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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 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.

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28   **Abstract**

29   Tufted Puffin (*Fratercula cirrhata*) populations have experienced dramatic declines since the

30   mid-19th century along the southern portion of the species range, leading citizen groups to

31   petition the United States Fish and Wildlife Service (USFWS) to list the species as endangered in

32   the contiguous U.S. While there remains no consensus on the mechanisms driving these trends,

33   decreases in the California Current Large Marine Ecosystem suggest climate-related factors, and

34   in particular the indirect influence of sea-surface temperature on puffin prey. Here, we use three

35   species distribution models (SDMs) to evaluate projected shifts in habitat suitable for Tufted

36   Puffin nesting for the year 2050 under two future Intergovernmental Panel on Climate Change

37   (IPCC) emission scenarios. Ensemble model results indicate warming marine and terrestrial

38   temperatures play a key role in the loss of suitable Tufted Puffin nesting conditions in the

39   California Current under both business-as-usual (RCP 8.5) and moderated (RCP 4.5) carbon

40   emission scenarios. Under both emission scenarios, ensemble model results suggest that more

41   than 93% of currently suitable nesting habitat in the California Current is likely to become

42   unsuitable. Moreover, the models suggest a net loss of greater than 18% of suitable nesting sites

43   throughout the entire North American range of the Tufted Puffin, regardless of emission-

44   reduction strategies. These model results highlight continued Tufted Puffin declines —

45   particularly among southern breeding colonies — and indicate a significant risk of near-term

46   extirpation in the California Current.

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48

Introduction

49

50   Worldwide, species are facing increasing challenges associated with rising sea and air

51   surface temperatures (Thomas et al., 2004). Warming climates have resulted in species range

52   shifts (Parmesan & Yohe, 2003), ecological responses (Walther et al., 2002) and changes in

53   habitat quality (Hickling et al., 2006). Foden et al. (2013) found that 83% of birds, 66% of

54   amphibians and 70% of corals that were identified as highly vulnerable to the impacts of climate

55   change are not currently considered threatened with extinction on the IUCN Red List of

56   Threatened Species, indicating that species' vulnerabilities are likely to be much greater than

57   conservation status alone would suggest.

58   In recent years in the United States, the USFWS and the National Marine Fisheries

59   Service (NMFS) have received several petitions to list species under the Endangered Species Act

60   based on the impacts of climate change (Siegel, K., Cummings, B. 2005; Wolf, S., Cummings,

61   B., Siegel, K., 2008). However, the link between climate change and risk to a species can be

62   difficult to assess. One approach to examining these linkages is to model the interaction between

63   climate and suitable habitat for a given species, given what is already known about the

64   relationship between the species and its habitat. This approach has become an integral

65   component of conservation planning in a world of changing environments (Hagen & Hodges,

66   2006; Richardson & Whittaker, 2010). Ultimately, understanding these linkages can help inform

67   conservation assessments and species and ecosystem management strategies (Carnaval & Moritz,

68   2008; Ponce-Reyes et al., 2017), for example, by estimating the likelihood of losing (or gaining)

69   particular suitable habitats of interest under future climate conditions.

70

71   **Tufted Puffins as a Pertinent Example**

72   The Tufted Puffin (*Fratercula cirrhata*) is an iconic species that is experiencing dramatic

73   population declines across the southern portion of its geographic range (Piatt & Kitaysky, 2002).

74   While Tufted Puffin populations in the Alaska Current have remained relatively stable (but see

75   Goyert et al., 2017), populations in the California Current large marine ecosystem (area of the

76   eastern Pacific Ocean spanning nearly 3,000 km from southern British Columbia, Canada to Baja

77   California, Mexico) have declined by approximately 90% relative to early 20th century estimates,

78   and are currently declining 9% annually (Hanson & Wiles, 2015). The number of occupied

79   breeding colony sites in Washington State has declined by 60% relative to the 1886-1977

80   average, and 45% relative to the 1978-1984 average (Hanson & Wiles, 2015). Range

81   contractions at the southern edge of the Tufted Puffin's habitat in both the eastern and western

82   Pacific Ocean have led to preliminary conservation actions by state agencies such as the

83   Washington Department of Fish and Wildlife and Japan Ministry of the Environment (MOE,

84   2011; Hanson & Wiles, 2015; WAC 232-12-014, 2016).

85

86   **Tufted Puffin Biology and Ecology**

87   Tufted Puffins are seabirds belonging to the family *Alcidae* and nest in colonies located

88   on both sides of the North Pacific, ranging in North America from the Channel Islands in

89   southern California (34° N) to coastal northern Alaska (68° N) (Piatt & Kitaysky, 2002) and in

90   Asia from Hokkaido, Japan (43° N) through the Kamchatka Peninsula (63° N) (WDFW, 2015).

91   They are central-place foragers during the nesting season, when they dig burrows or use crevices

92   for nesting on nearshore rocks, islands and sea stacks (Piatt & Kitaysky, 2002). During the

93   nesting season, puffins exhibit large foraging radii around their colonies (up to 40 km, e.g.,

94   Menza et al. (2016) Figure 12) and are able to carry more than twenty fish at a time while flying

95   back to the colony to feed their chicks (Piatt & Kitaysky, 2002; Hanson & Wiles, 2015). While

96   little is known about the wintering distribution and ecology of Tufted Puffins, summer (May-

97   September) breeding colonies are well documented and provide the most useful biological data

98   for conservation management (Piatt & Kitaysky, 2002). Extensive breeding colony surveys

99   dating back to the early 20th century allow us to examine any potential link between climate and

100   species range extent.

101   Tufted Puffins are subject to multiple well-documented ecological stressors—such as

102   increasing eagle predation, habitat degradation, declining prey availability, and fishing net

103   entanglement (Baird, 1991; Degange, et al., 1991; Ricca, et al., 2008)—but several mechanisms

104   associated with temperature stress may be important in driving puffin declines along their

105   southern range boundary. Gjerdrum et al. (2003) found dramatically reduced growth rates and

106   fledgling success in years with high Sea Surface Temperature (SST) anomalies. Other

107   researchers cite the nutritional demands of puffin chicks and the prey availability and preferences

108   correlating with fledgling success (Hipfner et al., 2007), suggesting a mechanism for the negative

109   effects of high sea surface temperature on puffin chicks. These and other studies point to a link

110   between temperature and demographic trends in the Tufted Puffin and help identify this species

111   as a candidate for distribution modeling. Modeling outputs may help expose proposed

112   interactions between high ocean temperatures, prey distribution in the water column and puffin

113   breeding success.

114   As a result of these potential threats and documented population declines, the USFWS

115   was petitioned to list the California Current population of the Tufted Puffin (*Fratercula cirrhata*)

116   as endangered under the Endangered Species Act (Sewell, 2014). In order to respond to this

117   petition, the USFWS is currently examining Tufted Puffin status and trends, evaluating threats to

118   its survival, the adequacy of existing regulatory mechanisms to conserve the species, the loss of

119   its habitat, and other relevant factors. Given that climate—specifically, increasing sea-surface

120   temperatures—may be a particularly important factor influencing puffin population dynamics

121   and ultimately reducing puffin breeding range, and given the vast geographic extent of puffin

122   nesting sites (34° of latitude and roughly 70° of longitude in North America) and historical data

123   on the occupancy of these sites, the Tufted Puffin is an excellent candidate for species

124   distribution modeling.

125   **Species Distribution Models in Conservation Planning**

126   Species distribution models (SDMs) are a powerful way to examine how climate

127   variables relate to species geographic distribution and the distribution of suitable habitat (Guisan

128   & Zimmermann, 2000; Guisan & Thullier, 2005). By associating species occurrence with

129   climate variables, these models can 1) test for associations in space and time between putative

130   environmental drivers and changes in species range and 2) project changes in suitable habitat

131   under future climate change scenarios (Bellard et al., 2012). SDMs use a variety of underlying

132   statistical models to capture the relationship between habitat and climate and create detailed

133   outputs highly useful for wildlife management (Carvalho et al., 2011; Guisan et al., 2013).

134   Recent Endangered Species Act listing decisions and management plans have drawn on SDM

135   results to provide critical spatial and temporal conservation information. For example, climate

136   envelope models were used to develop spatially explicit conservation strategies that account for

137   climate change, notably in the case of the North America Wolverine (*Gulo gulo*), where the

138   models were the basis of an ESA listing (81 FR 71670, 2016).

139   Here we use 50 years of species nesting habitat distribution information—ranging from

140   the Bering Sea to California—to map Tufted Puffin nesting habitat. We use this colony

141   occupancy data to model the relationship between nesting habitat and current environmental

142   conditions to project future suitable breeding sites in the same geographic range. We present

143   these results as an example of how this information can be used in a regulatory context (e.g.,

144   Endangered Species Act listing decisions) and in a conservation planning context.

145

Materials and Methods

147   **Environmental Data**

148   Environmental data for the current period, which we define here as the years 1950-2000,

149   were downloaded from WorldClim, a set of global climate layers derived from interpolation of

150   monthly climate observations (Hijmans et al., 2005, last accessed January 2017). After removing

151   WorldClim bioclimatic variables displaying high collinearity and considering factors relevant to

152   Tufted Puffin breeding phenology, we selected six environmental variables for analysis: annual

153   temperature range (ATR), mean diurnal temperature range (MDR), mean temperature of the

154   warmest quarter (MTWQ), annual precipitation (AP), precipitation of the warmest quarter

155   (PWQ) and distance-to-distance (DIST), a variable we created to help models discern suitable

156   nesting habitat as occurring only in rocky, coastal habitats within meters of the sea, a biological

157   requirement of puffins (Piatt & Kitaysky, 2002); (see Table 1 for measurements and units). Each

158   variable for the current period was scaled to a 5 arcmin grid cell size (ca 10 km x 10 km). After

159   scaling, all environmental variables within the relevant geographic range were cropped to only

160   include locations within 2 kilometers of the ocean, given the Tufted Puffin's obligate

161   nearshore nesting habitat.

162   The same 6 environmental variables above were averaged over the period of 1910-1950

163   to construct a 'past' climate regime used to project past Tufted Puffin range. Past climate

164   variables were selected using gridded climate data obtained from monthly observations from the

165   Climate Research Unit CRU TS v. 4.01 dataset (Harris et al., 2014 (crudata.uea.ac.uk), last

166   accessed March 2017). Past environmental data were similarly scaled down to the same 5 arcmin

167   grid cell size as the current data.

168   <u>Future Climate</u>

169   We selected emissions scenarios Radiative Concentration Pathways (RCP) 4.5 and 8.5 as

170   defined by the IPCC 5th Assessment Report (IPCC, 2014) as future environmental projections

171   against which to forecast changes in Tufted Puffin breeding distribution. Downscaled model

172   output for environmental variables for both future RCP scenarios were averaged across the

173   following general circulation models: Hadley Centre's HadGEM2-ES (Collins et al., 2011),

174   NOAA's GDFL-CM3 (Griffies et al., 2011) and NASA's GISS-E2-R (Nazarenko et al., 2015)

175   for the year 2050 (average of 2041-2060) (Hijmans et al., 2005, last accessed January 2017).

176   Utilizing the average of multiple prominent U.S. climate model outputs helps incorporate

177   variance in potential future climate projections within our model. The 2050 timeframe and these

178   emissions scenarios (roughly speaking, a moderate-reduction scenario and business-as-usual

179   scenario with no emission reductions) were selected as the most relevant to the conservation

180   decisions presently surrounding the Tufted Puffin (IPCC, 2014).

181

182 **Species Data**

183   Species distribution data were obtained courtesy of USFWS, Washington Department of

184 Fish and Wildlife and Environment Canada, and were derived from expansive U.S. and Canada

185 breeding colony surveys conducted by groups including USFWS, Washington Department of

186 Fish and Wildlife, Alaska Department of Fish and Game, Environment Canada, California

187 Department of Fish and Wildlife, and others (Speich & Wall, 1989; Hodum et al., unpubl.;

188 World Seabird Union (https://seabirds.net, last accessed March 2017); BCMCA (http://bcmca.ca,

189 2017, last accessed May 2017), see supplemental online materials). Count data consisted of

190 estimates of numbers of breeding individuals present at known nesting colonies and the spatial

191 coordinates of those observations. Biological data for the 'current' period of climate data (Table

192 2) represents the most recent survey data of known nesting sites from 1950-2009. While the

193 climatological data runs until the year 2000, biological data from up to 2009 were included to

194 incorporate recent detailed state-wide surveys in both Oregon and Washington, information

195 critical to examining trends across the puffin's southern range. We converted count data to

196 presence/absence values, given the nature of our analysis, which asked whether breeding habitat

197 was likely to be suitable ($\geq$1 nesting birds) or not (0) under future conditions. Some observations

198 were adjusted geographically up to one grid cell (ca 10 km) to fall within gridded terrestrial

199 environmental variables. Observations further than 15km from terrestrial grids (e.g., remote

200 islands) were removed from the analysis. The environmental variables described above were

201 selected to model potential interactions between climate conditions and puffin range during the

202 breeding season.

203   Given the low proportion of absence-to-presence observations for Tufted puffin surveys

204 and potential bias in survey locations, we added pseudo-absence (PA) observations (i.e.,

205 generated absence observations existing within the range of the SDM) to all models. SDMs using

206 both presence and absence have been shown to perform more accurately than models relying on

207 presence-only observations (Elith et al., 2006, Barbet-Massin et al., 2012). PA generation

208 methodology is also important in both model predictive accuracy and avoiding model over-

209 fitting (Barbet-Massin, Thuiller, & Jiguet, 2010, Barbet-Massin et al., 2012). Adapting these

210 recommendations in Barbet-Massin et al. (2012), 1000 PAs were randomly generated twice

211 across the SDM a minimum of 30km from any presence or true absence point.

212 **Model Parameterization**

213   Because Tufted Puffins rely heavily on both terrestrial and marine environments for

214 reproduction, we initially tested the correlation between sea-surface temperature and air-

215 temperature data across puffin colony observations. Sea surface temperature (SST) data for this

216 comparison comprised an average of mean monthly temperature for June, July and August,

217 months aligning with Tufted Puffin breeding season obtained from the Hadley Centre, UK

218 (Rayner et al., 2003 (metoffice.gov.uk/hadobs) last accessed March 2017) and the corresponding

219 air temperature readings (MTWQ) (Hijmans et al., 2005). Both sets of environmental variables

220 were scaled to a 5 arcmin grid cell size and represented means from the years 1950-2000. A high

221 correlation coefficient ($r = 0.96$) allowed us to use air temperature—which is available in higher

222 spatial resolution—than SST in the final analysis. This strong relationship between air- and sea-

223 surface temperature has also been documented across several other marine and aquatic species

224 distribution studies (Stefan & Preud'homme, 1993; Domisch et al., 2013). Additionally, within R

225 software (R Core Team, 2013), a principal component analysis (PCA) (Pearson, 1901) was

226 performed to compare variance in environmental variables between areas where colonies

227 collapsed in recent years to those that persist. This technique has been shown to help identify

228   differences in environmental niches of species occurrence data (eg. Broennimann et al., 2012;

229   Peña-Gómez et al., 2014); here, we use it to create an index of environmental variables to

230   identify likely drivers of Tufted Puffin declines after accounting for the covariances among

231   variables.

232   **Species Distribution Modeling**

233   <u>Model Algorithms</u>

234   SDMs were constructed with the R package BIOMOD2 (BIOdiversity MODelling)

235   (Thuiller et al., 2009; R Core Team, 2013). All SDMs were constructed for a spatial range larger

236   than the current estimated U.S. Tufted Puffin distribution (180°W to 120°W longitude and 33°N

237   to 69°N). Using a larger extent both increases the range of environmental gradients available for

238   model construction and introduces novel climates useful for projecting potential migration

239   (Thuiller et al., 2004; Fitzpatrick & Hargrove, 2009; Domisch et al., 2013). Models were also

240   constructed using a subset of all biological and environmental data from 126°W to 120°W and

241   33°N to 48.5°N. This measure is intended to account for the spatial variance of puffin

242   distribution and examine the temperature-habitat relationship in the California Current large

243   marine ecosystem exclusively —the portion of the range that has experienced the greatest

244   decline and has been petitioned for listing under the US Endangered Species Act.

245   To help acknowledge and estimate uncertainty, 3 different models using different

246   statistical approaches were selected from the BIOMOD framework; generalized linear models

247   (GLM) (McCullagh & Nelder 1989), generalized boosting models (GBM, also referred to as

248   boosted regression trees) (Ridgeway 1999) and random forests (RF) (Breiman, 2001). The GLM

249   models used a logit link between the response variable mean and combination of explanatory

250   variables (Guisan, Edwards, & Hastie, 2002) (i.e., logistic regression). GBMs incorporate

251   regression and machine-learning techniques through boosting many decision-tree models to

252   increase model performance (Elith et al., 2008). Decision models recursively partition sets of

253   explanitory and outcome variables in a stagewise manner until subsets of data are explained by

254   trees of bifurcating decisions (Elith et al., 2008). Boosting then sequentially fits decision trees to

255   training data, selecting the trees that best fit the data (Elith et al., 2008). Finally, RF represents a

256   machine-learning technique creating classification trees similar to those in GBMs, but instead

257   uses random bootstrap samples of data and explanatory variables upon the construction of each

258   tree (Breiman, 2001).

259   The significant differences in statistical and machine learning approaches across GLM,

260   GBM and RF algorithms provides variance across which to test sensitivity between models as

261   well as estimations of model uncertainty (Marmion et al., 2009; Rodríguez-Castañeda et al.,

262   2012). Additionally, using models with relatively more ensemble (GBM and RF) and

263   parsimonious (GLM) approaches to habitat selection as well as utilizing both parametric (GLM)

264   and non-parametric (RF) techniques provides robust analysis of environmental drivers of range

265   change (Marmion et al., 2009) and led to the selection of these three model algorithms.

266

267   <u>Model Calibration</u>

268   Having generated two variants of the dataset by generating distinct pseudo-absences, we

269   then constructed twenty models for each algorithm (GLM, GBM, RF), for each dataset variant,

270   for a total of 120 models. All models then utilized past environmental data as well as both future

271   emission scenarios to project both past and future puffin range changes. Each model run

272   performed a random 70:30 split of the biological data using 70% for model calibration and 30%

273   for model evaluation. This technique addresses spatial autocorrelation and is frequently utilized

274   when faced with dependent biological sampling (surveying of species around only areas of

275   known occurrence) (Araújo et al., 2005). Model selection and calibration parameters were kept

276   constant between past and current models to maintain consistency and repeatability. For all

277   models, the default modeling options of the BIOMOD package were utilized (Thuiller et al.,

278   2009).

279   <u>Ensemble Modeling and Evaluation</u>

280   The area under the receiver operating characteristic curve (AUC) and the True Skill

281   Statistic (TSS) were the two model metrics used to evaluate model performance. AUC maps

282   sensitivity rate (true positive) against (1-specificity) values (= false-positive rate) and is a

283   popular metric for species distribution model evaluations because it evaluates across all

284   thresholds of probability conversion to binary presence or absence (Fielding & Bell, 1997; Guo

285   et al., 2015). Higher AUC scores represent better model performance, with AUC scores between

286   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

287   scores display (sensitivity + specificity − 1) with sensitivity quantifying omission errors and

288   specificity quantifying commission errors (Allouche et al., 2006; Guo et al., 2015; Shabani et al.,

289   2016). TSS scores of zero or less indicate model performance no better than random and scores

290   of 1.0 indicating perfect performance. Both scores were emphasized in this analysis to provide

291   strong measure of ordinal model performance and to prediction accuracy in threshold-dependent

292   conservation planning (Allouche et al., 2006; Shabani et al., 2016).

293   Ensemble models were created using weighted averages of TSS scores both within and

294   across algorithms. This technique captures uncertainty stemming from random sampling of the

295   dataset as well as variance across modeling techniques (Gallardo & Aldridge, 2013), thereby

296   providing the user with a robust sense of model fit and sensitivity to particular parameters. TSS

297   scores below 0.7 were excluded from the ensemble to remove influence from poor predictive

298   models (Araújo et al., 2011). A proportional weight decay was used averaging model weights,

299   resulting in weights proportional to TSS evaluation scores. Additionally, binary conversions,

300   which maximized model TSS performance, were used in some range-change analyses. Range-

301   change analyses were performed allowing future migration to potential suitable future habitat as

302   well as with no potential migration. Ensemble binary thresholds and their impact on projections

303   are noted below.

304

305   **Results**

306   **Model Performance**

307   Models from all three algorithms, and especially the ensemble model, scored very high in

308   both model performance metrics (Table 3). GLM, GBM and RF algorithms displayed mean TSS

309   scores and standard deviations of 0.854 ± 0.023, 0.904 ± 0.017 and 0.915 ± 0.014, respectively.

310   Similarly, GLM, GBM and RF mean AUC scores were very high, indicating good model

311   accuracy (Table 3). Techniques utilizing machine learning methods (RF & GBM) consistently

312   displayed the highest performance by both AUC and TSS scores (Table 3), perhaps due to these

313   machine-learning (GBM & RF) models relying on boosting and ensemble learning, respectively,

314   compared to a single regression model approach within GLM algorithms. Despite the different

315   statistical and learning approaches of the selected modeling approaches, TSS and AUC scores

316   were high across all techniques and displayed low variance (Table 3).

317   **Variable Contribution**

318   <u>Response Plots</u>

319   After initial variable winnowing, both model response plots and PCA analysis indicate

320   that temperature variables ATR and MTWQ are strongly associated with Tufted Puffin breeding

321   habitat (Figure 1, 2). Importantly, MTWQ displayed a thermal maximum of suitable nesting

322   habitat (i.e., a threshold) around 15.5 °C, and the MTWQ variable also displayed the most

323   consensus across model members among all selected variables (Figure 1). This result highlights

324   consensus among GLM ensemble members surrounding the 15.5 °C threshold. ATR and MTWQ

325   are related to extreme summer temperatures and consensus among GLM ensemble members

326   across these variable response plots is consistent with the hypothesis that summer temperature

327   anomalies influence Tufted Puffin colonies.

328   Conversely, MDR and PWQ were not effective in predicting suitable habitat among all

329   models. In fact, the probability of Tufted Puffin occurrence remains high across the range of

330   MDR and PWQ values indicating that these variables are not helpful in predicting puffin

331   occupancy. Ensemble members do show a response to increased annual precipitation (AP)

332   values, but there remains a lack of consensus among model members around a particular

333   response cutoff.

334   <u>Principal Component Analysis</u>

335   Principal component analysis provided further support to the hypothesis identifying

336   summer temperature as a primary driver of variance in Tufted Puffin breeding habitat (Figure 2).

337   PCA components 1 (51%) and 2 (27%) together explained 78% of the variability in the data.

338   Component 2, with a strong loading of MTWQ of -0.730 and MDR loading of -0.491, indicates

339   that MTWQ and MDR explain the difference between presence and absence points as evidenced

340   by the separation of the 95% confidence ellipse along this component (Figure 2). The other four

341   variables loaded more strongly onto principal component 1 which does not help separate

342   presence and absence points. This result combined with the MTWQ response curves (Figure 2)

343   indicate the importance of MTWQ in predicting what habitat is suitable for Tufted Puffins

344   (Figure 1, 2).

345   **Range Forecasts**

346   <u>North American Projections - 2050</u>

347   After binary transformation of the future probabilistic projection maps ensemble model

348   range change analysis projects Tufted Puffins to lose 18% of their occupied range under RCP 4.5

349   and 25% under RCP 8.5 by 2050 (Table 3). RF models projected the greatest percent habitat loss

350   across North America under both emission scenarios (Table 3). There was uniform agreement

351   across ensemble members in projecting habitat loss, with variability among algorithms as to the

352   magnitude of that loss (Table 3). Spatially, losses were uniformly projected along the California

353   Current up to southeastern Alaska (Figure 3), although ensemble projections suggested continued

354   suitability of the Aleutian Islands under both emission scenarios (Figure 3). Ensemble model

355   results also reflected agreement on the opportunity for northward range expansion (Figure 3).

356   Both the projected southern range contraction and northward range expansion are further

357   consistent with the hypothesized relationship between puffin habitat and temperature.

358   <u>California Current - 2050</u>

359   Analysis of the California Current region within the overall ensemble models shows near

360   complete loss of suitable habitat between emission scenarios with both RCP 4.5 and 8.5 (Figure

361   4), although the individual component models showed variable amounts of habitat loss. GLM

362   models projected the most dramatic loss along the California Current with a predicted loss of

363   over 88% of suitable habitat (Table 3). GLM models also projected a negligible amount of

364   habitat as likely to become newly habitable in the California Current under either emission

365   scenario. Both GBM and RF models predicted less range change with GBM models projecting a

366   mean loss of about 30% and RF models projecting a mean loss of about 31%. Under both RCP

367   4.5 and 8.5, ensemble projections display complete loss of suitable habitat in Oregon and

368   virtually complete loss in California (Figure 4). GBM and RF models projected small portions of

369   northwestern Washington would become slightly more likely than not to become habitable by

370   2050 under both emission scenarios.

371

372   **Discussion**

373   Ensemble models uniformly support summer temperature as a predictor of Tufted Puffin

374   breeding habitat. High model evaluation metrics (Table 3) coupled with strong correlations

375   between temperature variables and Tufted Puffin range change (Figures 1, 2) provide confidence

376   that projected warmer summer temperatures are likely to be associated with the loss of greater

377   than 93% of Tufted Puffin breeding habitat in the California Current (Figure 4). North America-

378   wide, ensemble models project the overall loss of 18% and 25% of suitable habitat, respectively,

379   under moderate emission reductions and business as usual carbon emissions by 2050 (Table 3).

380   Figure 3 highlights that most nesting habitat will be lost along the southern portion of current

381   Tufted Puffin range as well as the opportunity for northward range expansion.

382   Important to the interpretation of ensemble projections is the binary transformation of

383   model outputs into suitable and unsuitable categories. For range change analyses, projections of

384   unsuitable habitat represent a weighted average of <50% probability of suitability, a cutoff

385   defined by ensemble calibration. In some cases we observed a majority of ensemble members

386   projecting a particular cell as marginally suitable while a minority of members strongly project

387   that cell as unsuitable. The subsequent result is unsuitable habitat despite being marginally

388   suitable in some models. This process of binary transformation can then reflect an aggregate of

389   probabilistic scores instead of the average of a binary projection. Binary transformations are thus

390   a useful tool to discuss and represent how changes in climate may affect the likelihood of

391   suitable breeding conditions throughout Tufted Puffin range, but are necessarily imprecise in that

392   they mask underlying variability.

393   Examining the variance among model results and the spatial variance in projections is

394   integral to the interpretation of model results in a conservation perspective (Guisan et al., 2013;

395   Porfirio et al., 2014). Tufted Puffins are a relatively rare species in the southern portion of their

396   range, are hard to survey, and occupy small areas of land (Hanson & Wiles, 2015). These

397   biological factors contribute to the difficulty of surveying (and therefore modeling) puffins and

398   can increase variance among model algorithms, making ensemble models more valuable for

399   interpretation of results (Segurado & Araújo, 2004; Hernandez et al., 2006). However, here we

400   use colony occupancy information rather than counts. Preliminary occupancy analysis suggest

401   that colony occupancy can be assessed with a high probability with a single relatively rapid visit

402   by boat even to a very small colony with few birds (Pearson et al., unpublished). Thus, our

403   colony occupancy approach likely reflects actual changes in colony occupancy throughout the

404   range. In addition, trends were consistent across algorithms in depicting significant losses of

405   suitability for habitat across the California Current, British Columbia and eastern Alaska (Figure

406   3). All algorithms also projected the opportunity for northward range expansion in the face of

407   accelerating northern latitude warming (Figure 3).

408   If suitable habitat expands as predicted by our ensemble models, biological and

409   ecological factors unrelated to climate such as eagle predation are predicted to continue and

410   likely to influence the probability of colonization (Hipfner et al., 2012; Hanson & Wiles, 2015).

411   Because colonization is uncertain, we depict in Figure 5 the loss of currently suitable habitat in

412   the California Current without the possibility of new colonization throughout the extent—a worst

413   case scenario. Variance among models as evidenced in Table 3 along the California Current

414   failed to result in more than a handful of consensus areas of suitability (Figure 4). While outlying

415   colonies such as the one in the Farallon Islands of California (where puffins remain at present) in

416   areas projected to be unsuitable are important to examine further, all models and especially

417   ensemble results support the trend of southern range contraction associated with warm summer

418   temperatures (Figures 1, 2, 3, 4). Additionally, while limitations on historical survey data make

419   interpretation of hindcasts difficult, preliminary hindcasting resulted in expansion across the

420   southern portion of current puffin habitat (see suppl. file). This result is further consistent with

421   the hypothesized relationship between high temperature and puffin success.

422   Our results are especially salient in light of the ongoing U.S. Fish and Wildlife Service's

423   analysis of puffin status following Natural Resources Defense Council's petition to list the

424   California Current population as endangered. When responding to the petition to list the puffin,

425   the Service can list the species throughout its range or can list a distinct population segment

426   (DPS) such as the breeding population south of the Canadian border or that in the California

427   Current. While determining which segments comprise a DPS as outlined by the ESA requires

428 more analysis, our results provide the spatial information to inform the threat that both of these

429 breeding range segments or "populations" will likely face. Based on our modeling, all potential

430 distinct populations segments from British Columbia, south, face a significant chance of near

431 extirpation or very significant habitat loss under a wide range of climate projections by 2050.

432   Conservation planning for species can greatly benefit from defining the portion(s) of their

433 range representing habitat critical to their survival (Hagen & Hodges, 2006). This designation is

434 essential for conservation planning both under the ⬜, in which it is required for listed species,

435 as well as for more localized conservation efforts (Taylor et al., 2005). Figure 3 highlights areas

436 where Tufted Puffins are currently at the highest risk of colony loss (low habitat suitability).

437 Many puffin nesting sites are already managed by the US Fish and Wildlife Service Refuge

438 system and many of these sites are also designated as "wilderness" (Sowles et al., 1980, Speich

439 and Wahl 1989, Naughton et al. 2007, US Fish and Wildlife Service 2017). Habitat projections

440 made for the year 2050 permits analysis of critical habitat in terms of species survival as well as

441 proposed conservation efficacy (Suckling & Taylor, 2006; Stein et al., 2013). Land acquisition

442 has proven to be an effective strategy for the management of endangered species and is a strategy

443 that has been utilized for the Tufted Puffin (Lawler et al., 2003; WDFW, 2016) and could be

444 used in the future. With limited resources to conserve species at the federal level, ranking the

445 conservation priorities and temporally analyzing threats can allow for prudent investment in

446 conservation lands (Lawler et al., 2003). Nesting colony sites throughout the Gulf of Alaska are

447 projected to remain suitable and results indicate the Aleutian Islands are the most likely habitat

448 to both continue to support large populations of Tufted Puffins as well as potentially becoming

449 suitable as new breeding sites (Figure 3). As these results suggest, we can use this information to

450 predict areas of future Tufted Puffin habitat to help outline areas for long-term conservation

451   action while also mapping areas where long-term conservation efforts may prove ineffective.

452   Such proactive conservation steps often result in greater conservation outcomes and are critical

453   for species struggling to adapt to changing climates (Morrison et al., 2011).

454

455   <u>Mechanisms Driving Decline</u>

456   Using the results reflected in Figure 3, wildlife managers can continue to explore the

457   causal mechanisms driving the discussed Tufted Puffin population declines and range

458   contraction. Currently numerous pathways are proposed to help determine puffin breeding

459   success and adult survival such as prey availability, SST, predation and habitat degradation

460   (Morrison et al., 2011; Hanson & Wiles, 2015). While many prey species do not show significant

461   population trends (MacCall, 1996), our results can provide spatial details to explore a potential

462   mechanistic explanation, vertical prey distribution (Gjerdrum et al., 2003). Exact measurements

463   are unknown but based on body size, Tufted Puffins exhibit the deepest maximum forage depths

464   across alcids, at approximately 110 meters, but typically forage at 60 meters or less (Piatt &

465   Kitaysky 2002). Tufted Puffins also forage much further offshore than most other alcids and in

466   deeper waters along continental shelf breaks (Ostrand et al., 1998 & Menza et al., 2016).

467   Foraging in deeper waters may leave Tufted Puffins susceptible to downward movement of prey

468   species in the water column during high temperatures (Ostrand et al., 1998; Gjerdrum et al.,

469   2003). Further research around these biological and ecological factors can be combined with our

470   model results to further explore the mechanisms behind the temperature-range relationship for

471   Tufted Puffins (Ostrand et al., 1998; Piatt & Kitaysky, 2002).

472   In addition to uncovering causal mechanisms, current conservation efforts are beginning

473   to examine diverging population patterns among related birds, Rhinoceros Auklets (*Cerorhinca*

474   *monocerata*), Cassin's auklets (*Ptychoramphus aleuticus*) as well as Tufted Puffins along the

475   California Current (Grémillet & Boulinier, 2009; Morrison et al., 2011). While these three alcids

476   fill similar ecological roles, recent years have seen dramatic population swings varying among

477   species (e.g. El-Niño of 1997-98) (Morrison et al., 2011). Cassin's auklets have displayed similar

478   ecological sensitivity to changing environmental conditions and have experienced recent large

479   scale mortality events as recently as 2015 (Syderman et al., 2006; Wolf et al., 2010; Hanson &

480   Wiles, 2015). Physiological and ecological differences between these related seabird species

481   such as forage radius, foraging depth, and diet composition may provide insights into the

482   mechanisms responsible for these differences in population trends among species (Syderman et

483   al., 2001; Wolf et al., 2009; Wolf et al., 2010; Morrison et al., 2011). For example, using SDMs

484   to model multiple species may provide insights into the relative influence of climate change on

485   populations trends (Johnson et al., 2017).

Conclusion

487   Our analysis shows a strong negative correlation between warm summer temperatures

488   and Tufted Puffin nesting range, particularly along the California Current. Construction of SDMs

489   utilizing two different emissions scenarios for the year 2050 show southern range contraction

490   and suggest a high risk of Tufted Puffin extirpation in the California Current large marine

491   ecosystem. Ensemble projections support preliminary analyses suggesting that temperature is

492   driving the current puffin population declines and colony loss. SDM model results can provide

493   valuable input for conservation decision processes. Specifically, our work provides the

494   foundation for evaluating the threat of climate change and increased summer temperatures on

495   Tufted Puffin breeding range.

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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

1

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.
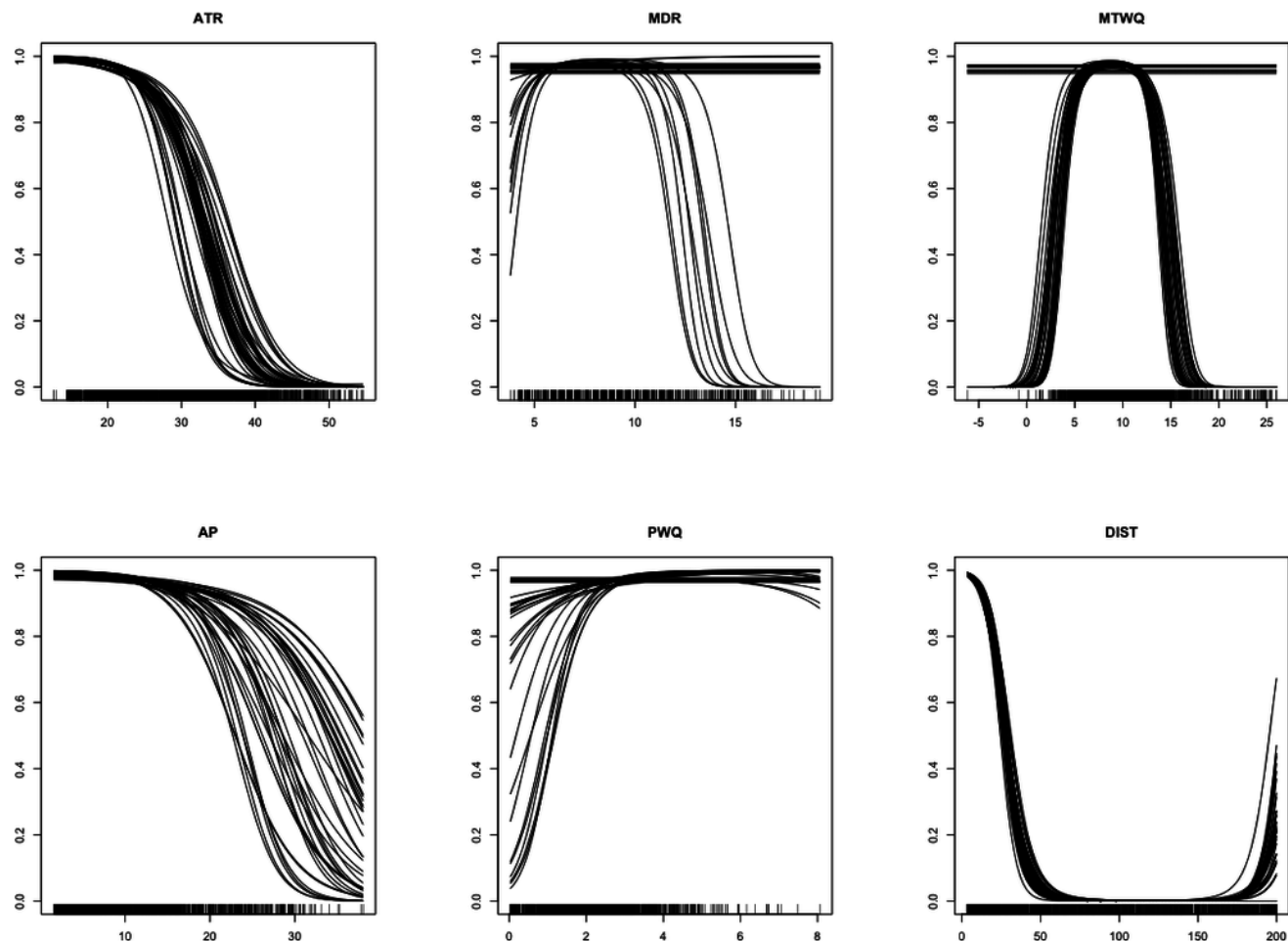
PeerJ

Figure 2

Principal component analysis.

Principal component analysis loadings 1 and 2 (95% confidence ellipses) for occupied and unoccupied nesting colonies.
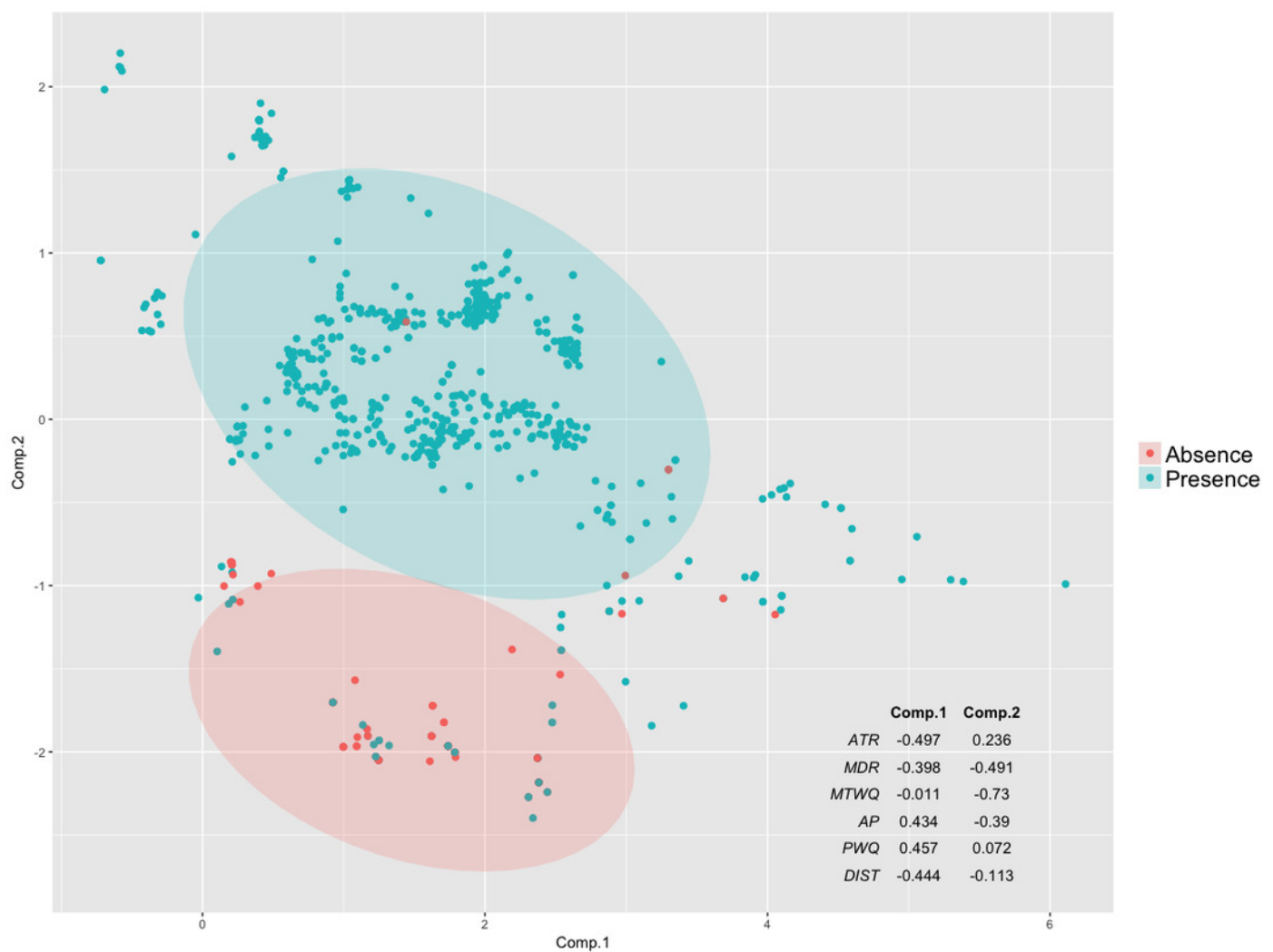
Figure 3

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
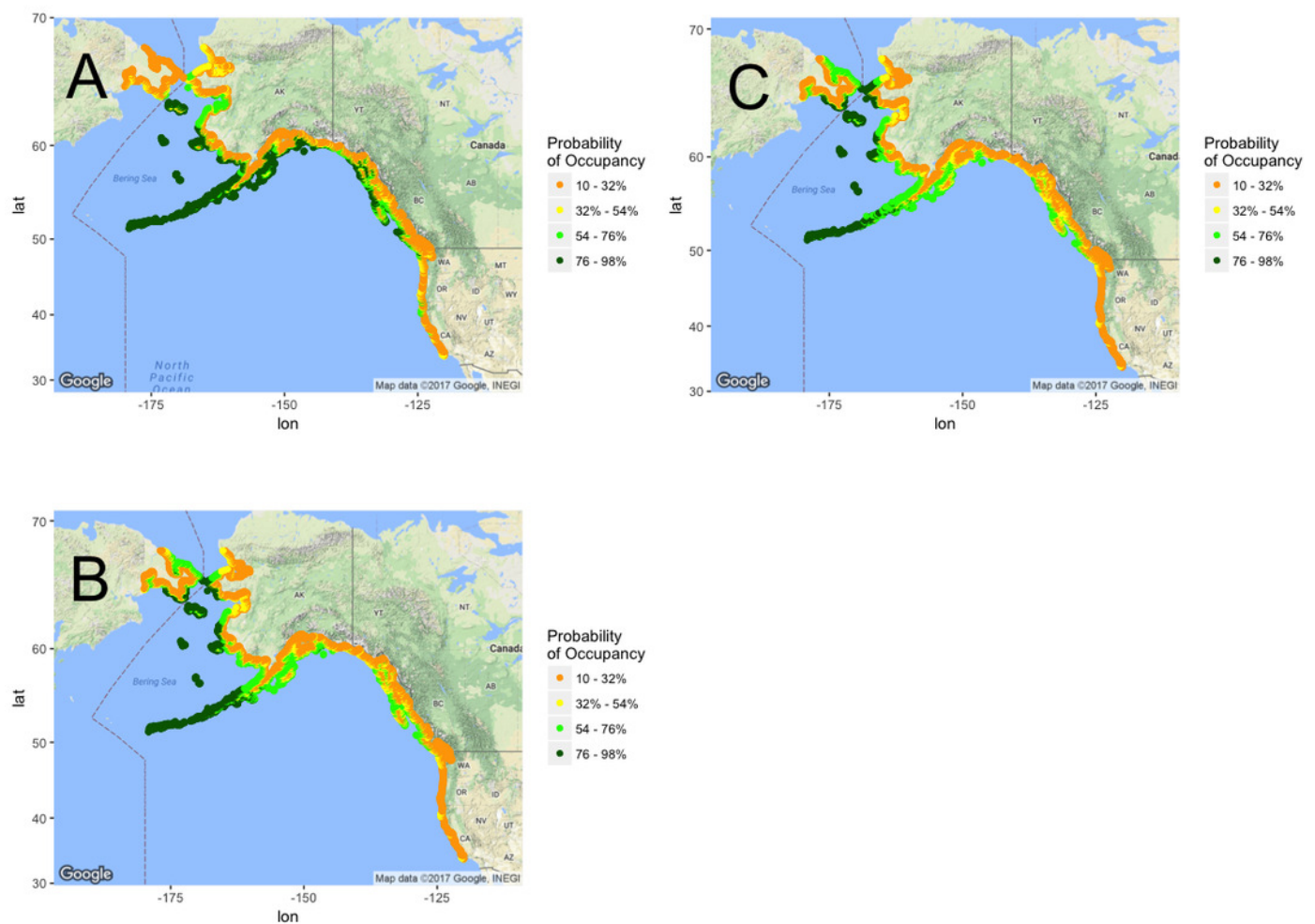
Figure 4

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.
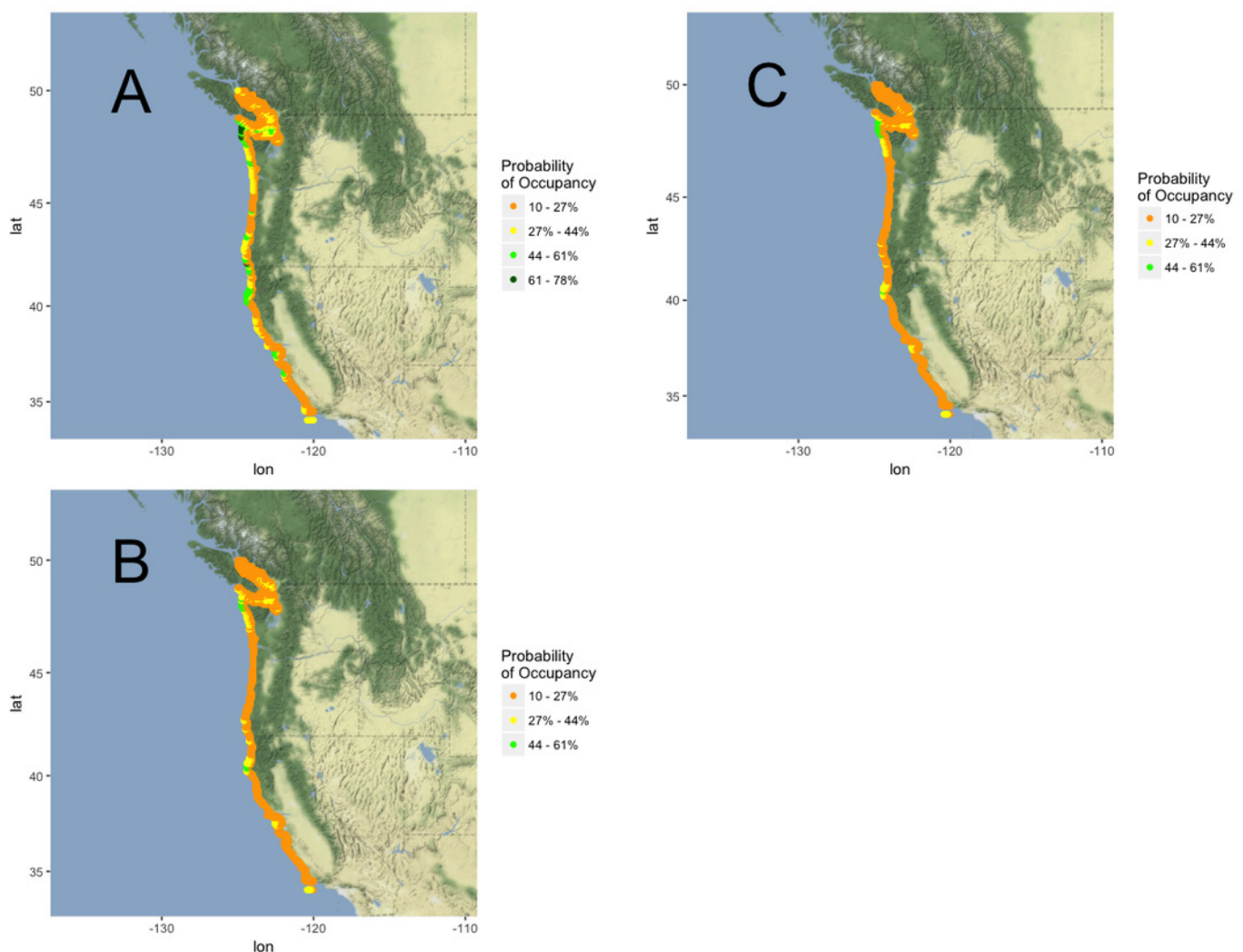
Figure 5

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.