THE INFLUENCE OF MICROCLIMATE AND LOCAL ADAPTATION FOR A CLIMATE-SENSITIVE SPECIES (*APLODONTIA RUFA*)

By

Jennie Jones Scherbinski

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Wildlife

Committee Membership

Dr. William Bean, Committee Chair

Dr. Joseph Szewczak, Committee Member

Dr. Micaela Szykman Gunther, Committee Member

Dr. William Zielinski, Committee Member

Dr. Alison O’Dowd, Program Graduate Coordinator

July 2018

ABSTRACT

THE INFLUENCE OF MICROCLIMATE AND LOCAL ADAPTATION FOR A CLIMATE-SENSITIVE SPECIES (*APLODONTIA RUFA*)

Jennie Jones Scherbinski

Climate change models and analyses predict a disproportionate impact on climatically sensitive species such as the mountain beaver (*Aplodontia rufa*). Mountain beavers have physiological constraints that limit their distribution to cool, moist climates. While mountain beavers have persisted through past periods of climate change, increasing temperature since the last glacial maximum is believed to have had a strong influence in reducing their range. This is particularly true for the Point Arena subspecies (*A. r. nigra*, “PAMB”), found towards the southwestern edge of their range on the coast of California. Here, I examined the climatic niche of mountain beavers at four scales: range-wide; by clade; PAMB rangewide; and PAMB microclimates to test whether PAMB exhibit different climatic requirements than other subspecies.

I examined the climatic space occupied by mountain beavers at four scales using the machine learning method MaxEnt and occurrence points from museum records, previous surveys conducted by USFS, and personal survey data. First, I modeled the distribution of mountain beaver range-wide and the distributions of the five individual genetic clades (Coastal, Californica, Olympica, Pacifica, and Rufa). To examine the microclimate use of PAMB, I developed fine-scale climate surfaces using temperatures recorded from dataloggers and topographic variables calculated from LiDAR data. These layers were incorporated with PAMB occurrence data to model distribution. Finally, I examined pairwise differences in microhabitat use between burrows and available space.

At all scales high temperatures were a limiting factor in distribution. Despite a low level of niche overlap at broad scales, mountain beavers appear to display some level of niche conservatism. PAMB does seem to exist in a warmer climate than other mountain beavers; however, they apparently persist by selecting the coolest places within that range. This suggests that niche overlap between the Coastal clade and all other clades may be higher than what is detected at the coarser scale. Further research is needed to understand the mechanisms limiting this distribution, but it may be that mountain beavers in marginal habitat are more adaptable to changes in climate.

ACKNOWLEDGEMENTS

There are many people who deserve my eternal gratitude for their assistance and guidance with this research. First, I would like to thank Dr. Tim Bean for his patience, guidance, and support as I battled through poison oak and R code. Thank you also to my committee members, Dr. Joe Szewczak, Dr. Micaela Szykman Gunther, and Dr. William Zielinski for their valuable insight into developing this project.

This project was made possible by funds from USFWS Arcata Office and BLM California Coastal Monument. Thanks to Greg Schmidt, John Hunter, Kay-Leigh Barnitz, David Ledig, and Bill Standley for helping to coordinate the funding and permits required for this research. A big thank you to Mendocino Redwood Company, The Conservation Fund, Soper Wheeler Company, and many individual landowners for providing access to their lands. Additionally, I must thank Robert Douglas, Hayley Ross, and Kim Fitts for sharing their knowledge of PAMB and survey techniques.

To the HSU Wildlife community, thank you for providing a supportive environment to foster my development as a conservation biologist. Thank you to Tamara Yanin for fighting through the terrors of PAMB habitat and somehow always keeping a smile on your face. The field work would have been even harder without you. I will forever be grateful to my fellow lab mates, Pairsa Belamaric, Alyssa Semerdjian, Ivy Widick, Adam Mohr, and Sarah Schooler. Your feedback was invaluable, the laughter incalculable, and the friendship incredible.

Lastly, I have to thank my family and friends for supporting me on this journey. Thanks to my Pinnacles family for introducing me to GIS and making my transition to a new species as painless as possible. To the Joneses and Scherbinskis, thank you for all the greeting cards and kind words of support. Finally, thank you to Scott for being my field technician, my editor, my advisor, my everything.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Understanding the limits to species distributions is a fundamental question in ecology, made all the more urgent by anthropogenic climate change (Elith et al. 2006). Most broadly, as global climate warms, species are expected to track the climatic conditions within which they are currently found, either upslope or towards the poles (Walther et al. 2002). This pattern has already been documented at broad scales in a wide array of species and ecosystems, and particularly evident in alpine and arctic species (Hughes 2000, Parmesan and Yohe 2003). However, recent, more fine-scale studies have complicated the relationship between a species' occurrence and its climatic limits (e.g., Moritz et al. 2008, Miller et al. 2018). Such work highlights the need to identify the specific mechanisms limiting species' distributions, especially at the trailing edge of their range, and particularly for species with characteristics that increase their sensitivity to climate change, such as those with physiological limitations or limited dispersal abilities (Ray et al. 2016, Case et al. 2015).

As the only living species from the once diverse family Aplodontiidae, the mountain beaver (*Aplodontia rufa*) has endured through historic periods of climate change. Due to high water requirements and a low heat tolerance, these small, fossorial rodents are currently limited to areas with cool, humid climates in California and the Pacific Northwest (Figure 1, Nungesser and Pfeiffer 1965, Kinney 1971, Johnson 1971). Despite their ability to persist morphologically unchanged since the Miocene, five of the seven subspecies are considered species of concern or endangered in all or part of their range due to current climate change and habitat loss (USFWS 1998, Environment Canada 2015, CADFW 2017). These imperiled populations (*A. r. californica, A. r. humboldtiana, A. r. olympica*, *A. r. nigra*, *and A. r. phaea*) represent the northern, southern, and eastern most edges of the mountain beaver range and likely exist at the species' climatic limits (Figure 1).

While the full extent of their historical range is unknown, fossil records suggest the mountain beaver range has contracted significantly since the late Pleistocene, likely tracking cooler climates and potentially leading to speciation (Wake 2006, Blois et al. 2010, Piaggio et al. 2013). Genetic work indicates that the seven subspecies can be further grouped into five distinct clades. The Point Arena mountain beaver (*A. r. nigra*, PAMB), Point Reyes mountain beaver (*A. r. phaea*), and Humboldt mountain beaver (*A. r. humboldtiana*) form a closely-related California coastal clade, while the remaining four subspecies (*A. r. olympica, A. r. rufa, A. r. californica, A. r. pacifica*) remain in separate clades (Piaggio et al. 2013, Figure 1).

Isolated, range-edge populations such as the California coastal clade may exist in climate refugia (Wake 2006, Blois et al. 2010). The subspecies of the California coastal clade may have developed local adaptations that allow them to occupy habitats, such as coastal scrub and coastal dunes, which are notably different from the primary habitat – forest understory – occupied by most mountain beavers (Zielinski and Mazurek 2006). Understanding whether these clades have retained their historical niche (niche conservatism) or adapted to local climates may provide valuable insight into how they have responded to climate change in the past and how they may respond in the future (Wiens et al. 2010, Pyron et al. 2015).

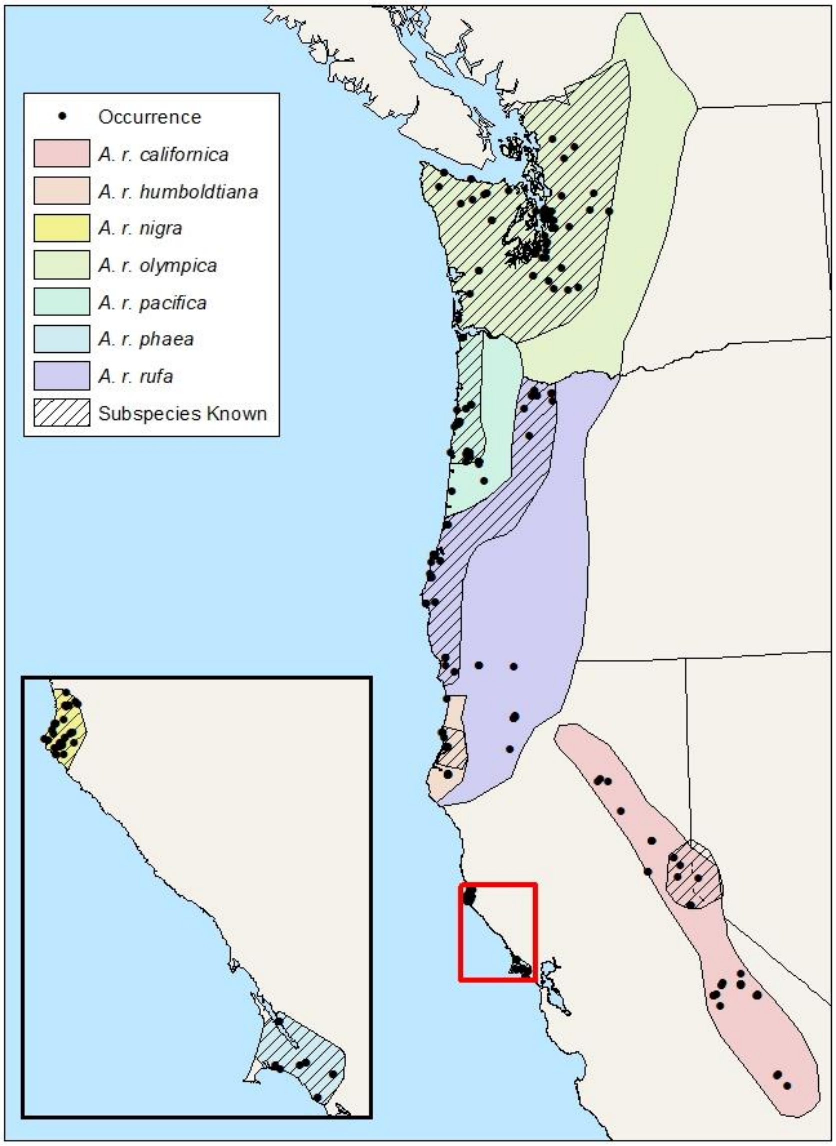


Figure 1. Mountain beaver subspecies distribution map adapted from Piaggio et al. 2013. Areas where genetic sampling occurred are represented as “Subspecies Known”. Subspecies for other areas was defined by a previous subspecies range map (Hall 1981). Points were acquired from Global Biodiversity Information Facility, personal surveys, and a previous study (Zielinski et al. 2015).

Response to previous climate change is particularly important to understand for climatically sensitive species such as the mountain beaver. The mountain beaver has a low capacity for urine concentration and water conservation that requires them to consume approximately 1/3 of their body weight in water daily, which may come from freestanding water or vegetation (Nungesser and Pfeiffer 1965). Ambient temperatures above 29º C cause the mountain beaver to enter hyperthermia, and exposure to temperatures between 32º-35º C is fatal (Johnson 1971). Burrows likely mitigate impacts of ambient temperature. However since most foraging occurs above ground, activity may be limited to cooler periods of the day in warmer climates (Ingles 1959).

One member of the California coastal clade, the federally endangered PAMB, has a small, disjunct distribution of ~235 km^2 along the Mendocino Coast in California making it an ideal candidate for understanding limits to species distributions (Zielinski et al. 2015, Figure 1). This subspecies inhabits inland forests, which provide increased cover and lower ambient temperatures at the ground level. They are also found in coastal scrub, where ambient ground temperatures are generally higher due to increased sun exposure, though fog may alleviate some of the impacts of decreased cover (Figure 2b, Torregrosa et al. 2016). PAMB is further genetically subdivided into three populations: two populations found exclusively inland and one population found on the coast and inland (Zielinski et al. 2013). It is unclear why PAMB are restricted to coastal Mendocino County when seemingly suitable climate and habitat exists both to the north and south of their current distribution. Once isolated, PAMB may have developed local adaptations allowing them to persist in hotter, drier conditions. Alternatively, PAMB on the coast may select microclimates that meet the typical needs of the species, a behavior that coarse-scale models would not reveal.

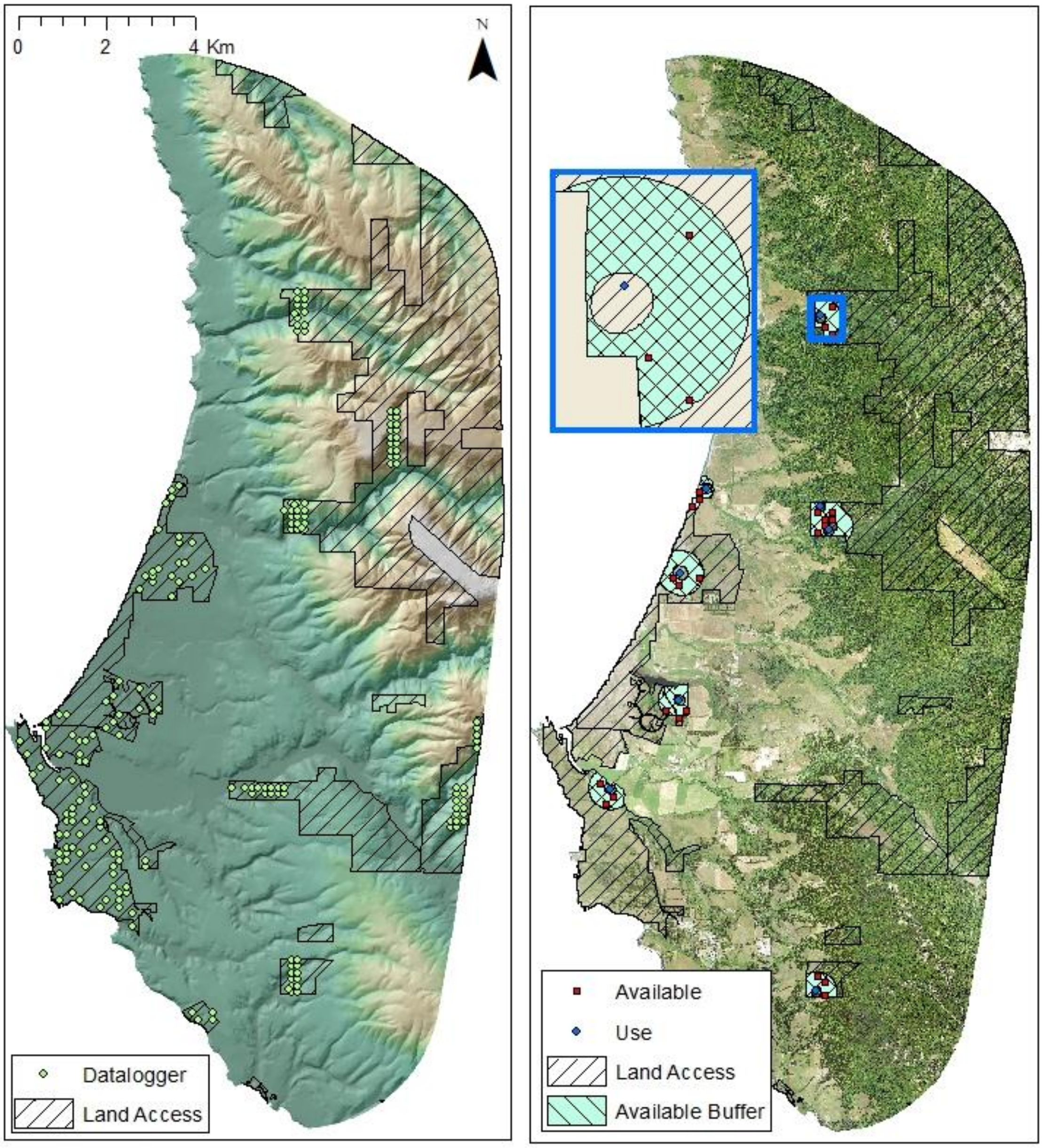


Figure 2. Elevation and orthophotos for the PAMB range overlaid with dataloggers deployed for fine-scale analysis. (A) The full datalogger deployment grid for boosted regression tree analysis. (B) Subset of dataloggers used for paired points analysis.

Species distributions models (SDMs) have increasingly been used to identify current geographic range, especially for rare species, and to compare niches among species (Elith et al. 2006, Warren et al. 2008). SDMs relate presence points to spatially explicit predictor variables using a variety of statistical approaches to predict a species' distribution (Elith et al. 2006). While they are generally effective at broad scales, SDMs are often unable to accurately assess fine scale details of distribution (Pearson and Dawson 2003, Guisan and Thuiller 2005). This is likely a result of the spatial mismatch between readily available predictor variables and the scale at which most species experience their environment and may be especially important to consider for species with limited mobility (Pearson and Dawson 2003, Guisan and Thuiller 2005, Potter et al. 2013).

Recent advances in downscaling climate data has allowed for the creation of fine resolution environmental predictors that better match the spatial scales at which animals are experiencing climate. LiDAR combined with microclimate dataloggers have successfully been used to create fine scale temperature models that better correspond to the scale at which a species experiences the environment (Frey et al. 2016, George et al. 2015). Incorporating climate variables at an appropriate scale will improve predictive ability and provide insight into direct mechanisms by which mountain beavers may respond to climate change. However, due to the amount of data involved in fine scale models, they are generally not feasible for range-wide modeling.

In this study, I attempted to understand range restrictions of the PAMB by modeling mountain beaver distribution at 3 levels: species, clade, and PAMB. If the climatic niche of PAMB were conserved, I expected that fine-scale PAMB models would match the climatic limits of the species as a whole. Conversely, if the genetically isolated PAMB had adapted to the hotter, drier conditions within which it's found, it would exhibit different responses to climatic predictors. Models were further tested to explain the disjunct distribution among the three subspecies forming the California clade. First, I created an SDM for the species as a whole. Next, I created SDMs for each of the five clades of mountain beaver and compared their ecological niches. If mountain beaver subspecies exhibited niche conservatism, I expected to find more overlap of the ecological niches of species that have contiguous distributions and the more closely related clades. Additionally, I developed fine scale climate models of the warm season in the PAMB range. I surveyed for PAMB throughout their range and combined this occurrence data with existing points from a previous study with the newly created climate layers to predict distribution within the range. I predicted that high temperatures would be the limiting factor for PAMB distribution. Finally, I compared climatic variables at burrow sites and paired available sites. I hypothesized that coastal PAMB and inland PAMB have selected habitats with similar microclimates, allowing them to persist in these seemingly distinct habitats. Based on this hypothesis, I predicted that paired non-use sites would have higher temperatures, and lower humidity.

METHODS

Study Area

The range of PAMB is currently limited to 235 km^2 area along the Mendocino County coast in California (Zielinski et al. 2015). The area is comprised of a variety of habitat types including coastal dunes, coastal scrub, riparian, and non-native grasslands along the coast, and forests and riparian areas inland (LANDFIRE 2017). Land use varies with approximately 25% of the range owned by timber companies, while the rest is divided among public land, ranches and dairy farms, and private parcels (ENPLAN 2017). The weather is moderate with annual mean temperatures between 10-12ºC (Fick and Hijmans 2017). Warmer temperatures are typically observed May-November (NOAA 2012). Summers have relatively high levels of fog and low-level clouds, particularly along the coast (Torregrosa et al. 2016).

Coarse-Scale Models

I examined the climatic niches of all subspecies of mountain beaver. First, I created niche space diagrams to visually compare the climates occupied by each subspecies compared with the species as a whole. Occurrence data for *A. rufa* were obtained from the Global Biodiversity Information Facility (GBIF 2017). Each occurrence was categorized by subspecies based on a distribution map adapted from Piaggio et al. 2013 (Figure 1). Any occurrence records with location uncertainty greater than 2 km were discarded from this analysis as they were considered too inaccurate to use with the ~1 km^2 resolution environmental predictor variables. I extracted mean annual temperature and mean annual precipitation from BioClim layers at each subspecies occurrence (Fick and Hijams 2017).

Next, I created distribution models using the machine learning method Maxent for the entire species and for each clade separately (Phillips et al. 2018). Maxent uses random points as “background data” (also referred to as pseudo-absences), allowing for presence only species modeling (Phillips et al. 2006). Environmental predictors, such as climate, are extracted at presence and background points to estimate the distribution of a species (Phillips et al. 2017). Additional occurrence points from the United States Forest Service and personal surveys (see below) were also included for PAMB. Points were thinned using ‘geothin’ in package enmSdm at a distance of 2 km to address sampling bias (Aiello-Lammens et al. 2015, Smith 2018).

Due to genetic similarity, the California Coastal Clade was grouped together for this analysis (Piaggio et al. 2013). The study area for each subspecies was defined as a 105 km buffer around occurrence points for that subspecies. While this buffer may be larger than the area that is currently available for this species, it is sufficiently large to connect the three disjunct coastal California distributions and was selected to assess whether climatic variables between these subspecies may explain their genetic isolation (Barve et al. 2011).

Ten climate variables were selected from BioClim as predictor variables (Table 1). Average summer fog was also used as a predictor variable for the coastal California subspecies, but was not available for the range of the other subspecies (Torregrosa et al. 2016). All possible combinations of these variables were used to create an initial candidate model set for each subspecies. Predictor variables within each study area were then evaluated for correlation using Pearson’s correlation. Any model that included variables with correlation above 0.5 were removed from the candidate model set (Dormann et al. 2013).

Table 1. Predictor variables used to calculate subspecies models. *Average fog was only available for the California coastal range.

Variable	**Description**
Bio1	Annual Mean Temperature
Bio5	Maximum Temperature of Warmest Month
Bio6	Minimum Temperature of Coldest Month
Bio10	Mean Temperature of Warmest Quarter
Bio11	Mean Temperature of Coldest Quarter
Bio12	Annual Precipitation
Bio13	Precipitation of Wettest Month
Bio14	Precipitation of Driest Month
Bio18	Precipitation of Warmest Quarter
Bio19	Precipitation of Coldest Quarter
Fog*	Average Summer Fog

Models were evaluated using AICc values and weights. Candidate models with ΔAICc less than or equal to 2 were considered top models, and their suitability rasters were evaluated for correlation (Burnham and Anderson 2004). If correlation was above 0.9, the model with the fewest parameters was selected as the top model. To assess accuracy, I calculated the Continuous Boyce Index (CBI) using the “enmSdm” package in R (Hirzel et al. 2006). CBI values range between -1 and 1, with more positive values indicating a more accurate model. Occurrence points were divided to create a training and testing data set, 75% of the data was used to create the model and the remaining 25%

were used to test accuracy. I conducted this evaluation 10 times, randomly sampling each time to calculate an average CBI. To assess whether closely related subspecies occupied more similar climatic niches, I calculated niche overlap range-wide for californica, olympica, pacifica, and rufa. I used Warren's *I* in the 'ENMTools' package in R (Warren et al. 2010). The top model for each clade was also projected into the Coastal California range and compared to the coastal clade.

PAMB Surveys and Fine-Scale Models

In the summer of 2017, I conducted surveys throughout PAMB range to determine patterns of occupancy and compare the climate at used locations versus those available to the population. Using ArcMap (Environmental Systems Research Institute, Inc., Redlands, CA) a points grid was placed over the range of PAMB, such that each point was 150 m from the nearest neighbor. From this grid, two subsets, one inland and one coastal, of 100 points were selected for PAMB surveys and datalogger deployment. Sites for the coastal grid were randomly selected in R (George et al. 2015). Sites were reselected if they were unsuitable for datalogger deployment (i.e. in a river or inaccessible due to topography or vegetation). Due to accessibility and a need to ensure that the full range of canopy cover, elevation, slope, and aspect were sampled, points for the inland grid were selected using a stratified approach (Fridley 2009, Frey et al. 2016). Inland points were along transects that were selected based on accessibility, presence of PAMB, and environmental variables. Histograms of elevation, slope, and aspect for the

PAMB range were compared to grid points to ensure the range of environmental variables was reflected by deployment sites.

Four inland sites and four coastal sites were selected to study the relationship between microclimate at use and available sites (Figure 2b). Use sites were identified based on signs of mountain beaver activity. Individual mountain beavers construct a burrow system with multiple burrow entrances that are distinct and easily identified as mountain beaver constructs (Camp 1918, Feldhammer et. al 2003, Zielinski et al. 2015). These systems may overlap and form burrow area; however, mountain beavers are not social, and their clumped dispersion tends to be a function of suitable habitat (Feldhammer et al. 2003). Use sites were defined as an individual burrow area separated from other burrows by at least 10 meters. Surveys radiated away from an identified burrow. If no additional burrows were found within a 10-meter distance, a GPS point was taken to designate a burrow area edge. Surveys continued around a burrow area until all edges were defined. Edges were also defined by topography (i.e. water features or cliff face), anthropogenic features, or vegetation edges.

Microclimate data were collected using iButton® (Maxim Integrated, San Jose, CA, USA) temperature loggers for two different analyses: (1) a downscaled microclimate model of PAMB habitat, and (2) comparison of microclimate at use vs. available sites. Each datalogger was placed in a shield constructed from PVC and fiberglass screen that allowed for airflow while limiting the effect of direct solar radiation and precipitation. All dataloggers were deployed during the summer, checked once in late summer/early fall, and collected in early winter. This deployment captured most of the typical warm season within the PAMB range (NOAA 2012).

At each site, one datalogger was placed directly outside a central burrow entrance, and three dataloggers were deployed at available sites. Available sites were randomly selected from the points grid 100-450 m from the burrow area (Figure 2b). This buffer is based on the maximum reported distance between locations for PAMB, which was 101.8 m (Zielinski and Mazurek 2006), and dispersal distances for other subspecies, which have been recorded from ~100 m (Arjo 2007) to over 450 m (Hacker 1991). Therefore, this distance should encompass areas that were potentially accessible to PAMB but not in use. Site selection was constrained by access and deployment points were reselected if the point fell within an area that would be uninhabitable or inaccessible for PAMB, such as roads, rivers, or solid rock. A 10-meter survey was conducted around available sites during the initial deployment and subsequent checks to confirm non-use. Soil moisture and temperature were recorded at use and non-use sites during initial deployment and subsequent data checks using 8” soil probes.

To generate a climate model at a scale appropriate to mountain beaver microclimate selection, I used a combination of fine-scale topographic data and known climate data recorded on the dataloggers. Climate data from the dataloggers were projected into the surrounding landscape using relevant predictors from the topographic data. Specifically, a Digital Terrain Model (DTM), Digital Surface Model (DSM), and Canopy Height Model (CHM) were calculated using LiDAR data from NASA’s Northern San Andreas Fault Study (OpenTopography.org). Environmental predictor variables were calculated using the DTM, DSM, and CHM at two spatial scales, 10 meters and 100 meters, to account for the impacts of these variables at a local and more widespread scale (Table 2). Distance to coast was calculated from a US shapefile at a 1-meter scale (GADM.org). Response variables, min, mean, and max temperature, were calculated for each datalogger during the 6-month deployment period. An additional response variable, upper critical temperature (“CT_{max}”), was calculated as the average number of times per day a data logger recorded temperatures above 32^{o}C, which is the lower temperature limit that causes mortality in mountain beavers with prolonged exposure. The CT_{max} analysis was incorporated to provide another metric for maximum temperature and control for extreme temperatures. Boosted regression trees in R package ‘dismo’ was used to analyze the relationship between topographic data at the datalogger locations and climate data recorded on the datalogger; these climate models were then projected onto topographic data throughout PAMB range (Hijmans et al. 2017).

Table 2. Predictor variables and the scales used to calculate fine scale temperature models from the Digital Terrain Model (DTM), Digital Surface Model (DSM), and Canopy Height Model (CHM).

Variable	**Spatial Scale**	**Description**
Distance to coast	1m	Euclidean distance from coast, proxy for fog
Mean cover	10m/100m	Mean percent cover from DTM and DSM
SD cover	10m/100m	Standard deviation of percent cover from DTM and DSM
Mean eastness	10m/100m	Mean sin (aspect *pi/180), between -1 and 1, DTM
Mean elevation	10m/100m	Mean elevation, DTM
SD elevation	10m/100m	Standard deviation of elevation, DTM
Elevation range	10m/100m	Range of elevation values, DTM
Mean northness	10m/100m	Mean cos(aspect*pi/180), between -1 and 1, DTM
Mean slope	10m/100m	Mean slope (%) from DTM
SD slope	10m/100m	Standard deviation of slope (%) from DTM
Topo Index	10m/100m	Difference in elevation between the point and mean elevation, indicating local low and high points, DTM
Mean veg height	10m/100m	Mean vegetation height, CHM
SD veg height	10m/100m	Standard deviation of vegetation height, CHM

Boosted Regression Trees are able to identify nonlinear relationships and explore complex interactions and can be particularly useful for a large number of predictor variables (Elith et al. 2008). Models were fit using a tree complexity of 3–5 and a bag fraction of 0.75 due to the small sample size. All models were initially run with a learning rate of 0.005 and decreased until at least 1000 trees were used to fit the model (Elith et al. 2008). Models were evaluated using cross validation, and the top model was then simplified by dropping non-informative predictor variables using methods outline in Elith et al. (2008). As the purpose of simplification is to improve the performance of the model, when the simplified model did not outperform the unsimplified model, the unsimplified model was considered the top model (Elith et al. 2008). The models were also tested for correlation between predicted and observed values using 10-fold cross validation. Low correlations between predicted and observed values indicates over-fitting of the model (Frey et al. 2016).

I combined the occurrence data I collected for PAMB with points from a previous study of PAMB distribution with the fine-scale climate data to construct local distribution models throughout PAMB range using Maxent (Zielinski et al. 2015). The mean, maximum, minimum, and critical temperature layers were used as predictive variables. All possible combinations of these four variables were considered candidate models and variables with >0.5 correlation were not included in the same model. The top model was selected using AICc (Warren and Seifert 2011). Accuracy of this model was also assessed using the Continuous Boyce Index (CBI), following the methods used for the broad scale models (Hirzel et al. 2006). Additional presence points provided from a variety of sources and collated by USFWS were also used as an independent testing data set but were not used as training data due to uncertainty in accuracy of location data.

Finally, I examined PAMB microclimate selection by comparing temperature and soil data at PAMB locations and nearby available locations. The mean, max, and minimum temperature from dataloggers at available points were averaged and compared to the use points using a paired t-test. Similarly, soil humidity and temperature were averaged at available sites and compared to readings from use sites.

RESULTS

Coarse-Scale Models

The niche space diagram showed that all the subspecies fell within a similar climatic niche (Figure 3). Californica occupied the driest and coldest niche, while pacifica occupied the wettest. The coastal clade inhabited a narrow niche on the hotter and drier end of the spectrum. Rufa and olympica appear to occupy a wider range of climatic conditions.

A total of 332 mountain beaver occurrence points with a location accuracy less than 2 km were available from GBIF, USFS, and personal surveys (Zielinski et al. 2015, GBIF 2017). After thinning, 178 occurrence points were used for modeling with 51 for the coastal clade, 27 for californica, 52 for olympica, 20 for pacifica, and 28 for rufa. The species-wide top model included maximum temperature of warmest month, minimum temperature of coldest month, and precipitation of the warmest quarter (Table 3, Figure 4). The mean CBI value for the range-wide model was 0.919 (Table 4). Maximum temperature had the greatest contribution to the model. Suitability for mountain beavers across their range peaked at a maximum temperature of the warmest month of 20ºC with a steep drop in suitability at higher temperatures (Appendix A1).

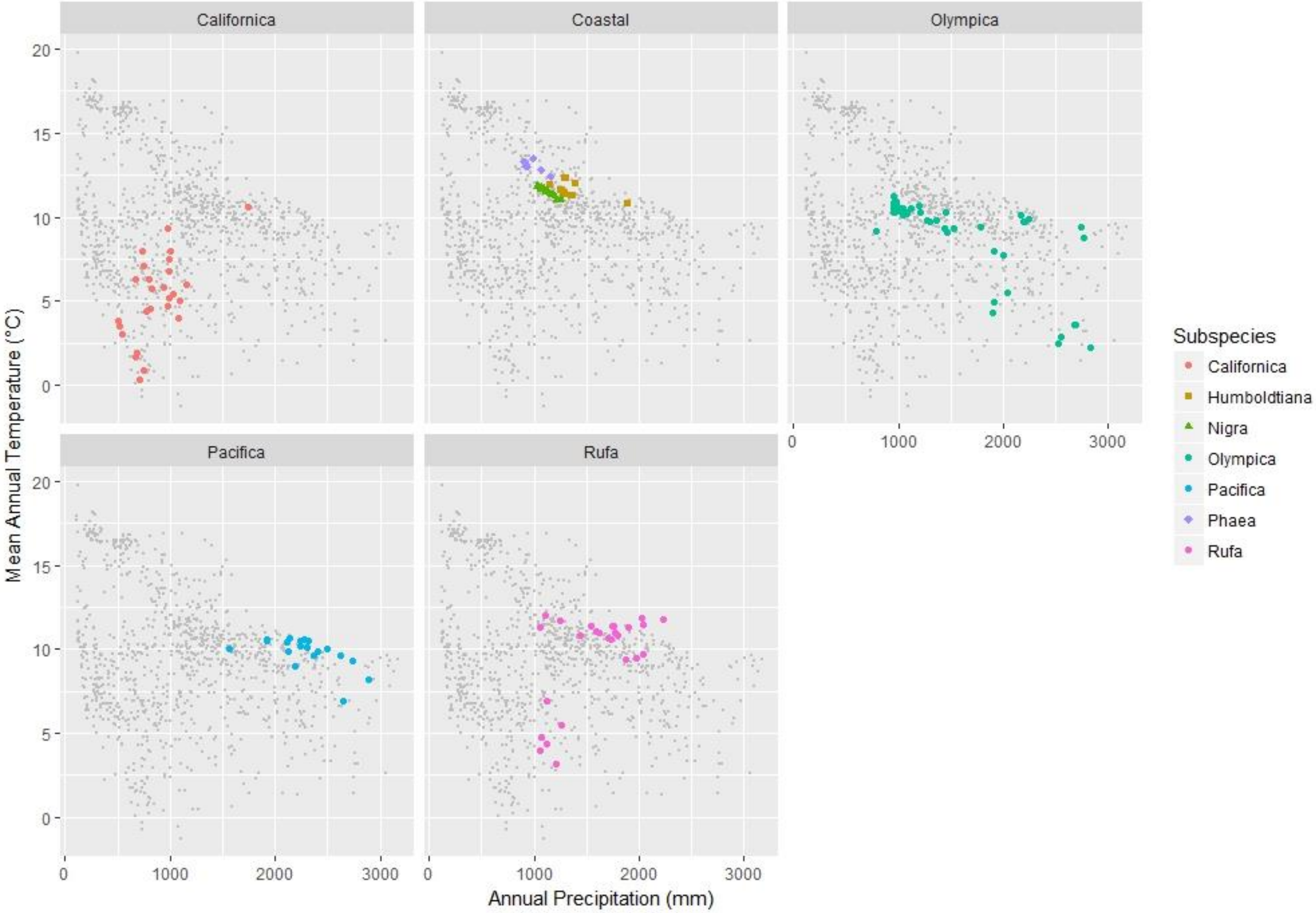


Figure 3. Mean annual temperature and annual precipitation at occurrence points for the five clades of mountain beaver. Smaller, gray points represent conditions at 1,000 random points within a 105 km buffer of all occurrence points.

Table 3. Top three suitability models for each clade of mountain beaver.

Clade	Predictors[1]	Beta	LogLik	K	AICc	ΔAICc	Weight
	Bio10 + Bio18 + Bio19	2.0	-212.99	3	433.03	0.00	0.38
Californica	Bio10 + Bio18 + Bio19	1.5	-212.03	4	433.88	0.85	0.25
	Bio5 + Bio18 + Bio19	1.5	-212.48	4	434.77	1.74	0.16
	Bio5 + Bio12 + Fog	1.0	-293.53	8	606.58	0.00	0.46
Coastal	Bio5 + Bio13 + Fog	1.0	-293.14	9	608.78	2.21	0.15
	Bio5 + Bio11 + Bio13 + Fog	1.5	-287.38	13	610.86	4.29	0.05
	Bio6 + Bio10 + Bio13	1.5	-390.64	15	825.82	0.00	0.54
Olympica	Bio6 + Bio10 + Bio13	2.0	-394.98	13	826.35	0.54	0.42
	Bio6 + Bio13	1.5	-401.78	11	832.69	6.87	0.02
	Bio1 + Bio19	0.5	-147.88	6	314.76	0.00	0.43
Pacifica	Bio6 + Bio10 + Bio13	1.0	-149.83	6	318.66	3.89	0.06
	Bio11 + Bio19	2.0	-154.30	4	319.45	4.69	0.04
	Bio5 + Bio11 + Bio14	1.5	-218.19	5	449.23	0.00	0.49
Rufa	Bio5 + Bio11 + Bio14	2.5	-220.10	5	453.06	3.83	0.07
	Bio5 + Bio18	1.0	-223.20	3	453.45	4.22	0.06
	Bio5 + Bio6 + Bio18	0.5	-1344.33	34	2773.65	0.00	0.90
All	Bio5 + Bio6 + Bio18	1.0	-1356.89	27	2778.07	4.42	0.10
	Bio5 + Bio6 + Bio13	0.5	-1344.57	39	2790.25	16.60	0.00

[1] Bio1 = Mean annual temperature, Bio5 = Maximum temperature of the warmest month, Bio6 = Minimum temperature of the coldest month, Bio10 = Mean temperature of the warmest quarter, Bio11 = Mean temperature of the coldest quarter, Bio12 = Annual precipitation, Bio13 = Precipitation of the wettest quarter, Bio14 = precipitation of the driest quarter, Bio18 = Precipitation of the warmest quarter, Bio19 = Precipitation of the coldest quarter, Fog = Mean summer fog

Table 4. The top model for each clade of mountain beaver including which predictor variables were used, the beta or regularization parameter, and evaluation metrics (AUC and CBI).

Clade	Model[1]	Beta	AUC	CBI	SD CBI
Californica	Bio10 + Bio18 + Bio19	2.0	0.906	0.774	0.221
Coastal	Bio5 + Bio12 + Fog	1.0	0.984	0.973	0.046
Olympica	Bio6 + Bio10 + Bio13	2.0	0.840	0.874	0.123
Pacifica	Bio1 + Bio19	0.5	0.905	0.830	0.236
Rufa	Bio5 + Bio11 + Bio14	1.5	0.822	0.920	0.104
All	Bio5 + Bio6 + Bio18	0.5	0.885	0.919	0.071

[1] Bio1 = Mean annual temperature, Bio5 = Maximum temperature of the warmest month, Bio6 = Minimum temperature of the coldest month, Bio10 = Mean temperature of the warmest quarter, Bio11 = Mean temperature of the coldest quarter, Bio12 = Annual precipitation, Bio13 = Precipitation of the wettest quarter, Bio14 = precipitation of the driest quarter, Bio18 = Precipitation of the warmest quarter, Bio19 = Precipitation of the coldest quarter, Fog = Mean summer fog.

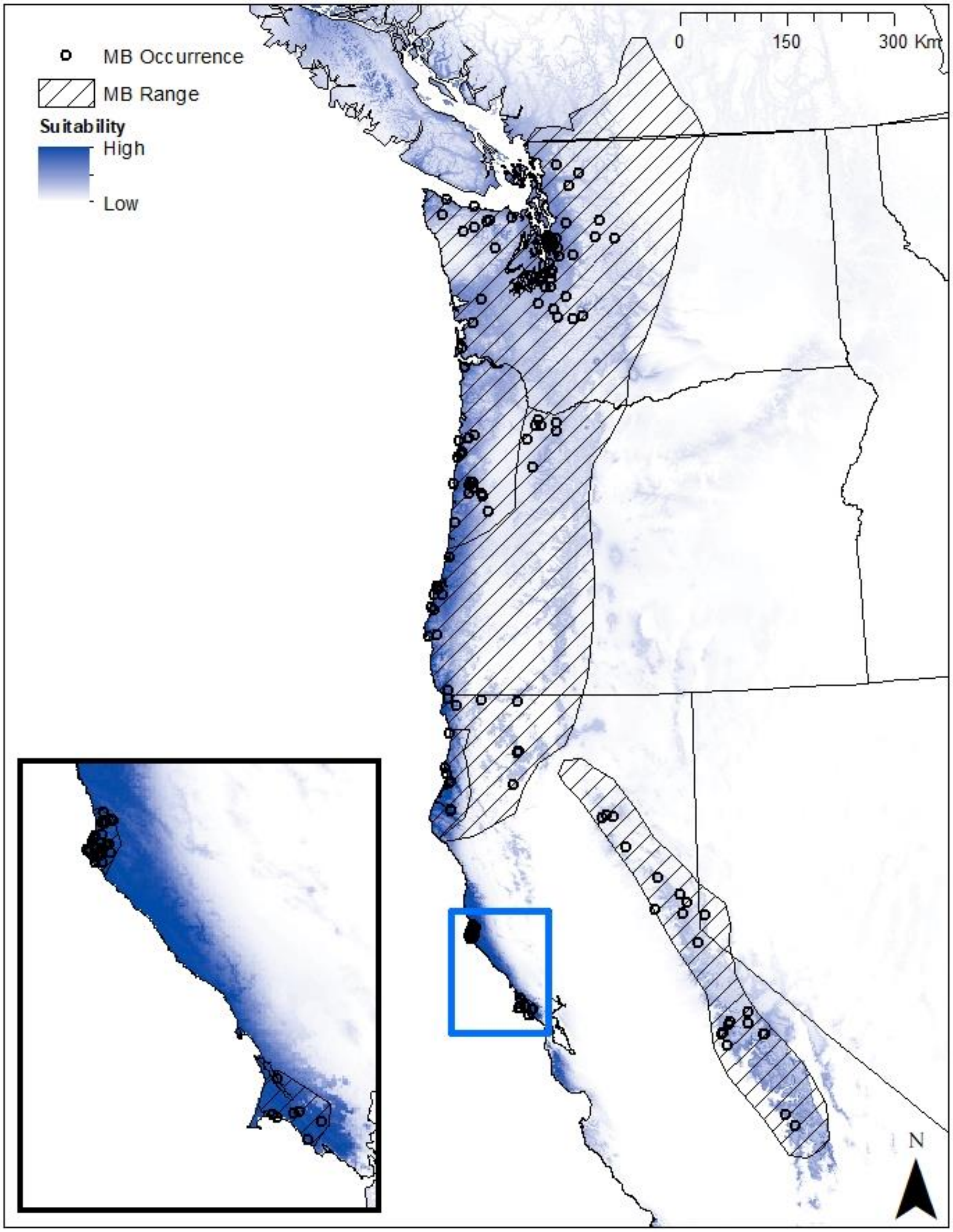


Figure 4. The range-wide model of climatic suitability for mountain beavers showed high suitability along the coast and limited suitability inland.

There was a definitive top model for the Coastal California Clade (“coastal”), *A. r. pacifica* (“pacifica”), and *A. r. rufa* (“rufa”). The predictors included in the best model for coastal were maximum temperature of the warmest month, annual precipitation and average summer fog (Table 3). Average summer fog had the highest percent contribution, but maximum temperature was shown to have the most useful information when used in isolation. Suitability peaked at 7 hours/day of fog, maximum temperature of the warmest month of 20ºC, and annual precipitation around 900 mm (Appendix A2). Maximum temperature of the warmest month and annual precipitation both had sharp peaks, while suitability remained high for a range of fog values.

The top model for pacifica included annual mean temperature and precipitation of coldest quarter (Table 3). While precipitation of the coldest quarter had greater contribution, mean temperature predicted a sharp decline in suitability at temperatures above 10.5ºC (Appendix A3). Suitability gradually increased as precipitation rose until a plateau of suitability at 1400 mm.

Predictors included in the top model for rufa were maximum temperature of warmest month, mean temperature of coldest quarter, and precipitation in the driest month (Table 3). All variables had similar importance in the model with maximum temperature of the warmest month again having the most useful information when used in isolation. There was very low probability of presence below 10 mm precipitation in the driest month and a decline in probability of presence above a maximum temperature in the warmest month of 10ºC (Appendix A4). Suitability increased below a mean temperature of the coldest quarter of -9.5ºC, decreased to a low at 0ºC and peaked at 9ºC.

The two-other subspecies, *A. r. californica* (“californica”) and *A. r. olympica* (“olympica”), each had two models within 2 ΔAICc, but both used the same predictor variables with different beta parameters. The two top models for californica and olympica were highly correlated (0.98 and 0.99 respectively), so the model with the fewest parameters was selected for further analysis. The predictors included in the top model for californica were mean temperature of the warmest quarter and precipitation of the warmest and coldest quarter (Table 3). Mean temperature of warmest quarter had the highest contribution and importance, showing highest probability of presence below 5ºC and steadily decreasing up to 20ºC where probability of presence dropped to 0 (Appendix A5). Any precipitation in the warmest quarter decreased suitability, while increasing precipitation to 450mm or higher in the coldest quarter peaked suitability.

The top model for olympica included minimum temperature of the coldest month, mean temperature of the warmest quarter, and precipitation of the wettest month. Minimum temperature of the coldest month had the highest contribution with probability of presence increasing sharply at temperatures above 0ºC (Appendix A6). Suitability had a sharp peak at a mean temperature of the warmest quarter of 30ºC and 130mm precipitation in the wettest month. CBI values varied between 0.774 for californica and 0.973 for coastal (Table 4).

Overall, the coastal clade had the least overlap in climatic suitability with the other clades, ranging between 0.083 for olympica and 0.231 for californica (Table 5, Figure 5). Pacifica had similarly low overlap with values ranging from 0.155 for californica (0.155), to 0.254 for rufa. The three remaining clades had moderate niche overlap. The highest overlap was between californica and rufa (0.523).

Table 5. Niche overlap for the five clades of mountain beaver. Overlap with the coastal clade was only calculated for the coastal range due to the lack of an available fog layer for inland areas, while all others were assessed for the entire range. Higher overlap suggests greater similarity of the model predictions.

	Californica	**Olympica**	**Pacifica**	**Rufa**
Coastal	0.231	0.083	0.186	0.219
Californica		0.414	0.155	0.523
Olympica			0.223	0.437
Pacifica				0.254

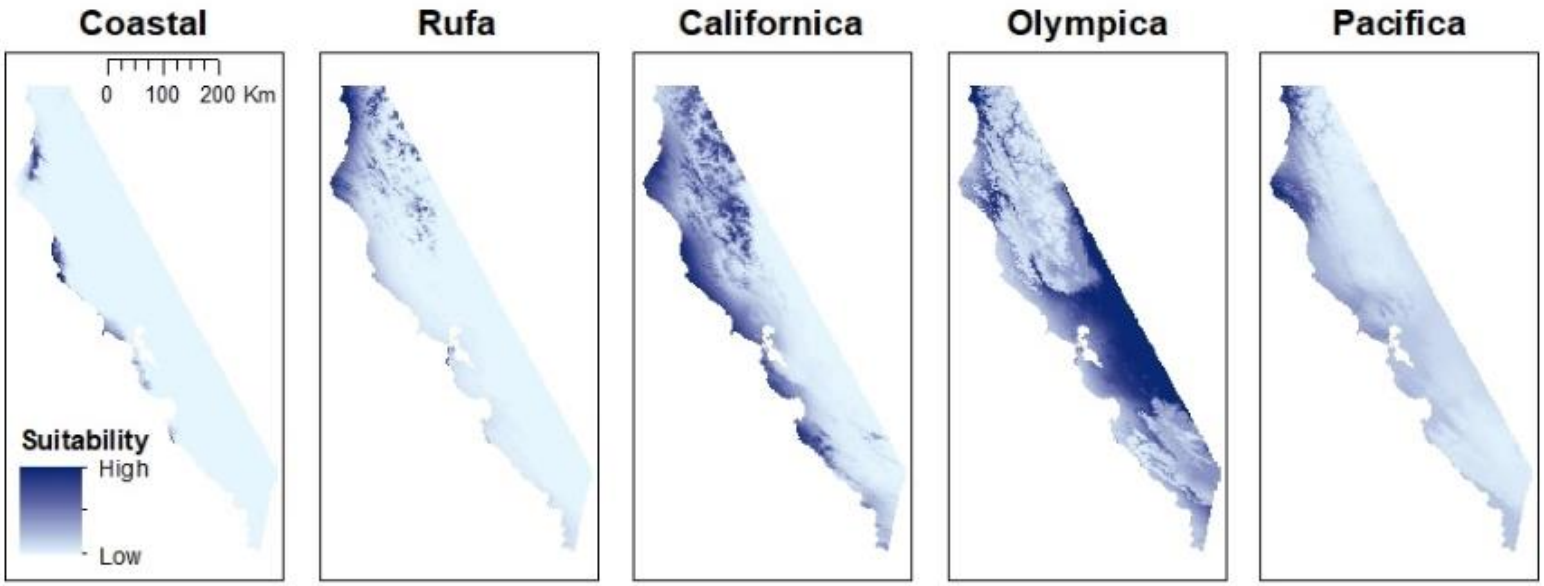


Figure 5. The top model for climatic suitability for each clade of mountain beaver projected into the coastal range for niche overlap comparison. Clades are in order of highest overlap with the coastal clade from left to right. Overlap was only compared with the coastal clade where a fog layer was available.

PAMB Surveys and Fine-Scale Analysis

I documented the occurrence of 20 PAMB burrow areas, eight of which were feasible to delineate the edges of the burrow area and were used for the paired points analysis. An additional 35 occurrences from USFS were used for a total of 55 PAMB occurrences for the suitability models. A total of 199 iButton data loggers were deployed during the summer of 2017 (Figure 2). Due to theft or loss, 27 data loggers were removed from the analysis. An additional four data loggers were placed later in the summer and excluded from the six-month microclimate modeling, leaving 168 locations for this analysis. Several of the data loggers recorded temperatures above a reasonable limit for the area, likely due to solar radiation and heat reflection from the soil. These were still included for analysis as they likely captured relative patterns of temperature if not absolute reliable values (Terando et al. 2017).

Creation of fine-scale climate layers from the dataloggers and LiDAR data resulted in accurate models for mean, minimum, and CT_{max} (Table 6, Figure 6). Deviance for these three layers range from 0.023 (CT_{max}) to 2.240 (minimum). However, the maximum temperature model had high deviance. The cross-validation correlation values were moderate (ranging from 0.586 to 0.794) indicating that there was some agreement between training and testing data.

Table 6. Model settings (tree complexity, learning rate, and number of trees) and performance metrics for the top model for each temperature variable. Additionally, whether the top model was simplified by removing uninformative predictor variables.

Variable	Complex	Learning Rate	No. trees	Deviance	Dev SE	CV corr	CV SE	Simplified
Mean	5	0.005	1000	0.517	0.053	0.784	0.041	No
Max	3	0.002	1300	33.258	2.206	0.64	0.034	No
Min	5	0.002	1400	2.24	0.292	0.794	0.029	Yes
CTmax	5	0.002	1300	0.023	0.004	0.586	0.101	Yes

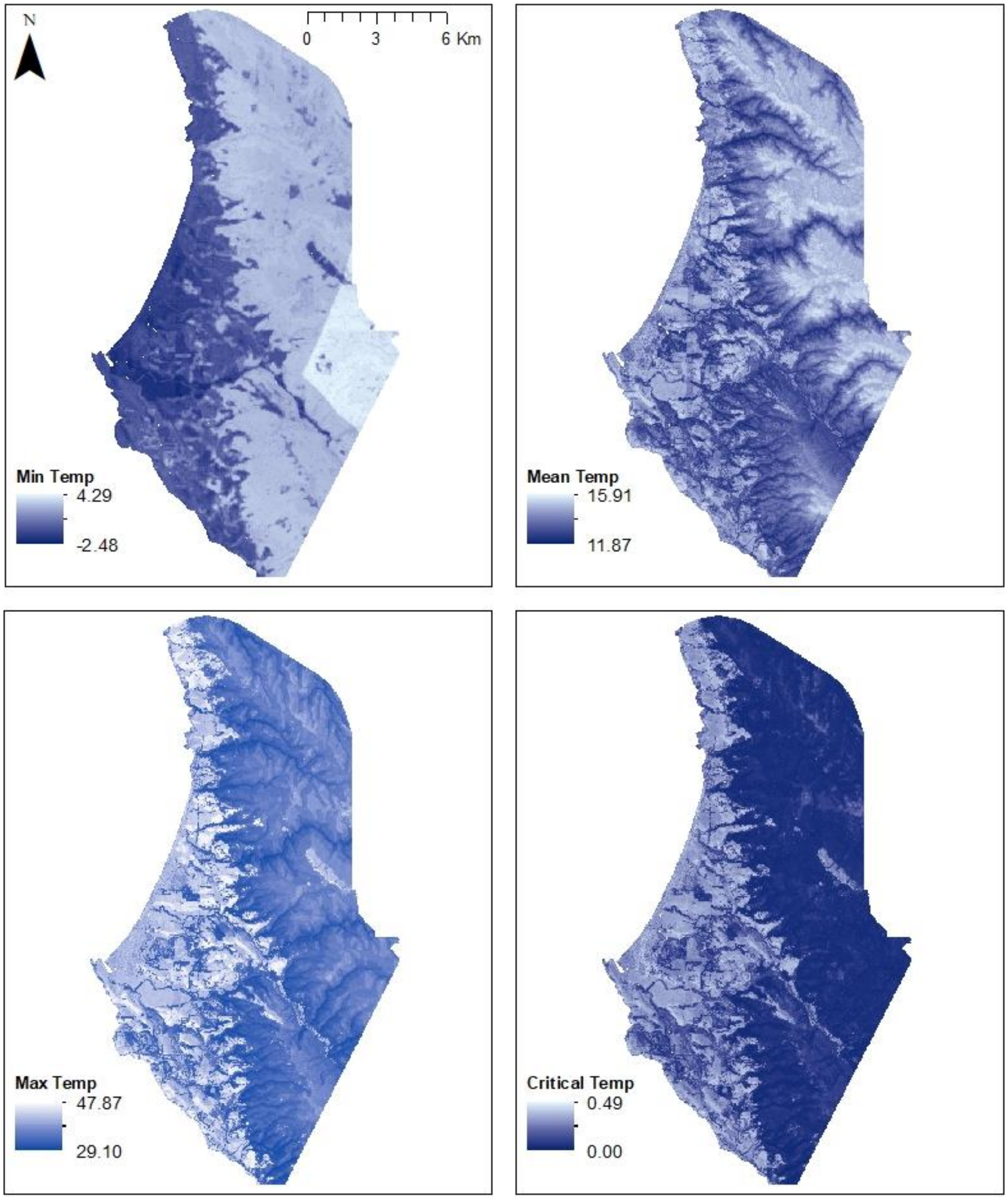


Figure 6. Results of the boosted regression tree analysis for each temperature metric (Minimum, Mean, Maximum, and Critical Temperature). Critical temperature was defined as the average number of times per day a datalogger recorded temperatures above 32ºC.

The top model for PAMB distribution included mean temperature and CT_{max} (Table 7, Figure 7). Mean temperature had a greater contribution (94.6%) than CT_{max}. Suitability decreased as mean temperature increased above 12.0ºC and increased as daily readings above CT_{max} increased to 0.45 (Appendix A7). The model had an AUC of 0.876. The mean CBI value for the top model was 0.96 when the original data were divided into training and testing datasets. The CBI value was 1.0 when the additional USFWS provided points were used as the testing dataset. The top five models all included these two layers, and some also incorporated minimum temperature (Table 7). Maximum temperature was not included in any of the best-supported models.

Table 7. Model selection table for PAMB microclimate suitability.

Model	Beta Mult	AICc	ΔAICc	AICc Weight
Mean + CTmax	3.0	895.29	0.00	0.65
Mean + CTmax	2.0	897.70	2.41	0.19
Mean + Min + CTmax	3.0	899.12	3.83	0.10
Mean + CTmax	2.5	901.26	5.98	0.03
Mean + Min + CTmax	2.0	901.59	6.30	0.03

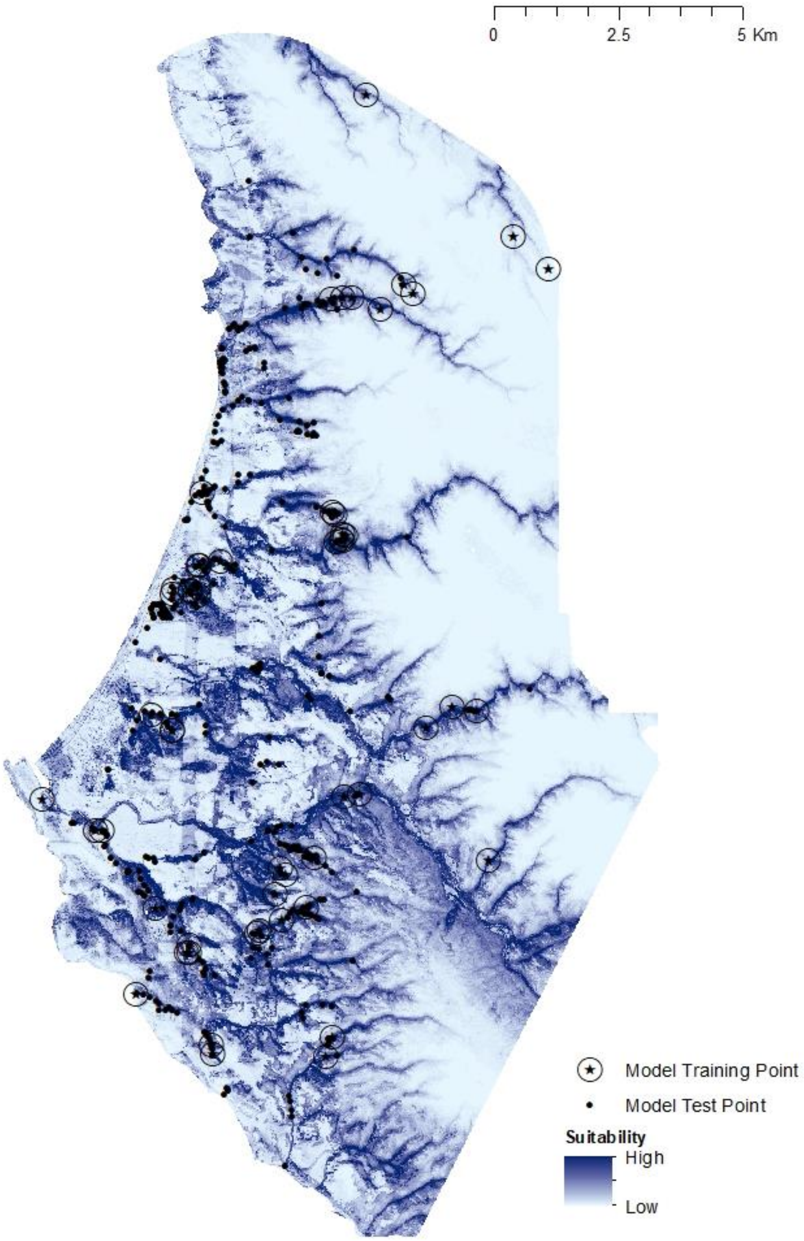


Figure 7. Climatic suitability model for Point Arena mountain beaver. Training points were used to create and assess the accuracy of the model. Test points were used as an additional accuracy assessment but were not used to create the model due to unknown accuracy.

At the finest scale, mean air temperature was an average 1.00ºC cooler at use sites than at available sites (t_7=-2.59, P = 0.036). Maximum and minimum air temperature were not significantly different at use and available sites (t_7 = -1.58, P = 0.159 and t_7 = 0, P = 1, respectively). Due to equipment failure, each burrow area had between 1-3 readings for soil temperature and humidity (Appendix B). Soil temperature was also cooler with use sites on average 1.42ºC than at available sites (t_{18}=-2.55, P = 0.020). Soil humidity varied across burrow areas with 3 burrow areas having higher humidity at use sites, and 4 with lower humidity at use sites (t_{20} = 0.21, P = 0.838). One burrow area in the coastal dunes had 0.0% humidity at all use and non-use sites.

DISCUSSION

I examined the climatic limits to mountain beavers at four spatial scales: range-wide, clade, and I created a fine-scale distribution model for the PAMB and a paired-microclimate analysis. At almost all scales, hot temperatures limited mountain beaver distribution. Overall, niche overlap between clades was low, however, the fine-scale models suggest that animals in different clades may select their niche at a finer scale and appear to have higher niche overlap than the coarser models indicated. Niche overlap was highest among clades that were genetically closest, indicating that this species has a tendency towards niche conservatism but has developed some local adaptations as well.

As expected, models at all scales showed a trend towards lower suitability at higher temperatures. High temperatures were important in identifying suitable habitat for all the clades, with the exception of pacifica. Pacifica was the only model that did not incorporate either maximum temperature of the warmest month or mean temperature of the warmest quarter. The models that included these variables had a clear trend of suitable habitat at lower temperatures. The pacifica model incorporated annual mean temperature but did not appear to be selecting for the coldest temperatures, suggesting a lower temperature limit as well. As genetic evidence supports pacifica as a separate species rather than subspecies, pacifica may have developed local adaptations that limit its niche to a specific range of temperatures (Piaggio et al. 2013). On the other hand, the range of pacifica is geographically limited by rivers to a small area on the north coast of

Oregon. In other words, the lack of a signal for warm temperature in the pacifica model may be an artifact of available climates rather than true climatic limits.

Pacifica and olympica are both geographically isolated by surrounding rivers, whereas the disjunct southern populations were likely separated by a changing climate (Blois et al. 2010, Piaggio et al. 2013). The lack of niche overlap between pacifica, olympica, and the southern clades may be a result of the coastal climates available to these northern populations. Additionally, these two clades diverged first, supporting the hypothesis that less related clades would have less niche overlap (Piaggio et al 2013). Even if mountain beavers have a tendency towards niche conservatism, these two clades would be the most likely to have distinct niches. The high level of overlap between rufa and californica also supports this hypothesis.

Similarly, the coastal clade had highest overlap with its two closest related clades, rufa and californica, but overlap for the coastal clade with other subspecies was overall low. This may be a result of their limited range and therefore restricted climatic niche. Additionally, niche overlap for the coastal populations could only be compared within the coastal range where a fog layer was available. Comparing fine scale models reveals that PAMB and members of the coastal clade are selecting a similar climatic niche, but at a finer scale. The niche space diagram showed that while the coastal clade is occupying the hotter, drier portion of the mountain beaver habitat spectrum, it still falls within the general range of climate occupied by the species as a whole (Figure 3). The most southern coastal subspecies, phaea exists in areas with the highest mean temperature, but is likely selecting for cooler areas within its range. PAMB can be further divided into three distinct genetic groupings, two of which only exist on the coast (Zielinski et al. 2013). The third grouping primarily inhabits the inland habitats, which more closely resemble other mountain beaver habitat. It is possible that the coastal groupings may be more adapted to hotter, drier climates and therefore critical to preserve in the face of climate change. A study into the physiology of California coastal mountain beavers could provide valuable insight into whether this species has adapted to a hotter, drier climate or if the fog in those areas is enough to sustain them.

The subtle differences in niche between clades are evidence for some local adaptation and, there are multiple mechanisms in which this adaptation can be realized. Behavioral adaptations, such as shifting foraging activities to cooler parts of the day, have been documented in other climatically-sensitive species and the activity patterns of mountain beavers have only been studied in californica (Smith 1974, Ingles 1959). Mountain beavers are active at various times throughout the day and night with increased activity and ranging at night (Ingles 1959). During summer months, mountain beavers shift to a more nocturnal lifestyle, potentially to avoid increased temperatures (Ingles 1959). This shift may be more conspicuous in populations living in areas with hotter temperatures and may occur seasonally or daily as weather conditions such as fog shift. Additionally, climatically-sensitive species have been shown to select habitat at a microclimatic scale (Wilkening et al. 2011, Shi et al. 2014, Varner and Dearing 2014). These microclimates may be particularly important at range margins such as the conditions experienced by PAMB (Ray et al. 2016). Both the fine scale SDM and paired points analysis suggest that PAMB are selecting for cooler microclimates within their range. Future studies on differences in active periods between clades could provide insight into behavioral adaptations. Overall, this species appears to favor niche conservatism which likely lead to the isolation of the southern populations.

The range-wide model over-predicted suitable climate for the coastal clade and under-predicted suitable climate for the inland populations. This may be due to a sampling bias along the coast. The entire northern California coast was identified as highly suitable for the species. Given the genetic isolation among the coastal subspecies, it is unlikely that these coastal areas are actually climatically suitable but unoccupied. Instead, this suggests that an additional facet of habitat or climate restricts the coastal subspecies to their respective distributions. Significantly, average summer fog cover contributed the most to the top model for this clade. The three California coastal populations exist in windward (N-NW facing) areas of the coast, areas that have increased fog cover (Torregrosa et al. 2015). The increased cover from fog may be the variable that allows this clade to persist in these warmer, climates, but not in the intervening areas. Similar to understanding the role of fog in limiting coastal redwood populations, understanding changing fog conditions into the future will be critical for projecting the impacts of climate change on these endangered subspecies (Dawson 1998).

It is unclear whether fog is important for mediating hotter summer temperatures on the coast or providing additional free moisture in the system. Mountain beavers can meet their water intake requirements without access to free-flowing water, however this requires significant moisture intake from vegetation (Crocker et al. 2007). Fog may provide additional moisture to drier coastal vegetation. Previous research has shown that

PAMB select areas with increased density of free-flowing water (Zielinski et al. 2015). Coastal habitats- such as the Dune burrow area where soil moisture was 0.0% and free-flowing water was not readily available- may be particularly reliant on moisture from fog. While there were no clear differences in soil moisture at burrow areas versus surrounding areas, soil humidity can vary greatly within a small area. Moisture is influence by soil type, which is itself likely a limiting factor for PAMB, as they require soil suitable for constructing burrows. Unfortunately, current digital soil layers were too coarse to incorporate into these models. Further research is needed to understand the interactions of soil moisture, fog, and free-flowing water on PAMB distribution.

While this study focused on the impacts of abiotic limits to mountain beaver distribution, there are likely biotic variables that also influence this species' distribution. Biotic variables are recognized as important factors in predicting distribution shifts in response to climate change, however there is debate over their relative importance at broad scales (Pearson and Dawson 2003, Wisz et al. 2013). Incorporating biotic factors, such as predation, competition, and dispersal abilities, into SDMs, particularly fine-scale SDMs, for mountain beavers may improve our understanding of how this species will respond to climate change (Wisz et al. 2013).

With the certainty of continued climate change, ecosystem conservation and preservation will escalate the importance of understanding the niche of climatically sensitive species such as the mountain beaver, as they lack the ability to adapt to changing temperatures (Rappaculio et al. 2014). These species are particularly vulnerable to increasing temperature and the associated changes in precipitation. While the lack of niche overlap suggests mountain beavers may have some ability to adapt to local conditions, this may be primarily focused on climatic limits such as the California coast. Subspecies like PAMB may exist on the climatic limit for mountain beavers, but they may also hold the key to their survival through climate change across the entirety of their range.

LITERATURE CITED

Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevic, B. Vilela, and R. P. Anderson. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541-545.

Arjo, W. M., R. E. Huenefeld, and D. L. Nolte. 2007. Mountain beaver home ranges, habitat use, and population dynamics in Washington. Canadian Journal of Zoology 85:328-337.

Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution. Ecological Modelling 222:1810-1819.

Blois, J. L., J. L. McGuire, and E. A. Hadly. 2010. Small mammal diversity loss in response to late-Pleistocene climatic change. Nature 465:771-775.

Burnham, K. P., and D. R. Anderson. 2004. Multimodal Inference: Understanding AIC and BIC in model selection. Sociological Methods & Research 33:261-304.

California Department of Fish and Wildlife [CADFW]. 2017. Special Animals List. California Department of Fish and Wildlife, Sacramento, CA, U.S.A.

Camp, D. L. 1918. Excavations of the burrows of the rodent *Aplodontia*, with observations on habitat of the animal. University of California Publications in Zoology 17:517-536.

Case, M. J., J. J. Lawler, and J. A. Tomasevic. 2015. Relative sensitivity to climate change of species in northwestern North America. Biological Conservation 187: 127-133.

Crocker, D. E., N. Kofahl, G. D. Fellers, N. B. Gates, and D. S. Houser. 2007. High rates of energy expenditure and water flux in free-ranging Point Reyes mountain beaver *Aplodontia rufa phaea*. Physiological and Biochemical Zoology: Ecology and Evolutionary Approaches 80:635-642.

Dawson, T. E. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117:476-485.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. García Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach.

2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27-48.

Elith, J., J. R. Leathwick, T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77:802-813.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijams, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. Overton, A. Townsend Peterson, S. J. Phillips, K. Richardson, R. Scachetii-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, N. E. Zimmerman, and M. Araujo. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151.

ENPLAN. 2017. ENPLAN Parcel Viewer Mendocino County. Accessed 05 May 2017.

Environment Canada. 2015. Management Plan for the Mountain Beaver (*Aplodontia rufa*) in Canada. *Species at Risk Act* Management Plan Series. Environment Canada, Ottawa, Canada.

Feldhammer, G. A., J. A. Rochelle, and C. D. Rushton. 2003. Mountain beaver (*Aplodontia rufa*). *In* G. A. Feldhammer, B. C. Thompson, and J. A. Chapman (editors). Wild Mammals of North America: Biology, Management, and Conservation. John Hopkins University Press, Baltimore, MD. Pp. 179-187.

Fick, S. E. and R. J. Hijmans. 2017. Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology.

Frey, S. J., A. S. Hadley, S. L. Johnson, M. Schulze, J. A. Jones, and M. G. Betts. 2016. Spatial models reveal the microclimatic buffering capacity of old-growth forests. Science Advances 2: e1501392.

Fridley, J. D. 2009. Downscaling climate over complex terrain. High finescale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). Journal of Applied Meteorology and Climatology 48:1033-1049.

Global Biodiversity Information Facility [GBIF]. 2017. GBIF Occurrence Download <https://doi.org/10.15468/dl.ydxkfg>. Accessed 18 October 2017.

George, A. D., F. R. Thompson III, and J. Faaborg. 2015. Using LiDAR and remote microclimate loggers to downscale near-surface air temperatures for site-level studies. Remote Sensing Letters 6:924 932.

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

Hall, E. R. 1981. The mammals of North America. 2nd ed. John Wiley & Sons Inc., New York.

Hacker, A. L. 1991. Population attributes and habitat selection of recolonizing mountain beaver (*Aplodontia rufa*). Thesis, Oregon State University, Corvallis, USA.

Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2017. Package 'dismo': species distribution modeling. R package version 1.1-4.

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

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? TREE 15:56-62.

Ingles, L. G. 1959. A quantitative study of mountain beaver activity. American Midland Naturalist 61: 419-423.

Johnson, S. R. 1971. The thermal regulation, microclimate, and distribution of the mountain beaver, *Aplodontia rufa pacifica* Merriam. Ph.D. dissertation, Oregon State University, Corvallis.

Kinney, J. L. 1971. Environmental physiology of a primitive rodent. Ph.D. dissertation, University of Oregon, Eugene.

LANDFIRE. 2017. Existing vegetation type layer. LANDFIRE 1.1.0. US Department of the Interior, Geological Survey. Accessed 23 February 2017.

Miller, C. I., D. L. Delany, K. A. Hersey, M. R. Jeffress, A. T. Smith, K. J. Van Gunst, and R. D. Westfall. Distribution, climatic relationships, and status of American pikas (*Ochotona princeps*) in the Great Basin, USA. Artic, Antarctic, and Alpine Research 50: e1436296.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261-264.

National Oceanic and Atmospheric Administration [NOAA]. 2012. National Data Buoy Center. Station ANVC1 – Climatic Summary Plots for air temperature. http://www.ndbc.noaa.gov/view_climplot.php?station=anvc1&meas=at Accessed 31 Aug 2017.

Nungesser, W. and E. Pfeiffer. 1965. Water balance and maximum concentrating capacity in the primitive rodent, *Aplodontia rufa*. Comparative Biochemistry and Physiology 14:289-297.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature. 421:37-42.

Pearson, R. G. and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelopes useful? Global Ecology and Biogeography 12:361-371.

Piaggio, A. J., B. A. Coghlan, A. E. Miscampbell, W. M. Arjo, D. B. Ransome, and C. E. Ritland. 2013. Molecular phylogeny of an ancient rodent family (Aplodontiidae). Journal of Mammalogy. 94:529-543.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling 190:231-259.

Phillips, S. J., R. P. Anderson, M. Dudík, R. E. Schapire, and M. E. Blair. 2017. Opening the black box: an open-source release of Maxent. Ecography 40:887-893.

Phillips, S. J., M. Dudík, and R. E. Schapire. 2018. Maxent software for modeling species niches and distributions (Version 3.4.1). http://biodiversityinformatics.amnh.org/open_source/maxent, Accessed on 05 March 2018.

Potter, K. A., H. A. Woods, S. Pincebourde. 2013. Microclimatic challenges in global change biology. Global Change Biology 19:2932-2939.

Pyron, R. A., G. C. Costa, M. A. Patten, and F. T. Burbrink. 2015. Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. Biological Reviews 90:1248-1262.

Ray, C., E. A. Beever, and T. J. Roadhouse. 2016. Distribution of a climate-sensitive species at an interior range margin. Ecosphere 7:e01379.

Rapacciuolo, G., S. P. Maher, A. C. Schneider, T. T. Hammond, M. D. Jabis, R. E. Walsh, K. J Iknayan, G. K. Walden, M. F. Oldfather, D. D. Ackerly, S. R. Beissinger. 2014. Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. Global Change Biology 20:2841-2855.

Shi, H., D. Paull, L. Broome, and H. Bates. 2014. Microhabitat use by mountain pygmy-possum (*Burramys parvus*): Implications for the conservation of small mammals in alpine environments. Austral Ecology 10.1111/aec.12220.

Smith, A. T. 1974. The distribution and dispersal of pikas: influences of behavior and climate. Ecology 55:1368-1376.

Smith, A. B. 2018. enmSdm: Tools for modeling species niches and distributions. R package version 0.2.2.5. http://www.earthskysea.org

Terando, A. J., E. Youngsteadt, E. K. Meinke, and S. G. Prado. 2017. Ad hoc instrumentation methods in ecological studies produce highly biased temperature measurements. Ecology and Evolution 7:9890-9904.

Torregrosa, A., C. Combs, and J. Peters. 2016. GEOS-derived fog and low cloud indices for coastal north and central California ecological analyses. Earth and Space Science 3(2):46-67.

U.S. Fish and Wildlife Service. 1998. Point Arena mountain beaver (*Aplodontia rufa nigra*) (Rafinesque)) recovery plan. Region 1, Portland, OR.

Varner, J., and M.D. Dearing. 2014. The importance of biologically relevant microclimates in habitat suitability assessments. PLoS ONE 9:e104648.

Wake, T.A. 2006. Archaeological sewellel (*Aplodontia rufa*) remains from Duncan's Point Cave, Sonoma County, California. Journal of Mammalogy 87:139-147.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J.C. Bebee, J. M. Fromentin, O. Hoegh-Guldber, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62: 2868-2883.

Warren, D. L. R. E. Glor, and M. Turelli. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33:607-611.

Warren, D. L., and S. N. Seifert. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecological Applications 21: 335-342.

Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, E. I. Damschen, T. J. Davies, J. A. Grytnes, S. P. Harrison, B. A. Hawkins, R. D. Holt, C. M. McCain, and P. R. Stephens. 2010. Niche conservatism as an emerging principle in ecology and conservation. Ecology Letters 13:1310-1324.

Wilkening, J. L., C. Ray, E. A. Beever, and P. F. Brussard. 2011. Modeling contemporary range retraction in Great Basin pikas (Ochotona princeps) using data on microclimate and microhabitat. Quaternary International 235:77-88.

Wisz, M. S., J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C .F. Damgaard, C. F. Dormann, M. C. Forchhammer, J. A. Grytnes, A. Guisan, R. K. Heikkinen, T. T. Høye, I. Kühn, M. Luoto, L. Maiorano, M. C. Nilsson, S. Normand, E. Öckinger, N. M. Schmidt, M. Termansen, A. Timmerman, D. A. Wardle, P. Aastrup, and J. C. Svenning. 2013. The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modelling. Biological Reviews 88:15-30.

Zielinski, W. J. F. V. Schlexer, J. R. Dunk, M. J. Lau, and J. J. Graham. 2015. A range-wide occupancy estimate and habitat model for the endangered Point Arena mountain beaver (*Aplodontia rufa nigra*). Journal of Mammalogy 96:380-393.

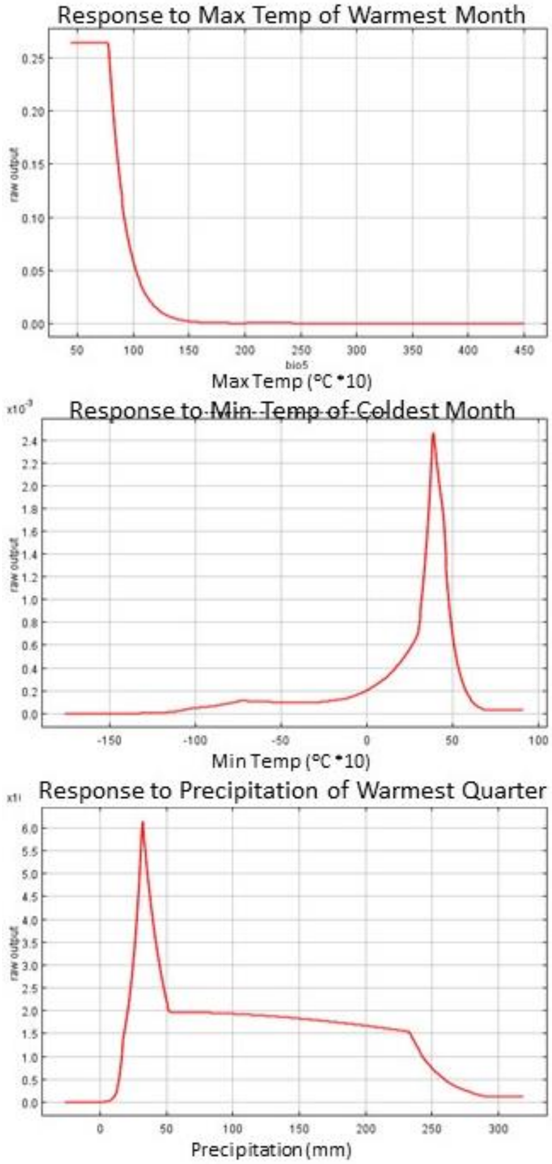
Zielinski, W. J., F. V. Schlexer, S. A. Parks, K. L. Pilgrim, and M. K. Schwartz. 2013. Small geographic range but not panmictic: how forests structure the endangered Point Arena mountain beaver (*Aplodontia rufa nigra*). Conservation Genetics 14:369-383.

Zielinski, W. J., and M. J. Mazurek. 2006. The reproductive ecology and home range of the Point Arena mountain beaver (*Aplodontia rufa nigra*). Unpublished report to the US Fish and Wildlife Service, Arcata Fish and Wildlife Office, Arcata, CA.

APPENDIX A

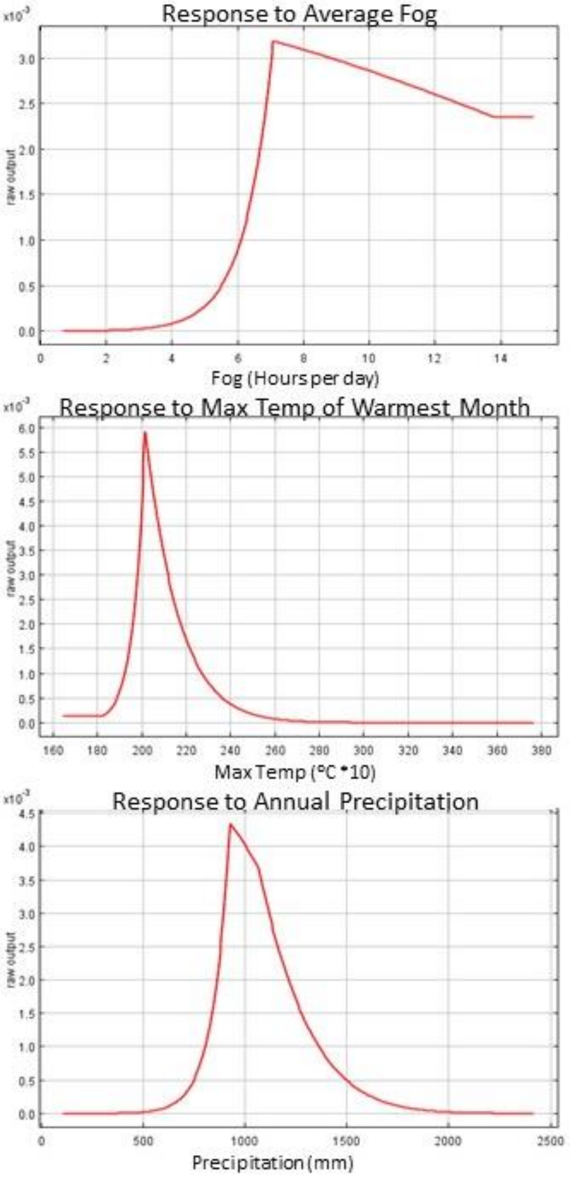
Appendix A. Responses curves, variable percent contribution and variable permutation importance for the mountain beaver species distribution models for (1) range-wide, (2) coastal, (3) pacifica, (4) rufa, (5) californica, (6) olympica, and (7) PAMB.

Appendix A1. Response curves and variable contributions for range-wide species distribution model.



Variable	Contribution	Importance
Max Temp Warmest Month	45.2%	58.0%
Min Temp Coldest Month	43.8%	25.5%
Precip Warmest Quarter	11.0%	16.5%

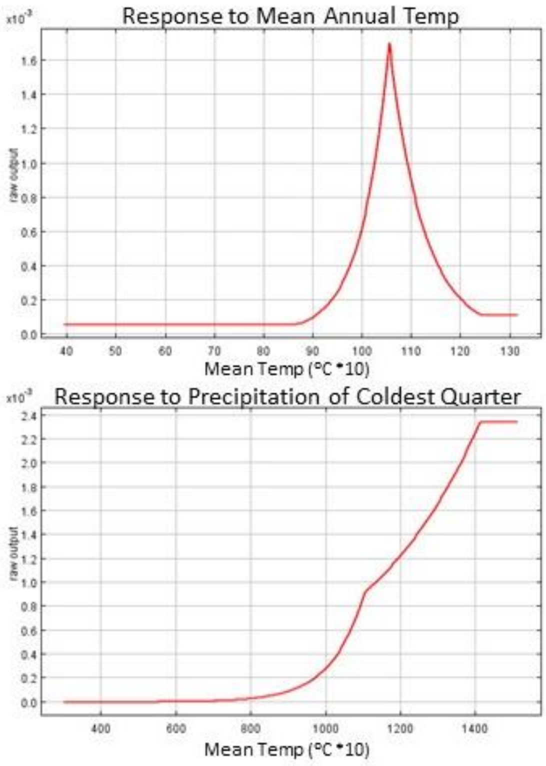
Appendix A2. Responses curves and variable contributions for the coastal species distribution model.



Variable	Contribution	Importance
Average Fog	65.3%	17.4%
Max Temp Warmest Month	11.6%	68.6%
Annual Precip	23.0%	14.0%

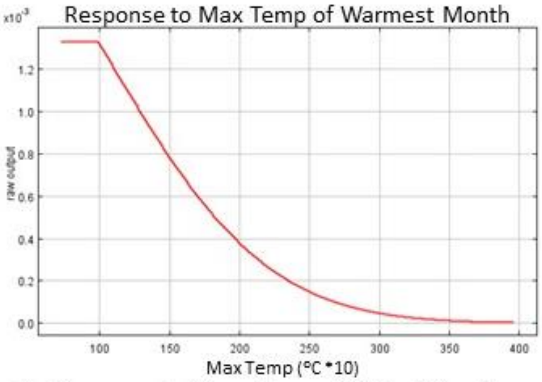
Appendix A3. Responses curves and variable contributions for the pacifica species distribution model.

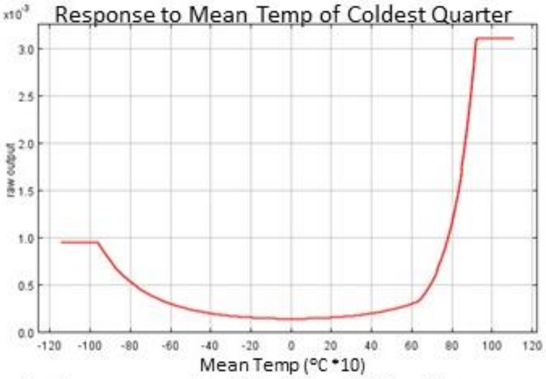
Variable	Contribution	Importance
Mean Annual Temp	22.2%	18.7%
Precip Coldest Quarter	77.8%	81.3%

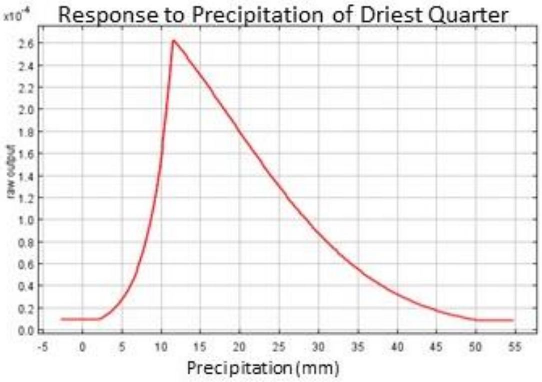


Appendix A4. Responses curves and variable contributions for the rufa species distribution model.

Variable	Contribution	Importance
Max Temp Warmest Month	14.4%	28.9%
Mean Temp Coldest Quarter	49.5%	30.4%
Precip Driest Quarter	36.1%	40.7%

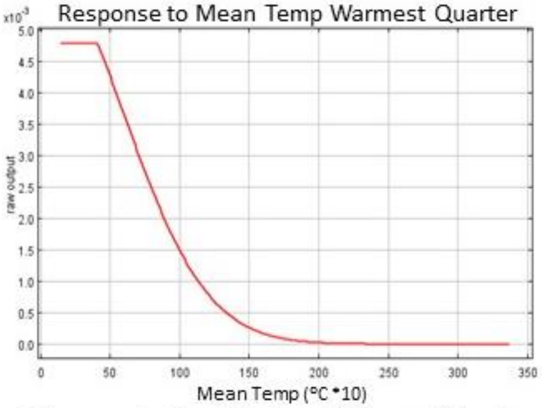


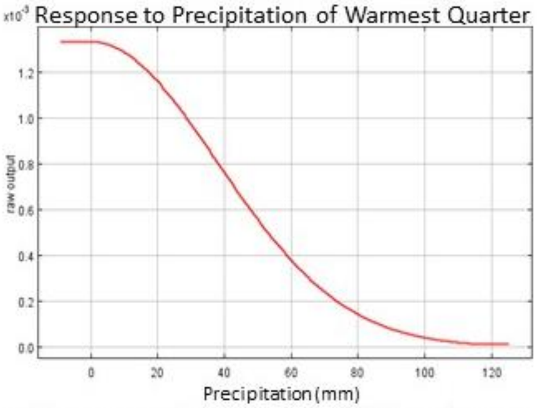


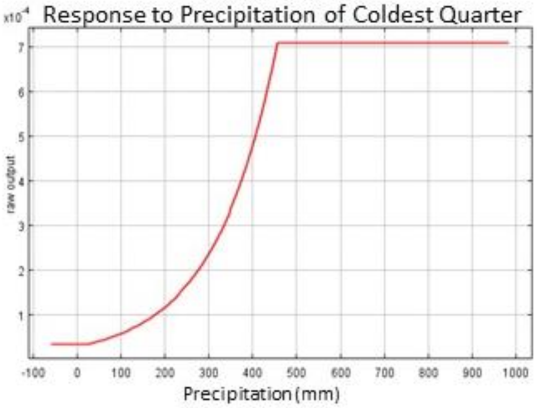


Appendix A5. Responses curves and variable contributions for the californica species distribution model.

Variable	Contribution	Importance
Mean Temp Warmest Quarter	61.2%	70.5%
Precip Warmest Quarter	9.2%	49.0%
Precip Coldest Quarter	29.6%	24.6%

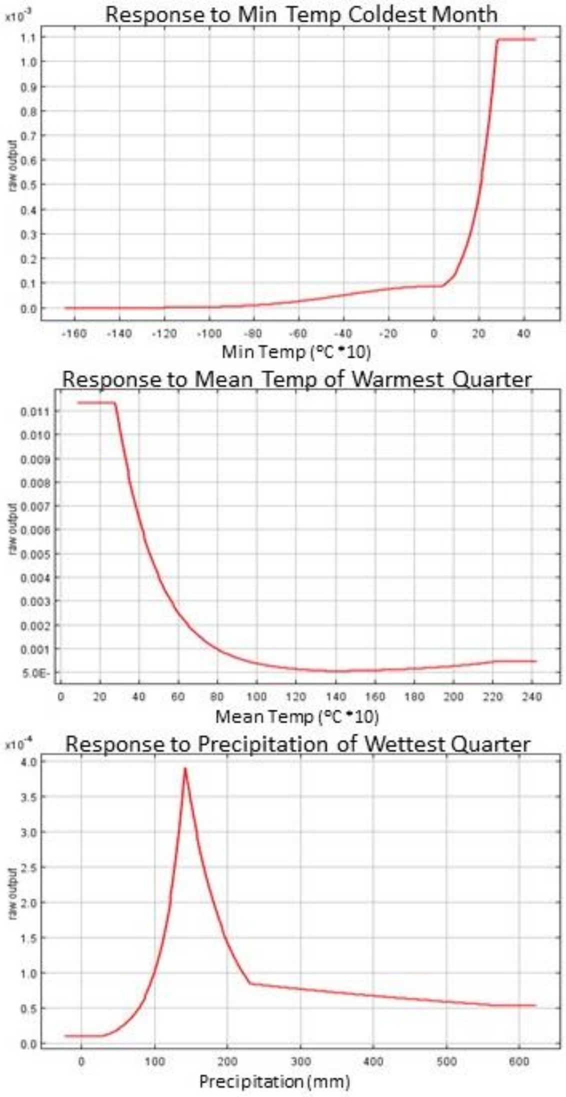






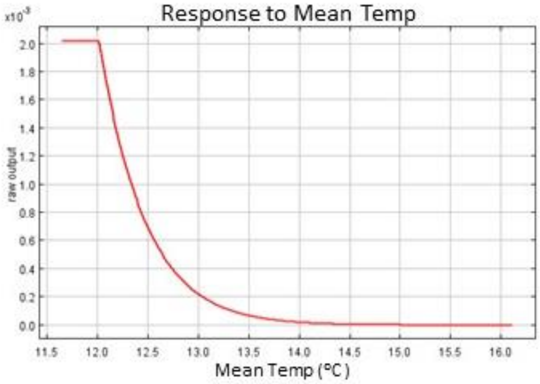
Appendix A6. Responses curves and variable contributions for the olympica species distribution model.

Variable	Contribution	Importance
Min Temp Coldest Month	64.6%	60.5%
Mean Temp Warmest Quarter	7.8%	19.3%
Precip Wettest Quarter	27.6%	20.2%

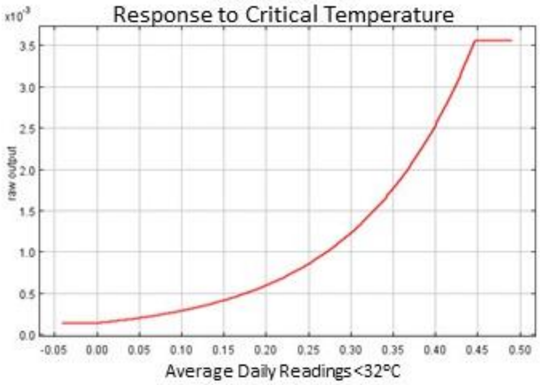


Appendix A7. Responses curves and variable contributions for PAMB species distribution model.

Variable	Contribution	Importance
Mean Temp	94.6%	84.1%
Critical Temp	5.4%	15.9%



Response to Mean Temp



Response to Critical Temperature

APPENDIX B

Appendix B. Soil moisture and temperature readings for 8 burrow areas used in paired points analysis. Use values are an average from the use sites for that reading. The average difference between the use and available sites for each burrow area are highlighted in blue for colder or moister at use sites and red for warmer or drier at use sites.

Location	Area	Reading	Temp			Humidity		
			Use	Available	Diff	Use	Available	Diff
Coastal	Miner	1	13.40	22.60	-9.20	9.90	3.60	6.30
		2	14.70	20.35	-5.65	14.50	11.15	3.35
		3	-	-	-	-	-	-
		Average			-7.43			4.83
	Davis	1	14.70	14.37	0.33	8.20	4.17	4.03
		2	13.60	14.25	-0.65	2.00	3.60	-1.60
		3	11.60	10.90	0.70	13.40	11.33	2.07
		Average			0.13			1.50
	Dune	1	16.40	19.17	-2.77	0.00	0.00	0.00
		2	14.70	16.85	-2.15	0.00	0.00	0.00
		3	-	-	-	-	-	-
		Average			-2.46			0.00
	AlderCoast	1	15.50	16.47	-0.97	1.50	5.33	-3.83
		2	14.30	15.77	-1.47	0.00	2.13	-2.13
		3	10.70	11.17	-0.47	11.10	13.53	-2.43
		Average			-0.97			-2.80
Inland	Moat	1	14.90	13.90	1.00	0.00	7.97	-7.97
		2	-	-	-	7.40	7.75	-0.35
		3	-	-	-	-	-	-
		Average			1.00			-4.16
	Alder	1	11.50	12.50	-1.00	0.00	0.87	-0.87
		2	13.00	13.70	-0.70	5.30	8.53	-3.23
		3	10.20	11.17	-0.97	-	-	-
		Average			-0.89			-2.05
	Owl	1	12.50	13.30	-0.80	9.50	9.07	0.43
		2	10.20	11.20	-1.00	8.70	9.77	-1.07
		3	-	-	-	11.40	14.93	-3.53
		Average			-0.90			-1.39
	Mallo	1	12.80	11.83	0.97	14.20	2.10	12.10
		2	12.80	12.67	0.13	3.00	0.23	2.77
		3	9.40	11.65	-2.25	9.20	2.95	6.25
		Average			-0.38			7.04