Predicted distribution of a rare and understudied forest carnivore: Humboldt martens (*Martes caurina humboldtensis*)

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Background. Many mammalian species have experienced range contractions. Following a reduction in distribution that has resulted in apparently small and disjunct populations, the Humboldt marten (*Martes caurina humboldtensis*) was recently designated as federally Threatened and state Endangered. This subspecies of Pacific marten occurring in coastal Oregon and northern California, also known as coastal martens, appear unlike martens that occur in snow-associated regions in that vegetation associations appear to differ widely between Humboldt marten populations. We expected current distributions represent realized niches, but estimating factors associated with long-term occurrence was challenging for this rare and little-known species. Here, we assessed the predicted contemporary distribution of Humboldt martens and interpret our findings as hypotheses correlated with the subspecies' niche to inform strategic conservation actions.

Methods. We modeled Humboldt marten distribution using a maximum entropy (Maxent) approach. We spatially-thinned 10,229 marten locations collected from 1996–2020 by applying a minimum distance of 500-m between locations, resulting in 384 locations used to assess correlations of marten occurrence with biotic and abiotic variables. We independently optimized the spatial scale of each variable and focused development of model variables on biotic associations (e.g., hypothesized relationships with forest conditions), given that abiotic factors such as precipitation are largely static and not alterable within a management context.

Results. Humboldt marten locations were positively associated with increased shrub cover (salal (*Gautheria shallon*)), mast producing trees (e.g., tanoak, *Notholithocarpus densiflorus*), increased pine (*Pinus sp.*) proportion of total basal area, annual precipitation at home-range spatial scales, low and high amounts of canopy cover and slope, and cooler August temperatures. Unlike other recent literature, we found little evidence that Humboldt martens were associated with old-growth structural indices. This case

study provides an example of how limited information on rare or lesser-known species can lead to differing interpretations, emphasizing the need for study-level replication in ecology. Humboldt marten conservation would benefit from continued survey effort to clarify range extent, population sizes, and fine-scale habitat use.

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2 **(*Martes caurina humboldtensis*)**

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29 **Abstract**

30 **Background.** Many mammalian species have experienced range contractions. Following a

31 reduction in distribution that has resulted in apparently small and disjunct populations, the

32 Humboldt marten (*Martes caurina humboldtensis*) was recently designated as federally

33 Threatened and state Endangered. This subspecies of Pacific marten occurring in coastal

34 Oregon and northern California, also known as coastal martens, appear unlike martens that

35 occur in snow-associated regions in that vegetation associations appear to differ widely

36 between Humboldt marten populations. We expected current distributions represent realized

37 niches, but estimating factors associated with long-term occurrence was challenging for this rare

38 and little-known species. Here, we assessed the predicted contemporary distribution of

39 Humboldt martens and interpret our findings as hypotheses correlated with the subspecies'

40 niche to inform strategic conservation actions.

41 **Methods.** We modeled Humboldt marten distribution using a maximum entropy (Maxent)

42 approach. We spatially-thinned 10,229 marten locations collected from 1996–2020 by applying

43 a minimum distance of 500-m between locations, resulting in 384 locations used to assess

44 correlations of marten occurrence with biotic and abiotic variables. We independently optimized

45 the spatial scale of each variable and focused development of model variables on biotic

46 associations (e.g., hypothesized relationships with forest conditions), given that abiotic factors

47 such as precipitation are largely static and not alterable within a management context.

48 **Results.** Humboldt marten locations were positively associated with increased shrub cover

49 (salal (*Gautheria shallon*)), mast producing trees (e.g., tanoak, *Notholithocarpus densiflorus*),

50 increased pine (*Pinus sp.*) proportion of total basal area, annual precipitation at home-range

51 spatial scales, low and high amounts of canopy cover and slope, and cooler August

52 temperatures. Unlike other recent literature, we found little evidence that Humboldt martens

53 were associated with old-growth structural indices. This case study provides an example of how

54 limited information on rare or lesser-known species can lead to differing interpretations,

55   emphasizing the need for study-level replication in ecology. Humboldt marten conservation

56   would benefit from continued survey effort to clarify range extent, population sizes, and fine-

57   scale habitat use.

58

59   **Key words**: California, distribution model, habitat relationships, Humboldt marten, *Martes*

60   *caurina humboltensis*, Maxent, rare species, Oregon, Pacific marten

61

62   **Introduction**

63   Modeling predicted distributions is important to direct conservation efforts yet creating

64   accurate predictions is challenging for rare, declining, or understudied species (Raphael

65   & Molina, 2007). For instance, constriction of the range available to a species – it's

66   realized niche – is the actualization of used conditions, but such conditions may change

67   (Colwell & Rangel, 2009). Contemporary location information may further associate a

68   species with conditions that were unaffected by prior agents of population decline, but

69   not with favored characteristics where the species resided prior (Caughley, 1994). For

70   instance, bison (*Bison bison*) were historically widely distributed throughout the Great

71   Plains of North America (Shaw, 1995), yet a contemporary species distribution model

72   would associate bison occurrence with conditions where the few relict populations

73   reside, including the extremely cold winters and thermal geysers of Yellowstone

74   National Park. Appropriate interpretation of the conditions that constitute suitable habitat

75   is requisite for species' management and spatial models may help predict occurrence

76   (Sofaer et al., 2019).

77   Humboldt martens (*Martes caurina humboldtensis*) are a distinct subspecies of

78   the Pacific marten (*M. caurina*) that historically occurred throughout coastal forests of

79   northern California and Oregon (Schwartz et al., 2020). Humboldt martens were thought

80   to be increasingly rare almost a century ago (Grinnell & Dixon, 1926) and were

81   considered to be extirpated in California and extremely rare in Oregon for the latter half

82   of the 20th century (Zielinski et al., 2001). In 1996, the Humboldt marten was

83   rediscovered in California (Zielinski & Golightly, 1996). Subsequent research efforts

84   over the last two decades have elucidated some aspects of Humboldt marten ecology

85   and demography (e.g., Linnell et al., 2018; Delheimer et al., In press), including surveys

86   to evaluate Humboldt marten distribution (e.g., Gamblin, 2019; Moriarty et al., 2019).

87   Such investigations have improved our knowledge of where Humboldt martens occur

88   yet the full geographic extent of the contemporary distribution remains unknown,

89   although it appears to compose a fraction of the historical distribution (USFWS, 2020).

90   This putative range contraction has resulted in apparently small and disjunct

91   populations (USFWS, 2019), which has engendered substantial concern for the species'

92   persistence. Consequently, Humboldt martens were listed as Endangered under the

93   state of California's Endangered Species Act (CDFW, 2019) and as Threatened under

94   the federal Endangered Species Act as a "coastal distinct population segment" of

95   Pacific martens (USFWS, 2020).

96   Clarifying the contemporary Humboldt marten distribution by identifying areas

97   where martens may occur that have not been surveyed and predicting the future

98   distribution (e.g., identifying areas where martens may not currently occur but could

99   colonize) is urgently needed for conservation planning. Nonetheless, modeling the

100 distribution of Humboldt martens is constrained by apparent non-stationary associations

101 between extant populations, and vegetation associations that contradict the prevailing

102   paradigm for North American martens. For instance, it has generally been recognized

103   that North American martens occur in mature forests characterized by dense canopy

104   cover, presence of large diameter and decadent trees and snags, and abundant coarse

105   woody debris (Thompson et al., 2012). Although initial investigations primarily

106   associated Humboldt martens with similar conditions (Slauson, Zielinski & Hayes,

107   2007), subsequent studies have indicated that Humboldt martens also occur in young

108   forests (<80 years old) with modest canopy cover and relatively small diameter trees

109   (Eriksson et al., 2019; Moriarty et al., 2019). Dense and spatially-extensive shrubs, also

110   an uncharacteristic vegetation association for martens elsewhere in North America, was

111   a consistent habitat component in most studies of Humboldt martens (Slauson, Zielinski

112   & Hayes, 2007; Eriksson et al., 2019; Gamblin, 2019; Moriarty et al., 2019). Similarly,

113   European pine martens (*Martes martes*) have long been considered a habitat specialist

114   associated with older forests (Storch, Lindstrom & de Jounge, 1990; Brainerd & Rolstad,

115   2002), yet have recently been documented in a wide variety of habitat types including

116   shrublands, grasslands, and agricultural areas (Lombardini et al., 2015; Balestrieri et al.,

117   2016; Moll et al., 2016; Manzo et al., 2018).

118   Observations that are limited in space or time may not identify the conditions

119   necessary for population persistence, which could result in a misrepresentation of a

120   species' niche. A previous range-wide Humboldt marten distribution model by Slauson

121   et al. (2019) emphasized a strong correlation between Humboldt marten occurrence

122   and an "old-growth structural index" (OGSI) variable, which is a composite index of

123   factors considered common to old-growth forests in the region, including density of large

124   live trees, snags, and downed wood, stand age, and diversity of tree sizes (Davis et al.,

125 2015). However, more recent and broader-scale research efforts suggest that

126 associations between OGSI and Humboldt marten distribution are much less clear (e.g.,

127 Barry 2018; Gamblin 2019; Linnell et al. 2018; Moriarty et al. 2019). A potential

128 mismatch in previously-predicted associations between vegetation and Humboldt

129 marten distribution could lead to a "wicked problem" by focusing management or

130 restoration in areas that may not benefit the species across its range (Gutiérrez, 2020).

131   Here, our objective was to create a contemporary range-wide model of predicted

132 Humboldt marten distribution that includes recent location data collected from broad-

133 scale randomized surveys throughout the historic range, combined with more recent

134 and accurate vegetation layers (e.g., shrub layers). Our goal was to predict factors

135 contributing to Humboldt marten distribution and to highlight areas for future surveys

136 and conservation efforts.

137

138 **Materials & Methods**

139 **Study Area**

140   We collected data throughout coastal northern California and Oregon. The

141 Humboldt marten is considered to occur in four Extant Population Areas (EPAs), which

142 were created using minimum convex polygons around clusters of marten detections, but

143 excluded clusters with smaller numbers of detections (<5) or detections >5 km from

144 other detections (USFWS 2019). As such, our surveys included both the recognized

145 EPAs (Central Coastal Oregon, Southern Coastal Oregon, California-Oregon Border,

146 and Northern Coastal California; Figure 1) but also extended between these designated

147 boundaries to include the historic range (USFWS 2019).

148   Surveys in California occurred in both near-coastal and montane areas (Klamath

149   Mountains, California Coast Range) that received substantial precipitation (100-300 cm

150   annual precipitation) with cooler (7-10°C) temperatures and drier summers dominated

151   with fog and low cloud moisture (Rastogi et al., 2016). Forest types included a mix of

152   coniferous and hardwood with a spatially-extensive shrub understory and dominant tree

153   species included redwood (*Sequoia sempervirens*) along the coast and Douglas-fir

154   (*Pseudotsuga menziesii*) in the mountains (Whittaker, 1960).

155   Surveys in Oregon similarly occurred in both near-coastal and montane areas

156   (Oregon Coast Range) where dominant forest types included Sitka spruce (*Picea*

157   *sitchensis*) and shore pine (*Pinus contorta*) along the coast and western hemlock

158   (*Tsuga heterophylla*) slightly inland (Franklin & Dyrness, 1973). The Sitka spruce zone

159   was characterized by a wet and moderately warm maritime climate with average annual

160   temperatures of 10-11 °C, average annual precipitation of 200-300 cm, and frequent fog

161   and cloud cover. The western hemlock zone, which was often co-dominated by

162   Douglas-fir, was somewhat cooler (7-10°C average annual temperature) and drier (150-

163   300 cm annual precipitation) with fairly extensive summer fog and low cloud cover (Dye

164   et al., 2020).

165   Common conifer species intermixed and included western hemlock, Port Orford

166   cedar (*Chamaecyparis lawsoniana*), and western redcedar (*Thuja plicata*). Hardwood

167   trees included tanoak (*Notholithocarpus densiflora*), giant chinquapin (*Castanopsis*

168   *chrysophylla*), coastal live oak (*Quercus agrifolia*), canyon live oak (*Q. chrysolepis*),

169   California bay (*Umbellularia californica*), red alder (*Alnus rubra*), bigleaf maple (*Acer*

170   *macrophyllum*), and Pacific madrone (*Arbutus menziesii*). Dominant shrubs throughout

171   the study area included salal *(Gautheria shallon)*, evergreen huckleberry *(Vaccinium*

172   *ovatum)*, Pacific rhododendron *(Rhododendron macrophyllum)*, and red huckleberry *(V.*

173   *parvifolium)*.

174

175   **Marten locations**

176   We used spatially-referenced Humboldt marten locations collected between 1996 and

177   2020 in California and Oregon. We excluded locations occurring in areas that were

178   modified by fire or timber harvest after the location date and prior to 2016, the date

179   represented by our vegetation data. If multiple locations occurred within a 500-m x 500-

180   m grid cell, we spatially-thinned locations to randomly include one in each cell,

181   attempting to achieve spatial independence for modeling (Kramer-Schadt et al., 2013).

182   Priority for location retention from highest to lowest was: (1) rest and den locations from

183   telemetry (Linnell et al., 2018; Delheimer et al., In press); (2) locations from scat dog

184   detection surveys (Moriarty et al., 2018; Moriarty et al., 2019); and (3) locations from

185   baited camera and/or track plate surveys (Slauson, Baldwin & Zielinski, 2012; Barry,

186   2018; Gamblin, 2019; Moriarty et al., 2019). We used presence-only data because

187   surveys that occurred prior to 2014 were often missing detection histories from non-

188   detection (e.g., absence) locations.

189   For the data for which the authors were responsible, our protocols were reviewed

190   and approved by the USDA Forest Service Research and Development Institutional

191   Care and Use Committee (permits 2015-002, 2017-005) or Humboldt State University

192   Institutional Care and Use Committee (permit 16/17.W.05-A). We obtained Scientific

193   Take Permits for hair snares and samples collected through the Oregon Department of

194   Fish and Wildlife (ODFW 119-15, 128-16, 033-16, 109-19, 107-20). Older verified

195   survey data were provided by the US Fish and Wildlife Service with no additional

196   information.

197

198   **Modeling approach**

199   Our modeling approach included Humboldt marten locations, biotic and abiotic predictor

200   variables, and randomly generated pseudo-absence points. We used a minimum

201   convex polygon (MCP) around Humboldt marten locations buffered by 10 km to define

202   the modeling region (Fig. 1b). We chose a 10 km buffer because it approximated the

203   upper quartile of daily marten movement (Moriarty et al., 2017). We projected our model

204   to available vegetation data from Gradient Nearest Neighbor (GNN) data supplied by

205   the Landscape Ecology, Modeling, Mapping and Analysis lab (Bell, Gregory & Davis,

206   2020; Bell et al., 2021), which included the coastal and Klamath level-3 eco-provinces

207   (U.S. Environmental Protection Agency, 2013). We removed urban areas and water

208   from the background data (Davis et al., 2016). We summarized the range, average, and

209   standard deviation for each variable within the modeling region and study area (Table 1,

210   Fig. 1).

211

212   **Biotic variables**

213   Biotic variables in our models included forest structure and composition, forest age,

214   canopy cover, OGSI, percent pine, percent mast, and predicted shrub cover, as

215   described below.

216   We used the 2016 version of GNN (Ohmann & Gregory, 2002) to incorporate

217 forest structure variables including forest age, canopy percent cover, OGSI, and percent

218 pine. Forest age was the basal area-weighted age based on field-recorded or modeled

219 ages of dominant and codominant trees. Canopy percent cover was calculated using

220 the Forest Vegetation Simulator (Crookston & Stage, 1999). Our OGSI index ranged

221 from 0-100 was based from 4 elements: density of large diameter live trees per hectare,

222 density of large diameter snags per hectare, percentage of downed wood greater than

223 25 cm in diameter, and an index of tree diameter diversity computed from tree densities

224 in different diameter classes (Davis et al., 2015). For live trees and snags, "large

225 diameter" was dependent on forest type and was defined for twelve vegetative zones,

226 each zone with a unique minimum diameter threshold (i.e., ranging 50-100 cm for live

227 trees, 50-75 cm for snags (Davis et al. (2015); see Supplemental information (Item S1)

228 for more information on integration of the OGSI variable into our model).

229   We created a variable called "percent pine", which was the combined percentage

230 of total basal area of shore pine, Jeffery pine (*P. jefferii*), and knobcone pine (*P.*

231 *attenuata*) from GNN. This variable was included because martens have been detected

232 in shore pine communities in the Oregon Central Coast population (Linnell et al., 2018;

233 Eriksson et al., 2019), and in areas with serpentine soils characterized by sparse cover

234 of Jeffery and knobcone pine, stunted tree growth, and dense shrub understories

235 (Kruckeberg, 1986; Safford, Viers & Harrison, 2005; Harrison et al., 2006; Slauson et

236 al., 2019). We visually inspected the congruence of the serpentine soil layer created by

237 the US Fish and Wildlife Service (Schrott & Shinn, 2020) with our percent pine layer,

238 confirming overlap between the two variables.

239   Humboldt martens have been associated with dense shrub cover throughout

240 their range (Slauson, Zielinski & Hayes, 2007; Moriarty et al., 2019). Salal and

241 evergreen huckleberry appear particularly important, as the berries of each occur in

242 Humboldt marten diets and provide food for marten prey species (Eriksson et al., 2019;

243 Manlick et al., 2019; Moriarty et al., 2019). We modeled probabilities of species

244 occurrence of salal and evergreen huckleberry, creating the model for evergreen

245 huckleberry following methods published for salal and other shrub species (Prevéy,

246 Parker & Harrington, 2020; Prevéy et al., 2020). We related locations to contemporary

247 (1981-2010) bioclimatic variables from the AdaptWest project (Wang et al., 2016) to

248 depict the probability of species occurrence (1-100%). Humboldt marten diet is

249 dominated by animals (e.g., passerines, ground squirrels) that feed on berries and mast

250 and Humboldt martens also directly consume berries (Slauson & Zielinski, 2017;

251 Eriksson et al., 2019; Manlick et al., 2019). The "mast" variable represented hardwood

252 tree and shrub species that produce nuts, seeds, buds, or fruits eaten by wildlife and

253 was estimated using the 2016 GNN layer as the percent of total basal area comprised

254 of tanoak, giant chinquapin, coastal live oak, canyon live oak, and California bay.

255

Abiotic variables

257 Abiotic variables included temperature (°C), precipitation (cm), cloud cover (%), coastal

258 proximity, percent slope, and topographic position index. We used 30-year normal

259 PRISM variables of Average Annual Precipitation converted to cm and Maximum

260 Temperature in August at an 800-m scale (1981-2010, PRISM Climate Group, Oregon

261 State University, http://prism.oregonstate.edu, created 10/17/2019) as a proxy for

262   maximum annual temperature. We explored annual data for temperature (2010-2018),

263   but the available 4 km resolution produced artifacts in the model.

264   We created models with the variable Coastal Proximity, which uses PRISM data

265   and combines coastal proximity and temperature advection influenced by terrain (Daly,

266   Helmer & Quiñones, 2003) modified for the western United States (Daly et al., 2008).

267   We derived percent slope and topographic position index from US Geological Survey

268   digital elevation models. Topographic position index is an indicator of slope position and

269   landform category; it is the difference between the elevation at a single cell and the

270   average elevation of the user-defined radius around that cell (Jenness, 2006).

271

272   **Scale optimization**

273   Given that martens select habitat at multiple scales (e.g., broad-scale landscape

274   features) and fine-scale features within home ranges (4th order selection; e.g., Minta,

275   Kareiva & Curlee, 1999), we optimized the spatial scale of each variable included in the

276   model. We smoothed variables using the extract function in package *raster* in R

277   (Hijmans, 2020; R Core Team, 2020) with a radius of 50 m, 270 m, 742 m, and 1170 m.

278   Our smallest scale (50 m, 0.81 ha) provided local and fine-scale conditions. We

279   assumed 270 m (20 ha) approximated the size of a Humboldt marten core area, similar

280   to optimized scales of vegetation characteristics used in predicting conditions for marten

281   rest structures elsewhere in California (Tweedy et al., 2019). The scale of 742 m (174

282   ha) represented an approximate female Humboldt marten home range size, calculated

283   as the average of female home range estimates (173 ha) from two previous studies

284   (Linnell et al., 2018; Supplemental Data S1; PSW, 2019).Our broadest scale was based

285 on the largest size of a Humboldt marten male home range (1170 m, 428 ha,

286 Supplemental Data S1), assuming a male would overlap multiple females and could be

287 interpreted as the smallest unit of population level selection (Linnell et al., 2018; PSW,

288 2019). We used individual univariate linear models (glm) for each spatial scale using our

289 training location data and a random background sample of 9,600 points (25 times the

290 location data) within the MCP at different locations than the Maxent generated pseudo-

291 absence data (Supplemental Data S2). Similar to prior examples (Wasserman et al.,

292 2010; McGarigal et al., 2016; Zeller et al., 2017), we selected the scale for each variable

293 that had the most extreme, and thus the most predictive, coefficient as well as the

294 lowest Akaike's Information Criterion (AIC) value. We also visually inspected the fit of

295 each spatial scale using boxplots (Supplemental Figs. S1, S2, S3).

296   We provided boxplots to visually estimate whether our final variables were similar

297 between all marten locations, thinned marten locations, available surveyed locations

298 without detections (non-detection), and random locations (Fig. 2).

299

300 **Predicted distribution**

301 We used Maxent modeling software v3.4.1 (Phillips, Anderson & Schapire, 2006) to

302 estimate the relative probability of Humboldt marten presence (Merow, Smith &

303 Silander, 2013). Maxent uses a machine learning process to develop algorithms that

304 relate environmental conditions at documented species' presence locations to that of

305 the surrounding background environment in which they occurred (Phillips & Dudík,

306 2008; Elith et al., 2011). We excluded variables with highly correlated predictors

307 (|Pearson coefficient| > 0.6), selecting the variable that was most interpretable for

308   managers (Table S2). During this process, we considered the variance inflation (Table

309   S3), which allows for evaluation of correlation and multicollinearity. Variance inflation

310   factors equal to 1 are not correlated and factors greater than 5 are highly correlated as

311   determined by $(1/(1-R_i^2))$, where R_i^2 is squared multiple correlation of the variable i

312   (Velleman & Welsch, 1981).

313   Within each model iteration, we selected the bootstrap option with 10 replicates,

314   random seed, and 500 iterations. We trained our models using a random subset of 75%

315   of presence locations and tested these using the remaining 25% with logistic output. We

316   used the default of 10,000 pseudo-absence background samples. We varied the

317   response functions to include linear, product, and quadratic features. We selected the

318   "auto features" option for all runs, which allows Maxent to further limit the subset of

319   response features from those selected by retaining only those with some effect.

320   Species distribution maps were produced from all models using the maximum

321   training sensitivity plus specificity threshold, which minimizes both false negatives and

322   false positives. We evaluated the AUC statistic to determine model accuracy and fit to

323   the testing data (Fielding & Bell, 1997). The AUC statistic is a measure of the model's

324   predictive accuracy, producing an index value from 0.5 to 1, with values close to 0.5

325   indicating poor discrimination and a value of 1 indicating perfect predictions (Elith et al.,

326   2006). We assessed variables using response curves, variable contributions, and

327   jackknife tests. We used percent contribution and permutation importance to determine

328   importance of input variables in the final model (e.g., Halvorsen (2013). Percent

329   contribution can be more informative with uncorrelated variables (Halvorsen 2013),

330   while permutation importance provides better variable assessment when models and

331   variables are correlated (Searcy & Shaffer (2016).

332   Because over-parameterized models tend to underestimate habitat availability

333   when transferred to a new geography or time period, we used selection methods

334   suggested by Warren & Seifert (2011). Maxent provides the option of reducing

335   overfitting with a regularization multiplier that can be altered by the user to apply a

336   penalty for each term included in the model (β regularization parameter) to prevent

337   overcomplexity or overfitting (Merow, Smith & Silander, 2013; Morales, Fernández &

338   Baca-González, 2017). A higher regularization multiplier will reduce the number of

339   covariates in the model, becoming more lenient with an increased sample size (Merow,

340   Smith & Silander, 2013). We did not include model replicates, an option in the interface,

341   to output the required data (lambda file) and set output to logistic. We altered the

342   Regularization Multiplier from 0.5 to 4 for each 0.5 increment (e.g., Radosavljevic &

343   Anderson (2014).

344   We ranked candidate models using AIC corrected for small sample sizes (AIC_c;

345   Burnham & Anderson 2002). We considered the model with the lowest AIC_c value to be

346   our top model with those with $\Delta AIC_c < 2$ to be competitive models. For our top model, we

347   generated predicted-to-expected (P/E) ratio curves for our model using only the testing

348   data to evaluate its predictive performance, which was based on the shape of the

349   curves, a continuous Boyce index (Boyce et al., 2002), and Spearman rank statistics.

350   We used the predicted-to-expected curve to inform our suitability thresholds following

351   Hirzel et al. (2006). We defined unsuitable in areas where the model performed equal to

352   or poorer than random chance (P/E ≤ 1) with the lower 95% confidence interval of the

353   P/E curve overlapping 0. For predicted suitable and highly suitable locations, we divided

354   P/E and their respective 95% confidence values greater than 1, categorizing the lower

355   half of data as suitable and the upper portion as predicted highly suitable.

356

357   **Results**

358   **Locations**

359   We compiled 10,229 Humboldt marten locations collected during 1996-2020 (542 baited

360   station, 263 detection dog team, 831 VHF telemetry, 8,537 GPS telemetry, 15 roadkill,

361   and 41 others). Our GPS data represented locations taken every 2.5-5 minutes on 7

362   individuals within the Central Coast (Linnell et al., 2018), and we did not display those

363   clustered data. After we spatially-thinned locations, 384 locations remained and were

364   spread among Extant Population Areas: Central Coastal Oregon *(n* = 77 locations)*,*

365   Southern Coastal Oregon (*n* = 77 locations), California-Oregon Border (*n* = 33

366   locations), and Northern Coastal California (*n* = 192 locations) (Fig. 1). There were 5

367   locations that did not occur within boundaries of any EPA (USFWS 2019). Location

368   types included den or rest structure locations (18%), genetically verified scats or

369   telemetry locations (32%), and baited camera or track plate locations (50%).

370   Thinned locations had similar medians and data distributions to the full location

371   dataset, except for mast and precipitation where the medians were slightly lower for the

372   thinned locations (Fig. 2). Non-detection locations had similar medians and data

373   distributions to random locations, with the most notable difference between medians for

374   salal (Table 1, Fig. 2). Differences between non-detection and random locations were

375   likely due to clustered sampling efforts (Fig. 1b).

376

Distribution modeling

378 Our final model included 8 variables after excluding correlated variables (Table S2,

379 Table S3). Variables in our model were optimized at the home range spatial scale

380 (1,170 m) except OGSI (50 m), but differences between scales were modest (Figs. S1-

381 S3). Our top model had a Regularization Multiplier of 1.5. Predictor variables, in order of

382 percent contribution, included a positive relationship with salal (23.3%), percent pine

383 (22.5%), average annual precipitation (21.6%), canopy cover (18.7%), and mast (5.4%)

384 followed by a negative relationship with average maximum August temperature (4.7%),

385 percent slope (2.7%), and OGSI (1.1%, Table 2). Permutation importance was similar

386 with the same top four variables highly contributing, but with a slightly modified order of

387 percent pine (30.3%), average annual precipitation (25.3%), canopy cover (20.2%), and

388 salal (15.5%; Table 2). The OGSI variable contributed least for both metrics.

389 We interpreted Maxent's univariate response curves and provide the marginal

390 plots as a supplemental figure (Fig. S4). Marten locations were correlated with both low

391 and high amounts of canopy cover and percent slope (quadratic response, Fig. 3).

392 Moderate amounts of canopy cover (e.g., 5-50%) appeared to be negatively correlated

393 with marten locations. Predicted marten distribution was positively correlated with salal

394 with some likelihood of a threshold at high values (Fig. 3), percent pine (Fig. 3), average

395 annual precipitation (Fig. 3), and mast (Fig. 3). There was a negative correlation

396 between marten locations and August temperature (Fig. 3) and a slightly negative to

397 neutral relationship between marten locations and OGSI (Fig. 3).

398   The predicted versus expected curve of our final model delineated unsuitable

399   areas as <14%, suitable areas as 15-30%, and predicted highly suitable at >30%

400   predicted probability (Fig. 4, Data S3) with an AUC value on the test data at 92%. The

401   model depicted southern Oregon and northern California as having the largest spatial

402   extent for predicted marten distribution, including areas south of the current known

403   distribution (Fig. 5, Data S3).

404

405   **Discussion**

406   We developed a range-wide species distribution model for the Humboldt marten based

407   on extensive survey effort and incorporation of contemporary vegetation and climatic

408   conditions. Our model is complementary, but not similar, to other Humboldt marten

409   distribution models (e.g., Slauson et al. 2019), which could lead to confusion when

410   attempting to understand Humboldt habitat associations. Instead of interpreting

411   differences between models as a conflict, we posit this as evidence of the conservation

412   challenge described by Caughley (1994) and representative of the difficulty in

413   establishing patterns of causality from observational studies. Nonetheless, our model

414   predicted areas where Humboldt martens are known to occur and identified areas of

415   potential occurrence outside of known population extents, which can be placed within

416   an ecological theory framework for managers. As with all models, there are limitations

417   associated with our predictions, and a clear assessment of these constraints is critical

418   for model results to be accurately used to inform management decisions (Sofaer et al.,

419   2019).

420 The role of biotic interactions in shaping the distribution of species has been

421 reported (e.g., Forchhammer et al., 2005; Guisan & Thuiller, 2005), yet evidence of the

422 importance of biotic variables alongside abiotic variables for predicting distributions at

423 larger spatial scales has been largely lacking (e.g., Wisz et al., 2013). High amounts of

424 shrub cover appears to be the most prevalent component of Humboldt marten locations

425 in both California (Slauson & Zielinski 2009, Slauson et al. 2007) and Oregon (Moriarty

426 et al., 2019) and accordingly, both salal and mast (including mast-producing shrubs)

427 had a strong contribution to our model. Although associations with shrub cover or mast

428 are generally uncharacteristic of martens, European pine martens may occur in areas of

429 dense shrubs (Lombardini et al., 2015) and American marten population numbers in

430 New York appear correlated with mast in hardwood forests (Jensen et al., 2012). Our

431 finding that Humboldt marten distribution was strongly correlated with canopy cover is

432 consistent with previous marten research (Bissonette et al. 1997, Hargis et al. 1999),

433 although our response was quadratic, suggesting marten locations were associated with

434 both low and high levels of canopy cover. Marten populations are typically associated

435 only with relatively dense and increasing canopy cover (Shirk, Raphael & Cushman,

436 2014) and we posit that a quadratic response to canopy cover by Humboldt martens

437 may be a function of shrub cover. Although additional information is needed to describe

438 fine-scale vegetation associations, forest conditions with a dense understory layer of

439 shrub and mast-producing species represent achievable targets that can guide

440 management or restoration.

441 Biotic variables influencing predicted Humboldt marten distribution in our model

442 were consistent with previous literature with some exceptions, most notably forest age

443   and OGSI. Within our model, the predicted relationship between Humboldt marten

444   distribution and higher OGSI values was not only weak but often negative

445   (Supplemental Item S1). The OGSI variable may, in fact, represent an interpretive

446   mismatch with shrub cover – some areas where Humboldt martens occur (e.g., mature

447   Douglas fir forest; Slauson et al. 2007) are characterized by both older forest conditions

448   (i.e., high OGSI values) and substantial shrub cover, while other areas (e.g., serpentine

449   or coastal pine forests; Eriksson et al. 2019, Moriarty et al. 2019) are characterized by

450   substantial shrub cover, but not older forest conditions (i.e., low OGSI values). As an

451   example of this mismatch, much of the putative distribution of Humboldt martens in

452   coastal Oregon and California is dominated by mature western hemlock forests with

453   high OGSI values, yet Humboldt martens are not strongly associated with such areas

454   (Moriarty et al. 2019), possibly because hemlocks are a shade-tolerant species that

455   prohibit understory growth such as shrubs (Kerns & Ohmann, 2004). When examining

456   our marten locations in a model only with the components of OGSI, downed wood was

457   the most influential variable (Supplemental Item S1). We suspect the differences

458   between our model and the Slauson et al. (2019) model resulted from non-stationary

459   vegetation associations that were only revealed by increased survey effort across a

460   broader geographic scope. While the Slauson et al. (2019) model relied on a modest

461   number of Humboldt marten detections from 1996–2010 with poor coverage outside of

462   northern California (USFWS 2019), our model included a relatively large number of

463   detections that occurred across a longer period of time (1996–2020), over a broader

464   geographic scope in both California and Oregon (Barry 2018; Gamblin 2019; Linnell et

465   al. 2018; Moriarty et al. 2019).

466   Range limit theorems have long postulated the importance of elevation, altitude,

467   and weather in determining the limits of species distributions (e.g., Darwin, 1859).

468   Precipitation was one of the top 3 predictive variables in all model simulations and

469   abiotic factors such as increased precipitation, proximity to the coast, and cool

470   temperatures likely influence vegetation type and composition. If these variables are

471   causally linked to marten occurrence, a plausible mechanism is that cooler wetter

472   conditions result in dense vegetation growth (e.g., shrubs). In areas with relatively low

473   canopy cover but dense shrubs, shrub cover may be functionally similar to canopy

474   cover by offering increased protection from predators (Hawley & Newby, 1957). High

475   shrub cover also likely results in an increased availability of berries and mast. Given that

476   martens consume prey items (e.g., birds, rodents) that feed on berries and mast, while

477   also consuming berries themselves, shrubs may both indirectly and directly subsidize

478   marten diets. If increased shrub cover decreases predation risk while simultaneously

479   providing abundant food resources, such areas may provide exceptional, if

480   uncharacteristic, marten habitat (Eriksson et al., 2019). If this is a potential mechanism,

481   an example includes the abundance of huckleberries that have been attributed to

482   increased reproduction and population growth for grizzly bears (*Ursus arctos*) over a 32-

483   year investigation (McLellan, 2015).

484   Species' distributions may also be strongly influenced by less-apparent factors

485   such as interspecific interactions with predators or competitors (Siren, 2020). As an

486   example, spotted owls (*Strix occidentalis*) closely align with old-growth forest conditions

487   which have been characterized with relatively high accuracy (Davis et al., 2016), yet

488   spotted owl population viability is dramatically decreased with presence of barred owls

489 (*S. varia*) due to interspecific competition and predation (Wiens, Anthony & Forsman,

490 2014; Diller et al., 2016; Dugger et al., 2016). Although few examples exist for

491 carnivores, a recent evaluation suggests that while lynx (*Lynx lynx*) distributions are

492 closely-tied to deep snow, the influence of reducing bobcat (*L. rufus*) competition was

493 stronger than the influence of snow itself (Siren, 2020). A directed research effort that

494 integrates the influence of vegetative and climatic associations with other factors such

495 as prey availability, predation pressure, and competition would provide better insight on

496 the drivers of Humboldt marten occurrence and a more holistic determination of marten

497 distribution.

498   Our results predict some of the components that comprise suitable marten

499 habitat but describing optimal habitat would be best informed by measures of survival

500 and fecundity. Future endeavors could develop site-specific models, ideally using

501 telemetry data that are biologically linked with fitness (e.g., long-lived adult female rest

502 and den structures) to address predicted habitat. We lack enough information regarding

503 where Humboldt martens resided historically to compare with our contemporary

504 distribution (Loehle, 2020), and we are generally ignorant of population densities, causal

505 associations of population declines, and population limitations. Such an understanding

506 is essential to describe expectations of future range (Brown, Stevens & Kaufman,

507 1996). Finally, the lack of consistency among Humboldt marten studies is suggestive of

508 imperfect knowledge of what components constitute Humboldt marten habitat. To avoid

509 differing views for rare species conservation (e.g., Gutiérrez, 2020; Jones et al., 2020),

510 amassing information collaboratively with a goal of prospective meta-analyses and

511 study-level replication will be essential (Facka & Moriarty, 2017; Nichols, Kendall &

512 Boomer, 2019).

513

514 **Conclusions**

515 Based on our modeling and an evaluation of available evidence, we conclude that the

516 most consistent range-wide characteristic with Humboldt marten distributions are forest

517 associations with extensive dense shrub cover or complex understory vegetation, which

518 may be indicative of increased food availability or predation escape cover. An

519 understanding of the strength of these interactions and factors that limit populations is

520 needed to make informed conservation decisions. An adaptive management framework

521 with integrated research components may allow for near-term conservation decision

522 making.

523

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Figure 1

Our study area and modelling region for Humboldt martens (*Martes caurina humboldtensis*) included all of coastal Oregon and northern California.

We modeled Humboldt marten predicted distributions in forested lands (Panel A, green mask) in 2 ecoregions [left]. We created a minimum convex polygon of known locations buffered by 10-km (hatched area). We compiled 10,229 marten locations, displaying 1,692 marten locations that were not GPS derived and clustered (icon color) from 5,153 surveyed sites with non-detections in light gray, collected during 1996-2020 (panel B). We spatially thinned locations to approximately 500m apart, prioritizing den and rest locations and resulting in 384 locations (black dots, panel C).

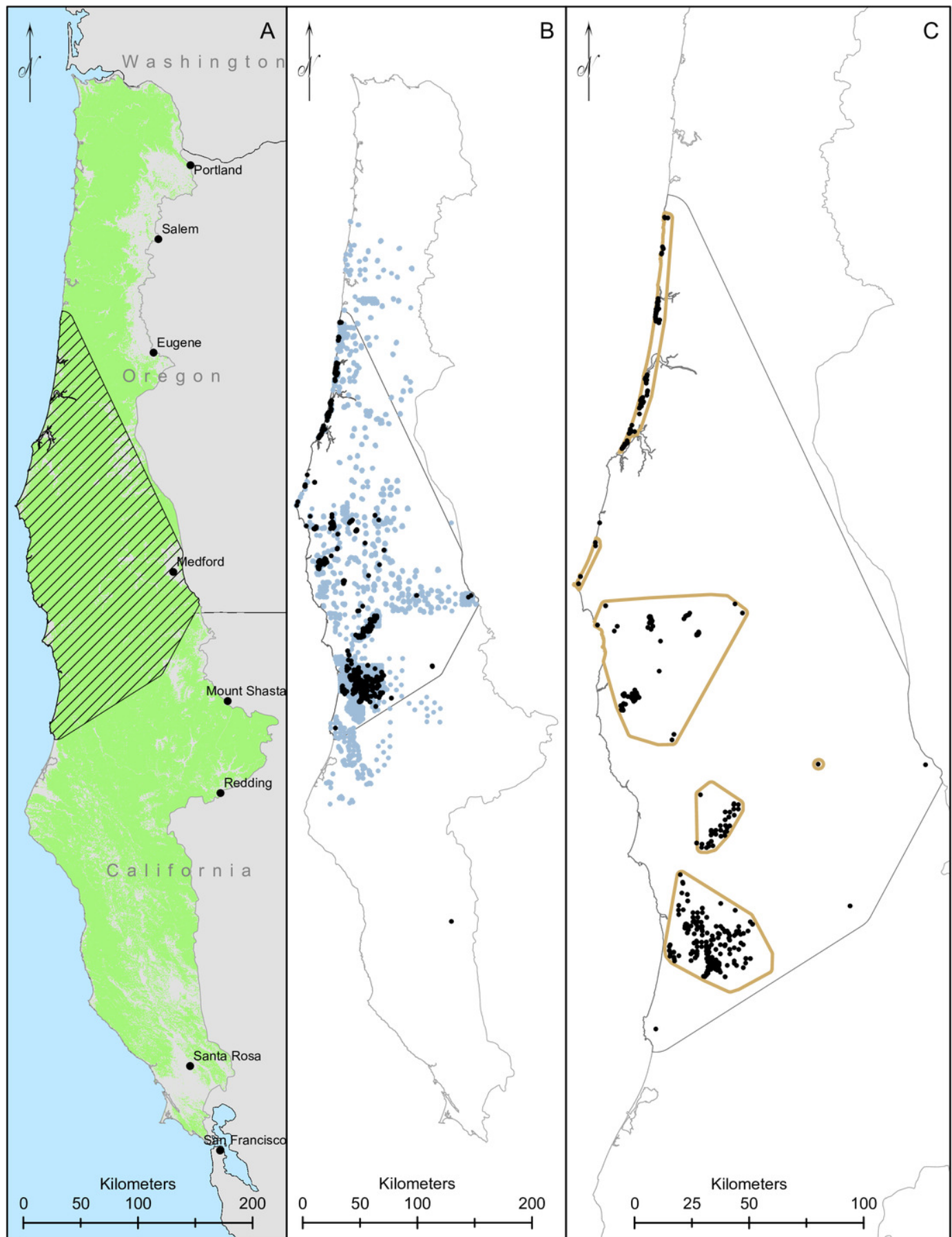



Figure 2

We investigate the range of variables in our thinned dataset compared to all marten locations and detection/non-detection data.

To provide the range of values observed in this study, we depict boxplots for the variables in the top model showing the thinned marten data (Marten), all non-GPS marten locations (Marten_DB), non-detected but surveyed locations (Non-detection), and random locations within the minimum convex polygon (9,600 random locations).

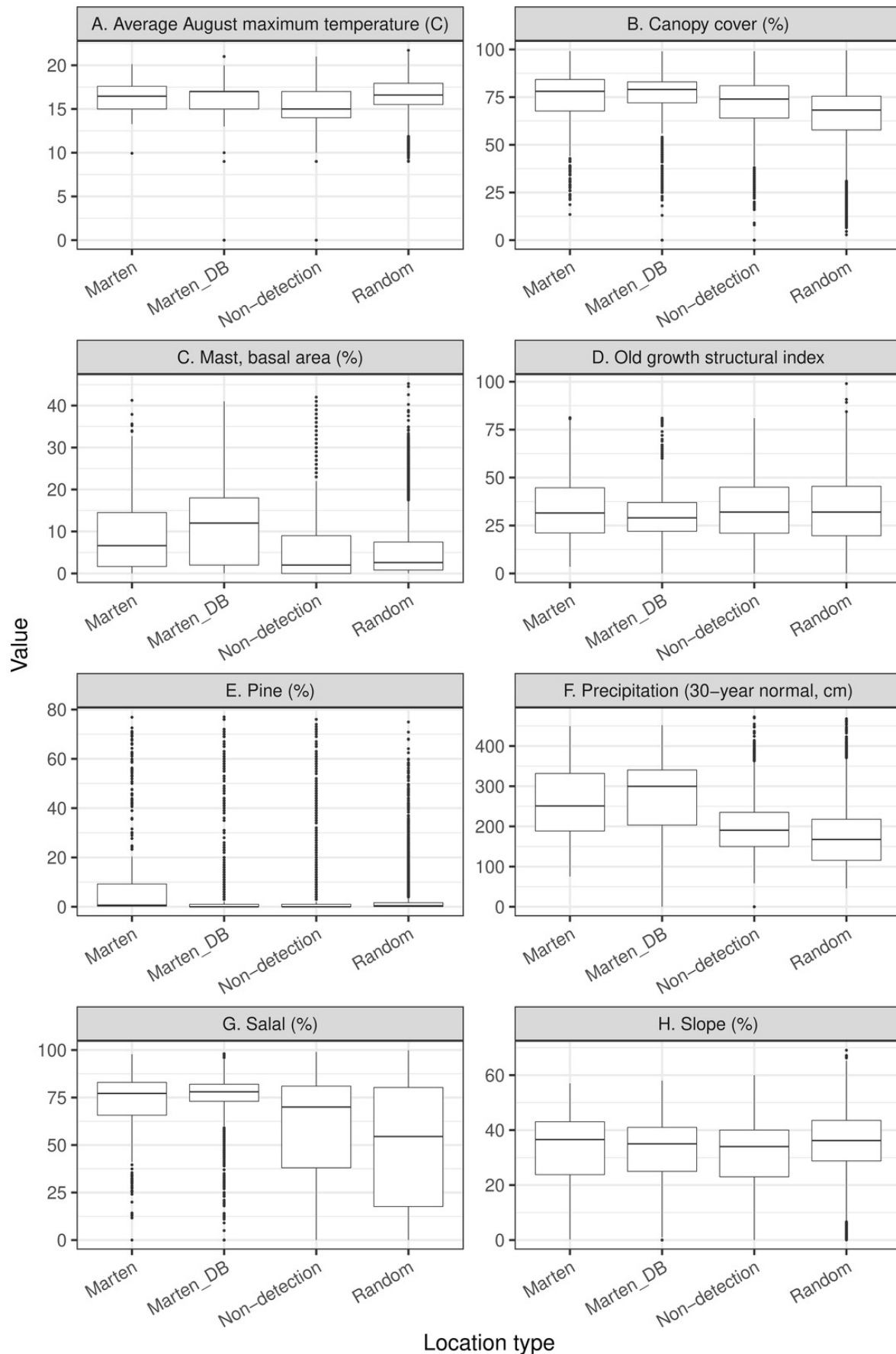



Figure 3

We depict predicted relationships between Humboldt marten locations and each of the variables within our final model.

Here, each curve is the predicted probability of presence with no conflicting influence of potentially correlated variables. Humboldt marten locations were correlated with both low and high amounts of canopy cover and percent slope (quadratic response). Predicted distribution was positively correlated with predicted salal (*Gaultheria shallon*) distribution, percentage of pine, precipitation, and mast. We observed a negative correlation between marten locations and August temperature. We observed a slight negative relationship between marten locations and the old growth structural index. Our figure order matches the percent contribution values reported in Table 2. The curves reveal the mean response (black) and standard deviation (gray) for 10 replicate Maxent runs.

Probability of presence

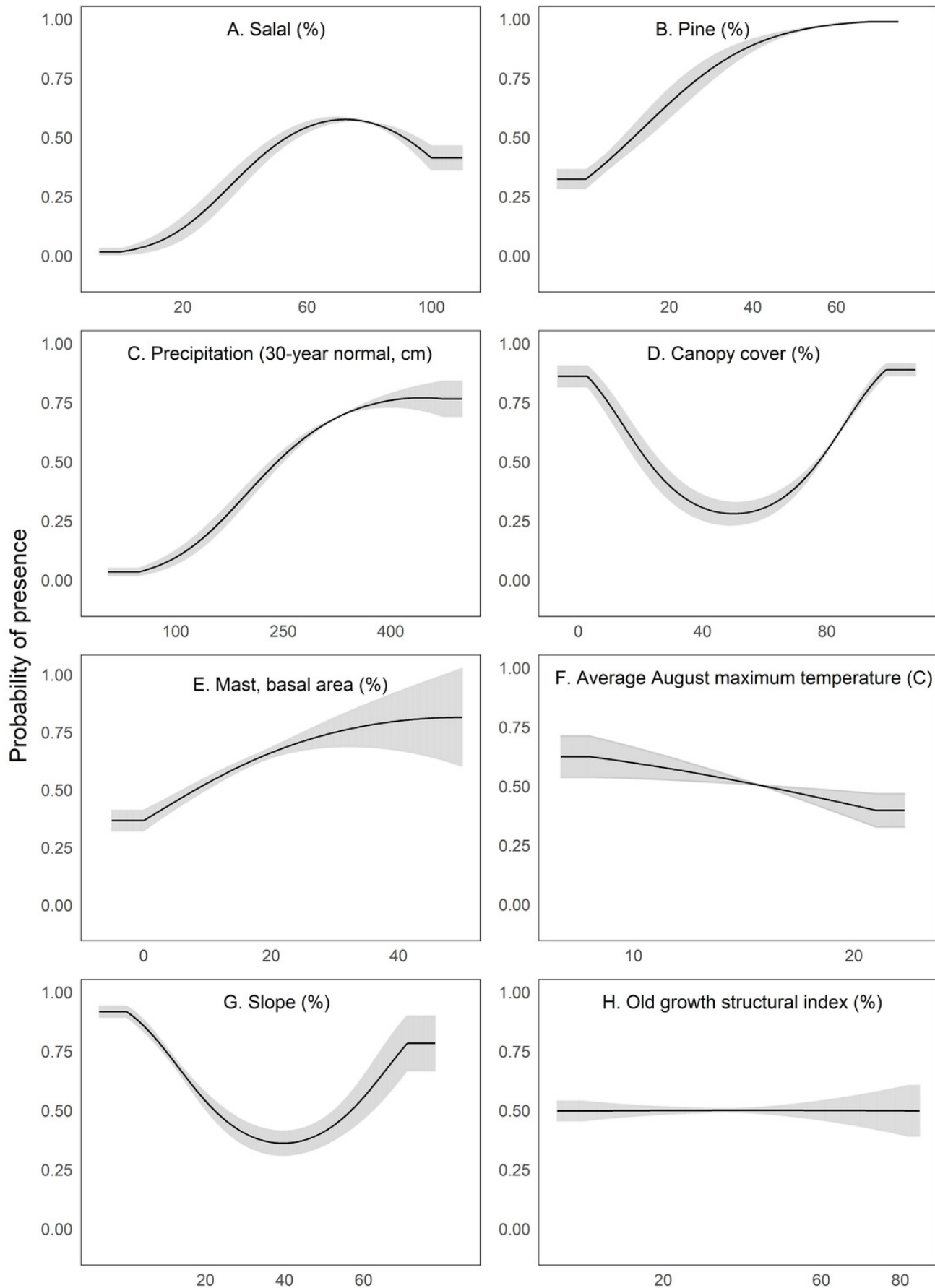



Figure 4

Our predicted suitable transitions for Humboldt marten (*Martes caurina humboldtensis*) range.

We present mean predicted vs. expected curve (solid black line) from our model replicates, showing 95-percent confidence intervals (gray-shaded vertical bars). The P/E = 1 threshold is where the curve crosses the random chance line (horizontal orange line), and the blue dashed vertical lines are the 95-percent confidence intervals. We used the predicted-to-expected curve to inform our suitability thresholds following Hirzel et al. (2006), including predicted unsuitable (P/E and confidence intervals 0-1), marginal (P/E > 1 but overlapping confidence intervals), and suitable (P/E and confidence intervals > 1; map depicted in Fig. 5).

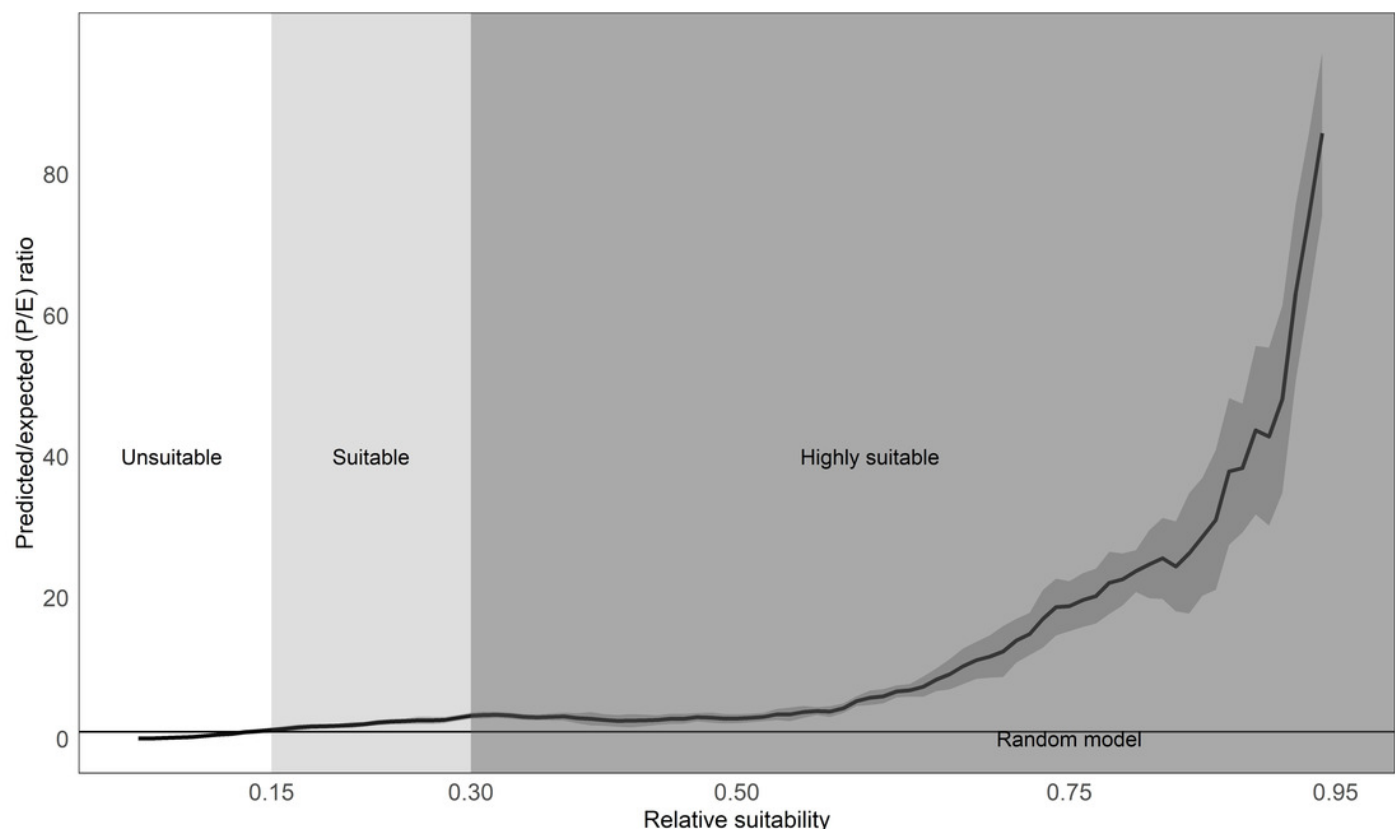
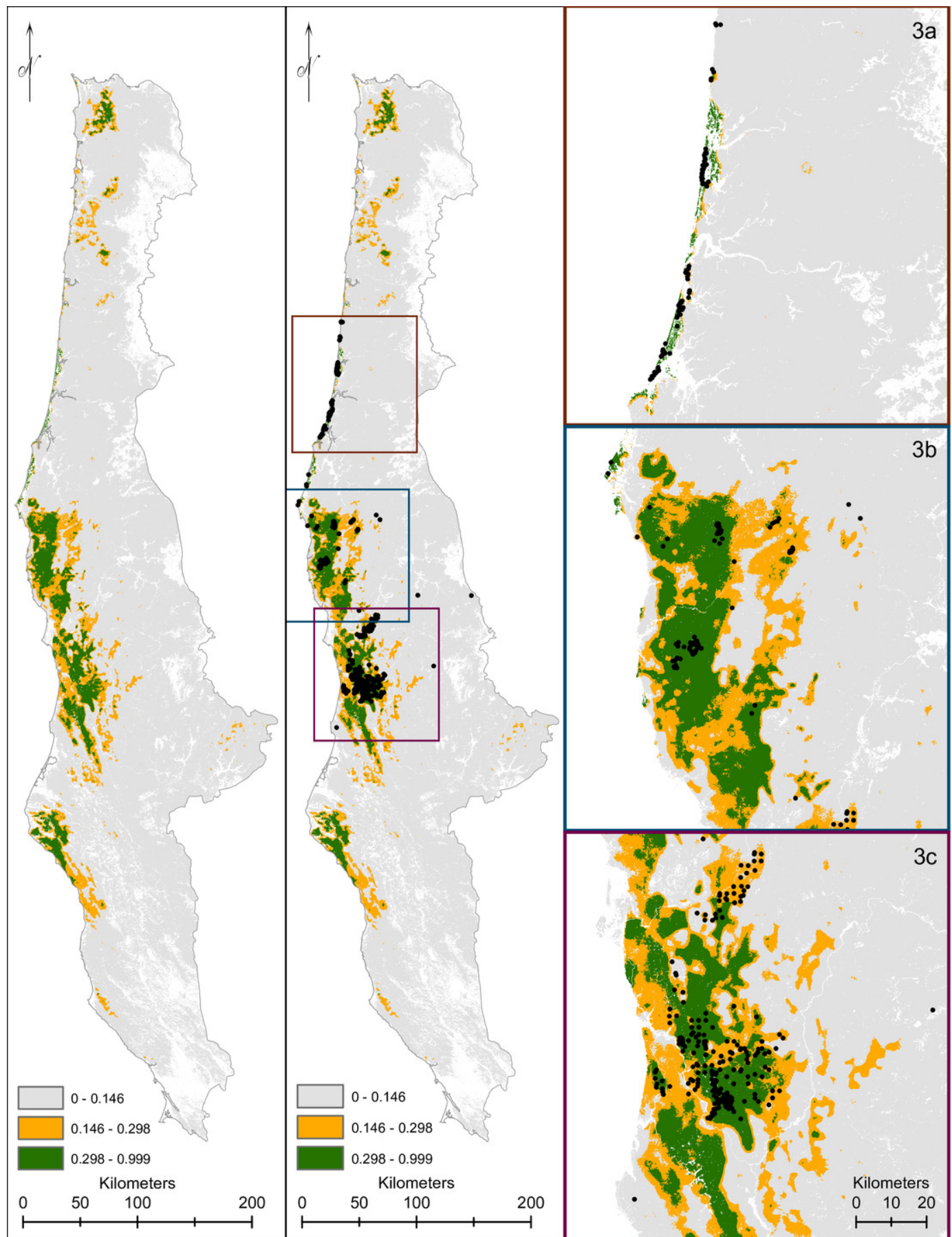



Figure 5

We display our modeled predicted range for Humboldt marten (*Martes caurina humboldtensis*).

For predicted range, we followed Hirzel et al. (2006) with predicted versus expected ratios transitioning between predicted highly suitable (green), suitable (orange), and marginal or not predicted suitable (gray). Marten location information was displayed (black dots). We zoomed to population extents to provide increased visual resolution within the Central Oregon Coast (Panel 3a), South coast (Panel 3b), and northern California (Panel 3c).

3a

3b

3c

	0 - 0.146
	0.146 - 0.298
	0.298 - 0.999

Kilometers
0   50   100   200

	0 - 0.146
	0.146 - 0.298
	0.298 - 0.999

Kilometers
0   50   100   200

Kilometers
0   10   20

Data ranges, means, and standard deviations for the model region, the contemporary Humboldt marten distribution, and at Humboldt marten locations.

We depict individual layer statistics within our Humboldt marten (*Martes caurina humboldtensis*) model region in coastal Oregon and northern California. We display the variable, optimized spatial scale with a radius in meters, value range from the coastal ecoregions, means and standard deviation (SD) for the model region, minimum convex polygon around all known marten locations (MCP), and values from spatially thinned marten locations (n = 384), our layer source, and a description of that variable. We only considered variables with < 60% correlation in our final model (Table S2).

1 **Table 1:**
2 **Data ranges, means, and standard deviations for the model region, the contemporary Humboldt marten distribution, and at**
3 **Humboldt marten locations.**
4 We depict individual layer statistics within our Humboldt marten (*Martes caurina humboldtensis*) model region in coastal Oregon and
5 northern California. We display the variable, optimized spatial scale with a radius in meters, value range from the coastal ecoregions,
6 means and standard deviation (SD) for the model region, minimum convex polygon around all known marten locations (MCP), and
7 values from spatially thinned marten locations (n = 384), our layer source, and a description of that variable. We only considered
8 variables with < 60% correlation in our final model (Table S2).

Variable	Scale	Value Range	Model Region (Mean ± SD)	Minimum convex polygon (Mean ± SD)	Marten Locations (Mean ± SD)	Source	Description
Forest age, years	270	0 – 712	95.5 ± 43	104.3 ± 49.4	109.8 ± 69.6	2016 GNN	Basal area weighted stand age based on field recorded or modeled ages of dominant/codominant trees
Canopy cover (%)	1170	2 – 99	65.9 ± 13	66.4 ± 14	71.3 ± 18.6	2016 GNN	Canopy cover percentage of all live trees
Coastal proximity	50	2 – 700	511.7 ± 193.1	516.3 ± 203.1	361.8 ± 197.9	PRISM	Optimal path length from the coastline accounting for terrain blockage (Daly et al. 2008)
Diameter diversity index	1170	26 – 811	433.9 ± 103	437.6 ± 111.7	459.4 ± 123.6	2016 GNN	Diameter diversity index - measure of stand structure based on tree densities in diff. DBH classes (x100)
Percent downed wood	270	0 – 797	69.3 ± 54.7	70.9 ± 50	68.5 ± 60.1	2016 GNN (created)	Created within GNN to estimated percentage of large downed wood, a component of OGSI
Salal	1170	0 – 100	35.7 ± 30.9	50.7 ± 32.3	72.7 ± 17.8	Prevéy	Probability of *Gautheria shallon* species occurrence (Prevéy et al. 2020)

Variable	N	Range	Mean ± SD	Mean ± SD	Mean ± SD	Source	Description
Masting vegetation	1170	0 – 72	5.9 ± 7.4	5.2 ± 6.7	9.3 ± 9	2016 GNN	Percent of stand basal comprised of tanoak (*Notholithocarpus densiflorus*; LIDE), giant chinquapin (*Castanopsis chrysophylla*; CHCH), coastal live oak (*Quercus agrifolia*; QUAG), canyon live oak (*Quercus chrysolepis*; QUCH), and California bay (*Umbellularia californica*; UMCA) (mast producing evergreen hardwoods, indicator of prey abundance)
Old growth structural index	50	0 – 100	32.7 ± 15.8	33.2 ± 16.1	33.8 ± 16.9	2016 GNN	Old-growth structure index based on abundance of large live trees, snags, down wood, and ddi
Percent pine	1170	0 – 94	1.2 ± 3.5	1.5 ± 4.5	10.9 ± 20.1	2016 GNN	Percent of pixel basal area comprised of shore pine (*Pinus contorta*; PICO), Jefferey pine (*Pinus jeffreyi*; PIJE) and knobcone pine (*Pinus attenuata*; PIAT). We use this as an indicator of serpentine and coastal dune environments.
Percent slope	1170	0 – 74	33.8 ± 10.9	36.2 ± 10.6	31.7 ± 15.8	USGS DEM	Percent slope in degrees
Precipitation	1170	13 – 198	66.9 ± 27	70 ± 30.1	102.4 ± 30.5	2016 GNN	Average annual precipitation 1981-2010 (inches)
Large snag density	742	0 – 48	4.9 ± 4.3	5.8 ± 4.6	6.9 ± 4.9	2016 GNN (created)	Created within GNN to estimated density of large snags, a component of OGSI
Temperature (August max)	1170	8 – 24	16.5 ± 2.3	16.1 ± 1.7	16.4 ± 1.7	PRISM	Average annual maximum temperature 1981-2010 (Celcius).
Topographic position index	270	-149 – 174	0.7 ± 26.7	1.1 ± 28.8	-0.3 ± 28.6	USGS DEM	Topographic position index - difference of cell elevation with mean of all cells w/in 450 m radius

| Large tree density | 1170 | 0 – 47 | 3.2 ± 3.5 | 4.4 ± 4.2 | 5.2 ± 5.9 | 2016 GNN (created) | Created within GNN to estimated density of large trees, a component of OGSI |
| Huckleberry | 1170 | 2 – 99 | 32.7 ± 24.6 | 39.1 ± 26 | 42.7 ± 27.2 | Prevéy | Probability of species occurrence for *Vaccinium ovatum* (created) |

We show the percent contribution and permutation importance from our top Maxent model.

We ordered variables by their percent contribution and report the optimized spatial scale (focal radius in meters), the univariate response type, and whether the univariate dependent plots were generally positively or negatively correlated with Humboldt marten (*Martes caurina humboldtensis*) locations.

1 **Table 2:**

2 **We show the percent contribution and permutation importance from our top Maxent model.**

3 We ordered variables by their percent contribution and report the optimized spatial scale (focal radius in meters), the univariate
4 response type, and whether the univariate dependent plots were generally positively or negatively correlated with Humboldt marten
5 (*Martes caurina humboldtensis*) locations.

Variable	Scale	Response	Univariate Relationship	Percent contribution	Permutation importance
Salal	1170	Quadratic	+	23.3	15.5
Percent pine	1170	Product	+	22.5	30.3
Precipitation_30-year average	1170	Product	+	21.6	25.3
Canopy cover	1170	Quadratic	+	18.7	20.2
Mast	1170	Product	+	5.4	1.3
August temperature_30-year average	1170	Linear	-	4.7	2.3
Percent slope	1170	Quadratic	-	2.7	4.4
Old growth structural index	50	Linear	-	1.2	0.7