Predicted distribution of a rare and understudied forest carnivore: Humboldt martens (*Martes caurina humboldtensis*) (#57298)

First revision

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

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Background. Several mammalian species have experienced contractions in distribution following European settlement and development of the North American continent. For example, local populations of North American martens (American marten, *Martes americana*; Pacific marten, *M. caurina*) have experienced substantial reductions in distribution and some extant populations are small and geographically isolated. The Humboldt marten (*M. c. humboldtensis*) is a subspecies of Pacific marten that occurs in coastal Oregon and northern California and was recently designated as federally threatened, following a reduction in distribution that has resulted in small and geographically isolated populations. Unlike martens that occur in snow-associated regions, vegetation associations appear to differ widely between Humboldt marten populations. We expect current distributions to represent realized niches, but estimating factors associated with long-term occurrence is challenging for rare and little-known species. Here, we assess the predicted 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 altered 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, and annual precipitation at home-range spatial scales, areas with 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. Conservation efforts and our assessment of potential risks to Humboldt marten populations would benefit from continued survey effort to clarify range extent, population sizes, and fine-scale habitat use.

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

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Abstract

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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 altered 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, and annual precipitation at home-range spatial scales, areas with 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. Conservation efforts and our assessment of potential risks to Humboldt marten populations would benefit from continued survey effort to clarify range extent, population sizes, and fine-scale habitat use.

Key words: California, distribution model, habitat relationships, Humboldt marten, *Martes caurina humboltensis*, Maxent, rare species, Oregon, Pacific marten

Introduction

Modeling predicted distributions of rare or declining species can direct conservation efforts, thus creating accurate predictions is important but challenging. For instance, constriction of the range available to a species – their realized niche – is the actualization of used conditions, but such conditions may change (Colwell & Rangel 2009). Contemporary location information may further associate a species with conditions that were unaffected by prior agents of population decline, but not with favored characteristics where the species resided prior (Caughley 1994). For instance, bison (*Bison bison*) were historically widely distributed throughout the Great Plains of North America (Shaw 1995), yet a contemporary species distribution model would associate bison occurrence with conditions where the few relict population reside. Conditions present for bison in Yellowstone National Park, such as extremely cold winters and thermal geysers, are uncharacteristic of the conditions where populations historically occurred. Challenges are more pronounced for understudied species

(Raphael & Molina 2007), but spatial models may help predict occurrence (Sofaer et al. 2019).

Humboldt martens (*M. c. humboldtensis*) are a distinct subspecies that historically occurred throughout coastal forests of northern California and Oregon (Schwartz et al. 2020). Humboldt martens were thought to be increasingly rare almost a century ago (Grinnell & Dixon 1926) and were considered to be extirpated in California and extremely rare in Oregon for the latter half of the 20th century (Zielinski et al. 2001). In 1996, the Humboldt marten was rediscovered in California (Zielinski & Golightly 1996). Subsequent research efforts over the last two decades have elucidated some aspects of Humboldt marten ecology and demography (e.g., Delheimer et al. In press; Linnell et al. 2018), including surveys to evaluate contemporary Humboldt marten distribution (e.g., Gamblin 2019; Moriarty et al. 2019). Although such investigations have improved our knowledge of where Humboldt martens occur, the full geographic extent of contemporary distribution remains unknown, although it appears to compose a fraction of the historical distribution (USFWS 2020). This putative range contraction has resulted in apparently small and isolated populations (USFWS 2019), which has engendered substantial concern for species' persistence. Consequently, Humboldt martens were listed as Endangered under the state of California's Endangered Species Act (CDFW 2019) and as Threatened under the federal Endangered Species Act as a "coastal distinct population segment of Pacific martens" (USFWS 2020).

Clarifying contemporary Humboldt marten distribution by identifying areas where martens may occur that have not been surveyed and predicting future distribution (e.g., identifying areas where martens may not occur but could colonize) is urgently needed for conservation planning. However, distribution modeling is constrained by apparent non-stationary associations with vegetation among Humboldt marten populations, which also contradicts the prevailing paradigm for vegetation associations of North American martens. For instance, it has been generally recognized that North American martens occur in mature forests characterized by dense canopy cover, presence of large diameter and decadent trees and snags, and abundant coarse woody debris (Thompson et al. 2012). Although initial investigations primarily associated Humboldt martens with similar conditions (Slauson et al. 2007), subsequent studies have indicated that Humboldt martens also occur in young forests (<80 years old) characterized by modest canopy cover and relatively small diameter trees with dense shrub cover (Eriksson et al. 2019; Moriarty et al. 2019). A dense and spatially-extensive shrub layer was associated with marten use or occurrence in most studies (Eriksson et al. 2019; Gamblin 2019; Moriarty et al. 2019; Slauson et al. 2007). Similarly, European pine martens (*Martes martes*) have long been considered a habitat specialist associated with older forests (Brainerd & Rolstad 2002; Storch et al. 1990), yet have recently been documented in a wide variety of habitat types including shrublands, grasslands, and agricultural areas (Balestrieri et al. 2016; Lombardini et al. 2015; Manzo et al. 2018; Moll et al. 2016).

Observations that are limited in space or time may not identify the conditions necessary for population persistence, which could result in a misrepresentation of a species' niche. A previous range-wide Humboldt marten distribution model Slauson et al. (2019) emphasized a strong correlation between Humboldt marten occurrence and an "old-growth structural index" (OGSI) variable, which is a composite index of factors considered common to old-growth forests in the region, including density of large live trees, stand age, snags and downed wood, and diversity of tree sizes (Davis et al. 2015). Nonetheless, their model relied on modest number of detections from 1996–2010 with poor coverage outside of northern California (USFWS 2019). Since 2010, we initiated large-scale surveys for Humboldt martens that greatly increased the spatial extent and number of Humboldt marten detections in both California and Oregon (e.g., Barry 2018; Gamblin 2019; Linnell et al. 2018; Moriarty et al. 2019). Recent research efforts suggest associations between OGSI and Humboldt marten distribution are less clear. A potential mismatch in previously-predicted associations between vegetation and Humboldt marten distribution could lead to a “wicked problem” by focusing management or restoration in areas that may not benefit the species across its range (Gutiérrez 2020).

Here, our objective was to create a contemporary range-wide model of predicted Humboldt marten distribution facilitated by including recent location data collected from broad-scale randomized surveys throughout the historic range, combined with more recent and accurate vegetation layers (e.g., shrub layers). Our goal was to predict factors contributing to Humboldt marten distribution and to highlight areas for future surveys and conservation efforts.

Materials & Methods

Study Area

We collected data throughout coastal northern California and Oregon. We included the four regions where Humboldt martens have been described - the Central

Coastal Oregon, Southern Coastal Oregon, California-Oregon Border, and Northern Coastal California populations (USFWS 2019; Fig. 1). Surveys in California occurred in both near-coastal and montane areas (Klamath Mountains, California Coast Range) that received substantial precipitation (100-300 cm annual precipitation) with cooler (7-10°C) temperatures and drier summers dominated with fog and low cloud moisture (Rastogi et al. 2016). Forest types included a mix of coniferous and hardwood with a spatially-extensive shrub understory and dominant tree species included redwood (*Sequoia sempervirens*) along the coast and Douglas-fir (*Pseudotsuga menziesii*) in the mountains (Whittaker 1960).

Surveys in Oregon similarly occurred in both near-coastal and montane areas (Oregon Coast Range) where dominant forest types included Sitka spruce (*Picea sitchensis*) and shore pine (*Pinus contorta*) along the coast and western hemlock (*Tsuga heterophylla*) slightly inland (Franklin & Dyrness 1973). The Sitka spruce zone was characterized by a wet and moderately warm maritime climate with average annual temperatures of 10-11 °C, average annual precipitation of 200-300 cm, and frequent fog and cloud cover. The western hemlock zone, which was often co-dominated by Douglas-fir, was somewhat cooler (7-10 °C average annual temperature) and drier (150-300 cm annual precipitation) with fairly extensive summer fog and low cloud cover (Dye et al. 2020).

Common conifer species intermixed included western hemlock, Port Orford cedar (*Chamaecyparis lawsoniana*), and western redcedar (*Thuja plicata*). Hardwood trees included tanoak (*Notholithocarpus densiflora*), giant chinquapin (*Castanopsis chrysophylla*), coastal live oak (*Quercus agrifolia*), canyon live oak (*Q. chrysolepis*), California bay (*Umbellularia californica*), red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*), and Pacific madrone (*Arbutus menziesii*). Dominant shrubs throughout the study area included salal *(Gautheria shallon*), evergreen huckleberry *(Vaccinium ovatum*), Pacific rhododendron *(Rhododendron macrophyllum*), and red huckleberry *(V. parvifolium*).

Marten locations

We used spatially-referenced Humboldt marten locations collected between 1996 and 2020 in all known regions with martens. We excluded locations occurring in areas modified by fire or timber harvest after the date of observation and prior to 2016, the date represented by our vegetation data. If multiple locations occurred within a 500-m x 500-m cell within a created grid, we spatially-thinned locations to randomly include one in each cell, attempting to achieve spatial independence for modeling (Kramer-Schadt et al. 2013). Priority for location retention from highest to lowest was: (1) rest and den locations from telemetry (Delheimer et al. In press; Linnell et al. 2018); (2) locations from scat dog detection surveys (Moriarty et al. 2018; Moriarty et al. 2019); and (3) locations from baited camera and/or track plate surveys (Barry 2018; Gamblin 2019; Moriarty et al. 2019; Slauson et al. 2012). We used presence-only data because older surveys (prior to 2014) were often missing detection histories from non-detection locations.

For the data for which the authors were responsible, our protocols were reviewed and approved by the USDA Forest Service Research and Development Institutional Care and Use Committee (permits 2015-002, 2017-005) or Humboldt State University

Institutional Care and Use Committee (permit 16/17.W.05-A). We obtained Scientific Take Permits for hair snares and samples collected through the Oregon Department of Fish and Wildlife (ODFW 119-15, 128-16, 033-16, 109-19, 107-20). Older verified survey data were provided by the US Fish and Wildlife Service with no additional information.

Modeling approach

Our modeling approach included Humboldt marten locations, biotic and abiotic predictor variables, and randomly generated pseudo-absence points (n = 10,000). We used a minimum convex polygon (MCP) around Humboldt marten locations buffered by 10 km to define the modeling region (Fig. 1b). We chose a 10 km buffer because it approximated the upper quartile of daily marten movement (Moriarty et al. 2017). We projected our model to available vegetation data from Gradient Nearest Neighbor (GNN) data supplied by the Landscape Ecology, Modeling, Mapping and Analysis lab (Bell et al. 2021; Bell et al. 2020), which included the coastal and Klamath level-3 eco-provinces (U.S. Environmental Protection Agency 2013). We removed urban areas and water from the background data (Davis et al. 2016). We summarized the range, average, and standard deviation for each variable within the modeling region and study area (Table 1, Fig. 1).

Biotic variables

Biotic variables in our models included forest structure and composition, forest age, canopy cover, OGSI, percent pine, percent mast, and predicted shrub cover, as described below.

We used the 2016 version of GNN (Ohmann & Gregory 2002) to incorporate forest structure variables including forest age, canopy percent cover, OGSI, and percent pine. Forest age was the basal area-weighted age based on field-recorded or modeled ages of dominant and codominant trees. Canopy percent cover was calculated using the Forest Vegetation Simulator (Crookston & Stage 1999). Here, OGSI was a slightly different composite index from the one used in Slauson et al. (2019) as it excluded stand age. The index ranged from 0-100 was based from 4 elements: density of large diameter live trees per hectare, density of large diameter snags per hectare, percentage of downed wood greater than 25 cm in diameter, and an index of tree diameter diversity computed from tree densities in different diameter classes (Davis et al. 2015). For live trees and snags, “large diameter” was dependent on forest type and was defined for twelve vegetative zones, each zone with a unique minimum diameter threshold (i.e., ranging 50-100 cm for live trees, 50-75 cm for snags (Davis et al. (2015); see Supplemental information (Item S1) for more information on integration of the OGSI variable into our model.

We created a variable called “percent pine”, which was the combined percentage of total basal area of shore pine, Jeffery pine (*P. jefferii*), and knobcone pine (*P. attenuata*) from GNN. This variable was included because martens have been detected in sparse shore pine communities in the Oregon Central Coast population (Eriksson et al. 2019; Linnell et al. 2018), and in areas with serpentine soils characterized by sparse cover of Jeffery and knobcone pine, stunted tree growth, and dense shrub understories (Harrison et al. 2006; Kruckeberg 1986; Safford et al. 2005; Slauson et al. 2019). We visually inspected the congruence of the serpentine soil layer created by the US Fish and Wildlife Service (Schrott & Shinn 2020) with our percent pine layer, confirming overlap between the two variables.

Humboldt martens have been associated with dense shrub cover throughout their range (Moriarty et al. 2019; Slauson et al. 2007). Salal and evergreen huckleberry appear particularly important, as the berries of each occur in Humboldt marten diets and provide food for marten prey species (Eriksson et al. 2019; Manlick et al. 2019; Moriarty et al. 2019). We modeled probabilities of species occurrence of salal and evergreen huckleberry, creating the model for evergreen huckleberry following methods published for salal and other shrub species (Prevéy et al. 2020a; Prevéy et al. 2020b). We related locations to contemporary (1981-2010) bioclimatic variables from the AdaptWest project (Wang et al. 2016) to depict the probability of species occurrence (1-100%). Humboldt marten diet is dominated by animals (e.g., passerines, ground squirrels) that feed on berries and mast and Humboldt martens also directly consume berries (Eriksson et al. 2019; Manlick et al. 2019; Slauson & Zielinski 2017). The “mast” variable represented hardwood tree and shrub species that produce nuts, seeds, buds, or fruits eaten by wildlife and was estimated using the 2016 GNN layer as the percent of total basal area comprised of tanoak, giant chinquapin, coastal live oak, canyon live oak, and California bay.

Abiotic variables

Abiotic variables included temperature (°C), precipitation (cm), cloud cover (%), coastal proximity, percent slope, and topographic position index. We used 30-year normal PRISM variables of Average Annual Precipitation converted to cm and Maximum Temperature in August at an 800-m scale (1981-2010, PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 10/17/2019). We explored annual data for temperature (2010-2018), but the available 4 km resolution produced artifacts in the model.

We created models with the variable Coastal Proximity, which uses PRISM data and combines coastal proximity and temperature advection influenced by terrain (Daly et al. 2003) modified for the western United States (Daly et al. 2008). We derived percent slope and topographic position index from US Geological Survey digital elevation models. Topographic position index is an indicator of slope position and landform category; it is the difference between the elevation at a single cell and the average elevation of the user-defined radius around that cell (Jenness 2006).

Scale optimization

Given that martens select habitat at multiple scales (e.g., broad-scale landscape features (1st order selection sensu Johnson 1980) and fine-scale features within home ranges (4th order selection; e.g., Minta et al. 1999), we optimized the spatial scale of each variable included in the model. We smoothed variables using the extract function in package *raster* in R (Hijmans 2020; R Core Team 2020) with a radius of 50 m, 270 m, 742 m, and 1170 m. Our smallest scale (50 m, 0.81 ha) provided local and fine scale conditions. We assumed 270 m (20 ha) approximated the size of a Humboldt marten core area, similar to optimized scales of vegetation characteristics used in predicting conditions for marten rest structures elsewhere in California (Tweedy et al. 2019). The scale of 742 m (174 ha) represented an approximate female Humboldt marten home range size, calculated as the average of female home range estimates (173 ha) from two previous studies (Linnell et al. 2018; Supplemental Data S1; PSW 2019).Our broadest scale was based on the largest size of a Humboldt marten male home range (1170 m, 428 ha, Supplemental Data S1), assuming a male would overlap multiple females and could be interpreted as the smallest unit of population level selection (Linnell et al. 2018; PSW 2019). We used individual univariate linear models (glm) for each spatial scale using our training location data and a random background sample of 9,600 points (25 times the location data) within the MCP (Supplemental Data S2). Similar to prior examples (McGarigal et al. 2016; Wasserman et al. 2010; Zeller et al. 2017), we selected the scale for each variable that had the most extreme, and thus the most predictive, coefficient. We also visually inspected the fit of each spatial scale using boxplots (Supplemental Figs. S1, S2, S3).

We provided boxplots to visually estimate whether our final variables were similar between all marten locations, thinned marten locations, available surveyed locations without detections (non-detection), and random locations (Fig. 2).

Predicted distribution

We used Maxent modeling software v3.4.1 (Phillips et al. 2006) to estimate the relative probability of Humboldt marten presence within the modeling regions (Merow et al. 2013). Maxent uses a machine learning process to develop algorithms that relate environmental conditions at documented species presence locations to that of the surrounding background environment in which they occurred (Elith et al. 2011; Phillips & Dudík 2008). We excluded variables with highly correlated predictors (|Pearson coefficient| > 0.6), selecting the variable that was most interpretable for managers (Table S2). During this process, we considered the variance inflation (Table S3), which allows for evaluation of correlation and multicollinearity. Variance inflation factors equal to 1 are not correlated and factors greater than 5 are highly correlated as determined by $(1/(1-R_i^2))$, where R_i^2 is squared multiple correlation of the variable *i* (Velleman & Welsch 1981).

Within each model iteration, we selected the bootstrap option with 10 replicates, random seed, and 500 iterations. We trained our models using a random subset of 75% of presence locations and tested these using the remaining 25% with logistic output. We used the default of 10,000 random background samples. We varied the response functions to include linear, product, and quadratic features. We selected the "auto features" option for all runs, which allows Maxent to further limit the subset of response features from those selected by retaining only those with some effect.

We used percent contribution and permutation importance to determine importance of input variables in the final model. Halvorsen (2013) produced simulation results suggesting percent contribution can be more informative with uncorrelated environmental variables. This metric is often used to assess variable significance (e.g., Warren et al. 2014). Searcy & Shaffer (2016) suggest that permutation importance provides better variable assessment when models and variables are correlated.

Species distribution maps were produced from all models using the maximum training sensitivity plus specificity threshold, which minimizes both false negatives and false positives. We evaluated the AUC statistic to determine model accuracy and fit to the testing data (Fielding & Bell 1997). The AUC statistic is a measure of the model's predictive accuracy, producing an index value from 0.5 to 1, with values close to 0.5 indicating poor discrimination and a value of 1 indicating perfect predictions (Elith et al. 2006). We assessed variables using response curves, variable contributions, and jackknife tests.

Because over-parameterized models tend to underestimate habitat availability when transferred to a new geography or time period, we used selection methods suggested by Warren & Seifert (2011). Maxent provides the option of reducing overfitting with a regularization multiplier that can be altered by the user to apply a penalty for each term included in the model (β regularization parameter) to prevent overcomplexity or overfitting (Merow et al. 2013; Morales et al. 2017). A higher regularization multiplier will reduce the number of covariates in the model, becoming more lenient with an increased sample size (Merow et al. 2013). We did not include model replicates, an option in the interface, to output the required data (lambda file) and set output to logistic. We altered the Regularization Multiplier from 0.5 to 4 for each 0.5 increment (e.g., Radosavljevic & Anderson (2014).

We ranked candidate models using Akaike's Information Criterion corrected for small sample sizes ($AIC_{c;}$ Burnham & Anderson 2002). We considered the model with the lowest AIC_c value to be our top model with those with $\Delta AIC_c<2$ to be competitive models.

For our top model, we generated predicted-to-expected (P/E) ratio curves ~~for our model~~ using only the testing data to evaluate its predictive performance, which was based on the shape of the curves, a continuous Boyce index (Boyce et al. 2002), and Spearman rank statistics. 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).

Results

Locations

We compiled 10,229 Humboldt marten locations collected during 1996-2020 (542 baited station, 263 detection dog team, 831 VHF telemetry, 8,537 GPS telemetry, 15 roadkill, and 41 others). Our GPS data represented locations taken every 2.5-5 minutes on 7 individuals within the Central Coast (Linnell et al. 2018), and we did not display those clustered data. We spatially-thinned locations, 384 locations remained and were spread among regions approximately in proportion to the area in each designated region as follows: Central Coastal Oregon *(n* = 77 locations, 6% of the designated Extant Population Area), Southern Coastal Oregon (*n* = 77 locations, 37% of the EPA), California-Oregon Border (*n* = 33 locations, 3% of the EPA), and Northern Coastal California (*n* = 192 locations, 54% of the EPA) populations (Fig. 1). There were 5 locations that did not occur within the boundaries of the designated populations

(USFWS 2019). Location types included den or rest structure locations (18%), genetically verified scats or telemetry locations (32%), and baited camera or track plate locations (50%).

The thinned locations had similar medians and data distributions to the complete location dataset except for mast and precipitation where the medians were slightly lower for the thinned locations (Fig. 2). Non-detection locations had similar medians and data distributions to random locations, with the most notable difference between medians for salal (Table 1, Fig. 2). Differences between non-detection and random locations were likely due to clustered sampling efforts (Fig. 1b).

Distribution modeling

Our model included 8 variables after excluding correlated variables (Table S2, Table S3). Variables in our model were optimized at the home range spatial scale (1,170 m) except OGSI (50 m), but differences between scales were modest (Figs. S1-S3). The top model had a Regularization Multiplier of 1.5. Predictor variables, in order of percent contribution, included a positive relationship with salal (23.3%), percent pine (22.5%), average annual precipitation (21.6%), canopy cover (18.7%), and mast (5.4%) followed by a negative relationship with average maximum August temperature (4.7%), percent slope (2.7%), and OGSI (1.1%, Table 2). Permutation importance was similar with the top four variables highly contributing - but with a slightly modified order of percent pine (30.3%), average annual precipitation (25.3%), canopy cover (20.2%), and salal (15.5%; Table 2). The OGSI variable contributed least for both metrics.

We interpreted Maxent's univariate response curves and provide the marginal plots as a supplemental figure (Fig. S4). Marten locations were correlated with both low and high amounts of canopy cover and percent slope (quadratic response, Fig. 3). We suspect these could be biologically correlated in that extensive flat areas in the Central Coast also have low tree canopy cover, but high shrub density. Moderate amounts of canopy cover (e.g., 5-50%) appeared to be negatively correlated with marten locations. Predicted marten distribution was positively correlated with salal with some likelihood of a threshold at high values (Fig. 3), percentage of pine (Fig. 3), average annual precipitation (Fig. 3), and mast (Fig. 3). There was a negative correlation between marten locations and August temperature (Fig. 3) and a slightly negative or neutral relationship between marten locations and OGSI (Fig. 3).

The predicted versus expected curve of our final model delineated unsuitable areas as <14%, suitable areas as 15-30%, and predicted highly suitable at >30% predicted probability (Fig. 4) with an AUC value on the test data at 92.1%. The model depicted southern Oregon and northern California as having the largest extent for predicted marten distribution, including areas south of the current known population (Fig. 5).

Discussion

We developed a range-wide species distribution model for the Humboldt marten based on extensive survey effort and incorporation of contemporary vegetation and climatic conditions. Our model is complementary, but not similar, to other Humboldt marten distribution models (e.g., Slauson et al. 2019b), which could lead to confusion when attempting to understand Humboldt habitat associations. Instead of interpreting differences between models as a conflict, we posit this as evidence of the conservation challenge described by Caughley (1994) and representative of the difficulty in establishing patterns of causality from observational studies. Nonetheless, our model predicted areas where Humboldt martens are known to occur and identified areas of potential occurrence outside of known population extents, which can be placed within an ecological theory framework for managers. As with all models, there are limitations associated with our predictions, and a clear assessment of these constraints is critical for model results to be accurately used to inform management decisions (Sofaer et al. 2019).

The role of biotic interactions in shaping the distribution of species has been reported (e.g., Forchhammer et al. 2005; Guisan & Thuiller 2005), yet evidence of the importance of biotic variables alongside abiotic variables for predicting distributions at larger spatial scales has been largely lacking (e.g., Wisz et al. 2013). High amounts of shrub cover appears to be the most prevalent component of Humboldt marten locations in both California (Slauson & Zielinski 2009, Slauson et al. 2007) and Oregon (Moriarty et al. 2019). Both salal and mast (including mast-producing shrubs) had a strong contribution to our model. Although associations with shrub cover or mast are generally uncharacteristic of martens, European pine martens may occur in areas of dense shrubs (Lombardini et al. 2015) and American marten population numbers in New York appear correlated with mast in hardwood forests (Jensen et al. 2012). Our finding that Humboldt marten distribution was strongly correlated with canopy cover is consistent with previous marten research (Bissonette et al. 1997, Hargis et al. 1999), although our response was quadratic, suggesting marten locations associated with both low and high levels of canopy cover. Marten populations are typically associated only with relatively dense and increasing canopy cover (Shirk et al. 2014) and we posit that a quadratic response to canopy cover by Humboldt martens may be a function of shrub cover. In areas with relatively low canopy cover but dense shrubs, shrub cover may functionally provide increased protection from predators (Hawley & Newby 1957). Although additional information is needed to describe fine-scale vegetation associations, forest conditions with a dense understory layer of shrub and mast-producing species represent achievable targets that can guide management or restoration.

Biotic variables influencing predicted Humboldt marten distribution in our model were consistent with previous literature with some exceptions, most notably forest age and OGSI. Within our model, the predicted relationship between Humboldt marten distribution and higher OGSI values was not only weak but often negative (Supplemental Item S1). The OGSI variable may, in fact, represent an interpretive mismatch with shrub cover – some areas where Humboldt martens occur (e.g., mature Douglas fir forest; Slauson et al. 2007) are characterized by both old~~er~~ forest conditions (i.e., high OGSI values) and substantial shrub cover, while other areas (e.g., serpentine or coastal pine forests; Eriksson et al. 2019, Moriarty et al. 2019) are characterized by substantial shrub cover, but not older forest conditions (i.e., low OGSI values). As an example, much of the putative distribution of Humboldt martens in coastal Oregon and California is dominated by mature western hemlock forests with high OGSI values, yet Humboldt martens are not strongly associated with such areas (Moriarty et al. 2019), possibly because hemlocks are a shade-tolerant species that prohibit understory growth

(Kerns & Ohmann 2004). When examining our marten locations in a model only with the components of OGSI, downed wood was the most influential variable (Supplemental Item S1). We suspect the differences between models resulted from non-stationarity in vegetation associations that were only revealed by increased survey effort across a broader geographic scope.

Range limit theorems have long postulated the importance of elevation, altitude, and weather in determining the upper limits of species distributions (e.g., Darwin 1859). Precipitation was one of the top 3 predictive variables in all model simulations and abiotic factors such as increased precipitation, proximity to the coast, and cool temperatures likely influence vegetation type and composition. If these variables are causally linked to marten occurrence, a plausible mechanism is that cooler wetter conditions result in dense vegetation growth, which likely aids martens in avoiding predators. Coupled with berries and mast that some shrubs provide and a suspected increased availability of prey items that eat berries (e.g., birds, rodents), such areas may provide exceptional, if uncharacteristic, marten habitat (Eriksson et al. 2019). As a potential mechanism, the abundance of huckleberries have been attributed to increased reproduction and population growth for grizzly bears (*Ursus arctos*) over a 32-year investigation (McLellan 2015). Species' distributions may also be strongly influenced by less-apparent factors such as interspecific interactions with predators or competitors (Siren 2020). As an example, spotted owls (*Strix occidentalis*) closely align with old-growth forest conditions which have been characterized with relatively high accuracy (Davis et al. 2016), yet spotted owl population viability is dramatically decreased with presence of barred owls (*S. varia*) due to interspecific competition and predation (Diller et al. 2016; Dugger et al. 2016; Wiens et al. 2014). Although few examples exist for carnivores, a recent evaluation suggests that while lynx (*Lynx lynx*) distributions are closely-tied to deep snow, the influence of reducing bobcat (*L. rufus*) competition was stronger than the influence of snow itself (Siren 2020). A directed research effort would be necessary to understand the relative importance of vegetation structures, vegetation types, prey, predation, and competition for Humboldt marten persistence.

Our results provide predictions for habitat components but describing optimal habitat would be best informed by measures of survival and fecundity. Future endeavors could develop site-specific models, ideally using telemetry data that are biologically linked with fitness (e.g., long-lived adult female rest and den structures) to address predicted habitat. We lack enough information regarding where Humboldt martens resided historically to compare with our contemporary distribution (Loehle 2020), and we are generally ignorant of population densities, causal associations of population declines, and population limitations. Such an understanding is essential to describe expectations of future range (Brown et al. 1996). Finally, the lack of consistency among Humboldt marten studies is suggestive of imperfect knowledge of what components constitute Humboldt marten habitat. To avoid differing views for rare species conservation (e.g., Gutiérrez 2020; Jones et al. 2020), amassing information collaboratively with a goal of prospective meta-analyses and study-level replication will be essential (Facka & Moriarty 2017; Nichols et al. 2019).

Conclusions

Based on our modeling and an evaluation of available evidence, we conclude that the most consistent range-wide characteristic with Humboldt marten distributions are forest associations with extensive dense shrub cover or complex understory vegetation, which may reflect an association with increased food availability or predation escape cover. An understanding of the strength of these interactions and factors that limit populations is needed to make informed conservation decisions. An adaptive management framework with integrated research components may allow for near-term conservation decision making.

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Literature cited

Balestrieri A, Bogliani G, Boano G, Ruiz-González A, Saino N, Costa S, and Milanesi P. 2016. Modelling the distribution of forest-dependent species in human-dominated landscapes: patterns for the pine marten in intensively cultivated lowlands. *PLoS ONE* 11:e0158203.

Barry BR. 2018. Distribution, habitat associations, and conservation status of Pacific fisher (*Pekania pennanti*) in Oregon Thesis. Oregon State University.

Bell DM, Acker SA, Gregory MJ, Davis RJ, and Garcia BA. 2021. Quantifying regional trends in large live tree and snag availability in support of forest management. *Forest Ecology and Management* 479:118554. https://doi.org/10.1016/j.foreco.2020.118554

Bell DM, Gregory MJ, and Davis R. 2020. Gradient nearest neighbor map data quality summary: GNN-2020. In: Service UF, editor: USDA Forest Service and Oregon State University.

Boyce MS, Vernier PR, Nielsen SE, and Schmiegelow FKA. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281-300. http://dx.doi.org/10.1016/S0304-3800(02)00200-4

Brainerd SM, and Rolstad J. 2002. Habitat selection by Eurasian pine martens *Martes martes* in managed forests of southern boreal Scandinavia. *Wildlife Biology* 8:289-297.

Brown JH, Stevens GC, and Kaufman DM. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27:597-623.

Caughley G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.

CDFW. 2019. Title 14: OAL Matter Number: 2019-0201-02 Endangered Status for Humboldt marten, tri-colored blackbird, fisher southern Sierra ESU. California Department of Fish and Wildlife; 18 Mar 2019 Amendment.

Colwell RK, and Rangel TF. 2009. Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences* 106:19651-19658.

Crookston N, and Stage A. 1999. Percent canopy cover and stand structure statistics from the forest vegetation simulator. USDA Forest Service, Rocky Mountain Research Station. Gen. Tech. Rep. RMRS-GTR-24.

Daly C, Halbleib M, Smith JI, Gibson WP, Doggett MK, Taylor GH, Curtis J, and Pasteris PP. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology: A Journal of the Royal Meteorological Society* 28:2031-2064.

Daly C, Helmer EH, and Quiñones M. 2003. Mapping the climate of Puerto Rico, Vieques and Culebra. *International Journal of Climatology: A Journal of the Royal Meteorological Society* 23:1359-1381.

Darwin C. 1859. *The origin of species. 6th edition*: John Murray, London.

Davis R, Ohmann J, Kennedy R, Cohen W, Gregory M, Yang Z, Roberts H, Gray A, and Spies T. 2015. Northwest Forest Plan – the first 20 years (1994-2013): status and trends of late-successional and old-growth forests USDA Forest Service: Portland, OR, USA.

Davis RJ, Hollen B, Hobson J, Gower JE, and Keenum D. 2016. Northwest Forest Plan—the first 20 years (1994–2013): status and trends of northern spotted owl habitats. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. General Technical Report PNW-GTR-929. p 54.

Delheimer MS, Moriarty KM, Slauson KM, Roddy AM, Early DA, and Hamm KA. In press. Comparative reproductive ecology of two subspecies of Pacific marten (*Martes caurina*) in California. *Northwest Science*.

Diller LV, Hamm KA, Early DA, Lamphear DW, Dugger KM, Yackulic CB, Schwarz CJ, Carlson PC, and McDonald TL. 2016. Demographic response of northern spotted owls to barred owl removal. *The Journal of Wildlife Management* 80:691-707.

Dugger KM, Forsman ED, Franklin AB, Davis RJ, White GC, Schwarz CJ, Burnham KP, Nichols JD, Hines JE, and Yackulic CB. 2016. The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. *The Condor* 118:57-116.

Dye AW, Rastogi B, Clemesha RE, Kim JB, Samelson RM, Still CJ, and Williams AP. 2020. Spatial patterns and trends of summertime low cloudiness for the Pacific Northwest, 1996–2017. *Geophysical Research Letters* 47:e2020GL088121.

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Sobero´n J, Williams S, Wisz MS, and Zimmermann NE. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129-151.

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, and Yates CJ. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17:43-57.

Eriksson CE, Moriarty KM, Linnell MA, and Levi T. 2019. Biotic factors influencing the unexpected distribution of a Humboldt marten (Martes caurina humboldtensis) population in a young coastal forest. *PLoS ONE* 14:e0214653. 10.1371/journal.pone.0214653

Facka AN, and Moriarty KM. 2017. An approach to foster a new generation of broad-scale collaboration within the *Martes* Working Group. In: Zalewski A, Aubry KB, O'Mahony D, Birks JDS, and Proulx G, eds. *The Martes complex in a new millennium*: Mammal Research Institute; Polish Academy of Sciences.

Fielding AH, and Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38-49.

Forchhammer MC, Post E, Berg TB, Høye TT, and Schmidt NM. 2005. Local-scale and short-term herbivore–plant spatial dynamics reflect influences of large-scale climate. *Ecology* 86:2644-2651.

Franklin JF, and Dyrness CT. 1973. Natural vegetation of Oregon and Washington. *USDA Forest Service General Technical Report, Pacific Northwest Forest and Range Experiment Station*.

Gamblin HE. 2019. Distribution and habitat use of a recently discovered population of Humboldt martens in California Master of Science. Humboldt State University.

Grinnell J, and Dixon J. 1926. Two new races of the pine marten from the Pacific Coast of North America. *University of California Publications in Zoology*:411–417.

Guisan A, and Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993-1009.

Gutiérrez R. 2020. Invited commentary: when a conservation conflict comes full circle — the spotted owl conflict is a wicked problem. *Journal of Raptor Research* 54:337-348.

Halvorsen R. 2013. A strict maximum likelihood explanation of MaxEnt, and some implications for distribution modelling. *Sommerfeltia* 36:1-132.

Harrison S, Safford HD, Grace JB, Viers JH, and Davies KF. 2006. Regional and local species richness in an insular environment: serpentine plants in California. *Ecological Monographs* 76:41-56.

Hawley VD, and Newby FE. 1957. Marten home ranges and population fluctuations. *Journal of Mammalogy* 38:174-184.

Hijmans RJ. 2020. raster: Geographic data analysis and modeling. In: 3.3-13 Rpv, editor. https://CRAN.R-project.org/package=raster.

Hirzel AH, Le Lay G, Helfer V, Randin C, and Guisan A. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199:142-152.

Jenness J. 2006. Topographic Position Index (tpi_jen. avx) extension for ArcView 3. x, v. 1.3 a. Jenness Enterprises (accessed May 2019.

Jensen PG, Demers CL, Mcnulty SA, Jakubas WJ, and Humphries MM. 2012. Marten and fisher responses to fluctuations in prey populations and mast crops in the northern hardwood forest. *Journal of Wildlife Management* 76:489-502.

Johnson DH. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71. doi:10.2307/1937156

Jones GM, Gutiérrez R, Block WM, Carlson PC, Comfort EJ, Cushman SA, Davis RJ, Eyes SA, Franklin AB, and Ganey JL. 2020. Spotted owls and forest fire: Comment. *Ecosphere* 11.

Kerns BK, and Ohmann JL. 2004. Evaluation and prediction of shrub cover in coastal Oregon forests (USA). *Ecological Indicators* 4:83-98.

Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM, Cheyne SM, Hearn AJ, Ross J, Macdonald DW, Mathai J, Eaton J, Marshall AJ, Semiadi G, Rustam R, Bernard H, Alfred R, Samejima H, Duckworth JW, Breitenmoser-Wuersten C, Belant JL, Hofer H, and Wilting A. 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions* 19:1366-1379. 10.1111/ddi.12096

Kruckeberg AR. 1986. An essay: the stimulus of unusual geologies for plant speciation. *Systematic Botany*:455-463.

Linnell MA, Moriarty K, Green DS, and Levi T. 2018. Density and population viability of coastal marten: a rare and geographically isolated small carnivore. *PeerJ* 6:e4530 - '4521 pg. 10.7717/peerj.4530

Loehle C. 2020. Quantifying species' geographic range changes: conceptual and statistical issues. *Ecosphere* 11.

Lombardini M, Cinerari CE, Murru M, Rosin AV, Mazzoleni L, and Meriggi A. 2015. Habitat requirements of Eurasian pine marten *Martes martes* in a Mediterranean environment. *Mammal Research* 60:97-105.

Manlick PJ, Petersen SM, Moriarty KM, and Pauli JN. 2019. Stable isotopes reveal limited Eltonian niche conservatism across carnivore populations. *Functional Ecology* https://doi.org/10.1111/1365-2435.13266.

Manzo E, Bartolommei P, Giuliani A, Gentile G, Dessì-Fulgheri F, and Cozzolino R. 2018. Habitat selection of European pine marten in central Italy: from a tree dependent to a generalist species. *Mammal Research* 63:357-367.

McGarigal K, Wan HY, Zeller KA, Timm BC, and Cushman SA. 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology*:1-15. 10.1007/s10980-016-0374-x

McLellan BN. 2015. Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *The Journal of Wildlife Management* 79:749-765. https://doi.org/10.1002/jwmg.896

Merow C, Smith MJ, and Silander JA. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36:1058-1069. 10.1111/j.1600-0587.2013.07872.x

Minta SC, Kareiva PM, and Curlee AP. 1999. Carnivore research and conservation: learning from history and theory. In: Clark TW, Curlee AP, Minta SC, and Kareiva PM, eds. *Carnivores in ecosystems: the Yellowstone experience*. London, United Kingdom: Yale University Press, 323-404.

Moll RJ, Kilshaw K, Montgomery RA, Abade L, Campbell RD, Harrington LA, Millspaugh JJ, Birks JDS, and Macdonald DW. 2016. Clarifying habitat niche width using broad-scale, hierarchical occupancy models: a case study with a recovering mesocarnivore. *Journal of Zoology* 300:177-185. https://doi.org/10.1111/jzo.12369

Morales NS, Fernández IC, and Baca-González V. 2017. MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. *PeerJ* 5:e3093. 10.7717/peerj.3093

Moriarty KM, Linnell MA, Chasco B, Epps CW, and Zielinski WJ. 2017. Using high-resolution short-term location data to describe territoriality in Pacific martens. *Journal of Mammalogy* 98:679-689.

Moriarty KM, Linnell MA, Thornton JE, and Watts III GW. 2018. Seeking efficiency with carnivore survey methods: a case study with elusive martens. *Wildlife Society Bulletin* 42:403-413.

Moriarty KM, Verschuyl J, Kroll AJ, Davis R, Chapman J, and Hollen B. 2019. Describing vegetation characteristics used by two rare forest-dwelling species: Will established reserves provide for coastal marten in Oregon? *PLoS ONE* 14:e0210865. 10.1371/journal.pone.0210865

Nichols JD, Kendall WL, and Boomer GS. 2019. Accumulating evidence in ecology: Once is not enough. *Ecology and Evolution* 9:13991-14004.

Ohmann JL, and Gregory MJ. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. *Canadian Journal of Forest Research* 32:725-741.

Phillips SJ, Anderson RP, and Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231-259.

Phillips SJ, and Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161-175.

Prevéy JS, Parker LE, and Harrington CA. 2020a. Projected impacts of climate change on the range and phenology of three culturally-important shrub species. *PLoS ONE* 15:e0232537. https://doi.org/10.1371/journal.pone.0232537

Prevéy JS, Parker LE, Harrington CA, Lamb CT, and Proctor MF. 2020b. Climate change shifts in habitat suitability and phenology of huckleberry (*Vaccinium membranaceum*). *Agricultural and forest meteorology* 280:107803.

PSW. 2019. Humbodlt marten data summary and report for the northern coastal California population: distribution and population parameter estimates. USDI Fish and Wildlife Service, USDA Forest Service Pacific Southwest Research Station. p 33.

R Core Team. 2020. R: a language and environment for statistical computing. https://www.R-project.org/. Vienna, Austria: R Foundation for Statistical Computing.

Radosavljevic A, and Anderson RP. 2014. Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography* 41:629-643. https://doi.org/10.1111/jbi.12227

Raphael MG, and Molina R. 2007. *Conservation of rare or little-known species: biological, social, and economic considerations*. Washington D.C., USA: Island Press.

Rastogi B, Williams AP, Fischer DT, Iacobellis SF, McEachern K, Carvalho L, Jones C, Baguskas SA, and Still CJ. 2016. Spatial and temporal patterns of cloud cover and fog inundation in coastal California: Ecological implications. *Earth Interactions* 20:1-19.

Safford H, Viers J, and Harrison S. 2005. Serpentine endemism in the California flora: a database of serpentine affinity. *Madrono* 52:222-257.

Schrott GR, and Shinn J. 2020. A landscape connectivity analysis for the coastal marten (*Martes caurina humboldtensis*). Arcata, CA. https://www.fws.gov/arcata/shc/marten/#report: USDI Fish and Wildlife Service. p 123.

Schwartz MK, Walters AD, Pilgrim KL, Moriarty KM, Slauson KM, Zielinski WJ, Aubry KB, Sacks BN, Zarn KE, and Quinn CB. 2020. Pliocene-early Pleistocene geological events structure Pacific martens (*Martes caurina*). *The Journal of heredity*.

Searcy CA, and Shaffer HB. 2016. Do ecological niche models accurately identify climatic determinants of species ranges? *The American Naturalist* 187:423-435.

Shaw JH. 1995. How many bison originally populated western rangelands? *Rangelands* 17:148-150.

Shirk AJ, Raphael MG, and Cushman SA. 2014. Spatiotemporal variation in resource selection: insights from the American marten (*Martes americana*). *Ecological Applications* 24:1434-1444.

Siren AP. 2020. Interacting effects of climate and biotic factors on mesocarnivore distribution and snowshoe hare demography along the boreal-temperate ecotoneDissertation. University of Massachusetts, Amherst.

Slauson KM, Baldwin JA, and Zielinski WJ. 2012. Occupancy estimation and modeling in *Martes* research and monitoring. In: Aubry KB, Zielinski W, Raphael MG, Proulx G, and Buskirk SW, eds. *Biology and conservation of martens, sables, and fishers: a new synthesis*. Ithaca, New York, USA: Comstock Publishing Associates, 343-370.

Slauson KM, and Zielinski WJ. 2017. Seasonal specialization in diet of the Humboldt marten (*Martes caurina humboldtensis*) in California and the importance of prey size. *Journal of Mammalogy* 98:1697-1708. 10.1093/jmammal/gyx118

Slauson KM, Zielinski WJ, and Hayes JP. 2007. Habitat selection by American martens in coastal California. *Journal of Wildlife Management* 71:458-468.

Slauson KM, Zielinski WJ, LaPlante DW, and Kirk TA. 2019. A landscape suitability model for the Humboldt marten (*Martes caurina humboldtensis*) in coastal California and coastal Oregon. *Northwest Science*.

Sofaer HR, Jarnevich CS, Pearse IS, Smyth RL, Auer S, Cook GL, Edwards Jr TC, Guala GF, Howard TG, and Morisette JT. 2019. Development and delivery of species distribution models to inform decision-making. *BioScience* 69:544-557.

Storch I, Lindstrom E, and de Jounge J. 1990. Diet and habitat selection of the pine marten in relation to competition with the red fox. *Acta Theriologica* 35:311-320.

Thompson I, Fryxell J, Harrison D, Aubry K, Zielinski W, Raphael M, Proulx G, and Buskirk S. 2012. Improved insights into use of habitat by American martens.

Biology and conservation of martens, sables, and fishers Edited by KB Aubry, WJ Zielinski, MG Raphael, G Proulx, and SW Buskirk Cornell University Press, Ithaca, USA:209-230.

Tweedy PJ, Moriarty KM, Bailey JD, and Epps CW. 2019. Using fine scale resolution vegetation data from LiDAR and ground-based sampling to predict Pacific marten resting habitat at multiple spatial scales. *Forest Ecology and Management* 452:117556.

U.S. Environmental Protection Agency. 2013. Level III ecoregions of the continental United States. EPA- National Health and Environemental Effects Research Laboratory: Corvallis, Oregon, USA.

USFWS. 2019. Species Status Assessment for the coastal marten (*Martes caurina*), Version 2.1. Arcata, CA, USA: US Fish and Wildlife Service, Region 8. p 141.

USFWS. 2020. Endangered and threatened wildlife and plants; threatened species status for coastal distinct population segment of the Pacific marten with a Section 4(d) rule *Federal Register* 85:63806-63831.

Velleman PF, and Welsch RE. 1981. Efficient computing of regression diagnostics. *The American Statistician* 35:234-242. 10.2307/2683296

Wang T, Hamann A, Spittlehouse D, and Carroll C. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE* 11:e0156720.

Warren DL, and Seifert SN. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications* 21:335-342.

Warren DL, Wright AN, Seifert SN, and Shaffer HB. 2014. Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 C alifornia vertebrate species of concern. *Diversity and Distributions* 20:334-343.

Wasserman TN, Cushman SA, Schwartz MK, and Wallin DO. 2010. Spacial scaling and multi-model Inference in landscape genetics: *Martes americana* in northern Idaho. *Landscape Ecology* 25:1610-1612.

Whittaker RH. 1960. Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs* 30:279-338.

Wiens JD, Anthony RG, and Forsman ED. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. *Wildlife Monographs* 185:1-50.

Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes JA, and Guisan A. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88:15-30.

Zeller KA, Vickers TW, Ernest HB, and Boyce WM. 2017. Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study. *PLoS ONE* 12:e0179570. 10.1371/journal.pone.0179570

Zielinski WJ, and Golightly R. 1996. The status of marten in redwoods: is the Humboldt marten extinct. Conference on Coast Redwood Forest Ecology and Management

(J LeBlanc, ed) Humboldt State University, Arcata, California. Arcata, California, USA. p 115-119.

Zielinski WJ, Slauson KM, Carroll CR, Kent CJ, and Kudrna DG. 2001. Status of American martens in coastal forests of the Pacific states. *Journal of Mammalogy* 82:478-490.

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).

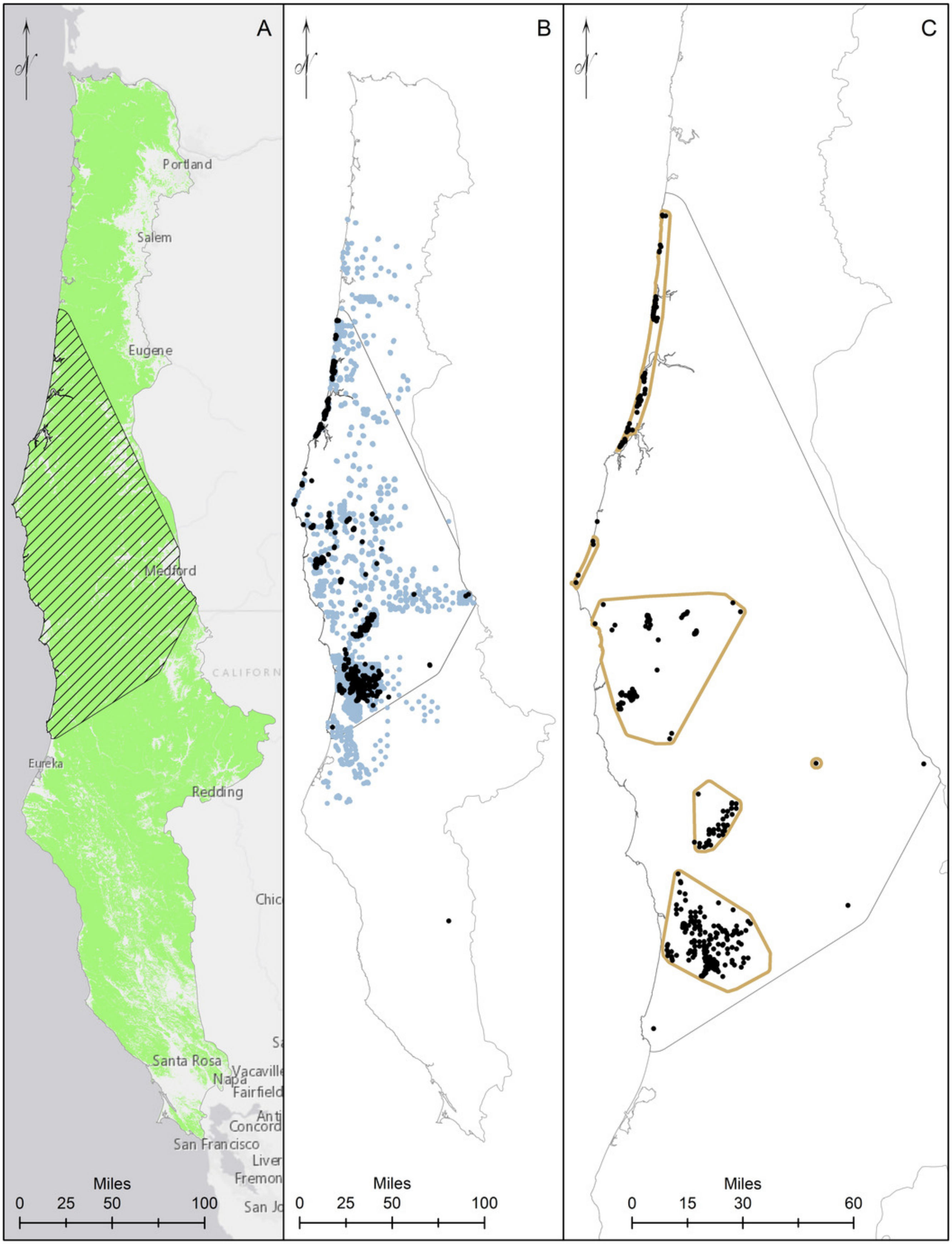

A
B
C
Portland
Salem
Eugene
Medford
CALIFORN
Eureka
Redding
Chic
Santa Rosa
Napa
Vacaville
Fairfield
Anti
Concord
San Francisco
Liver
Fremon
San Jo
Miles
0 25 50 100
Miles
0 25 50 100
Miles
0 15 30 60

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).

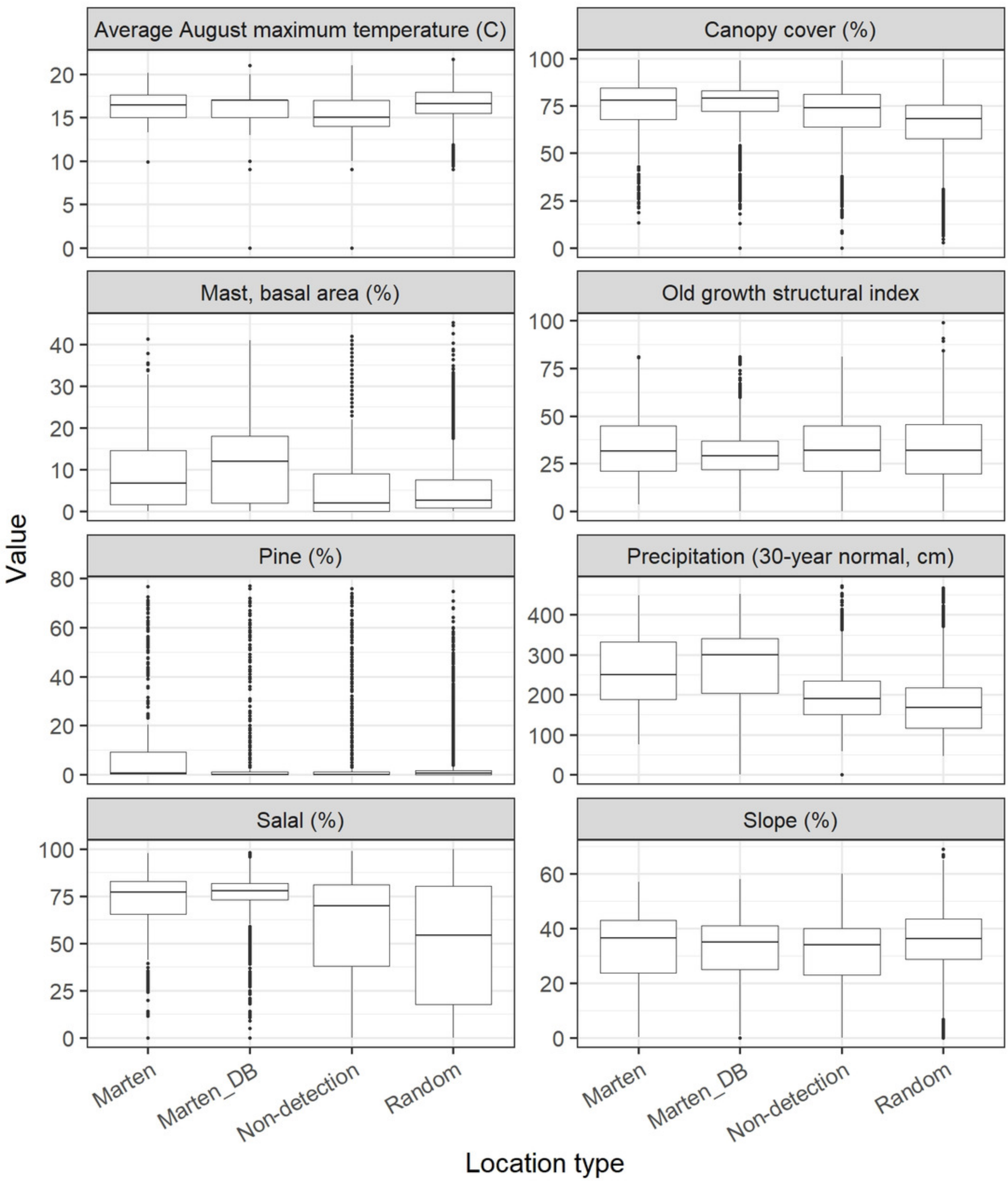
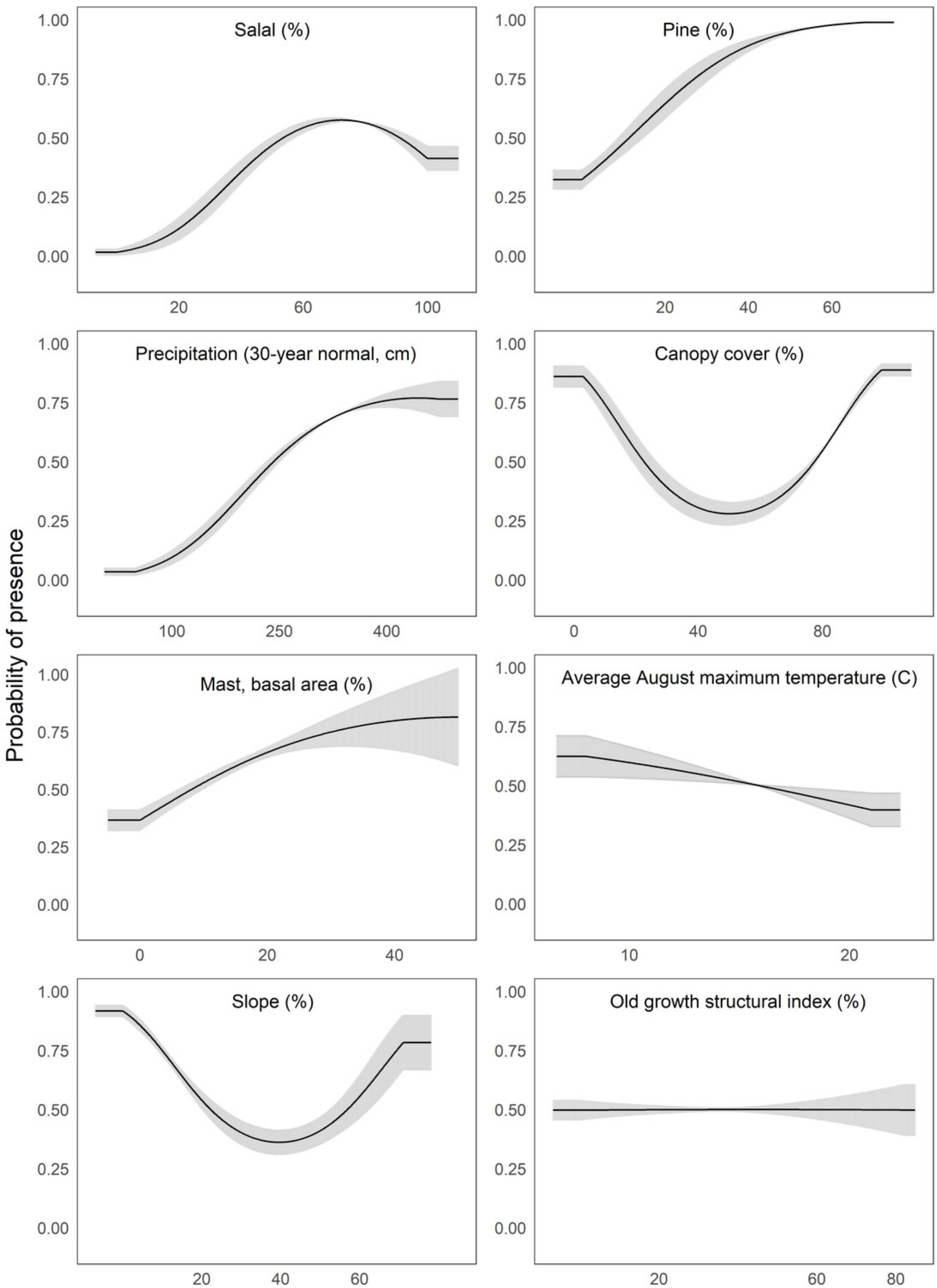

Average August maximum temperature (C)
Canopy cover (%)
Mast, basal area (%)
Old growth structural index
Pine (%)
Precipitation (30-year normal, cm)
Salal (%)
Slope (%)
Value
Marten
Marten_DB
Non-detection
Random
Location type

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
Salal (%)
Pine (%)
Precipitation (30-year normal, cm)
Canopy cover (%)
Mast, basal area (%)
Average August maximum temperature (C)
Slope (%)
Old growth structural index (%)
1.00
0.75
0.50
0.25
0.00

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).

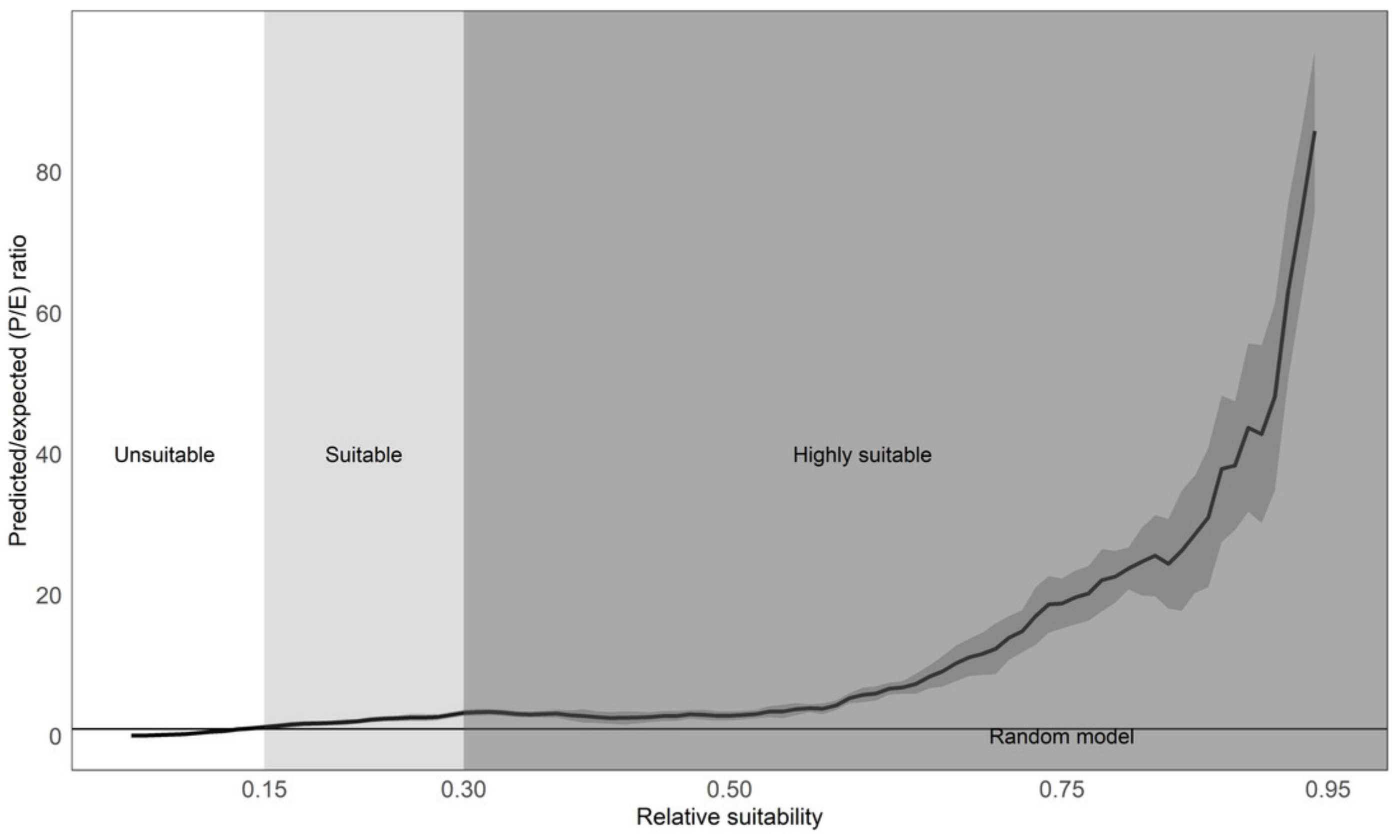


Figure 5

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).

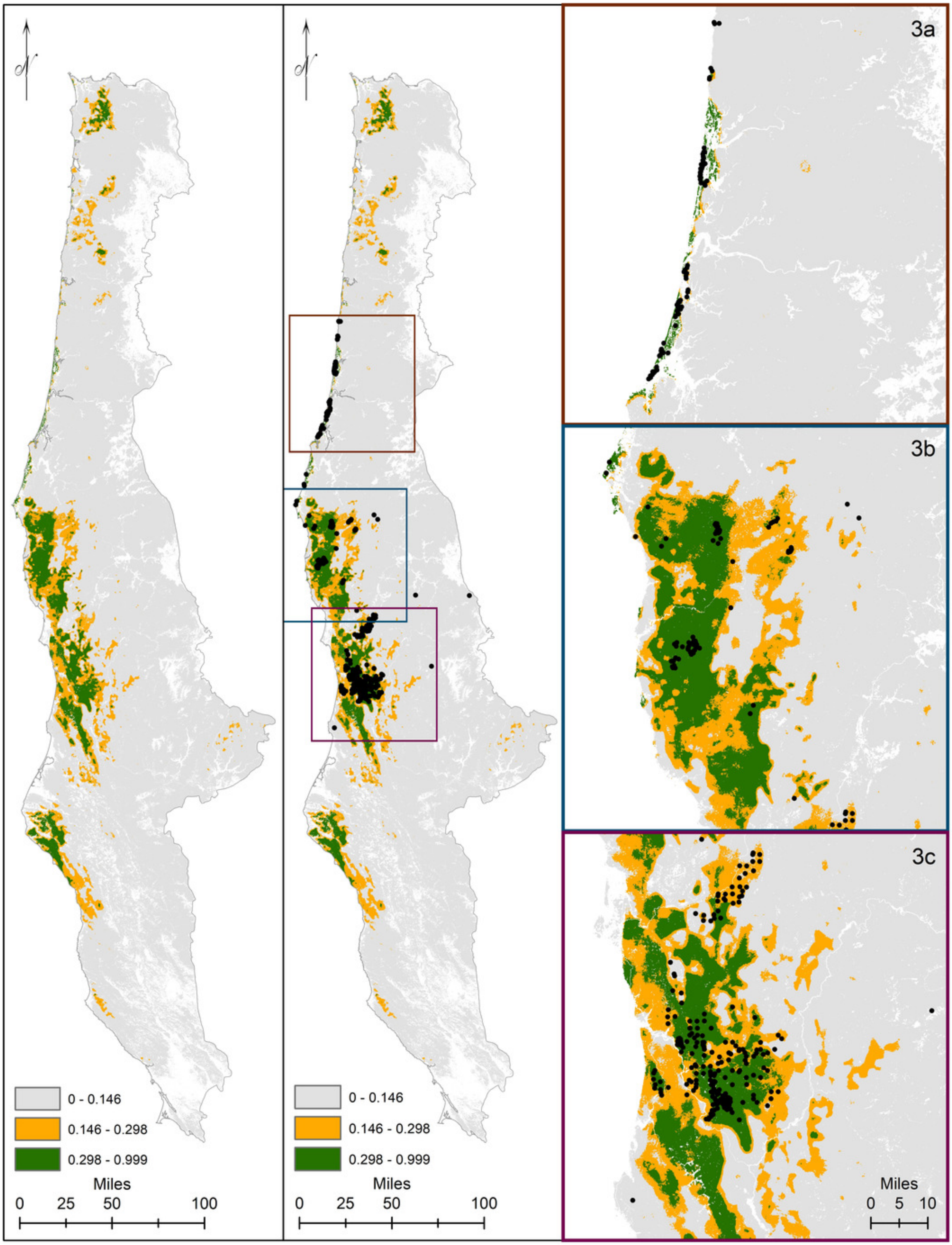

3a
3b
3c
0 - 0.146
0.146 - 0.298
0.298 - 0.999
Miles
0 25 50 100
0 5 10

Table 1 (on next page)

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).

Table 1:
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).

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)

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)

Table 2 (on next page)

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.

Table 2:

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.

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