Will the Continental U.S. Lose its Tufted Puffins?

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Abstract

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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. 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 sea-surface temperature, play a role. This study uses 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. Temperature variables demonstrated the largest contribution to model construction and ensemble model results suggest the key role of warming marine and terrestrial temperatures on the loss of Tufted Puffin habitat in the California Current under both carbon emission scenarios. By 2050, under both emission scenarios RCP 4.5 and 8.5, ensemble model results suggest the loss of greater than

26% of Tufted Puffin nesting habitat throughout its North American range. Ensemble model results also project that 100% of currently suitable habitat along the California Current is more likely than not to become unsuitable by 2050, regardless of emission mitigation strategies. These model results highlight a continuation of Tufted Puffin declines among southern breeding colonies and indicate a significant risk of near-term extirpation in the continental U.S.

Acknowledgements

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Introduction

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). As a result of these population declines, the United States Fish and Wildlife Service (USFWS) was petitioned to list the Tufted Puffin (*Fratercula cirrhata*) under the Endangered Species Act (ESA) (NRDC, 2014). Consistent with the ESA, the USFWS is currently examining the status and trends of the Tufted Puffin and evaluating the threats this species faces. Literature on puffin reproductive success and the southerly spatial distribution of population declines suggest temperature plays an important role in puffin population dynamics (Gjerdrum et al., 2003; Hanson & Wiles, 2015). Documenting the Tufted Puffin's role in the ecosystem and its relationship with changing climatic conditions can serve as an important indicator of ecosystem health (Hatch & Sanger, 1992; Piatt et al., 2007).

In addition to studying ecosystems, modeling the interaction between climate and suitable habitat for endangered species has become an integral component of conservation planning in a world of changing environments (Hagen & Hodges, 2006; Richardson & Whittaker, 2010). Understanding of these linkages can help inform both individual species and ecosystem management strategies (Carnaval & Moritz, 2008; Ponce-Reyes et al., 2017). To provide insight into these linkages for the Tufted Puffin, I use climate-envelope modeling to quantify the relationship between temperature and Tufted Puffin breeding habitat over the past 50 years. I then use these results to forecast predicted near-term changes in puffin nesting habitat.

Across the southern portion of the species range, many Tufted Puffin colonies have experienced precipitous declines or have collapsed altogether (Piatt & Kitaysky, 2002). While Alaskan Tufted Puffin populations have remained relatively stable, populations in the continental United States have declined by approximately 90% relative to early 20th century estimates, and are currently declining 9% annually (Hanson & Wiles, 2015). Similarly, 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). Documented range contractions at the southern edge 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 (Hanson & Wiles, 2015; WAC 232-12-014, 2016).

Tufted Puffin Biology

Tufted Puffins are seabirds belonging to the family *Alcidae* and are notable for their bright orange bill and distinct yellow tufts. Tufted Puffins historically nested in colonies located on both sides of the North Pacific, ranging in the U.S. from the Channel Islands in southern California (34° N) to coastal northern Alaska (68° N) (Piatt & Kitaysky, 2002). Alcids are noted for their exceptional ability to “fly” under water while diving for forage fish (Piatt & Kitaysky, 2002). They exhibit large foraging radii around their colonies and are able to carry more than 20 fish in their bills while flying back to the colony to feed their chicks (Piatt & Kitaysky, 2002; Hanson & Wiles, 2015). Tufted Puffins breed along rocky outer coasts, seeking soft substrate to dig their burrows (Piatt & Kitaysky, 2002). 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 additional pressures such as fishing net entanglement (Baird, 1991; Degange, et al., 1991; Ricca, et al., 2008). For example, Gulf of Alaska puffin populations declined by more than 60% coinciding with a period of limited prey availability during the 1970s-1990s (Piatt & Anderson, 1996). However, it remains unclear which stressors are particularly important to the puffin decline in the southern portion of its range (Hanson & Wiles, 2015).

Leading researchers have proposed several mechanisms associated with temperature stress as driving puffin declines along their southern range boundary. Gjerdrum et al. examined the connection between temperature and fledgling success and their results highlight Tufted Puffin sensitivity to high temperatures, showing dramatically reduced growth rates and fledgling success in years with high Sea Surface Temperature (SST) anomalies (Gjerdrum et al., 2003). Other researchers cite the nutritional demands of puffin chicks and the prey availability and preferences correlating with fledgling success (Hipfner et al., 2007). Hipfner et al. used stable-isotope ratios in egg yolk to examine differences in feeding ecology between subcolonies of Puffins and how those variations relate to large scale environmental processes to influence breeding success (Hipfner et al., 2007). These and other studies point to a link between temperature and demographic trends in the Tufted Puffin.

Ecological Modeling

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 changes 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 ESA listing decisions and management plans have drawn on SDM results to provide critical spatial and temporal conservation recommendations. 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, where the models were the basis of an ESA listing (81 FR 71670, 2016).

In this study, I use species nesting habitat distribution information to map Tufted Puffin habitat and to project future changes in suitable habitat under two different carbon emission scenarios. Exploration of this habitat-climate linkage seeks to explain the contraction of Tufted Puffin breeding range and to help understand how climate change is likely to influence the distribution of suitable habitat in the future. Additionally, I aim to present this spatial information in a manner useful for the ESA listing decision process and conservation planning.

Materials and Methods

Environmental Data

Environmental data for the current period, representing 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 the timeline of Tufted Puffin breeding biology, 6 environmental variables were selected: 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 ocean distance (DIST) (see table below 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 geographic range listed below were cropped to only include locations within 200 kilometers of the ocean. This procedure more accurately reflects potential puffin range given coastal habitat requirements while still providing environmental gradients upon which to construct models and incorporate potential future environmental conditions.

Future Climate

Emissions scenarios Radiative Concentration Pathways (RCP) 4.5 and 8.5 as defined by the IPCC 5th Assessment Report (IPCC, 2014) were selected as future environmental projections against which to forecast changes in Tufted Puffin 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) (Hijmans et al., 2005, last accessed January 2017). Incorporating multiple projections of future environmental variables further captures projection uncertainty. This timeframe (near-term future) 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

I obtained species distribution data courtesy of USFWS and Washington Department of Fish and Wildlife (WDFW), which derived from expansive U.S. breeding colony surveys conducted by groups including USFWS, WDFW, Alaska Department of Fish and Game and California Department of Fish and Wildlife (Speich & Wall, 1989; Hodum et al., unpubl.; World Seabird Union (seabirds.net), last accessed March 2017). Count data consisted of estimates of breeding individuals present at known nesting colonies and the spatial coordinates of these observations. Biological data for the 'current' period of climate data (Table 1) 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. Count data were then converted to presence/absence readings. Some observations were adjusted 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 (Table 2). I created a sixth environmental variable 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). This variable, distance to the ocean, mapped every land grid cell's distance in km to the nearest ocean grid cell and inclusion of this variable increased model performance.

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

	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

Table 1: Time spans corresponding to model biological and environmental inputs

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

Table 2: Environmental Variables, measurements and units

Model Parameterization

Because Tufted Puffins rely heavily on both terrestrial and marine environments, I 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 the use of air temperature as opposed to SST readings for better spatial coverage and for future projections. This relationship 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, I use it to create an index of environmental variables to identify likely drivers of Tufted Puffin declines after accounting for the covariances among variables.

Hindcasting

Hindcast models were created to further analyze the relationship between temperature and puffin habitat. Hindcasts can increase confidence in future projections and help shed light on ecological interactions over time (Raxworthy et al., 2003; Labay et al., 2011). These 'hindcast' models utilize current puffin distribution projections and the past environmental data detailed above to project past puffin range. 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. 4.00 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. A limited amount of historical survey data along the California Current makes scoring the hindcast projections against past survey data difficult. However, examining past model projections at specific known historical locations (such those in Hanson & Wiles, 2015) in a past, cooler climate helps interpret the influence of a warming climate in the future (Labay et al., 2011).

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). Utilizing 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). Given the much greater density and population size of Tufted Puffin nesting colonies in Alaska, 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 among the California Current exclusively.

To help acknowledge and estimate uncertainty, 3 different models utilizing 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 input data using decisions based on explanitory variables in a stagewise manner until subsets of data are explained by trees of decisions (Elith et al., 2008). Boosting then sequentially fits decision trees to training data and minimizes the loss function through addition at each step of a new tree (Elith et al., 2008). Finally, RF represents a machine learning technique creating classification trees similar to those in GBMs but utilizes random bootstrap samples of data upon the construction of each tree. Additionally, unlike normal tree construction which uses all explanatory variables, each node within a tree is split using only a subset of explanatory variables (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 2 variants of the dataset by permuting pseudo-absences, I 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) and is a popular metric for species distribution model evaluations due to evaluating across all thresholds of continuous probability conversion to binary presence or absence (Fielding & Bell, 1997; Guo et al., 2015). Higher AUC scores represent higher model performance with AUC scores, as described in Guo et al. (2015) between 0.7-0.8 classified as 'fair', 0.8-0.9 as 'good' and 0.9-1.0 as 'excellent'. 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 data set 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 both allowing future migration to potential suitable future habitat (Table 3, Figure 4) as well as with no potential migration (Figure 5). 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 0.852 ± 0.021, 0.907 ± 0.019 and 0.919 ± 0.017, respectively. Similarly, GLM, GBM and RF mean AUC scores were very high, suggesting 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), though all algorithms received high evaluation metric scores. Since machine learning (GBM & RF) models rely on boosting and ensemble learning, respectively, compared to a single regression model approach within GLM algorithms, output models of the former are optimized to achieve high evaluation scores. 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). The ensemble model achieved a TSS score of 0.932 which lends high confidence to the ensemble model's ability to project both suitable and unsuitable habitat under the current climate using the 6 selected environmental variables (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). First, variable response curves confirmed the significance of temperature variables in driving puffin distribution (Figure 1). MTWQ and ATR displayed strong responses across higher environmental values of each variable (Figure 1). Importantly, MTWQ displayed a thermal maximum of suitable nesting habitat (i.e., a threshold) around 15.5 °C. MTWQ also displayed the most consensus across model members among all selected variables (Figure 1). This result highlights consensus among GLM ensemble members on the distinctness of the 15.5 °C threshold.

Conversely, MDR and PWQ response plots display consensus among model members on the insensitivity of puffins to these variables. Across the environmental gradients of both variables, the probability of Tufted Puffin occurrence remains high and suggests these variables are not driving puffin range. AP ensemble members do show a response to increased AP values, but there remains a lack of consensus among model members on the distinctness of a response cutoff. ATR and MTWQ are related to extreme summer temperatures and consensus among GLM ensemble members across these variable response plots further supports the hypothesis of summer temperature anomalies influencing Tufted Puffin colonies.

Further examination of the influence of warm temperature on puffin range in the California Current–that is, excluding Alaska and British Columbia–model runs display similar thresholds for environmental variable response plots (Appendix A.1). While the signal is significantly weaker with the exclusion of data north of British Columbia, MTWQ and ATR again emerged as the variables strongly correlating with Tufted Puffin occurrence. Given that these condensed models only relied on a small subset of the data in the full model, their use in generating projection maps is limited. However, the inclusion of condensed runs isolating the U.S. California Current provides further support that temperature is driving puffin nesting habitat and importantly shows that this trend is evident when analyzing just the continental U.S. Tufted Puffin range (Appendix A.1).

Principal Component Analysis

Principal component analysis provided further support to the hypothesis identifying summer temperature as the primary driver of variance in Tufted Puffin breeding habitat (Figure 2). PCA analysis highlighted MTWQ primarily explaining the significant differences between presence and absence points in the second principal component (Figure 2). Significant differences in MTWQ between presence and absence sites led to the deviation in principal component 2 which was responsible for 27% of total variance in the data (Figure 2). The other 5 variables loaded more strongly onto principal component 1. While DIST is known to not vary among presence or true absence locations, MDR and PWQ did not display significant response in Figure 1. The response plot results and no significant differences across principal component 1 between presence and absence sites lends further support that MDR and PWQ are not driving puffin habitat. Acknowledging that principal component 2 is comprised most heavily of MTWQ, examining the difference between presence and absence sites across the component reveals that absence sites have a significantly higher MTWQ value than presence sites using a 95% confidence ellipse (Figure 2). This result combined with the MTWQ response plots present strong support to the significance of MTWQ in predicting what habitat is suitable for Tufted Puffins (Figure 1, 2).

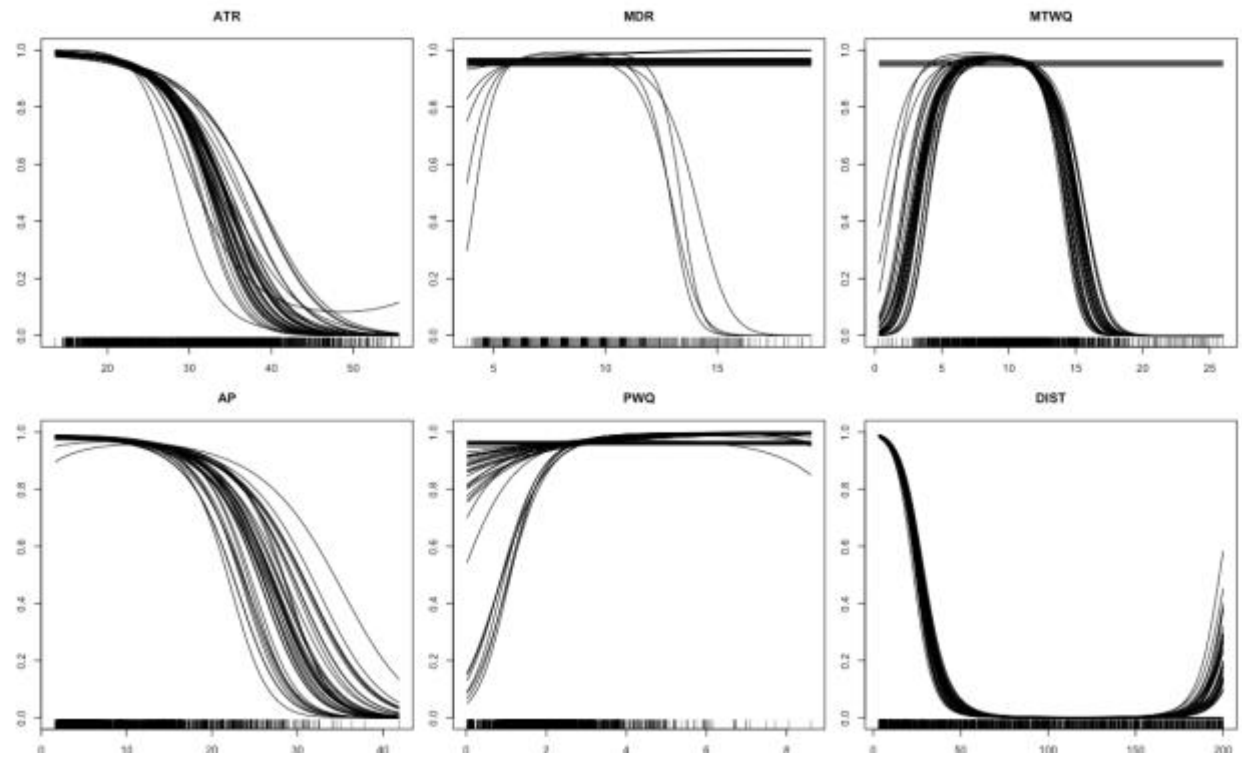


Figure 1: Response curves across GLM algorithms for all environmental variables. Each line represents one GLM model run (N=40). Y-axis displays probability of occurrence. X-axis displays environmental variable values, with each tick on X-axis representing value of one data point. Results display distinct cutoffs between ATR, MTWQ and occurrence probability.

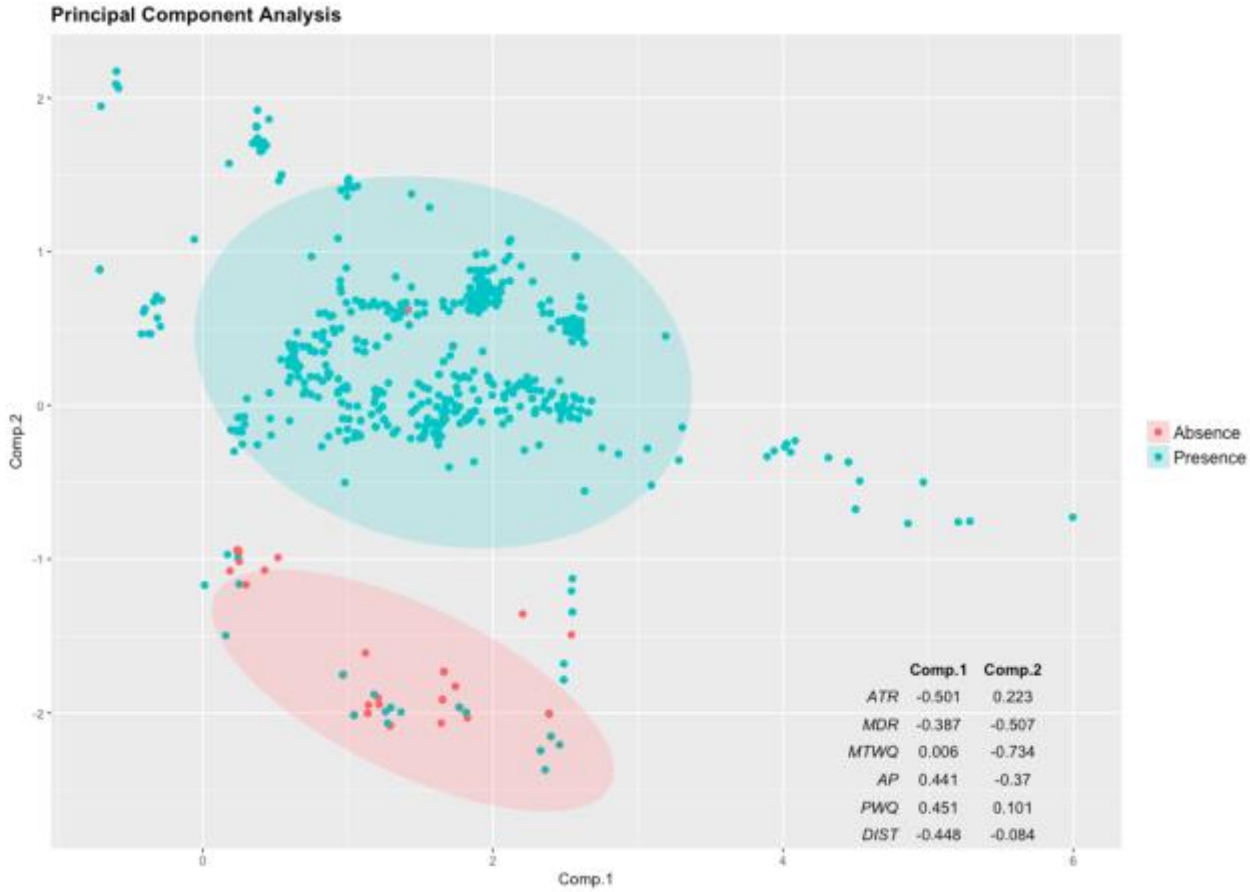
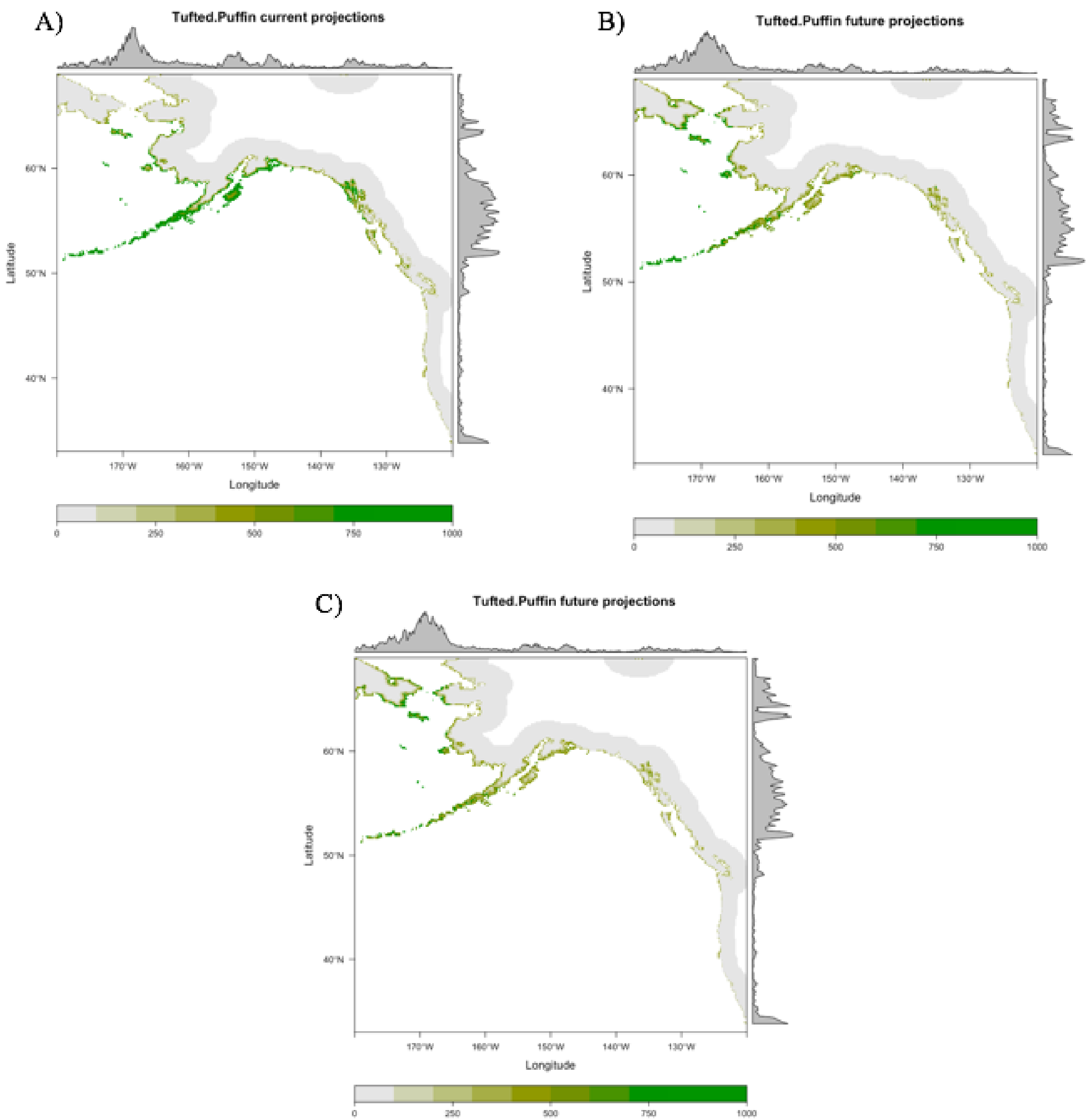


Figure 2: Principal component analysis loadings 1 and 2 (95% confidence ellipses) for occupied and unoccupied nesting colonies.

	Ensemble	GLM	GBM	RF
A) Model Evaluation				
AUC	.995	.977 ± .006	.987 ± .004	.988 ± .005
TSS	.936	.852 ± .021	.907 ± .019	.919 ± .017
B) % Range Change				
4.5 Species-Wide	-26.93	-12.37 ± 16.71	-33.83 ± 15.93	-50.39 ± 13.54
California Current	-100	-94.41 ± 17.59	-18.04 ± 21.59	-26.64 ± 22.63
8.5 Species-Wide	-34.50	-19.26 ± 20.18	-37.12 ± 18.40	-60.32 ± 14.55
California Current	-100	-94.66 ± 16.92	-17.97 ± 22.84	-29.54 ± 22.14

Table 3: 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. Species-wide and 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.



<u>Figure 3</u>: Tufted Puffin breeding habitat range projection maps. Probabilistic maps, color scale displays probability of grid cell representing suitable habitat x 1000. A) Current projections. B) 2050 projections under RCP 4.5. C) 2050 projections under RCP 8.5.

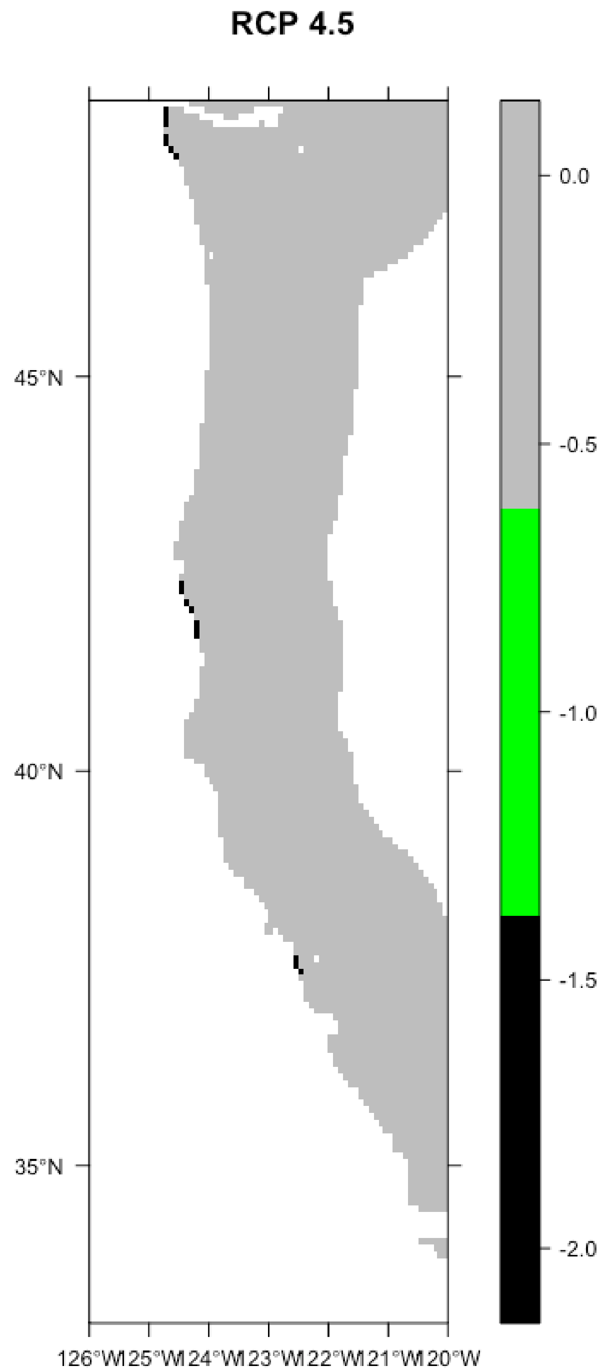


Figure 4: Range change along the U.S California Current extent (32°N-48.5°N, 126°W-120°W) for 2050 RCP 4.5. Black cells (-2 on scale) represent currently suitable habitat projected to become unsuitable, Green cells (-1 on scale) represent stable habitat and Grey cells (0 on scale) represent continued unoccupied habitat. Blue cells (not pictured, 1 on scale) represent newly suitable habitat.

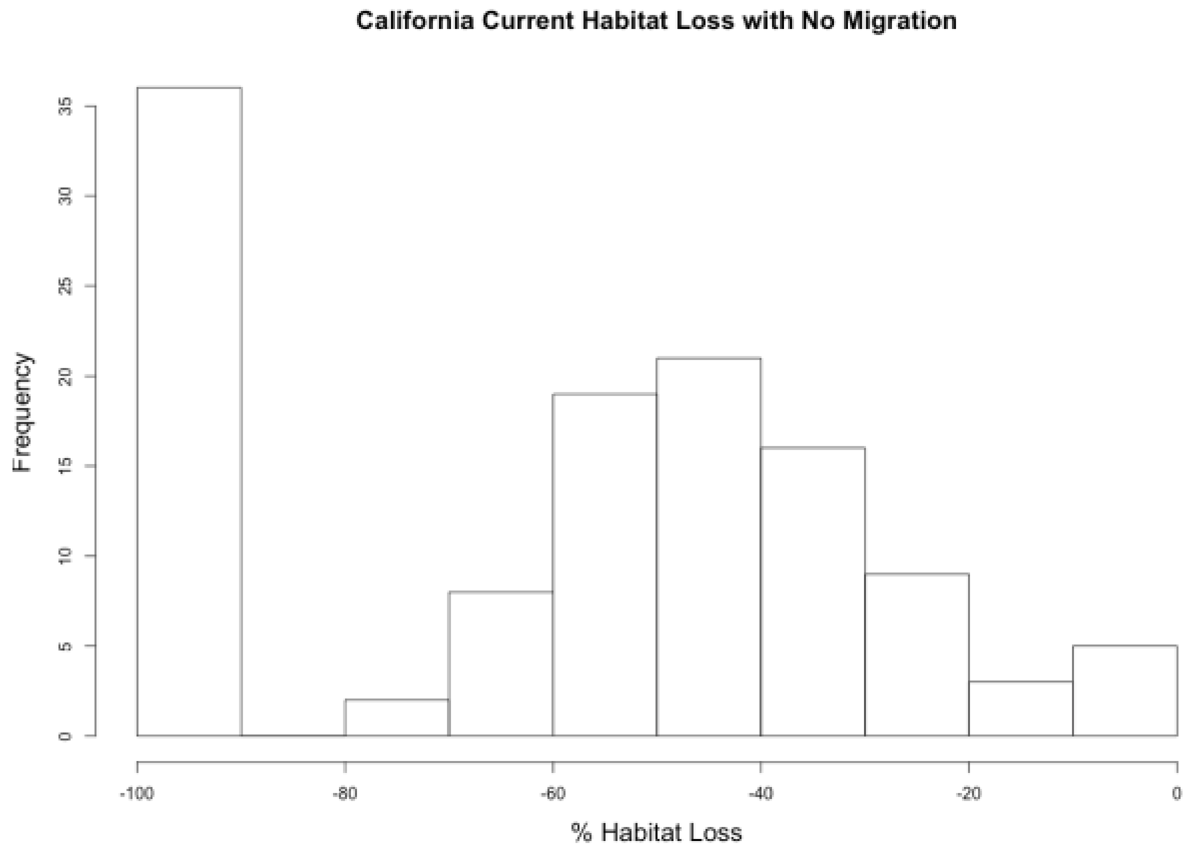


Figure 5: Histogram displaying the amount of current California Current Extent suitable habitat projected to become unsuitable by 2050 under RCP 4.5 (N=120). In this analysis, there is an assumption of no migration or dispersal to potentially suitable new habitat.

Range Forecasts

Hindcast 1950

Current models projected to the past using historical climate data show southern range stability and some expansion, mirroring historical records and estimates of Tufted Puffin range (See Appendix A.2) (Hanson & Wiles, 2015). This importantly shows that models project expansion in the southern portion of Tufted Puffin range with past, cooler climate data. This is consistent with both the limited survey data from that period as well as consensus past range estimates (Hanson & Wiles, 2015). Ensemble projections failed to map suitable habitat in northern and central California but showed expansion, relevant to current-day, in suitable habitat to cover most of the Washington and Oregon coastline (Appendix A.2). These trends provide further support to the influence of temperature in the driving the current Tufted Puffin range contraction along the California Current.

Species Wide 2050

The results of preliminary analyses and model evaluation metrics provide confidence in the predictive power of ensemble projections as well as the environmental drivers behind any resulting changes (Figures 1, 2, Table 3). After binary transformation of the future probabilistic projection maps (Figure 3) ensemble model range change analysis projects Tufted Puffins to lose 27% of their current range under RCP 4.5 and 35% under RCP 8.5 (Table 3). Stated another way, ensemble model projections show at least 27% of current Tufted Puffin habitat becoming more likely than not to represent unsuitable environmental conditions by 2050. RF models projected the greatest percent of habitat loss under both emission scenarios (Table 3). While all algorithms displayed variance in magnitude, there was uniform agreement across ensemble members in projecting habitat loss (Table 3). Spatially, losses were uniformly projected along the California Current up to eastern Alaska (Figure 3). Ensemble projections were clear in the continued suitability of the Aleutian Islands under both emission scenarios (Figure 3). Ensemble model results also reflected agreement between members on the opportunity for northward range expansion (Figure 3). Southern range contraction and northward range expansion projections both support the relationship between puffin habitat and temperature.

California Current (Continental U.S.) 2050

Analysis of the California Current region within the overall ensemble models shows complete loss of suitable habitat between emission scenarios with both RCP 4.5 and RCP 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 94% of suitable habitat. GLM models also projected a negligible amount of habitat as likely to become habitable in continental U.S. under either emission scenario. Both GBM and RF models predicted less range change with GBM models projecting a mean loss of about 18% and RF models projecting a mean loss of about 28%. All algorithms were consistent in projecting complete loss of suitability throughout California and Oregon (Figure 4). GBM and RF models projected small amounts 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 habitat. High model evaluation metrics (Table 3) coupled with strong correlations between temperature variables and Tufted Puffin range (Figures 1, 2) provide confidence that warm summer temperatures are driving the projected loss of 100% of Tufted Puffin breeding habitat in the continental U.S. (Figure 4). These ensemble projections show that all the currently suitable modeled habitat along the U.S. California Current extent is more likely than not to become unsuitable by 2050 under both emission scenarios.

Important to the interpretation of ensemble projections is the binary transformation of model outputs. For range change analyses such as Figure 4, projections of unsuitable habitat represent a weighted average of probability of suitability of 0.490 or less (that is, <50% likelihood of suitability), a cutoff defined by ensemble calibration. In some cases I 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. This process of binary transformation can then reflect an aggregate of probabilistic scores instead of the average of a binary projection. Species wide, ensemble models project the overall loss of 27% and 35% of suitable habitat, respectively, under moderate emission reductions and business as usual carbon emissions (Table 3). Figure 3 highlights the spatial concentration of lost habitat along the southern portion of current Tufted Puffin range as well as the opportunity for northward range expansion. Ensemble results provide strong support of the significant chance of Tufted Puffin extirpation from the continental U.S. by the year 2050 regardless of carbon emission scenarios.

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 rare species throughout portions 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). Here, 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). Potential range expansion also influenced the results of the California Current range change in Table 3. Biological and ecological factors unrelated to climate such as eagle predation are predicted to continue, making the colonization of all potentially climatically suitable habitat unlikely (Hanson & Wiles, 2015). Figure 5 highlights this possibility and displays an analysis of the percent of currently suitable habitat projected to be lost without the possibility of new colonization. Variance among models as evidenced in Table 3 along the California Current failed to result in consensus areas of suitability (Figure 4). While exceptions such as the Farallon Islands (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).

These results are especially salient in light of the ongoing USFWS analysis following NRDC's petition. Analysis of the continental U.S. portion of Tufted Puffins for an ESA listing relies on the Distinct Population Segment (DPS) portion of the ESA (61 FR 4722, 1996). DPSs are defined as subgroups of a species that are discrete to the remainder of the species, of significance to the species and their conservation status must be relayed in relation to the ESA criteria (61 FR 4722, 1996). While there remains no definitive genetic analyses proving continental U.S. Tufted Puffins are distinct from Alaskan puffins, the international boundary separating these populations can inform a "discreteness" finding. The ESA designates international borders may serve in designating discrete segments when certain conditions are met, importantly including conservation status (61 FR 4722, 1996). Continental U.S. Tufted Puffins are shown in this analysis to face different conservational threats and the Canadian border separating the U.S. Tufted Puffin populations can then define the discreteness and importance of the continental U.S. puffin DPS (61 FR 4722, 1996). Aside from demonstrating discreteness and significance of the proposed DPS, outlining the threats facing Tufted Puffins remains the largest question to answer in the ESA decision making process. Here, my analysis strongly suggests temperature poses a significant and immediate threat to continued puffin nesting in the continental U.S. Agreement is evident among both ensemble model projections on the extent of suitable habitat loss by 2050 under RCP 4.5 and 8.5, with both projecting complete loss of suitable habitat in the continental U.S. (Figure 4, Table 3). Model outputs define the magnitude and spatial variance of climate change as a threat to Tufted Puffins within the ESA framework.

Species can greatly benefit from defining the portion 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 abandonment (low habitat suitability). Nesting habitat along the California Current such as Destruction Island, WA and Haystack Rock, OR already receive protection from other ecological stressors to ensure provision of high quality habitat along the California Current (Hanson & Wiles, 2015). 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). Given the unique requirements of Tufted Puffin breeding habitat, many suitable sites are currently owned by government agencies (WDFW, 2016; USFWS, 2007), however these SDM results can highlight efficient future investments. 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 continue to support large populations of Tufted Puffins (Figure 3). In this way, these results can be used 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 of 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), my 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 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 my 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 as Tufted Puffins and have experienced recent large scale die offs as recently as 2015 (Syderman et al., 2006; Wolf et al., 2010; Hanson & Wiles, 2015). Minor physiological and ecological differences between these analogous seabird species such as forage radius, forage area depth and forage depth may shed light on these trends and guide future analyses on the underlying mechanisms (Syderman et al., 2001; Wolf et al., 2009; Wolf et al., 2010; Morrison et al., 2011). Figure 1 highlights the sensitive threshold of warmest quarter temperature and probability of puffin occurrence. While varying between model algorithms, emergent climate thresholds driving Tufted Puffin habitat provides valuable information upon which to examine difference in the ecological drivers of seabirds across the California Current. SDMs modeling multiple species can examine variance in similar species' sensitivity to environmental factors and provide input for directed conservation efforts (Johnson et al., 2017).

In conclusion, my analysis shows a strong correlation between warm summer temperatures and Tufted Puffin geographic range, particularly along the California Current. Construction of SDMs utilizing two different emissions scenarios for the year 2050 show southern range contraction and project a significant chance of Tufted Puffin extirpation in the continental U.S. Ensemble projections support preliminary analyses indication that temperature is driving the current puffin population declines and colony abandonment. SDM model results can provide valuable input for the ESA listing process in analyzing the threat that climate change and increased summer temperatures pose and for projecting how long Tufted Puffins will inhabit the continental U.S.

Appendix 1

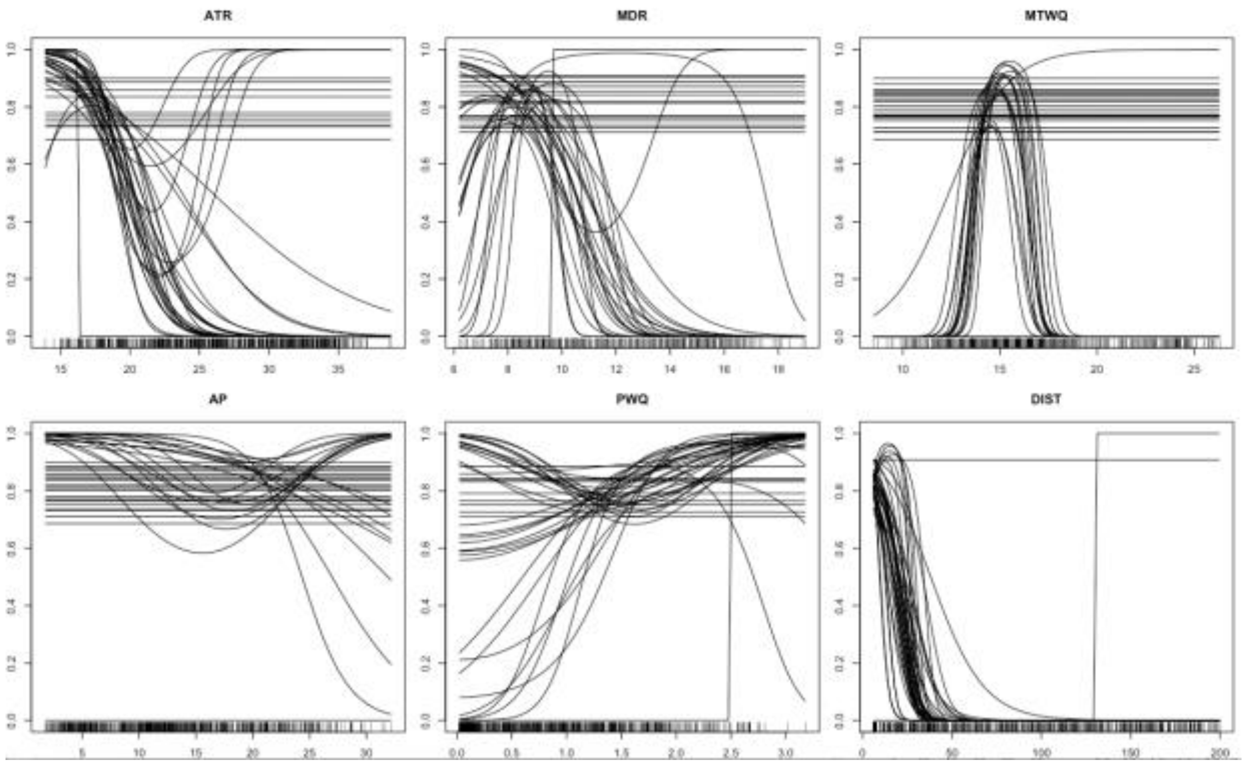


Figure A.1: Response plot for U.S. California Current extent (33°N - 50°N, 126°W- 120°W). Y-axis represents probability of occurrence. X-axis represents gradient for environmental variables.

<u>**Appendix 2**</u>

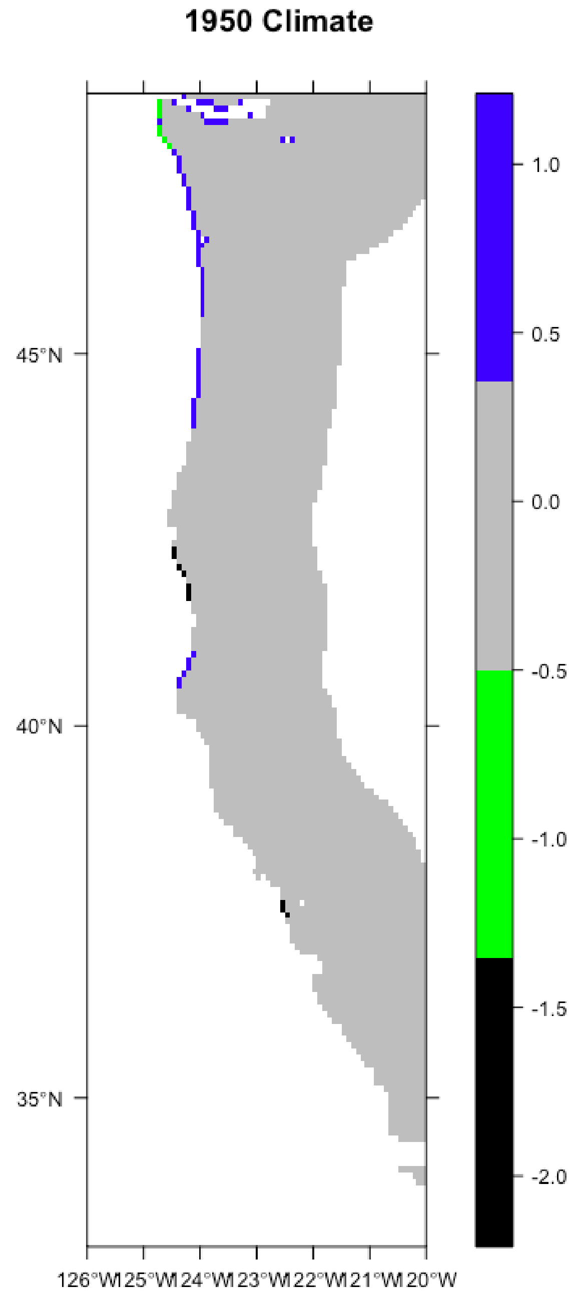


Figure A.2: Range change along the U.S California Current extent (32°N-48.5°N, 126°W-120°W) for 1950 climate. Black cells represent lost habitat, Green cells represent stable habitat, Grey cells represent continued unoccupied habitat and Blue cells represent habitat not suitable under the projected climate.

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