning (GBM & RF) models relying on boosting and ensemble learning, respectively, compared to a single regression model approach within GLM algorithms. Despite the different statistical and learning approaches of the selected modeling approaches, TSS and AUC scores were high across all techniques and displayed low variance (Table 3).

Variable Contribution

Response Plots

After initial variable winnowing, both model response plots and PCA analysis indicate that temperature variables ATR and MTWQ are strongly associated with Tufted Puffin breeding habitat (Figure 1, 2). Importantly, MTWQ displayed a thermal maximum of suitable nesting habitat (i.e., a threshold) around 15.5 °C, and the MTWQ variable also displayed the most consensus across model members among all selected variables (Figure 1). This result highlights consensus among GLM ensemble members surrounding the 15.5 °C threshold. ATR and MTWQ are related to extreme summer temperatures and consensus among GLM ensemble members across these variable response plots is consistent with the hypothesis that summer temperature anomalies influence Tufted Puffin colonies.

Conversely, MDR and PWQ were not effective in predicting suitable habitat among all models. In fact, the probability of Tufted Puffin occurrence remains high across the range of MDR and PWQ values indicating that these variables are not helpful in predicting puffin occupancy. Ensemble members do show a response to increased annual precipitation (AP) values, but there remains a lack of consensus among model members around a particular response cutoff.

Principal Component Analysis

Principal component analysis provided further support to the hypothesis identifying summer temperature as a primary driver of variance in Tufted Puffin breeding habitat (Figure 2). PCA components 1 (51%) and 2 (27%) together explained 78% of the variability in the data. Component 2, with a strong loading of MTWQ of -0.730 and MDR loading of -0.491, indicates

that MTWQ and MDR explain the difference between presence and absence points as evidenced by the separation of the 95% confidence ellipse along this component (Figure 2). The other four variables loaded more strongly onto principal component 1 which does not help separate presence and absence points. This result combined with the MTWQ response curves (Figure 2) indicate the importance of MTWQ in predicting what habitat is suitable for Tufted Puffins (Figure 1, 2).

Range Forecasts

North American Projections - 2050

After binary transformation of the future probabilistic projection maps ensemble model range change analysis projects Tufted Puffins to lose 18% of their occupied range under RCP 4.5 and 25% under RCP 8.5 by 2050 (Table 3). RF models projected the greatest percent habitat loss across North America under both emission scenarios (Table 3). There was uniform agreement across ensemble members in projecting habitat loss, with variability among algorithms as to the magnitude of that loss (Table 3). Spatially, losses were uniformly projected along the California Current up to southeastern Alaska (Figure 3), although ensemble projections suggested continued suitability of the Aleutian Islands under both emission scenarios (Figure 3). Ensemble model results also reflected agreement on the opportunity for northward range expansion (Figure 3). Both the projected southern range contraction and northward range expansion are further consistent with the hypothesized relationship between puffin habitat and temperature.

California Current - 2050

Analysis of the California Current region within the overall ensemble models shows near complete loss of suitable habitat between emission scenarios with both RCP 4.5 and 8.5 (Figure

4), although the individual component models showed variable amounts of habitat loss. GLM models projected the most dramatic loss along the California Current with a predicted loss of over 88% of suitable habitat (Table 3). GLM models also projected a negligible amount of habitat as likely to become newly habitable in the California Current under either emission scenario. Both GBM and RF models predicted less range change with GBM models projecting a mean loss of about 30% and RF models projecting a mean loss of about 31%. Under both RCP 4.5 and 8.5, ensemble projections display complete loss of suitable habitat in Oregon and virtually complete loss in California (Figure 4). GBM and RF models projected small portions of northwestern Washington would become slightly more likely than not to become habitable by 2050 under both emission scenarios.

Discussion

Ensemble models uniformly support summer temperature as a predictor of Tufted Puffin breeding habitat. High model evaluation metrics (Table 3) coupled with strong correlations between temperature variables and Tufted Puffin range change (Figures 1, 2) provide confidence that projected warmer summer temperatures are likely to be associated with the loss of greater than 93% of Tufted Puffin breeding habitat in the California Current (Figure 4). North America-wide, ensemble models project the overall loss of 18% and 25% of suitable habitat, respectively, under moderate emission reductions and business as usual carbon emissions by 2050 (Table 3). Figure 3 highlights that most nesting habitat will be lost along the southern portion of current Tufted Puffin range as well as the opportunity for northward range expansion.

Important to the interpretation of ensemble projections is the binary transformation of model outputs into suitable and unsuitable categories. For range change analyses, projections of unsuitable habitat represent a weighted average of <50% probability of suitability, a cutoff defined by ensemble calibration. In some cases we observed a majority of ensemble members projecting a particular cell as marginally suitable while a minority of members strongly project that cell as unsuitable. The subsequent result is unsuitable habitat despite being marginally suitable in some models. This process of binary transformation can then reflect an aggregate of probabilistic scores instead of the average of a binary projection. Binary transformations are thus a useful tool to discuss and represent how changes in climate may affect the likelihood of suitable breeding conditions throughout Tufted Puffin range, but are necessarily imprecise in that they mask underlying variability.

Examining the variance among model results and the spatial variance in projections is integral to the interpretation of model results in a conservation perspective (Guisan et al., 2013; Porfirio et al., 2014). Tufted Puffins are a relatively rare species in the southern portion of their range, are hard to survey, and occupy small areas of land (Hanson & Wiles, 2015). These biological factors contribute to the difficulty of surveying (and therefore modeling) puffins and can increase variance among model algorithms, making ensemble models more valuable for interpretation of results (Segurado & Araújo, 2004; Hernandez et al., 2006). However, here we use colony occupancy information rather than counts. Preliminary occupancy analysis suggest that colony occupancy can be assessed with a high probability with a single relatively rapid visit by boat even to a very small colony with few birds (Pearson et al., unpublished). Thus, our colony occupancy approach likely reflects actual changes in colony occupancy throughout the range. In addition, trends were consistent across algorithms in depicting significant losses of

suitability for habitat across the California Current, British Columbia and eastern Alaska (Figure 3). All algorithms also projected the opportunity for northward range expansion in the face of accelerating northern latitude warming (Figure 3).

If suitable habitat expands as predicted by our ensemble models, biological and ecological factors unrelated to climate such as eagle predation are predicted to continue and likely to influence the probability of colonization (Hipfner et al., 2012; Hanson & Wiles, 2015). Because colonization is uncertain, we depict in Figure 5 the loss of currently suitable habitat in the California Current without the possibility of new colonization throughout the extent—a worst case scenario. Variance among models as evidenced in Table 3 along the California Current failed to result in more than a handful of consensus areas of suitability (Figure 4). While outlying colonies such as the one in the Farallon Islands of California (where puffins remain at present) in areas projected to be unsuitable are important to examine further, all models and especially ensemble results support the trend of southern range contraction associated with warm summer temperatures (Figures 1, 2, 3, 4). Additionally, while limitations on historical survey data make interpretation of hindcasts difficult, preliminary hindcasting resulted in expansion across the southern portion of current puffin habitat (see suppl. file). This result is further consistent with the hypothesized relationship between high temperature and puffin success.

Our results are especially salient in light of the ongoing U.S. Fish and Wildlife Service's analysis of puffin status following Natural Resources Defense Council's petition to list the California Current population as endangered. When responding to the petition to list the puffin, the Service can list the species throughout its range or can list a distinct population segment (DPS) such as the breeding population south of the Canadian border or that in the California Current. While determining which segments comprise a DPS as outlined by the ESA requires

more analysis, our results provide the spatial information to inform the threat that both of these breeding range segments or “populations” will likely face. Based on our modeling, all potential distinct populations segments from British Columbia, south, face a significant chance of near extirpation or very significant habitat loss under a wide range of climate projections by 2050.

Conservation planning for species can greatly benefit from defining the portion(s) of their range representing habitat critical to their survival (Hagen & Hodges, 2006). This designation is essential for conservation planning both under the ESA, in which it is required for listed species, as well as for more localized conservation efforts (Taylor et al., 2005). Figure 3 highlights areas where Tufted Puffins are currently at the highest risk of colony loss (low habitat suitability). Many puffin nesting sites are already managed by the US Fish and Wildlife Service Refuge system and many of these sites are also designated as “wilderness” (Sowles et al., 1980, Speich and Wahl 1989, Naughton et al. 2007, US Fish and Wildlife Service 2017). Habitat projections made for the year 2050 permits analysis of critical habitat in terms of species survival as well as proposed conservation efficacy (Suckling & Taylor, 2006; Stein et al., 2013). Land acquisition has proven to be an effective strategy for the management of endangered species and is a strategy that has been utilized for the Tufted Puffin (Lawler et al., 2003; WDFW, 2016) and could be used in the future. With limited resources to conserve species at the federal level, ranking the conservation priorities and temporally analyzing threats can allow for prudent investment in conservation lands (Lawler et al., 2003). Nesting colony sites throughout the Gulf of Alaska are projected to remain suitable and results indicate the Aleutian Islands are the most likely habitat to both continue to support large populations of Tufted Puffins as well as potentially becoming suitable as new breeding sites (Figure 3). As these results suggest, we can use this information to predict areas of future Tufted Puffin habitat to help outline areas for long-term conservation

action while also mapping areas where long-term conservation efforts may prove ineffective. Such proactive conservation steps often result in greater conservation outcomes and are critical for species struggling to adapt to changing climates (Morrison et al., 2011).

Mechanisms Driving Decline

Using the results reflected in Figure 3, wildlife managers can continue to explore the causal mechanisms driving the discussed Tufted Puffin population declines and range contraction. Currently numerous pathways are proposed to help determine puffin breeding success and adult survival such as prey availability, SST, predation and habitat degradation (Morrison et al., 2011; Hanson & Wiles, 2015). While many prey species do not show significant population trends (MacCall, 1996), our results can provide spatial details to explore a potential mechanistic explanation, vertical prey distribution (Gjerdrum et al., 2003). Exact measurements are unknown but based on body size, Tufted Puffins exhibit the deepest maximum forage depths across alcids, at approximately 110 meters, but typically forage at 60 meters or less (Piatt & Kitaysky 2002). Tufted Puffins also forage much further offshore than most other alcids and in deeper waters along continental shelf breaks (Ostrand et al., 1998 & Menza et al., 2016). Foraging in deeper waters may leave Tufted Puffins susceptible to downward movement of prey species in the water column during high temperatures (Ostrand et al., 1998; Gjerdrum et al., 2003). Further research around these biological and ecological factors can be combined with our model results to further explore the mechanisms behind the temperature-range relationship for Tufted Puffins (Ostrand et al., 1998; Piatt & Kitaysky, 2002).

In addition to uncovering causal mechanisms, current conservation efforts are beginning to examine diverging population patterns among related birds, Rhinoceros Auklets (*Cerorhinca*

monocerata), Cassin's auklets (*Ptychoramphus aleuticus*) as well as Tufted Puffins along the California Current (Grémillet & Boulinier, 2009; Morrison et al., 2011). While these three alcids fill similar ecological roles, recent years have seen dramatic population swings varying among species (e.g. El-Niño of 1997-98) (Morrison et al., 2011). Cassin's auklets have displayed similar ecological sensitivity to changing environmental conditions and have experienced recent large scale mortality events as recently as 2015 (Syderman et al., 2006; Wolf et al., 2010; Hanson & Wiles, 2015). Physiological and ecological differences between these related seabird species such as forage radius, foraging depth, and diet composition may provide insights into the mechanisms responsible for these differences in population trends among species (Syderman et al., 2001; Wolf et al., 2009; Wolf et al., 2010; Morrison et al., 2011). For example, using SDMs to model multiple species may provide insights into the relative influence of climate change on populations trends (Johnson et al., 2017).

Conclusion

Our analysis shows a strong negative correlation between warm summer temperatures and Tufted Puffin nesting range, particularly along the California Current. Construction of SDMs utilizing two different emissions scenarios for the year 2050 show southern range contraction and suggest a high risk of Tufted Puffin extirpation in the California Current large marine ecosystem. Ensemble projections support preliminary analyses suggesting that temperature is driving the current puffin population declines and colony loss. SDM model results can provide valuable input for conservation decision processes. Specifically, our work provides the foundation for evaluation the threat of climate change and increased summer temperatures on Tufted Puffin breeding range.

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747 170.00000 (accessed 28 March 2017).

Table 1(on next page)

Environmental variables, measurements and units.

Environmental variables, measurements and units.

Environmental Variable	Measurement	Unit
Annual Temperature Range (ATR)	Maximum temperature – minimum temperature	°C
Mean diurnal range (MDR)	Mean of monthly (max temp-min temp)	°C
Mean temperature of the warmest quarter (MTWQ)	Mean temperature of warmest quarter	°C
Annual Precipitation (AP)	Annual Precipitation	cm
Precipitation of the warmest quarter (PWQ)	Precipitation of warmest quarter	cm
Distance to ocean (DIST)	Distance of grid cell to ocean	km

1

Table 2(on next page)

Time periods corresponding to model biological and environmental inputs.

Time periods corresponding to model biological and environmental inputs.

	Climate Data	Biological Data
Past Period	1910-1950	Habitat projections
Current Period	1950-2000	1950-2009
Future	2050 IPCC RCP 4.5, RCP 8.5	Habitat projections

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2

Table 3 (on next page)

Evaluation metrics and range change analysis.

Evaluation metrics and range change analysis for ensemble model and by model algorithm (N=40). A) Model area under the receiver operating characteristic curve (AUC) and true skill statistic (TSS) for ensemble model and by algorithm. AUC represents sensitivity rate (true positive) against 1-specificity values (false positive) and TSS represents (sensitivity + specificity - 1). Scores presented are mean plus or minus standard deviation B) Percent of projected change in range by model algorithm. North America-wide and U.S. California Current (32°N-48.5°N) independent analyses. Both RCP 4.5 (4.5 also shaded light grey) and RCP 8.5 (8.5 also shaded darker grey) represented. Scores presented are mean plus or minus standard deviation.

	Ensemble	GLM	GBM	RF
A) Model Evaluation				
AUC	.995	.979 ± .006	.989 ± .004	.989 ± .003
TSS	.924	.854 ± .023	.904 ± .017	.915 ± .014
B) % Range Change				
4.5 Species-Wide	-18.14	-16.32 ± 17.59	-15.45 ± 10.90	-24.77 ± 20.00
California Current	-93.75	-88.55 ± 26.60	-30.15 ± 19.49	-30.34 ± 18.06
8.5 Species-Wide	-24.57	-22.94 ± 21.38	-16.56 ± 12.99	-29.47 ± 22.82
California Current	-93.75	-88.61 ± 26.18	-30.02 ± 18.94	-31.36 ± 19.76

Figure 1

GLM model algorithm variable response plots.

Response curves across GLM algorithms for all environmental variables. Each line represents one GLM model run (N=40). Y-axis displays probability of occurrence. X-axis displays environmental variable values, with each tick on X-axis representing value of one data point. Results display distinct cutoffs between ATR, MTWQ and occurrence probability.

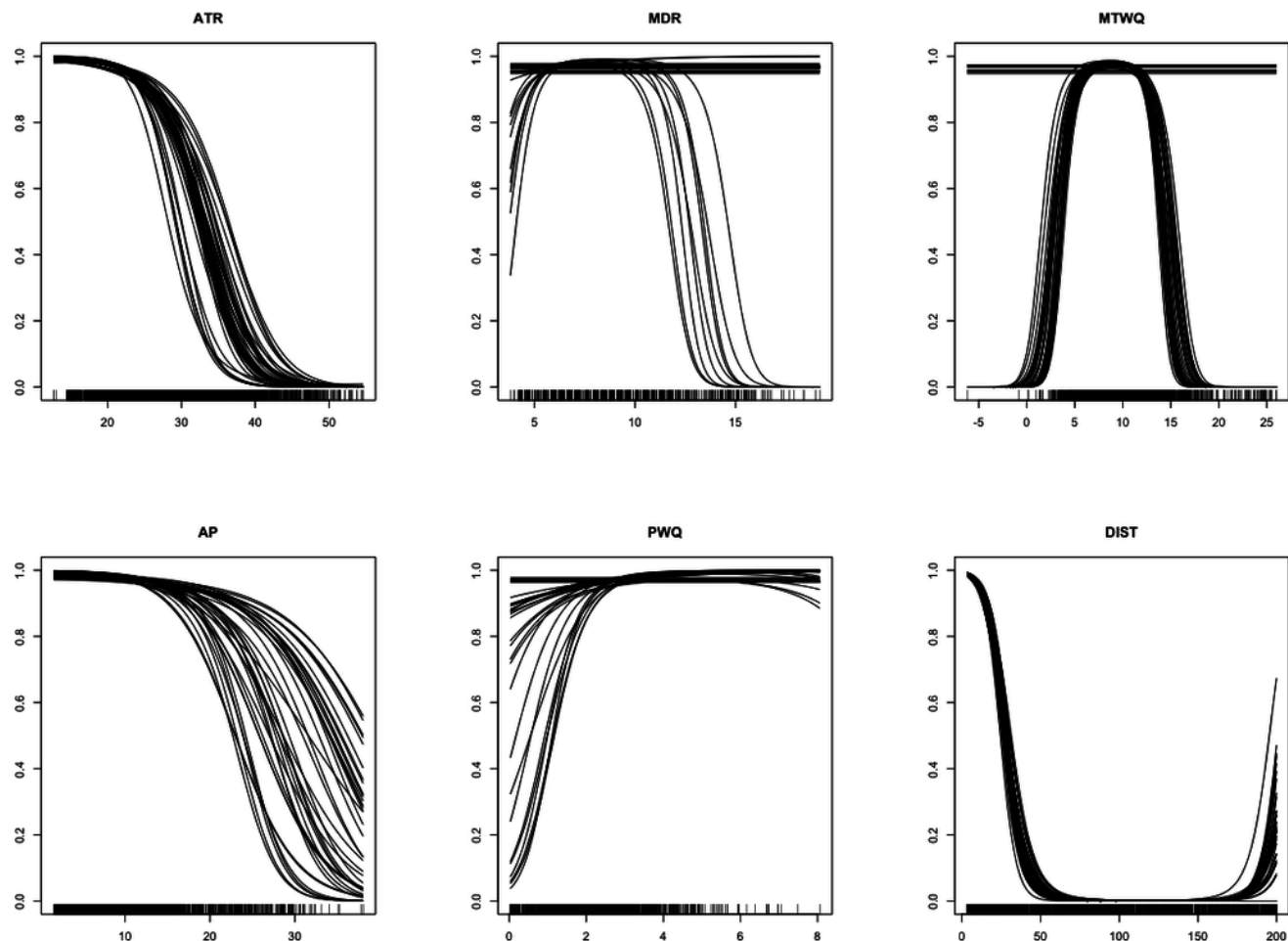


Figure 2

Principal component analysis.

Principal component analysis loadings 1 and 2 (95% confidence ellipses) for occupied and unoccupied nesting colonies.

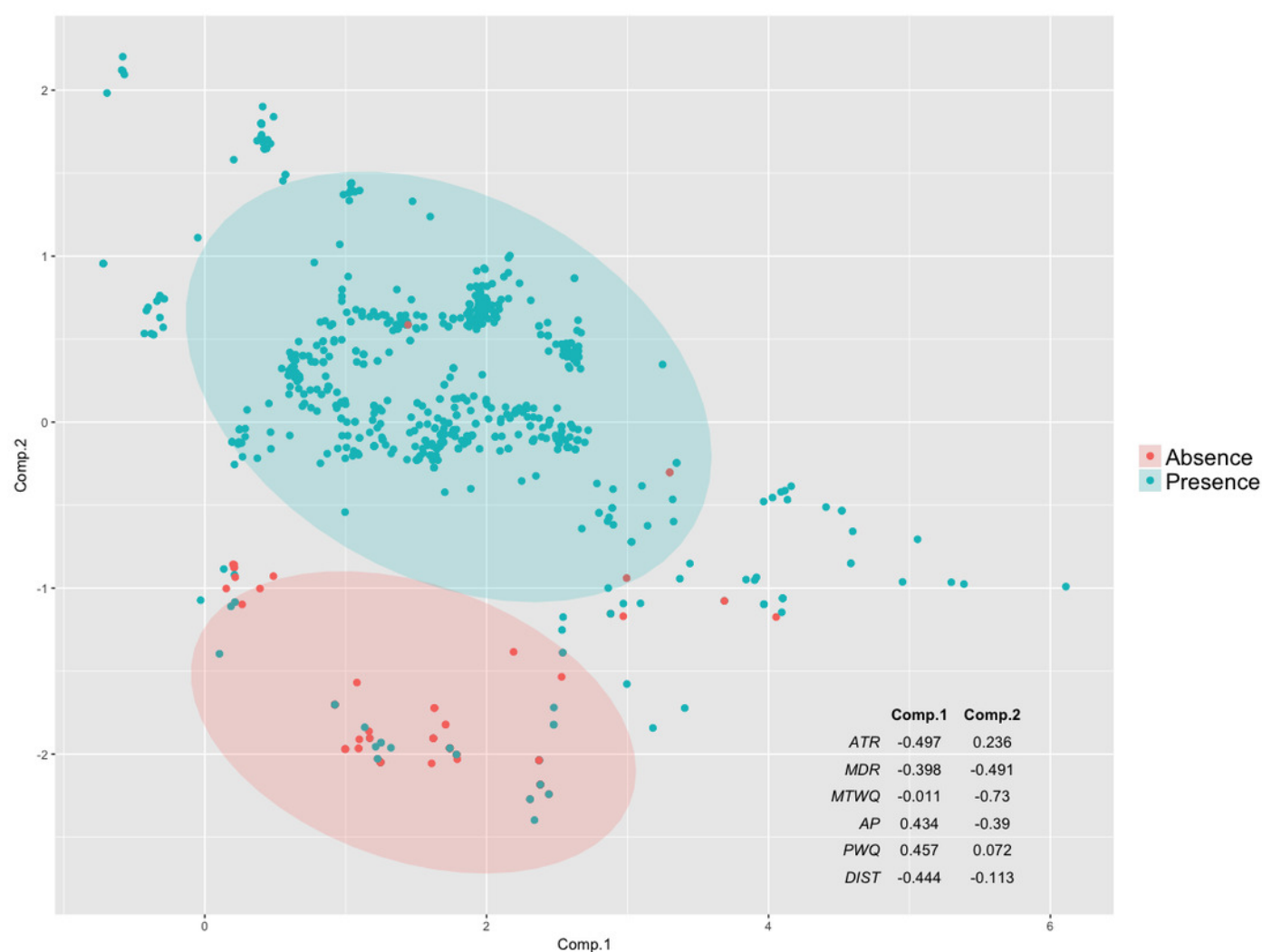


Figure 3

North-America-wide habitat projection maps.

Tufted Puffin breeding habitat range projection maps. Probabilistic maps, color bins display percent probability of grid cell representing suitable habitat. A) Current projections. B) 2050 projections under RCP 4.5. C) 2050 projections under RCP 8.5. Map data © 2017 Google

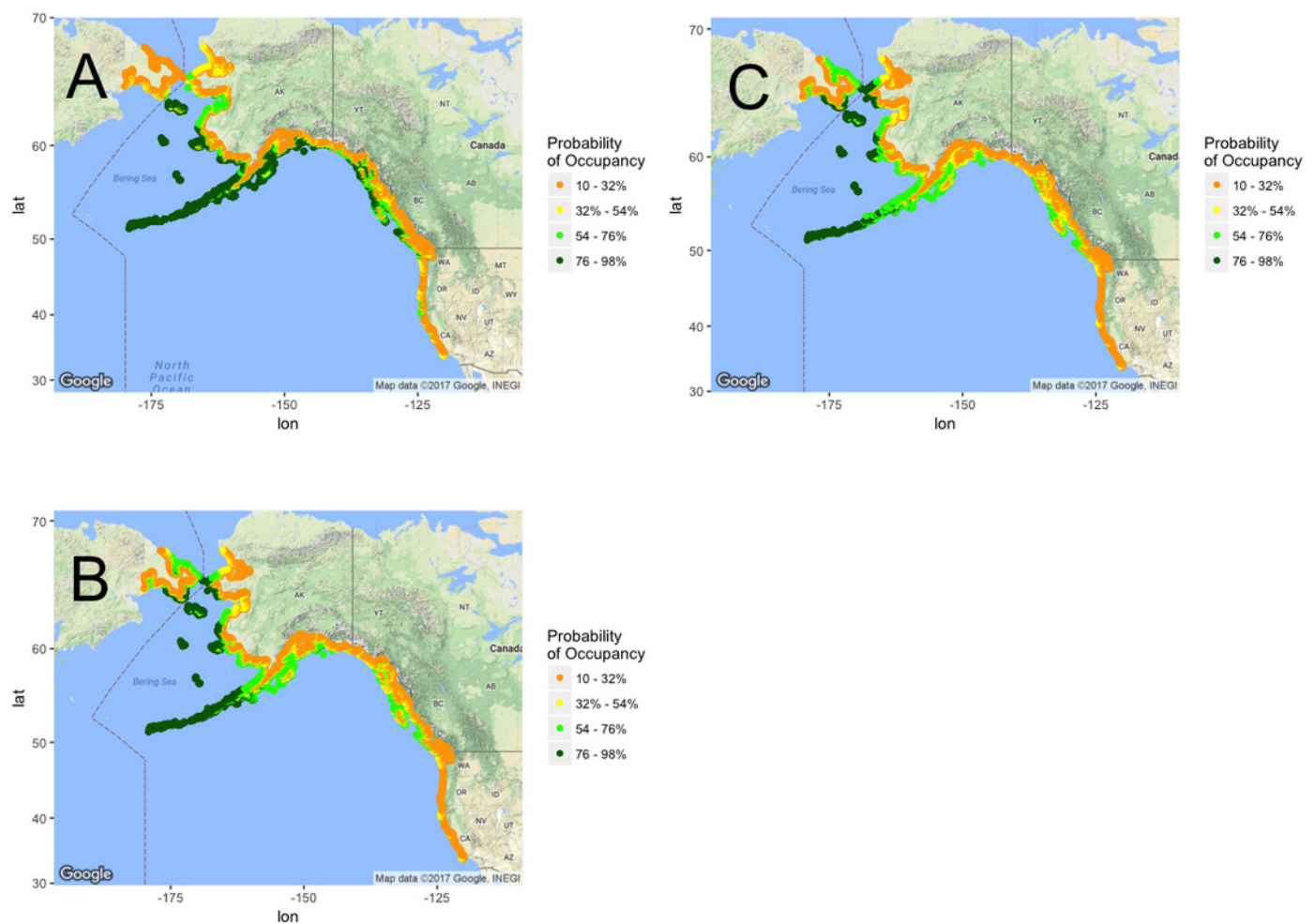


Figure 4

California Current habitat projection maps.

Tufted Puffin breeding habitat range projection maps exclusive to the California Current (32°N-48.5°N). Probabilistic maps, color bins display percent probability of grid cell representing suitable habitat. A) Current projections. B) 2050 projections under RCP 4.5. C) 2050 projections under RCP 8.5.

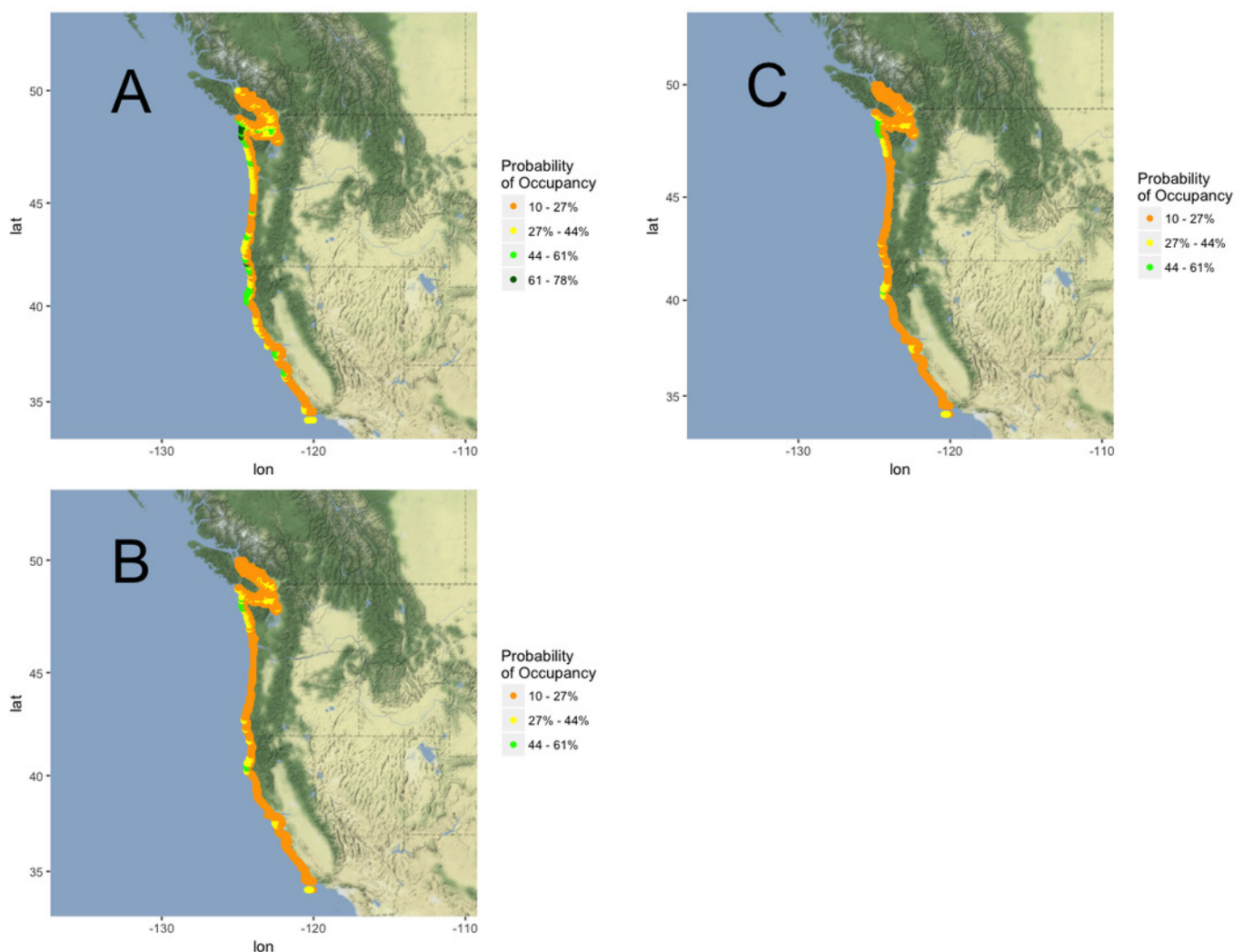


Figure 5

Histogram of habitat loss in the California Current with no migration.

Histogram displaying the amount of current California Current Extent suitable habitat projected to become unsuitable by 2050 under RCP 8.5 (N=120). Colors represent model algorithms. In this analysis, there is an assumption of no migration or dispersal to potentially suitable new habitat.

