Regional Habitat Variation for Pygmy Rabbits

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by Lindsey M. Rush

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AUTHORIZATION TO SUBMIT THESIS

This thesis of Lindsey M. Rush, submitted for the degree of Master of Science with a Majorin Natural Resources and titled, "Regional Habitat Variation for Pygmy Rabbits," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

The pygmy rabbit (*Brachylagus idahoensis*) is a sensitive species endemic to the sagebrush steppe ecosystem of the western USA. As ecosystem engineers and sagebrush obligates, pygmy rabbits and their connection to sagebrush have made the species fascinating to study. In Idaho, federal and state agencies are currently focusing on conservation and restoration of sagebrush habitats, and for certain species like pygmy rabbits, information about their distribution and habitat relationships is incomplete. Sagebrush habitats available to pygmy rabbits across their range are diverse, and a better understanding of the characteristics that influence their presence is necessary for future conservation actions. This thesis investigates how habitat relationships of pygmy rabbits differ across five ecological regions in Idaho and how certain environmental characteristics influence habitat suitability.

We modeled predicted species distribution for five distinct ecological regions in Idaho, identifying environmental characteristics that influence suitable habitat for the species, while also identifying areas of predicted suitable habitat within each region. We created inductive species distribution models (SDMs) using maximum entropy methods that included a suite of environmental predictor variables representing topography, vegetation, climate, and soil characteristics. Results of the regional models identified substantial variation in habitat associations across the five regions, with each retaining a unique set of environmental predictors. Bioclimatic variables were the most influential environmental parameters in all five regions, but the specific variables differed among all regions. The models that were developed at regional extents predicted smaller areas of habitat (an average of 15% less for suitable habitat and 80% less for primary habitat) than predictions generated from a model developed at the extent of the entire range of the species. Lastly, we projected the regional models using future climate scenarios to explore how future climate conditions might affect predicted suitable habitat for pygmy rabbits. Significant reductions in suitable habitat were projected across the study area, but variation among regions also was apparent. Although these projections should be interpreted with caution, they suggest that climate-driven changes in the environment could have large and varying effects on persistence of habitat for pygmy rabbits in Idaho.

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DEDICATION

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CHAPTER 1: ENVIRONMENTAL RELATIONSHIPS VARY ACROSS REGIONS FOR A HABITAT SPECIALIST: COMPARING SPECIES DISTRIBUTION MODELS FOR PYGMY RABBITS

(manuscript in preparation, coauthors: Leona K. Svancara, Ian T. Smith, Sonya J. Knetter, Jason W. Karl, Janet L. Rachlow)

ABSTRACT

Habitat relationships can differ across the geographic range of species, especially for widespread generalists. In contrast, habitat specialists are believed to exhibit relatively consistent habitat use throughout their ranges. The pygmy rabbit is a sagebrush-dependent habitat specialist of conservation concern that has a broad but patchy distribution across the sagebrush biome of the western USA. Our goal was to model habitat associations for pygmy rabbits to evaluate regional variation and contrast predictions from models developed at more local extents with results from a model developed at a rangewide extent. We created inductive species distribution models (SDMs) using maximum entropy methods within five ecological regions that encompassed about 20% of the species rangewide distribution and spanned environmental gradients in climate, topography, and vegetation. We included a suite of environmental predictor variables representing topography, vegetation, climate, and soil characteristics. Results of the regional models identified substantial variation in habitat associations across the five regions, with each retaining a unique set of environmental predictors. Bioclimatic variables were the most influential environmental parameters in all five regions, but the specific variables differed among all regions. The models that were developed at regional extents predicted smaller areas of habitat (an average of 15% less for suitable habitat and 80% less for primary habitat) than predictions generated from a model developed at the extent of the entire range of the species. Because bioclimatic variables were effective in discriminating areas used by pygmy rabbits, they also provided an opportunity to assess potential future habitat distribution under various climate change projections. Habitats modeled under two climate scenarios projected substantial reductions in suitable habitat for pygmy rabbits across most regions and pronounced variation among regions in the magnitude and direction of the climate effects. Collectively, results of this work underscore the need to incorporate regional variation in habitat associations into planning for current and future conservation and management strategies.

Keywords: bioclimatic, climate, habitat specialist, Maxent, pygmy rabbit, sagebrush, species distribution models, SDM

INTRODUCTION

Habitat relationships can differ substantially across the geographic range of a species. Both theoretical (Brown 1984) and more recently empirical evidence (Slatyer et al. 2013) support a positive relationship between geographic range size and niche breadth. Variation in availability or distribution of resources can result in context-dependent habitat selection (i.e., functional response; Mysterud & Ims 1998; Holbrook et al. 2015) that differs across environmental gradients. In addition, species characterized as generalists can live in a broader range of environments and thus, exhibit greater variation in habitat associations (Fridley et al. 2007; Grassel & Rachlow 2009; Pandit et al. 2009). In contrast, habitat specialists, by definition, persist within a narrower range of environmental conditions and are more likely to exhibit consistency in habitat use throughout their distribution (McPeek 1996). However, the generalist-specialist classification represents an ecological continuum (Fridley et al. 2007, Shipley et al. 2009), and widespread specialists are likely to encounter and respond to greater habitat heterogeneity across their ranges (Doherty et al. 2016) and thus, exhibit local adaptability.

Because habitat specialists are affected by habitat change to a greater degree than generalists (Devictor et al. 2008; Berger et al. 2014; Matthews et al. 2014), understanding the factors that shape their distributions is critical for guiding land management and developing conservation and habitat restoration strategies. Assumptions about consistent habitat associations for habitat specialists throughout their range, however, might be misleading with respect to strategic habitat conservation, and for uncommon specialists, might result in omitting suitable habitats from field surveys aimed at documenting species occurrence. The importance of these issues is heightened given ongoing anthropogenic changes to ecosystems and their disproportionate effects on specialist species (Davies et al. 2011; Travis 2003). Globally, human activities tend to expand the distribution of widespread habitat generalists while restricting the ranges of specialists (Newbold et al. 2018; Pandit et al. 2009). Effective conservation of habitat specialists will be advanced by incorporating an understanding of diversity in habitat relationships and adaptability to environmental variation. Indeed, failing to integrate intra-specific variation in response to climate change could contribute to misinterpreting mechanisms influencing population persistence and misdirecting conservation efforts aimed at mitigating the consequences (Hällfors et al. 2016, Nice et al. 2019).

Species distribution models (SDMs) are commonly used in conservation planning to evaluate relationships between species and their environments and to predict distributions of species and their habitats based on statistical relationships between known occurrences and environmental gradients (Franklin 2013; Guisan et al. 2013). SDMs are useful for identifying suitable habitats provided important environmental characteristics associated with the presence of a species are included in the model (Elith & Leathwick 2009) and the environmental variables identify characteristics that constrain the species distribution (Jarnevich et al. 2015). SDMs that incorporate climatic conditions also provide a mechanism for exploring how distribution of habitats and species might change under future climate scenarios (Guisan & Thuiller 2005).

The scales at which SDMs are constructed can vary from global to local, which influences both model performance and utility for different objectives (Fois et al. 2018). As the scale of a model changes, tradeoffs occur between specificity and the ability to generalize model outcomes (Elith & Leathwick 2009; Phillips et al. 2017a). Models developed with fine-resolution environmental data over small extents are hypothesized to be more accurate with respect to characterizing habitat suitability and predicting species occurrence, while SDMs developed across broad extents with coarse-scale environmental data are likely to result in greater commission errors (Fernández et al. 2013; Manzoor et al. 2018). Similarly, broad rangewide models are likely to miss or underestimate any local adaptability. Understanding the limits and implications of uncertainty in distribution models is important for both model development and application of model results.

We quantified habitat associations and predicted distributions of suitable habitat for an uncommon habitat specialist of conservation concern. Our study focused on the pygmy rabbit *(Brachylagus idahoensis)*, a small mammal endemic to sagebrush biome in the western USA. Pygmy rabbits are a sagebrush (*Atremisia* spp.) specialist and are currently designated as vulnerable, imperiled, or critically imperiled in all nine states within which it occurs (IDFG 2015; NatureServe 2020). Although the sagebrush biome encompasses over 65 million hectares, many processes have reduced and fragmented sagebrush landscapes, including fires, livestock grazing, energy development, agriculture and other anthropogenic land uses, and invasion of non-native plants (Davies et al. 2012; Remington et al. 2021). Consequently, the extent and quality of sagebrush habitats are decreasing, which directly and indirectly affects wildlife communities (Carr et al. 2015; Remington et al. 2021). Some of the >350 vertebrates that occupy sagebrush landscapes, like American badgers (*Taxidea taxus*) and red-tailed hawks (*Buteo jamaicensis*), are widespread habitat generalists (Dobkin & Sauder 2004). Other species like Greater sage-grouse (*Centrocercus urophasianus*), sagebrush voles (*Lemmiscus curtatus*), and pygmy rabbits, are considered obligate species that only occur in sagebrush-dominated environments, and consequently, are particularly vulnerable to loss, modification, and fragmentation of sagebrush habitats (Aldridge et al. 2008; Pierce et al. 2011).

Sagebrush vegetation serves several functions for pygmy rabbits. Despite the presence of plant secondary metabolites (Ulappa et al. 2014), sagebrush accounts for >95% of the diet of pygmy rabbits during winter and about 50% during summer (White et al. 1982; Shipley et al. 2006). Sagebrush shrubs also provide habitat structure, security from predators (McMahon et al. 2017; Jimenez et al. 2020), and thermal shelter (Milling et al. 2017). Because pygmy rabbits are obligate burrowers (Green & Flinders 1980), soil properties that support burrow construction and integrity also influence their distribution (Gabler et al. 2001; Larrucea & Brussard 2008a). Deeper, loamy soils not only accommodate burrowing, but also support greater growth potential for sagebrush shrubs (Barnard et al. 2019).

Sagebrush communities across the western USA are diverse, encompassing sagebrush steppe and sagebrush shrublands (Kulcher 1964). This heterogeneous region spans six floristic provinces (Ertter & Moseley 1992) with elevations from 150 m to >3,000 m, and environments ranging from semi-arid basins to subalpine (Miller & Heyerdahl 2018). Although presence of sagebrush and suitable soil properties likely limit the distribution of pygmy rabbits, use of these resources and other environmental conditions may vary across their geographic range, and despite being habitat specialists, pygmy rabbits are distributed across much of the sagebrush biome (Smith et al. 2019a).

We explored intra-specific variability in habitat associations for the pygmy rabbit and how predicted distribution of habitat differed between rangewide and more localized scales.

We used locations of pygmy rabbits recorded since 2000 to create a series of localized SDMs encompassing portions of the species range in Idaho, USA. Our objectives were to: 1) model the distribution of suitable habitat for pygmy rabbits within distinct ecological regions and contrast habitat factors that predict species distribution among regions; 2) compare region-specific predictions with outcomes from a model created at the extent of the species range (Smith et al. 2019a); and 3) use the regional models to evaluate how the distribution of suitable habitats for pygmy rabbits might change under future climate scenarios. We hypothesized that variables defining suitable habitat for pygmy rabbits would differ among regions because of variation in environmental characteristics and potential local adaptations. We predicted that climate variables would influence distributions to a greater extent in the southwestern and southern regions that are characterized by relatively hot and dry summers, and that topographic features would be more important in the northern and eastern regions that have greater diversity in elevation, slope, and topography. Second, although we expected substantial overlap between the rangewide and regional habitat model predictions, we hypothesized that the regional SDMs would identify significantly smaller areas of suitable habitat because they are fine-tuned to the location data and environmental variables within each regional extent. Finally, because we expected that climatic variables would influence the current distribution of pygmy rabbits, we evaluated the extent to which predicted habitat distribution might change under future climate scenarios.

METHODS

Study Area

Our study focused on the distribution of pygmy rabbits in Idaho, USA, in the central portion of the species' geographic range (Fig. 1 inset). We defined five ecological regional extents occupied by pygmy rabbits across southern Idaho for development of region-specific SDMs. To determine the regional extents, we first examined polygons defined by the Bureau of Land Management (BLM) to designate fine-scale habitat management regions for the greater sage-grouse (*Centrocercus urophasianus*). Boundaries of those polygons reflect hydrologic units and barriers to movement of grouse based on telemetry data (Stiver et al. 2015). We overlaid known occurrences of pygmy rabbits on the sage-grouse polygons and then merged fine-scale polygons to five create ecological regions that encompassed distinct areas occupied by pygmy rabbits (Regions: 1 - Owyhee Desert, 2 - Southern Desert, 3 - Central Desert, 4 - Bear Lake, and 5 - Lemhi-Salmon). Three of the five regions overlap slightly with the neighboring states of Oregon, Nevada, Utah, and Wyoming (Fig. 1).

The climate in southern Idaho is characterized by cold winters and hot, dry summers with most precipitation occurring during the cool season months (November-May; Runkle et al. 2017). The low-elevation areas of southern Idaho are shielded by mountains to the east and west resulting in generally limited precipitation (Runkle et al. 2017). Variation in precipitation and temperature patterns exists among the five modeling regions (Table 1; WWRC 2018). In general, the southwestern portion of our study area has the lowest historical precipitation values and highest mean annual temperatures, and the eastern portion has the lowest mean annual temperatures and highest precipitation (PRISM data; PRISM Climate Group 2012; Table 1).

Vegetation characteristics vary across the study area. The five ecological regions we defined coincide with five divisions of Idaho's floristic provinces (Ertter & Moseley 1992). Within our study area, big sagebrush (*Artemesia tridentata*) and green rabbitbrush (*Chrysothamnus viscidiflorus*) are common shrub species across lower elevations, especially along drainages and alluvial fans. On the lower elevation flats, isolated areas of low sagebrush (*Artemesia arbuscula*), bitterbrush (*Purshia tridentata*), shadscale (*Atriplex confertifolia*), and spiny greasewood (*Glossopetalon spinescens*) are also common. The dominant tree species found within the sagebrush-steppe ecosystem are western juniper (*Juniperus occidentalis*) and Utah juniper (*J. osteosperma*), but there are also populations of pinyon pine (*Pinus monophylla*) scattered throughout. Many of the sagebrush-steppe habitats in southern Idaho include an understory of mixed native grasses (e.g., bluebunch wheatgrass, *Pseudoroegneria spicata;* Sandberg's bluegrass, *Poa secunda*; bottlebrush squirreltail, *Elymus elymoides*; Indian ricegrass, *Achnatherum hymenoides*), seeded perennial grasses (e.g., crested wheatgrass, *Agropyron cristatum*), and annual invasive species (e.g., cheatgrass, *Bromus tectorum*).

The study area is characterized by a diversity of topographic features. In general, the eastern portion of the study area is characterized by higher elevations and a greater range of slopes (Table 2). The Lemhi-Salmon Region (Region 5) in east-central Idaho has broad valleys bounded by high mountain ranges including the Continental Divide of the Rocky

Mountains, which runs along the eastern border. The Owyhee Desert Region (Region 1) is characterized by a combination of mountains and deep river canyons. In addition, the distribution of land ownership and land use differ markedly across the five regions. In general, populations of pygmy rabbits in Idaho occur on multiple-use public rangelands managed by the BLM and at higher elevations, open lands managed by the US Forest Service (FS). Public rangelands are often embedded in a mosaic of private lands managed as pastures or agricultural land with native habitat adjacent or nearby. Across public and private lands, livestock grazing is one of the most common land uses. Like much of the sagebrush ecosystem in the western USA, fires have increasingly impacted sagebrush communities in our study region (Mata-Gonzalez et al. 2018; Miller & Heyerdahl 2018).

Location Data

We acquired occurrence records for pygmy rabbits collected during 2000-2019 within the five regional extents across southern Idaho and portions of Oregon, Nevada, Utah, and Wyoming from multiple sources (Fig. 1). Most of the data were obtained from the Idaho Species Diversity Database (ISDD: https://idfg.idaho.gov/species/). We used additional locations from recent studies of pygmy rabbits completed in the Salmon-Lemhi Region (Region 5; e.g., Camp et al. 2013; McMahon et al. 2017) and locations from recent field surveys conducted by BLM biologists in southwestern Idaho (Region 1). Location data from neighboring states were provided by individual state agencies and used in a rangewide modeling effort for this species (Smith et al. 2019a). We vetted all data to ensure reliability and retained only records for which species identification was confirmed via photographs, sightings, collection of field specimens, or confirmed pellets at burrow sites. The verified occurrences were then buffered to remove locations closer than 250 m, which is the approximate diameter of a female home range (Estes-Zumpf and Rachlow 2009). Lastly, we removed any occurrences within a recent fire perimeter that burned during 2000-2019. In total, 1,584 presence locations were included within the five regional extents (n = 421, 103, 167, 159, 734 in Regions 1-5, respectively). We also randomly generated approximately 10,000 background points, or pseudo absences, within each region using ArcMap 10.6.1 for use in the modelling process; these points also were spatially buffered by 250 m, and the actual number per region (n = 9,045 to 9,904) differed with region size. Areas with no vegetation information in the land cover data (e.g., water, cities) were not included in the background points.

Environmental Data

We used environmental data layers to evaluate a suite of habitat variables potentially associated with occurrence of pygmy rabbits. Environmental data used for the SDMs included bioclimatic variables, soil characteristics, vegetation properties and topography (Table 3). Because the data were collected from multiple sources, the scales differed among layers, so we resampled all data to 30-m resolution. We ensured that all layers had the same projection and coordinate system (Albers equal-area conic projection, North American Datum (NAD) 1983, Contiguous United States), geographic bounds, and cell size, and that all raster files were converted to ASCII file format for input into R 3.5.2 (R Core Team 2018) and Maxent 3.4.0 (Phillips et al. 2017b).

Land cover – Land cover variables used for modeling habitat for pygmy rabbits included vegetation types known to be used (e.g., sagebrush), or alternately, avoided by the species (e.g., trees). Tree canopy cover has been negatively associated with pygmy rabbits, presumably because trees provide perches for avian predators, and increasing tree cover is associated with a reduction of the sagebrush shrub understory (Larrucea & Brussard 2008b; Woods et al. 2013; Edgel et al. 2014). Agricultural lands also are expected to be avoided by pygmy rabbits, although some rabbits may use sagebrush habitats adjacent to agricultural lands. During this project, multiple national datasets were updated, and consequently, we incorporated components from both newly updated and previous versions. Primarily, we used the updated Rangeland Fractional Components dataset from the National Land Cover Database (USGS 2020; Rigge et al. 2019). In addition, we included variables from the 2016 land cover database (i.e., agricultural land cover; USGS 2016a), the 2016 NLCD USFS Tree Canopy Cover (i.e., tree canopy cover; USGS 2016b), and the Provisional Remote Sensing Shrub/Grass NLCD Base Products for the Western US (i.e., sagebrush canopy cover; USGS 2016c).

Although pygmy rabbits are associated with relatively high densities of sagebrush and other shrub species, many studies also have reported the importance of an understory of grasses and forbs (e.g., Heady & Laundré 2005; Larrucea & Brussard 2008a). The Rangeland Fractional Components dataset included a layer depicting percent herbaceous cover, along with a nested subset layer for cover of annual herbaceous plants. Because grasses and forbs comprise roughly half of the summer diet of pygmy rabbits (Shipley et al. 2009; Schmalz et al. 2014), we also included a measure of vegetation productivity, Normalized Difference Vegetation Index (NDVI), estimated for the late summer period. We used cloud-free eMODIS 7-day composite NDVI images (USGS 2016d) from July, August, and September to calculate the mean monthly maximum NDVI values, and the intra-seasonal average and standard deviation from 2000 to 2016. This variable was used in previous work to model distributions for both sage-grouse and pygmy rabbits in Idaho (Smith et al. *in review*). Lastly, because studies have linked presence of pygmy rabbit burrows to areas of reduced ground litter and microbiotic crust (e.g., Weiss & Vert 1984; Himes & Drohan 2007; Edgel et al. 2014) or reduced herbaceous cover (Gabler et al. 2001), we also included percent litter and percent bare ground variables to reflect these ground covers from the updated Rangeland Fractional Component dataset (Rigge et al. 2019).

Topography – We included topographic features in the regional models because they can also influence animal habitat, usually by altering soil deposition, vegetation composition and growth, thermal environments, and properties of precipitation (Table 3). We resampled a 1/3 arc-second, 10-m resolution national elevation dataset (NED; USGS 2019) to create 30-m resolution raster data layers for elevation, slope, and curvature using *Topography Tools* (ArcGIS 2010; Dilts et al. 2015) in ArcMap 10.7.1. We created a data layer for a topographic position index (TPI) by calculating the normalized difference between elevation at a central pixel and the surrounding average elevation, and we selected 500m focal radius to represent slope position and general landforms (Weiss 2001). We also estimated an index of terrain roughness at a 200-m scale by calculating the standard deviation of elevation to represent terrain ruggedness associated with the approximate size of an individual's home range.

Soils – We included soil properties because pygmy rabbits are obligate burrowers and relatively deep, loamy soils that retain integrity of burrows are associated with their presence (Green & Flinders 1980). Soil depth and texture also serve as indicators for ecological conditions that influence potential vegetation, and relatively deep, well-drained soils in areas used by rabbits also support greater shrub growth (Weiss & Verts 1984). We included soil parameters in the models from the POLARIS soils database (Chaney et al. 2016). We calculated mean values for eight soil characteristics (bulk density, pH, organic matter percentage, clay percentage, sand percentage, silt percentage, saturated water content (Theta-S), and depth to restrictive layer; Table 3).

Climate – Pygmy rabbits are small-bodied endotherms that can be affected by climate directly because seasonal thermal extremes are often outside of their thermal neutral zone (Katzner & Parker 1997; Milling et al. 2018). Pygmy rabbits do not migrate or shift space use seasonally, but instead use burrows and above-ground micro-sites as thermal refuges during both winter and summer seasons (Milling et al. 2018). Climate also can influence the distribution of pygmy rabbits indirectly through effects on vegetation growth and soil development. We modeled the influence of temperature and precipitation by including 19 bioclimatic variables (Hijmans et al. 2005) from long-term datasets describing average conditions during 1981-2010 (PRISM Climate Group, 2012; Table S1). These variables are commonly used to model the bioclimatic conditions shaping species distributions (e.g., Elith et al. 2006; Anderson & Gonzalez 2011; Stanton et al. 2012).

Model Development and Testing

We modeled predicted habitat for pygmy rabbits within the five ecological regions using maximum entropy modeling (Maxent 3.4.0, Phillips et al. 2006). This inductive approach uses species presence data, randomly generated background locations, and environmental information in the form of spatial raster data to estimate the relative probability of occurrence across the modeled region based on similarity with habitat conditions at known locations. With each model run, a randomly selected subset representing 80% of the presence locations was used to train the model, and predictions were tested with the held-out samples.

Prior to running the Maxent models, we completed steps to promote model fit and reduce model complexity. Our first step was to optimize the feature type and regularization multiplier using the R package *dismo* (Hijmans et al. 2020), along with function *enmSdm* v0.3.4.6 (Smith 2019b). Within Maxent, users can choose to allow the program to run a default set of feature types, which are mathematical transformations of the variables used in the modeling process that constrain the variable response curves; available feature types are linear, quadratic, product, threshold, and hinge (Elith et al. 2011; Merow et al. 2013). Instead, we chose to use the occurrence data to determine which combination of feature types was optimized to fit the relationship between occurrences and environmental characteristics. Regularization multipliers penalize the inclusion of parameters that result in little or no "gain" to the model (Merow et al. 2013). We tested a range of multipliers (values 0.5 to 5 in increments of 0.5, and values 6 to 20 in increments of 1) with different feature types to identify the best performing combination based on Akaike Information Criteria corrected for small sample size (AICc; Warren & Seifert 2011; Wright et al. 2015).

We appended the values of all environmental variables to both the occurrence locations and background points for each of the five study regions to independently model pygmy rabbit distribution and suitable habitat specific to each region. Using the optimized *enmSdm* parameters, we created full models starting with 53 environmental variables (Table 3). We selected the Cloglog output, which scales the model results (i.e., probability of species presence) to values between 0 and 1 (Phillips & Dudik 2008).We assessed model performance using a 10-fold cross-validation, in which a random subset (20%) of locations was withheld for model testing. We used the area under the receiver operating curve (AUC) to evaluate model fit using the withheld samples to assess the model's success in discriminating between presence locations and background points (Elith et al. 2011; Merow et al. 2013).

Once the full models were completed, we analyzed the contributions of each environmental variable to the model and iteratively removed highly correlated variables and those that did not contribute to the model. We interpreted two contribution-related values associated with environmental variables: percent contribution and permutation importance (PI). Percent contribution is an algorithm used by Maxent that increases the gain of the model by modifying the coefficient for a single variable; the program assigns the increase in the gain to the environmental variable(s) that the feature depends on and then converts those values into percentages at the end of the training process. Permutation importance is a relative value that measures the contribution of a single variable to the full strength of the model. When a variable's PI was low (<2%), we removed it from the model for that region; we chose this threshold to be consistent with the model building process used to create the rangewide model for pygmy rabbits (Smith et al. 2019a). To accomplish a reduction of correlated variables, we constructed a pairwise correlation matrix to identify pairs that were highly correlated ($\geq$0.8) and eliminated the variable with the lower PI. We iteratively reduced variables, reoptimized model parameters, and reran models until correlation and contribution criteria were reached. This interactive process resulted in a final "reduced" model for each region that best fit occurrence data and habitat conditions within the regional extent.

We used variable response curves to interpret how environmental variables influenced the predicted distribution of pygmy rabbits and their habitat. Two sets of response curve plots are produced by Maxent: one set displays the predicted habitat suitability as a function of one environmental variable in the model, while setting all other environmental variables in the model to the average sample values. The second set of curves represents a model that only uses a single environmental variable, showing the marginal effect of changing exactly one variable, whereas the plot including the average values of all other variables may take advantage of sets of variables changing together. Both plots reflect the dependence of predicted presence (or habitat suitability) both on the selected variable and on dependencies induced by correlations between the selected variable and other variables (Phillips et al. 2016).

Mapping Predicted Habitats

The final models for each region produced a raster dataset at 30-m resolution with a continuous range of values from 0 to 1. However, thresholds are needed to create and map classes of habitat suitability. We used two types of thresholds to categorize habitat into categories of non-habitat, suitable habitat, and primary habitat. To distinguish non-habitat from suitable habitat, we chose the value that maximized the sum of testing sensitivity plus specificity, which is often used for presence-only SDMs because it is relatively unaffected by changes in the ratio of occurrences to background points (Liu et al. 2005). For the higher threshold separating suitable from primary habitat, we used the average predicted value at occurrence locations. Consequently, all primary habitat was predicted to be the same or higher quality than the average value in places where the species was confirmed to be present. This threshold was chosen for consistency in comparing our regional models to a rangewide model and also because literature supports this "conservative" approach (Liu et al. 2016).

Predictions Under Future Climate Scenarios

To explore how potential changes in climate might influence the distribution of pygmy rabbits and their habitats, we projected the final model for each region including values for climate variables from future climate scenarios for 2050. We used two projected climate scenarios from NOAA's climate models (Representative Concentration Pathways, RCPs), identified as RCP 4.5 and RCP 8.5. The future climate data were projected by multiple climate models and shared socio-economic pathways in the Coupled Model Intercomparison Project Phase 5 (CMIP5) (AdaptWest Project 2015). A stabilization scenario, RCP 4.5, assumes that radiative forcing level conditions will stabilize at 4.5 Watt/m^2 before 2100 (Taylor et al. 2012). In contrast, RCP 8.5 represents a more extreme emissions scenario in which the radiative forcing level hits 8.5 Watt/m^2, which is typical for projections in the literature resulting in high greenhouse gas concentration levels (Taylor et al. 2012). The dataset was downloaded from the AdaptWest Project (2015) in Lambert Conformal Conic projection, at 1-km resolution, covering North America. The original dataset consisted of 48 monthly temperature and precipitation variables; we used R package *dismo* (Hijmans et al. 2020) and the function "biovars" to clip and recalculate the 48 monthly variables into the 19 bioclimatic variables that were used in the current climate model projections (Tables S1, S2). Both sets of future climate projections, RCP 4.5 and RCP 8.5, were reprojected to Albers equal-area conic projection, NAD 1983 Contiguous United States, resampled to a 30-m resolution, and then clipped to the five regional extents.

Quantifying Habitat Overlap

We compared results of our regional models with predictions generated by rangewide model by Smith et al. (2019a). Using the same methods to identify thresholds, we quantified geometric overlap for both suitable and primary habitats predicted by each model within the five regions. In addition, we mapped areas of overlap and non-overlap between the regional and rangewide models to examine differences in spatial distributions of model results.

We used a similar approach to compare predictions of the current and future regional models. Under future climate scenarios, we expected a reduction in the amount of suitable habitat and a shift in the distribution of habitat within regions. Given uncertainty in climate projections, we examined overlap between current and potential future habitat by combing suitable and primary habitat categories. We used the same thresholds and mapped non-habitat and habitat to identify areas of habitat contraction, persistence, and expansion under the two future climate scenarios.

RESULTS

Regional Habitat Models

The amount of predicted habitat for pygmy rabbits varied markedly among regions, as did the percentage of each region identified as habitat for the species. The area of predicted suitable habitat per region ranged from 20,829 to 434,307 ha, and the area of primary habitat ranged from 12,632 to 380,706 ha (Table 4). Across regions, these predictions represented 5-18% of the total area classified as suitable habitat and 1-18% identified as primary habitat. These values were higher for two regions (Regions 3 & 5) in comparison with the other regional extents (Figs. 2a & 3a). The regions differed substantially in size; Region 1 in the southwest is the largest, at >8 times larger than the smallest region (Region 4). Nonetheless, percentages of predicted habitat were not correlated with size of the regions. The largest percentage of both suitable and primary habitat was identified in Region 5 (Table 4, Fig. 3a). The AUC values for the regional models ranged from 0.821 to 0.939, indicating high discriminatory power (Table 5).

The suite of final regional models included different combinations of environmental variables, supporting the hypothesis of regional variability in habitat associations for pygmy rabbits across our study area. Each regional model retained 4 to 14 variables with unique sets of bioclimatic, land cover, topographic, and soil characteristics (Table 5). Across the five regions, no models had the same top variable or any variables in the same order of permutation importance, and no individual variable was retained in more than two regional models (Table 5).

Climate had a prominent effect on the predicted distribution of habitat across all regions. Bioclimatic variables were the most influential environmental parameters in all five regions, representing the top 1 to 4 variables in each regional model. Indeed, every regional model included at least three bioclimatic variables (Table 5). Climate variables retained in the final models included both temperature ($n = 8$) and precipitation ($n = 6$) features, however, variables associated with temperature were the most influential in four of the five regions with the exception being Region 2 (Southern Desert) where annual precipitation (BIO12) had the greatest permutation importance (Table 5).

As expected, climatic factors strongly influenced predicted distributions in the warmer and drier western portions of our study area. One bioclimatic variable (maximum temperature of the warmest month, BIO5) was the most influential variable for Region 1 in southwestern Idaho, and the next most influential variable was winter precipitation (BIO19; Table 5). Distribution was correlated with intermediate values for both variables suggesting that areas of thermal and precipitation extremes were less suitable habitat (Fig. S1). Contrary to our expectation, however, climatic variables were also influential in the cooler, eastern portion of our study area (Regions 4 & 5). Those eastern regions were more strongly influenced by temperature variables associated with annual temperature (BIO1 - annual mean temperature), the difference between summer and winter temperatures (BIO7 - annual temperature range), and winter temperatures (BIO11 - mean temperature of the coldest quarter). Response curves indicated highest predicted suitability at intermediate values for each of these variables within the ranges exhibited in the regions (Fig. S1).

Distribution across the five regions also was influenced by vegetation, however, the variables differed among regions. Although pygmy rabbits are considered sagebrush obligates, canopy cover of sagebrush was retained in only two regional models (Region 1 & 2), and in neither was it ranked among the top variables (Table 5). In those western regions, both herbaceous cover and annual herbaceous cover also were influential, which suggested that ground cover in addition to sagebrush was useful in distinguishing areas occupied by pygmy rabbits. Highest habitat suitability was associated with relatively low values of herbaceous cover (Fig. S1). Phenology (i.e., NDVI) also was retained in the model for Region 1. As expected, predicted habitat for pygmy rabbits was negatively related to tree canopy cover (Fig. S1), and this variable was strongly influential in the mountainous terrain in Region 5, where 20% of the region was characterized by tree canopy cover (Table 2). Predicted distribution also was affected by avoidance of agriculture in Region 3, which had the greatest percent of area in agriculture land cover of any region (Table 2, Fig. S1).

Soil and topographic features also exhibited a modest influence on the distribution of pygmy rabbits across most regions, but the specific environmental features differed. The only terrain or soil variable with a permutation importance >10% was roughness of the terrain in

Region 1. This southwest region is characterized by rugged canyons associated with desert rivers (i.e., Owyhee Canyonlands). Predicted habitat was strongly associated with low (0-5%) values of slope in Regions 2 and 4 (Fig. S1). Soil properties were retained only in the southwestern regions (Region 1 & 2) and included clay and sand content in the 30-100-cm stratum (Table 5).

Overlap Between Regional and Rangewide Models

As expected, models developed at the regional extents predicted smaller and more focused areas of suitable habitat for pygmy rabbits than the SDM developed at the rangewide extent (Figs. 2 & 3). Across all regions, the amount of primary habitat identified by the regional models was only 7-42% of the area predicted by the rangewide model. The pattern was similar but less pronounced for predicted suitable habitat across three of the five regions (26-61%), however, within two regions (Regions 3 & 5), greater areas of the suitable habitat category were predicted by the regional models, even though total habitat was lower (Fig. 2).

Spatial overlap between predictions from the regional and rangewide models was greater for the primary habitat category than the suitable habitat category. Across regions, an average of 60% (range = 13-85%) of the primary habitat predicted by the regional models overlapped with the same category mapped from the rangewide model (Table 6). In contrast, only 19% (range = 12-28%) of suitable habitat overlapped between models. Spatial overlap between predicted habitat from the regional and rangewide models also varied among regions (Table 6, Fig. 3). Predictions were most similar for the northcentral and northeastern regions (Region 3 & 5) and least similar for the southwestern regions (Regions 1 & 2). In those two regions, the rangewide model predicted large areas of primary and suitable habitats in areas without occurrence records for the species (Figs. 1 & 3).

Projected Habitat Under Future Climate Scenarios

Models of habitat for pygmy rabbits generated under future climate scenarios projected substantial decreases in habitat for pygmy rabbits within our study area (Fig. 4). Total predicted area of potential habitat (suitable and primary habitats combined) was reduced by 73% under the RCP 4.5 model, and four regions were projected to lose all or almost all potential habitat (Table 7). Influential bioclimatic variables that showed the largest projected changes for those regions (Table S2) indicated an increase in maximum summer temperature (BIO5; 7°C in Region 1) and an increase in mean annual temperature (BIO1; 2.4°C in Region 5). Relatively large areas of expansion and persistence of potential habitat under the RCP 4.5 model parameters were concentrated in the northeastern portion of Region 3 (Central Desert) despite overall reduction in amount of habitat within the region (Fig. 4a).

Under the more extreme climate projection (RCP 8.5), the trend was similar but more pronounced for 4 of the 5 regions for which projected habitat was reduced by an average of 82% (Table 7). Similar to the RCP 4.5 projection, potential habitat persisted in parts of Region 3, however, in the southeastern region (Region 4, Bear Lake), potential habitat was projected to increase from 9% of the region to 32% under the more extreme climate projection (Table 7, Fig. 4b). For that region, three temperature-related bioclimatic variables were the most influential (Table 5). Projected values for those variables for the RCP 8.5 model indicate a 3.4°C increase in mean annual temperature (BIO1), a 1.5°C decrease in winter temperature (BIO11), and a modest increase of 1°C for annual range of temperatures (BIO7; Table S2).

DISCUSSION

Our work demonstrates the importance of using localized, region-specific information about habitat associations for conservation and land management. Although habitat specialists are expected to be tightly coupled with a relatively narrow range of environmental conditions, we documented pronounced variation in habitat associations for pygmy rabbits, despite their status as a habitat specialist. Unique combinations of climatic, land cover, soil, and topographic features were useful in predicting the distribution of habitat for the species across diverse regions, and bioclimatic variables had strong effects on predicted habitat in all regions. The models developed at regional extents predicted smaller areas of habitat (an average of 15% less for suitable habitat and 80% less for primary habitat) than predictions generated from Smith et al.'s (2019a) model developed across the entire species range. These focused predictions can help biologists target areas for surveys, habitat conservation, restoration, or other management actions. Because climatic variables were effective in discriminating areas used by pygmy rabbits across the study area, they also provided an opportunity to incorporate potential future climate into projections of habitat distribution for the species. Although results of such models should be interpreted with caution, habitats modeled under two different climate scenarios projected substantial reductions in potential habitat for pygmy rabbits across most regions and pronounced variation among regions in the magnitude and direction of the climate effects. Collectively, results of this work underscore the need to incorporate regional variation into planning for current and future conservation strategies.

We modeled habitat for pygmy rabbits across an area that represents approximately 20% of the species geographic range and encompassed environmental gradients across multiple dimensions. These gradients likely influence habitat quality for wildlife in diverse ways, and we expected that such variation would contribute to measurable differences in habitat associations for pygmy rabbits. We expected a contrast in habitat associations from west to east across our study area, however, only some of our expectations were met.

The variables effective at discriminating occurrence locations from background points differed among all our study regions. Our expectation that topographic variables would be more influential in the higher-elevation eastern regions that exhibit greater variability in topography was not supported. In fact, only one variable (slope) was retained in the model for Region 4, and it had relatively low influence (Table 5). In contrast, climatic factors strongly influenced the distribution of the species in the western and southern regions as we expected, however, bioclimatic variables were highly influential across all regional models (although the specific variables differed among regionals). Even though the variables differed, model fit was high for all regions (Table 5), suggesting that the variability we documented across the five regional models was well-supported. An important consequence of such regional variation in habitat associations is the opportunity to fine-tune conservation and habitat management actions.

Key characteristics associated with habitat use by pygmy rabbits related to sagebrush and soil were retained in some of the regional models, however, their relative importance was overshadowed by climatic variables. As a sagebrush obligate that relies on the sagebrush shrubs for forage (Shipley et al. 2006) as well as security and thermal shelter (Milling et al. 2017), we expected that sagebrush cover would be an influential variable in the SDMs, however, only two of the five regional models included sagebrush canopy cover (Table 5). In contrast, the variables that shaped the bioclimatic envelope in each region were stronger predictors of species distribution, likely through their indirect influence on vegetation composition (Elith & Leathwick, 2009; Morales-Barbero & Vega-Álvarez 2018). Some climate variables also might directly influence pygmy rabbits. For example, BIO3 (Isothermality) represents the daily swing in temperatures relative to the annual difference between summer and winter temperatures (O'Donnell & Ignizio 2012). A similar parameter that quantifies daily temperature variability (diurnal temperature range) has direct fitness consequences for organisms that exceed the influence of elevated temperatures associated with climate change (Maguire et al. 2018; Briga & Verhulst 2015; Vasseur et al. 2014).

Similar to sagebrush, soil characteristics were retained in the final variable set for only 2 regional models. As obligate burrowers, pygmy rabbits are often associated with micro-topographic features (e.g., mima mounds, Parsons et al. 2016) and drainages, alluvial fans and hillsides that favor soil deposition (Weiss & Verts 1984). Soils data available over large spatial extents tend to be relatively coarse, and are unlikely to map such fine-scale variability. Although sagebrush and soil variables were not as useful as bioclimatic variables in predicting distribution of pygmy rabbits and their habitat at the scales of our regional models, they are required by the species. These results illustrate an important difference between habitat selection studies that generate resource selection functions and species distribution models across landscapes.

The geographic range of pygmy rabbits spans >8 degrees of latitude and >15 degrees longitude across the western USA, and given the breadth of environmental variation that exists across this range, we might expect even greater variation in habitat associations than we documented in our study area as a consequence of behavioral plasticity and adaptation to local environments. Consistent with this expectation, our regional models identified much less predicted habitat than the similarly developed rangewide model (Smith et al. 2019a, Fig. 2). Another line of evidence that supports the contention of local adaptation for this species was revealed following translocation of pygmy rabbits from surrounding states to support re-establishment of the species in the Columbia Basin in Washington, USA. Males with greater percentages of Columbia Basin ancestry were more successful in reproduction than males from other lineages, despite having limited genetic diversity (DeMay et al. 2016; DeMay et al. 2017), and this trend has continued during more recent translocation efforts (Nerkowski 2021).

Spatial overlap in predicted habitat between the rangewide and regional habitat models was evident in all regions, however, the rangewide model also identified large areas of suitable and primary habitat where no occurrence locations were documented in our study area. This result was especially evident in Regions 1 & 2 (Figs. 1 & 3). The rangewide model was built with occurrence locations from throughout the species range, and consequently, reflects habitat associations from populations elsewhere (e.g., Nevada, Wyoming, and California). This tradeoff between model specificity and generality is typical of modeling efforts at broader versus narrower extents (Elith & Leathwick 2009). Regional variation in habitat associations was documented for another wide-ranging sagebrush specialist, the greater sage-grouse (Doherty et al. 2016; State of Idaho 2019). Doherty et al. (2016) documented functional habitat responses for several environmental parameters across management zones that emphasize the importance of regional variation in conservation planning, even for highly specialized species. Intra-specific niche variation has been documented across diverse taxa (e.g., Pearman et al. 2010, Maguire et al. 2018) with implications for models of current as well as future species distributions.

Models that incorporated future climate projections resulted in substantial reductions in the amount of potential habitat for pygmy rabbits. The exception to this trend occurred in the eastern portion of the study area (Region 4 - Bear Lake) under the more extreme climate model (RCP 8.5). This region is projected to get warmer and slightly wetter (Table S2) and to support an area of habitat expansion (Fig. 4b). Similarly, despite an overall decrease in area, expansion and persistence of potential habitat was projected in the northeastern portion of Region 3 under both climate scenarios (Fig. 4). We explored the potential influence of climate change by using projected values for bioclimatic variables that strongly influenced our current SDMs. However, our projections of habitat under these future climate scenarios did not include explicit data about changes in other key environmental variables, such as soil moisture, vegetation or fire, and inclusion of such information would refine the ability to project potential habitat (Adler et al. 2021). Despite the uncertainty associated with future climate projections, however, these results also suggest that patterns of habitat change could vary regionally for this species.

Several uncontrollable factors could influence our model results. First, we obtained the most comprehensive information available on occurrence of pygmy rabbits in our study area for building the SDMs, however, knowledge about the distribution of this cryptic species is incomplete. Number of occurrences was unequal among regions, and two (Regions 1 & 5) had over 2 times the number of locations compared to the others. Studies have suggested that the strength of predictive models like Maxent is affected by the amount and distribution of presence data (El-Gabbas and Dormann 2018). We cannot determine the degree to which disparity in the number of occurrences influenced our models of predicted habitat; however, efforts to locate populations of pygmy rabbits increased following the petition to list the species under the Endangered Species Act in the 2000s (Federal Register 2005; Rachlow & Svancara 2006), which resulted in field surveys and documentation of populations throughout our study area. Consequently, known occurrences, while undoubtedly incomplete, likely reflect the distribution of pygmy rabbits across our study area. Certainly, one important outcome of this work is the opportunity to focus field surveys in areas where suitable habitat is predicted for the species but occurrences have not been documented (e.g., southeastern portion of Region 5 and northeastern portion of Region 3).

Second, given the coarse resolution of our remotely sensed environmental variables, we cannot capture the fine-scale aspects of the habitat that influence occupancy by this species. This factor is perhaps most limiting in evaluation of the effects of soil properties on distributions of pygmy rabbits. Consequently, we expect that commission errors are likely common in our predictions given that pygmy rabbits have a patchy distribution and one assumption of SDMs is that species are at equilibrium with available habitat (Pearson & Dawson 2003). Finally, although we chose thresholds to produce comparable habitat suitability categories for comparison with Smith et al. (2019a), those choices influence the amount and distribution of predicted habitats, and other threshold values would produce different estimates.

Pygmy rabbits are a habitat specialist endemic to the sagebrush ecosystem. The species is unique among mammalian vertebrates in almost exclusive consumption of sagebrush vegetation (Shipley et al. 2006) and the ability to tolerate plant secondary metabolites that characterize sagebrush (Shipley et al. 2012). Yet even these habitat specialists exhibited apparent variation in habitat use across their range. This result demonstrates that regional ecological context is important, even for species that are tightly coupled to specific habitats. Understanding the processes that underlie this variation in habitat association is necessary for anticipating how species might adapt to climate change and other anthropogenic factors that alter the environment. For example, another lagomorph that is an alpine habitat specialist, the American pika (*Ochotona princeps*), is expected to be strongly and negatively influenced by climate change. However, pikas also exhibit diverse habitat associations and behavioral responses throughout their range (Beever et al. 2017; Rodhouse et al. 2018, Smith et al. 2019b) that could modulate the species response to environmental change (Smith et al. 2019c). The degree to which pygmy rabbits can adjust behaviors (e.g., use of burrow systems) to adapt to changing climatic conditions is unknown, but research on current patterns of activity suggest that burrow use is responsive to seasonal and diurnal fluctuations in temperature (Milling 2018).

MANAGEMENT IMPLICATIONS

Our work has implications for conservation of pygmy rabbits and their habitats throughout their range. Given that pygmy rabbits are uncommon and have traits that make the species challenging to detect without targeted field surveys (i.e., patchy distribution across a variety of scales, low population densities, cryptic behaviors), the SDMs we developed can help biologists to refine field surveys to better understand patterns of occurrence within our study area, and this approach could be applied to guide surveys in other regions. As new information becomes available, the SDMs can be reevaluated and updated to support increased understanding of the species ecology and distribution.

Second, the regional variation we documented lays a foundation for investigating processes that shape variation in habitat associations and other factors that might constrain the species' distribution disproportionately across regions. Finally, habitat suitability models that are tuned to specific regions can help land managers target habitat conservation and restoration efforts, and provide guidance for siting infrastructure (e.g., energy development, roads, fire breaks) to reduce impacts on potential habitat for this species of conservation concern while still providing for multiple land uses. Additionally, models that incorporate future climate scenarios for this species suggest large changes in the distribution and amount of potential habitat, and such information can inform a proactive approach to conserve habitats for pygmy rabbits and other sagebrush-dependent wildlife. More broadly, this work demonstrates that even habitat specialists exhibit regional variation in habitat associations.

Advancing our understanding of why such variation exists and how it may contribute to population characteristics like survival and reproduction can help design effective conservation strategies that are responsive to changing environments.

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Table 1. *Representative climate conditions for five regions defined to model regional habitat for pygmy rabbits in Idaho and neighboring states, USA. Values represent averages for the period of 1980-2020 recorded by Remote Automatic Weather Stations (RAWS) located close to populations of pygmy rabbits within each region.*

	Maximum summer temp. (°C)	Minimum summer temp. (°C)	Maximum winter temp. (°C)	Minimum winter temp. (°C)	Winter snow depth (cm)	Total annual precipitation (cm)
Region 1	28.6	8.8	4.4	-7.3	0.0	21.1
Region 2	28.1	9.7	1.2	-8.3	5.8	27.9
Region 3	27.6	6.5	-0.3	-13.7	34.5	36.8
Region 4	26.3	4.3	-0.3	-14.6	5.1	20.3
Region 5	25.9	9.1	-0.4	-13.1	13.5	26.4

Table 2. *Environmental characteristics within five regions defined to model regional habitat for pygmy rabbits in Idaho and neighboring states, USA. Data were accumulated for each regional extent from the model input data layers (see Table 3).*

Environmental Variables	**Region 1**	**Region 2**	**Region 3**	**Region 4**	**Region 5**
Avg. elevation (m)	1,562	1,713	1,485	2,096	2,057
Elevation range (m)	666-2,971	785-3,299	755-3,136	1,803-2,990	1,143-3,858
Avg. slope (%)	6.1	8.14	4.64	10.45	11.87
Slope range (%)	0-75	0.73.4	0-68.6	0-64.2	0-77.5
Avg. sagebrush cover (%)	8.5%	8.6%	8.9%	10.9%	10.9%
Area of region with ≥15% sagebrush (ha)	400,966	397,552	443,415	150,218	623,459
Percent of regional extent with ≥15% sagebrush cover	12%	20%	19%	39%	29%
Area of region with ≥10% tree cover (ha)	132,711	177,930	50,290	104,386	440,202
Percent of regional extent with ≥10% tree cover	4%	9%	2%	27%	20%
Annual precipitation range (cm) (BIO12)	16.8-13.9	21.1-125.1	17.7-93.3	26.5-130.5	15.9-121.1
Annual temperature range (°C) (BIO1)	0.9-11.8	-0.1-11.3	-0.3-11.4	1.4-5.7	-3.9-7.6
Area of region in agriculture (ha)	17,267	47,226	89,069	2,559	54,553
Percent of region in agriculture	1%	2%	4%	1%	3%

Table 3. *Environmental variables used to model habitat distribution for pygmy rabbits in Idaho and neighboring states, USA. Listed are the data's original scale prior to being resampled to 30-meter scale for consistency. NDVI was resampled from 250m to 90m using the nearest neighbor. Scale refers to the area or neighborhood used in variable calculations.*

Type	Environmental Variable	Scale (m)	Data Source and Notes
LANDCOVER and PRODUCTIVITY	Sagebrush cover (%)	30	NLCD 2016 Sagebrush Rangeland Fractional Component (USGS 202; Rigge et al. 2019)
	Big sagebrush cover (%)	30	
	Total shrub cover (%)	30	
	Mean sagebrush height (cm)	30	
	Shrub height (cm)	30	
	Herbaceous cover (%)	30	
	Annual herbaceous cover (%)	30	
	Bare ground (%)	30	
	Litter cover (%)	30	
	Mean sagebrush cover (%)	200	Provisional Remote Sensing Shrub/Grass NLCD Base Products for the Western US (USGS 2016c)
	Mean agricultural cover (%)	200	NLCD 2016 Land Cover (USGS 2016a)
	Mean tree canopy cover (%)	200	NLCD 2016 USFS Tree Canopy (Analytical Version) (USGS 2016b)
	Mean Normalized Difference Vegetation Index (NDVI) during July-Sept; avg. of monthly maximums	250	NDVI (USGS 2016d); Metrics were calculated annually, averaged from 2000–2016.
TOPOGRAPHY	Aspect (°)	30	10-m Digital Elevation Model (USGS 2019), Dilts (2015) [TPI]; TPI is the difference between elevation at a central point and the surrounding average elevation
	Slope (%)	30	
	Elevation (m)	30	
	Curvature	30	
	Terrain roughness (SD of elevation)	200	
	Topographic Position Index (TPI) normalized	500	
CLIMATE	19 bioclimatic variables (Hijmans et al. 2005)	800	PRISM 30-year normals of precipitation and temperature (PRISM Climate Group 2012)
SOILS	Clay in 0-30cm & 30-100cm (%)	30	POLARIS Soil Data (Chaney et al. 2016)
	Sand in 0-30cm & 30-100cm (%)	30	
	Silt in 0-30cm & 30-100cm (%)	30	
	pH in 0-30cm & 30-100cm	30	
	Bulk density in 0-30cm & 30-100cm (g/cm^3)	30	
	Organic matter in 0-30cm & 30-100cm log10 (%)	30	
	Saturated soil water content in 0-30cm & 30-100cm (m^3/m^3)	30	
	Depth to restrictive layer (cm)	30	

Table 4. *Total area and area of predicted suitable and primary habitat for pygmy rabbits within five modeling regions in Idaho and neighboring states, USA. Percentage of regional extent represented within each habitat suitability category is reported. Results are based on region-specific SDMs.*

	Total area of region (ha)	Suitable habitat (ha)	Suitable habitat (% of region)	Primary habitat (ha)	Primary habitat (% of region)
Region 1	3,368,554	187,281	6%	57,756	2%
Region 2	1,986,546	132,174	7%	24,464	1%
Region 3	2,348,962	434,307	18%	158,188	7%
Region 4	386,517	20,829	5%	12,632	3%
Region 5	2,166,213	260,302	12%	380,707	18%

Table 5. *Environmental variables used in the final habitat models for pygmy in five regions in Idaho and neighboring states, USA. Permutation importance representing relative variable importance is included for environmental variables in the final models. The last four rows of the table include values for each regions' model fit (AUC), optimized model parameters (both regularization multiplier and feature types), and thresholds used to categorize potentially suitable habitat and primary habitat.*

Environmental Variables	**Region 1**	**Region 2**	**Region 3**	**Region 4**	**Region 5**
Mean sagebrush cover (%)	6.1	3.3			
Herbaceous Cover (%)		4.2	12		
Annual Herbaceous Cover (%)	6.2	2.4			
Bare ground (%)		6.8			
Litter cover (%)				13.3	
Mean Agricultural Cover (%)			10.5		
Mean Tree Canopy Cover (%)	2.7				33.5
Mean Normalized Difference Vegetation Index (NDVI) during July-Sept; avg. of monthly maximums	11.5				
Slope (%)		7.6		5.3	
Elevation (m)			4.7		
Terrain Roughness (SD of elevation)	14.1				
Topographic Position Index (TPI) (normalized)	5.7				
Annual Mean Temperature (BIO1)				16.6	49.6
Isothermality (BIO3)		13		11.1	
Temperature Seasonality (BIO4)		9.9			
Max. Temperature of Warmest Month (BIO5)	28.2				
Min. Temperature of Coldest Month (BIO6)		7.9	29.3		
Temperature Annual Range (BIO7)				26.3	12.9
Mean Temperature of Wettest Quarter (BIO8)			11.6		
Mean Temperature of Coldest Quarter (BIO11)				22	
Annual Precipitation (BIO12)		25.2			
Precipitation of Wettest Month (BIO13)			11.6		
Precipitation of Driest Month (BIO14)	7.5			5.4	
Precipitation Seasonality (BIO15)			20.4		
Precipitation of Wettest Quarter (BIO16)					4
Precipitation of Warmest Quarter (BIO18)		4			
Precipitation of Coldest Quarter	15.7				

(BIO19)					
Clay in 30-100 cm (%)	2.3	5			
Sand in 30-100 cm (%)		4.5			
Bulk Density in 0-30 cm (g/cm^3)		2.9			
Organic matter in 30-100 cm log10 (%)		3.3			
Model AUC	0.939	0.927	0.861	0.936	0.821
Regularization multiplier	2	1	0.5	0.5	4.5
Feature Types (l=linear, q=quadratic, p=product, h=hinge)	l,q,p,h	l,p,h	l,q	l,q,p	l,p,h
Threshold Values; [1]MTSS/[2]AVE. PRES.	0.2831/ 0.6955	0.2202/ 0.7023	0.3835/ 0.6563	0.3887/ 0.6973	0.424/ 0.6884

[1]MTSS: Maximum test sensitivity plus specificity

[2]AVE.: Average predicted values occurrence locations

Table 6. *Spatial overlap between predicted habitat for pygmy rabbits generated from models developed within five regional extents (Regional Models, Fig. 3a) in Idaho and neighboring states, USA, and a model developed across the species geographic range (Rangewide Model, Fig. 3b; Smith et al. 2019a). Percentages represent the area of overlap as a percentage of the area of predicted habitat from the Regional Models.*

	Suitable habitat (ha)		Primary habitat (ha)	
Region 1	27,886	15%	42,915	74%
Region 2	33,844	26%	3,290	13%
Region 3	122,671	28%	69,722	44%
Region 4	2,528	12%	10,688	85%
Region 5	31,966	12%	314,449	83%

Table 7. *Area of projected potential habitat (suitable and primary categories combined) for pygmy rabbits in five regions of Idaho and neighboring states, USA, under a current model and two climate scenarios (RCP 4.5 and RCP 8.4). Percentages represent the area of predicted habitat as a percentage of the regional extents.*

	Current model (ha)		RCP 4.5 (ha)		RCP 8.5 (ha)	
Region 1	245,036	7%	113,416	3%	92,339	3%
Region 2	156,638	8%	128	0%	54	0%
Region 3	592,495	25%	362,371	15%	201,050	9%
Region 4	33,460	9%	6,918	2%	122,972	32%
Region 5	641,009	30%	48,420	2%	7,883	0%

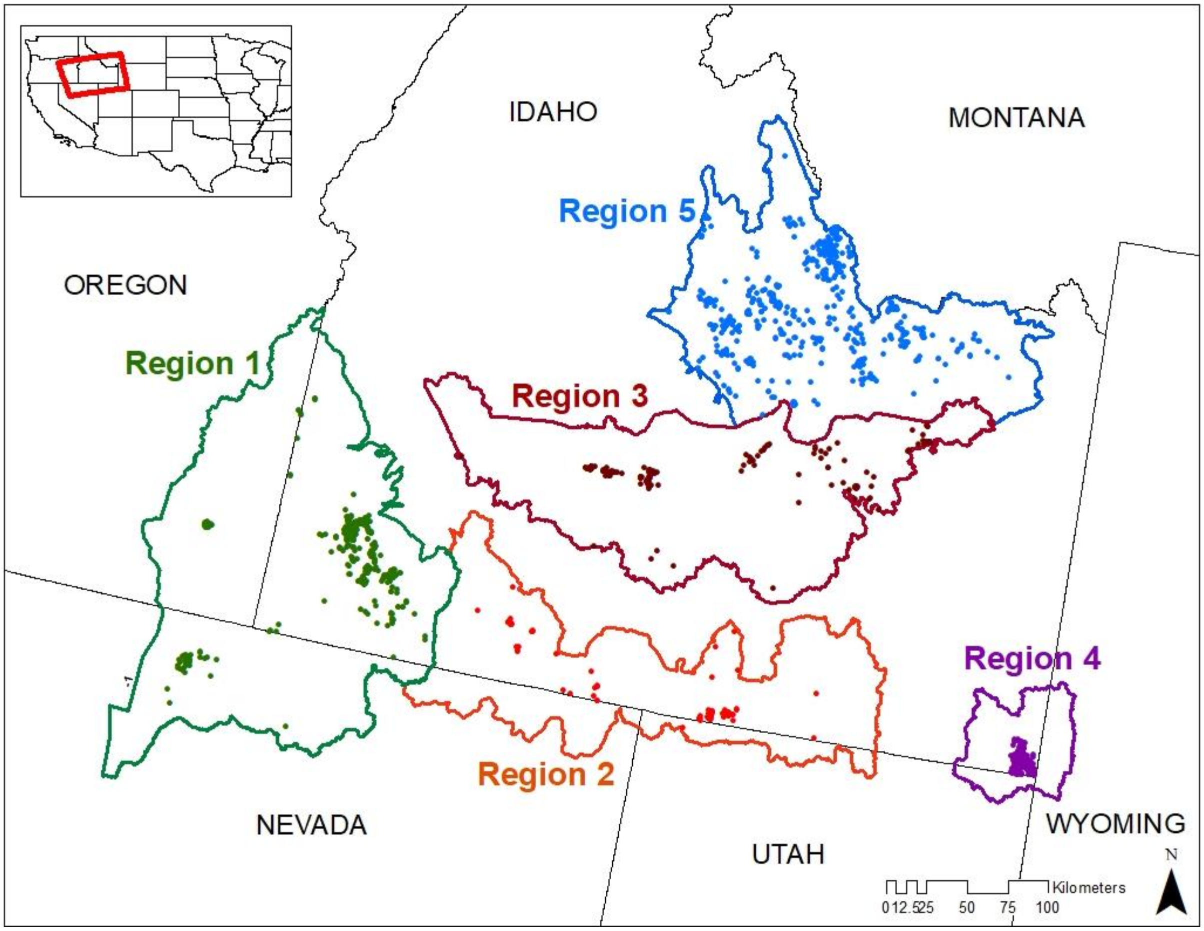


Figure 1. *Location of the study area (inset) and five regions where habitat distribution for pygmy rabbits was modeled in Idaho and neighboring states, USA. Confirmed occurrences used to build models were collected during 2000-2019.*

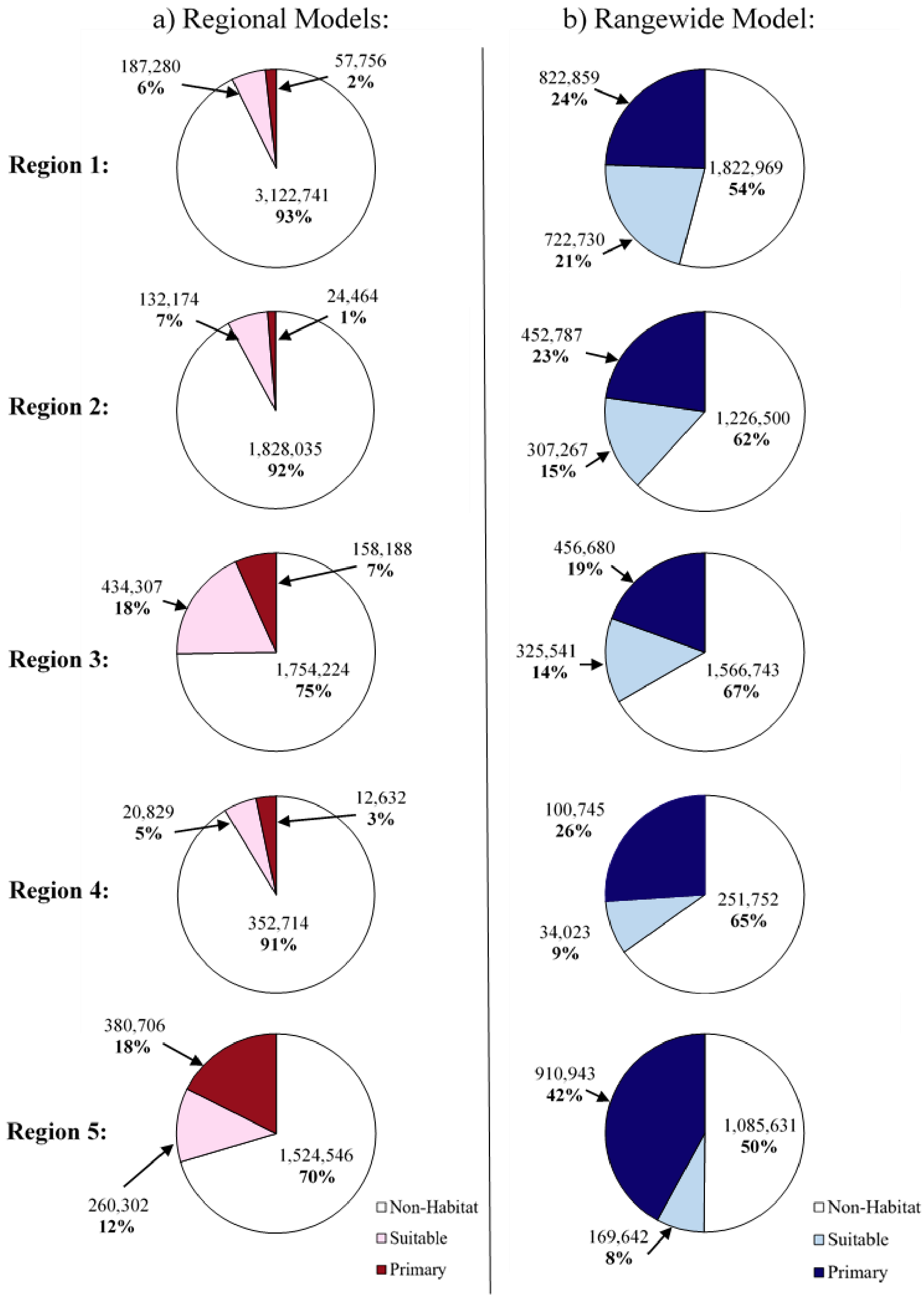
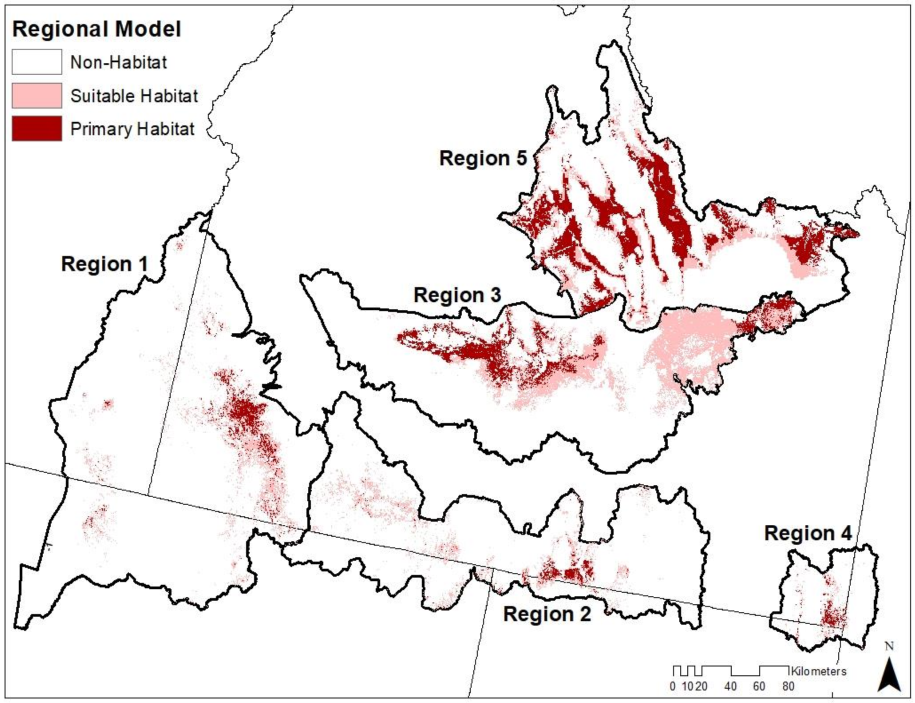
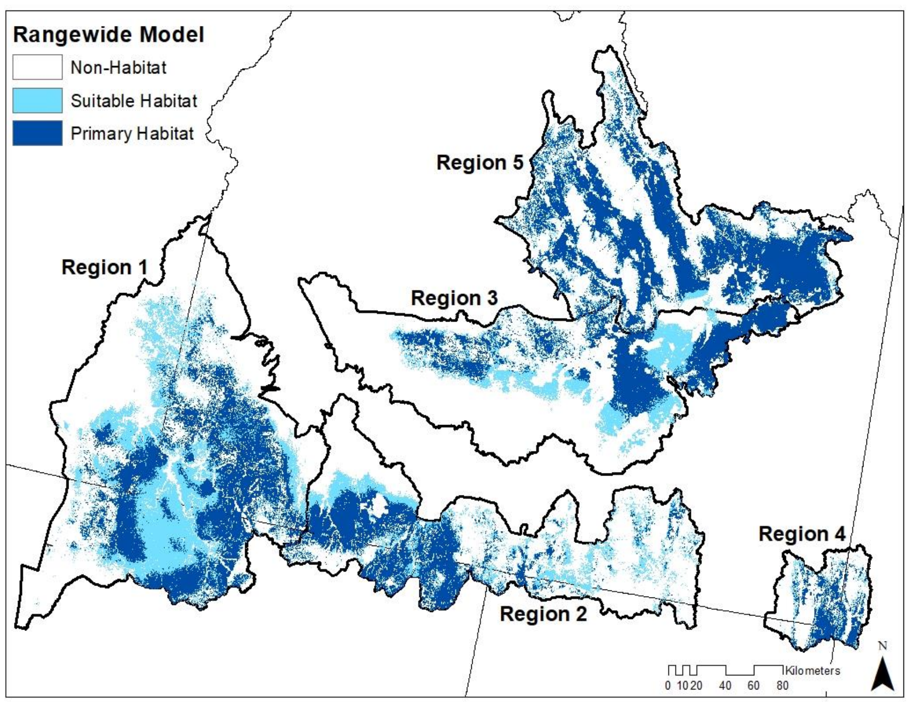


Figure 2. *Areas and percentages of predicted habitat for pygmy rabbits modeled within five regional extents in Idaho and neighboring states, USA. a) Regional model predictions and b) Rangewide model predictions (from Smith et al. 2019a).*

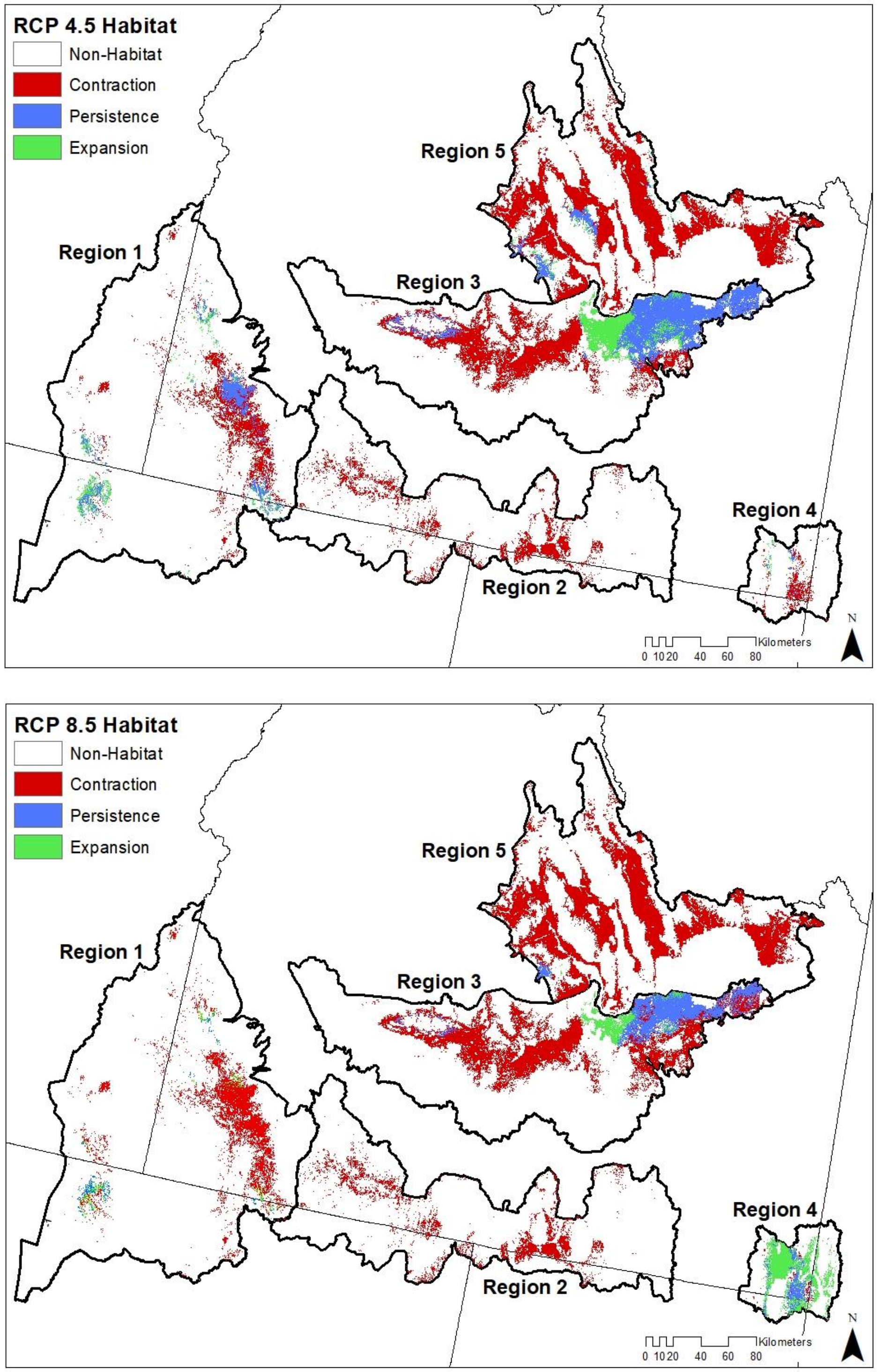


a)



b)

Figure 3. *Predicted habitat distribution for pygmy rabbits in five regions in Idaho and neighboring states, USA. Thresholds for suitable and primary habitat designations were values that maximized the sum of test sensitivity and specificity and the average predicted values at presence points, respectively. a) Regional model predictions and b) Rangewide model predictions (from Smith et al. 2019a).*



a)

b)

Figure 4. *Changes in potential habitat for pygmy rabbits in Idaho and neighboring states, USA, from current predictions based on regional models (Fig. 3a) to future projections under two climate scenarios a) RCP 4.5 and b)RCP 8.4. Mapped habitat includes both suitable and primary habitat categories combined. Contraction = change from habitat to non-habitat, Persistence = remain as habitat, and Explansion = change from non-habitat to habitat.*

APPENDIX A: SUPPLEMENTAL TABLES

Table S1. *Bioclimatic variables derived from monthly temperature and precipitation data (PRISM Climate Group 2012) used to model habitat for pygmy rabbits in five regions of Idaho and neighboring states, USA. Variables are of three types: annual trends (e.g., mean annual temperature), seasonality (e.g., annual range in precipitation), and extreme or limiting environmental factors (e.g., precipitation of the wet and dry quarters). A quarter is a period of three consecutive months.*

Variable	**Description**
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp – min temp))
BIO3	Isothermality (BIO 2/BIO 7) x100
BIO4	Temperature Seasonality (standard deviation x 100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO 5-BIO 6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
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
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

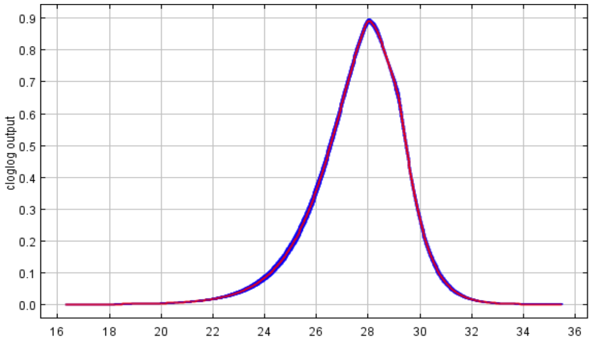
Table S2. *Mean (+/- range) values for bioclimatic variables (Table S1)included within five regional models used to predict current habitat and project potential future habitat distribution for pygmy rabbits in Idaho and neighboring states, USA. Current values were derived from monthly temperature and precipitation data (PRISM Climate Group 2012), and potential future values were calculated from monthly data generated under two climate projections, RCP 4.5 and RCP 8.5 (AdaptWest Project, 2015).*

	Climate Model	**Region 1**	**Region 2**	**Region 3**	**Region 4**	**Region 5**
BIO1	Current	-	-	-	4.4 (1.4-5.7)	3.8 (-3.9-7.7)
	RCP 4.5	-	-	-	6.8 (4.4-8.1)	6.4 (0.8-10.2)
	RCP 8.5	-	-	-	7.8 (5.3-9.1)	7.3 (1.7-11.1)
BIO3	Current	-	36.8 (27.7-43.7)	-	37.3 (31.7-40.0)	-
	RCP 4.5	-	36.1 (25.2-43.1)	-	36.3 (30.9-39.0)	-
	RCP 8.5	-	35.9 (25.2-42.8)	-	36.0 (30.7-38.8)	-
BIO4	Current	-	857.3 (718.5-969.8)	-	-	-
	RCP 4.5	-	876.7 (761.0-981.6)	-	-	-
	RCP 8.5	-	886.5 (770.4-989.3)	-	-	-
BIO5	Current	29.9 (17.9-34.1)	-	-	-	-
	RCP 4.5	37.9 (23.7-37.9)	-	-	-	-
	RCP 8.5	34.9 (24.9-39.2)	-	-	-	-
BIO6	Current	-	-8.5 (-13.0- -4.7)	-10.5 (-15.4- -5.2)	-	-
	RCP 4.5	-	-5.9 (-2.5- -10.3)	-8.1 (-2.9- -13.3)	-	-
	RCP 8.5	-	-4.99 (-9.30- -1.5)	-7.1 (-12.3- -2)	-	-
BIO7	Current	-	-		39.1 (31.6-44.6)	38.4 (28.5-45.9)
	RCP 4.5	-	-		40.7 (33.1-46.1)	40.4 (27.6-46.9)
	RCP 8.5	-	-		40.9 (33.3-46.3)	40.8 (28.0-47.1)
BIO8	Current	-	-	2.8 (-8.1-12.2)	-	-
	RCP 4.5	-	-	4.36 (-6.03-16.48)	-	-
	RCP 8.5	-	-	4.92	-	-

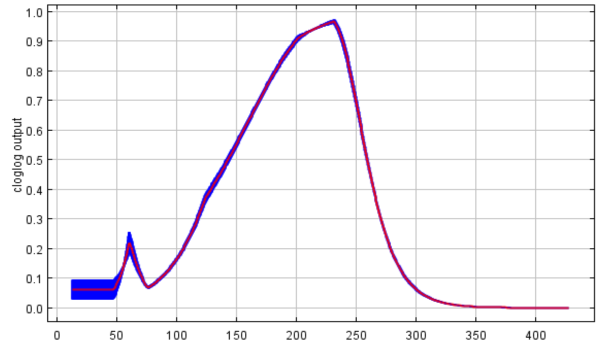
				(-5.35-17.42)		
BIO11	Current	-	-		-4.7 (-6.8- -3.3)	-
	RCP 4.5	-	-		-4.1 (-5.4- -2.8)	-
	RCP 8.5	-	-		-3.2 (-4.4- -1.8)	-
BIO12	Current	-	399.2 (211.0-1251.3)	-	-	-
	RCP 4.5	-	425.9 (224.0-1335.0)	-	-	-
	RCP 8.5	-	429.5 (223.0-1358.0)	-	-	-
BIO13	Current	-	-	46.7 (26.1-141.7)	-	-
	RCP 4.5	-	-	47.0 (28.0-164.0)	-	-
	RCP 8.5	-	-	47.6 (28.0-169.0)	-	-
BIO14	Current	8.3 (4.7-20.3)	-	-	23.9 (14.3-39.7)	-
	RCP 4.5	11.3 (5.0-25.0)	-	-	27.3 (13.0-46.0)	-
	RCP 8.5	11.3 (5.0-25.0)	-	-	26.96 (14-46)	-
BIO15	Current	-	-	39.5 (22.9-68.1)	-	-
	RCP 4.5	-	-	37.4 (17.6-65.6)	-	-
	RCP 8.5	-	-	38.3 (17.5-67.2)	-	-
BIO16	Current	-	-	-	-	151.8 (55.4-433.7)
	RCP 4.5	-	-	-	-	153.4 (62.0-452.0)
	RCP 8.5	-	-	-	-	152.6 (61.0-470.0)
BIO18	Current	-	65.6 (29.6-170.7)	-	-	-
	RCP 4.5	-	77.0 (28.0-148.0)	-	-	-
	RCP 8.5	-	74.9 (27.0-145.0)	-	-	-
BIO19	Current	117.3 (45.9-395.6)	-	-	-	-
	RCP 4.5	112.9 (39.0-485.0)	-	-	-	-
	RCP 8.5	117.7 (41.0-506.0)	-	-	-	-

APPENDIX B: SUPPLEMENTAL FIGURES

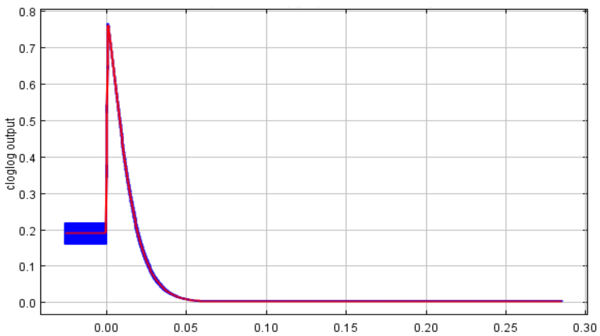
Figure S1. *Region 1 Final Variable Response Curves*



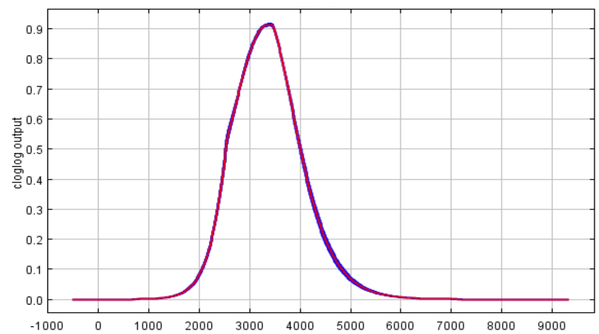
MAX. TEMPERATURE OF WARMEST MONTH (BIO5)



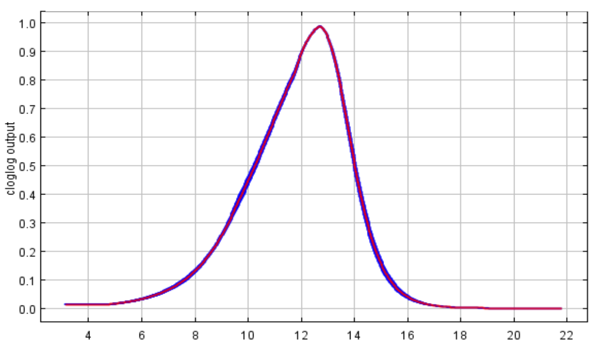
PRECIPITATION OF COLDEST QUARTER (BIO19)



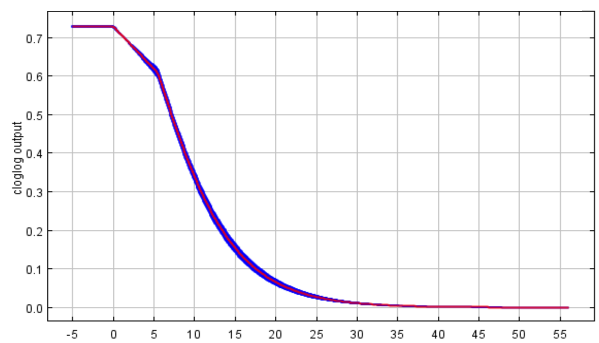
TERRAIN ROUGHNESS



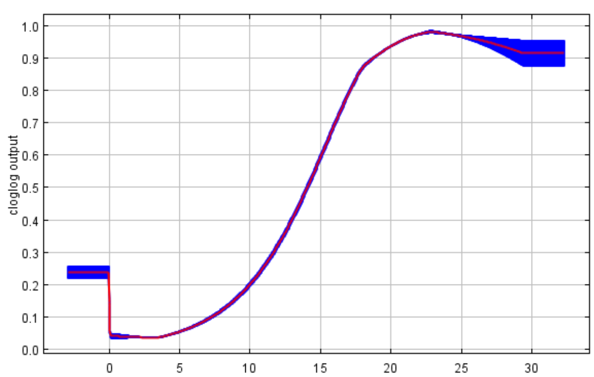
NDVI (NORMALIZED DIFFERENCE VEGETATION INDEX)



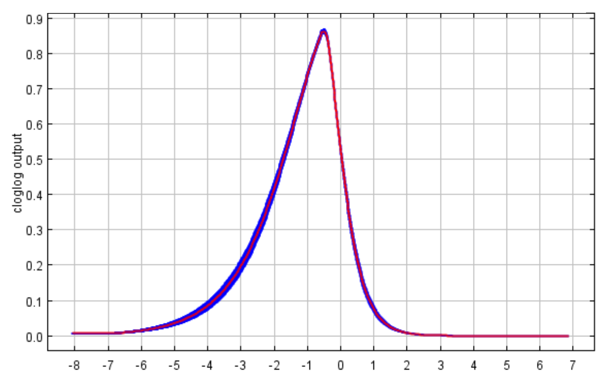
PRECIPITATION OF DRIEST MONTH (BIO14)



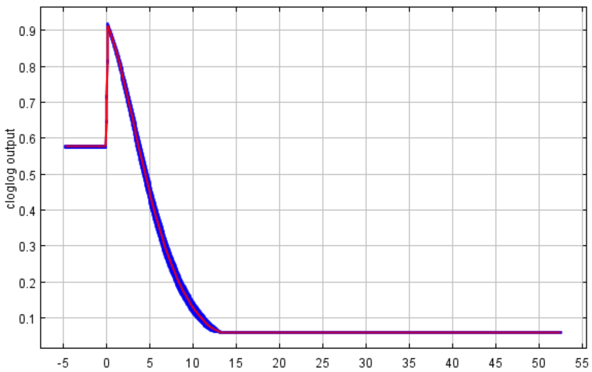
ANNUAL HERBACEOUS COVER



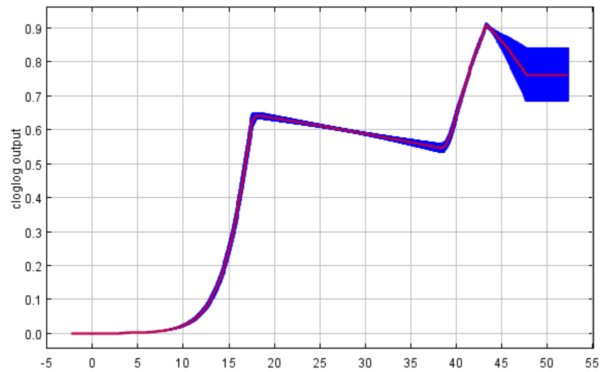
SAGEBRUSH CANOPY COVER



TOPOGRAPHIC POSITION INDEX

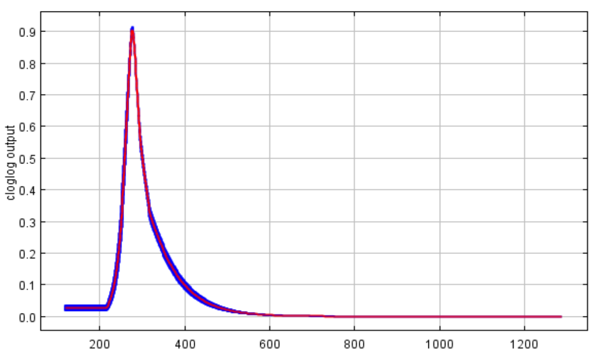


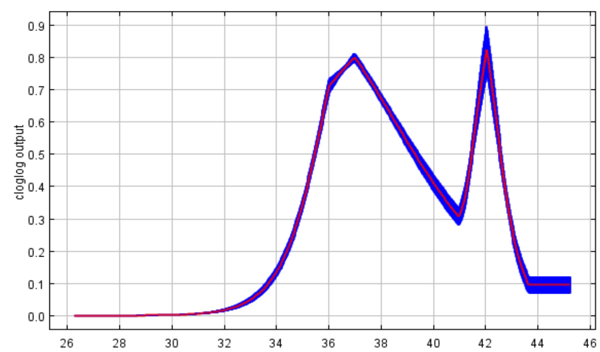
TREE CANOPY COVER



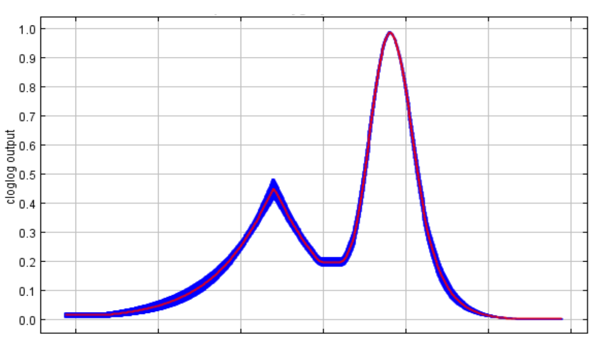
CLAY PERCENTAGE (30-100 CM)

Region 2 Final Variable Response Curves

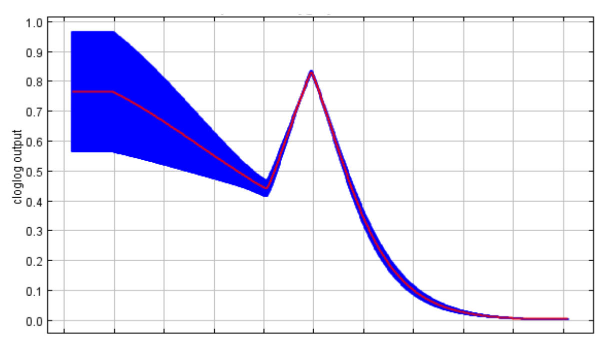




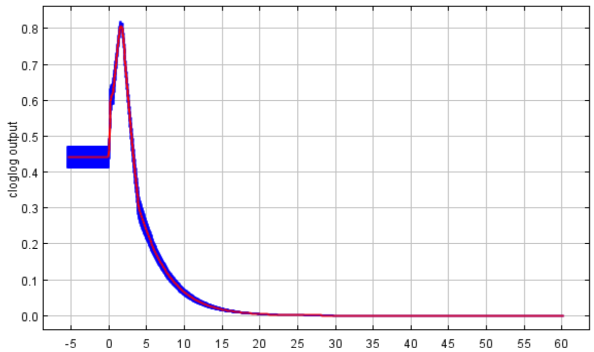
ISOTHERMALITY (BIO3)



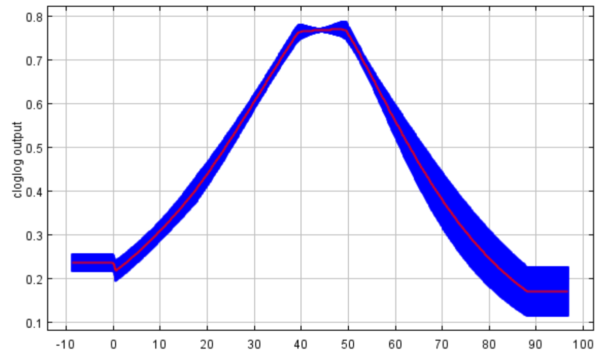
TEMPERATURE SEASONALITY (BIO4)



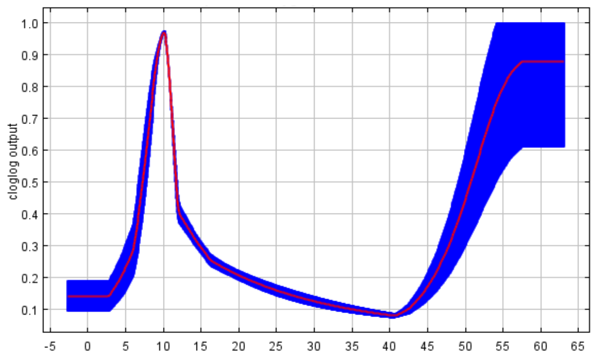
MIN. TEMPERATURE OF COLDEST MONTH (BIO6)



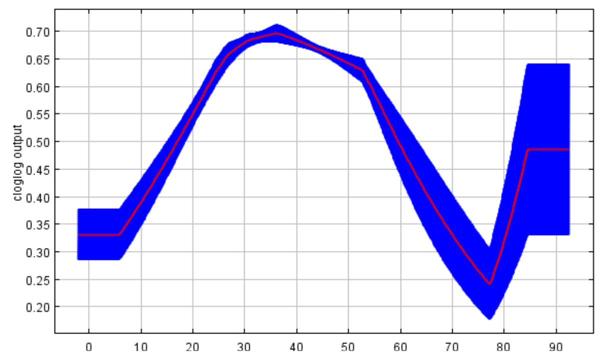
SLOPE



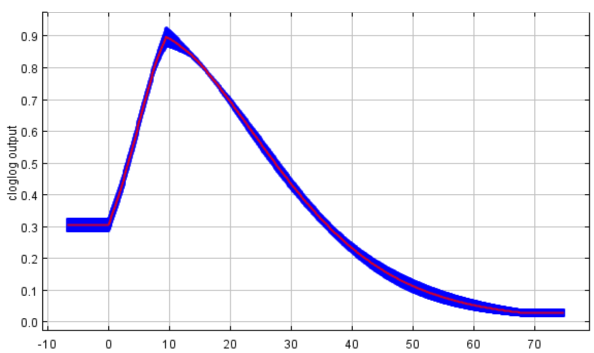
BARE GROUND PERCENTAGE



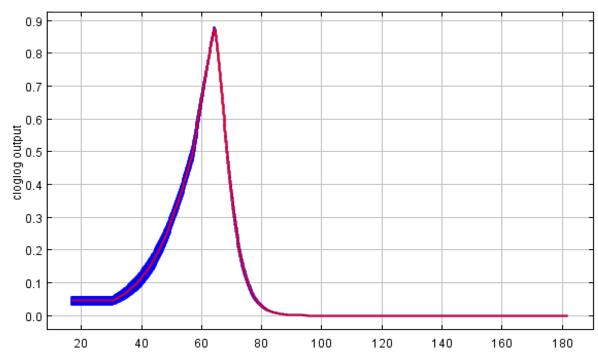
CLAY PERCENTAGE (300-100 cm)



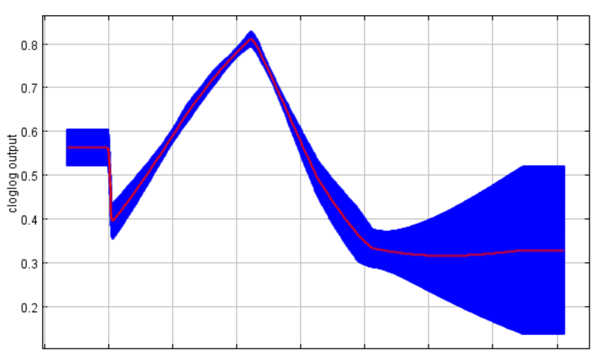
SAND PERCENTAGE (30-100 cm)



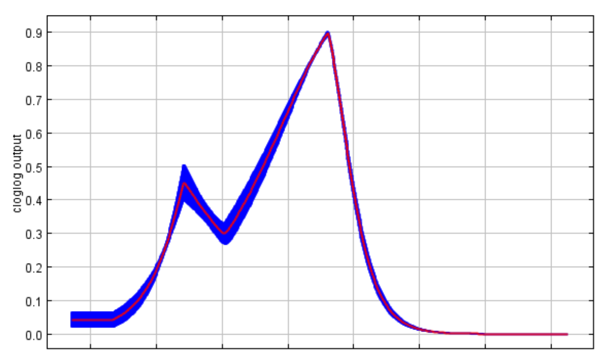
HERBACEOUS COVER



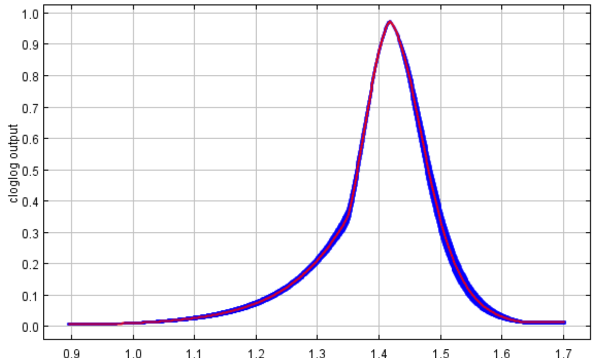
PRECIPITATION OF WARMEST QUARTER (BIO18)



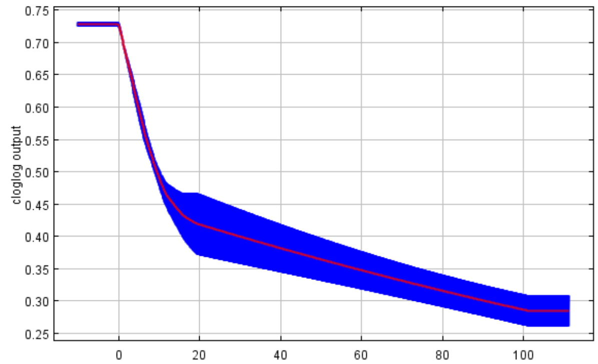
SAGEBRUSH CANOPY COVER



SOIL ORGANIC MATTER PERCENTAGE (30-100 cm)

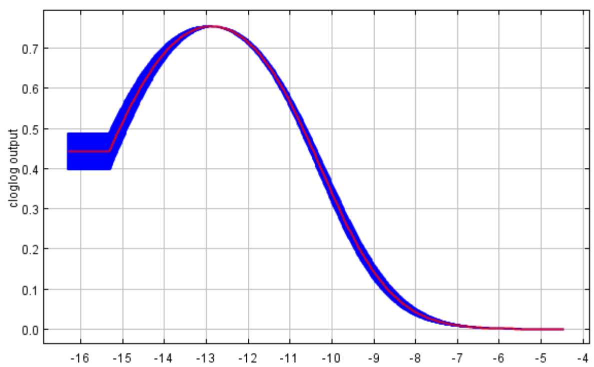


SOIL BULK DENSITY (0-30 cm)

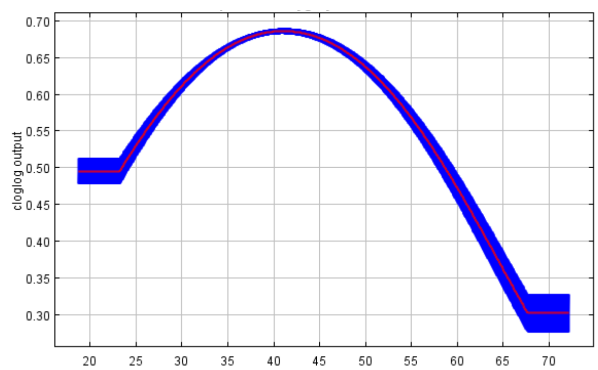


ANNUAL HERBACEOUS COVER

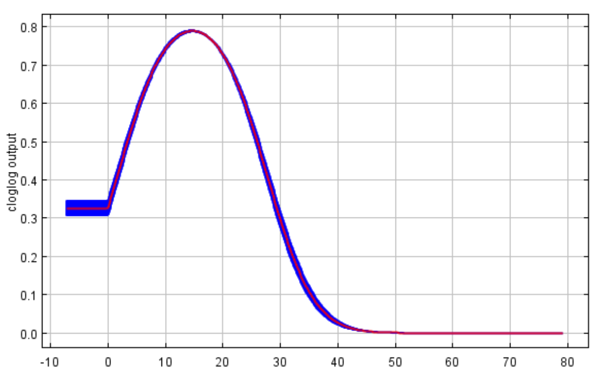
Region 3 Final Variable Response Curves



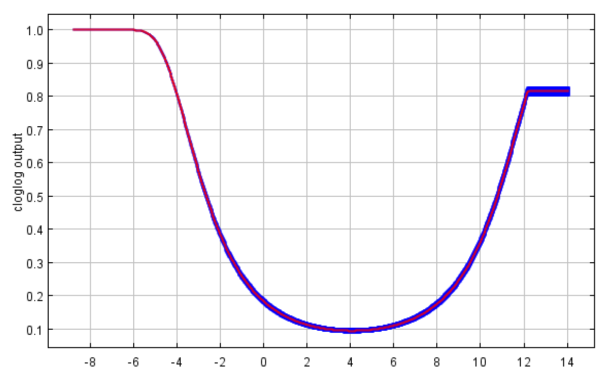
MIN. TEMPERATURE OF COLDEST MONTH (BIO6)



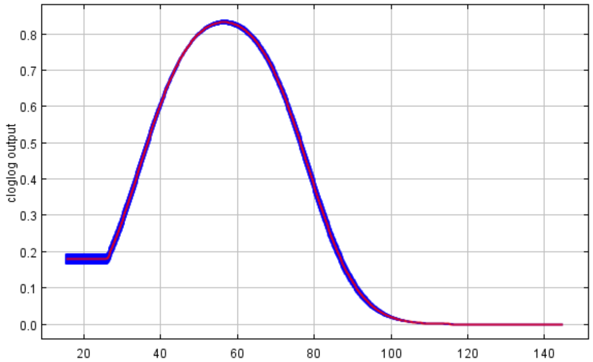
PRECIPITATION SEASONALITY (BIO15)



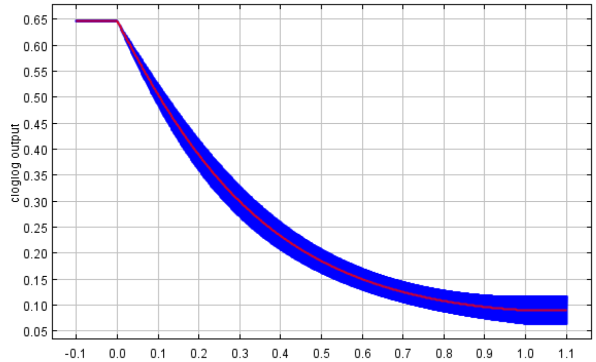
HERBACEOUS COVER



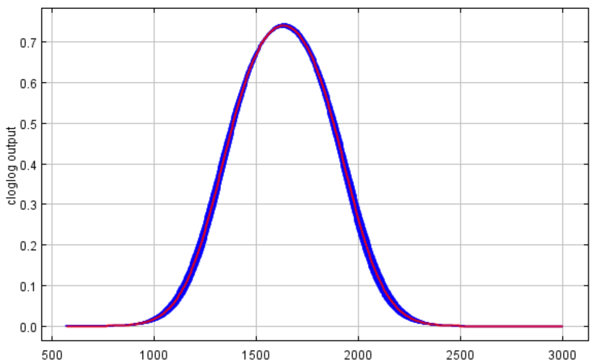
MEAN TEMPERATURE OF WETTEST MONTH
(BIO8)



PRECIPITATION OF WETTEST MONTH (BIO13)

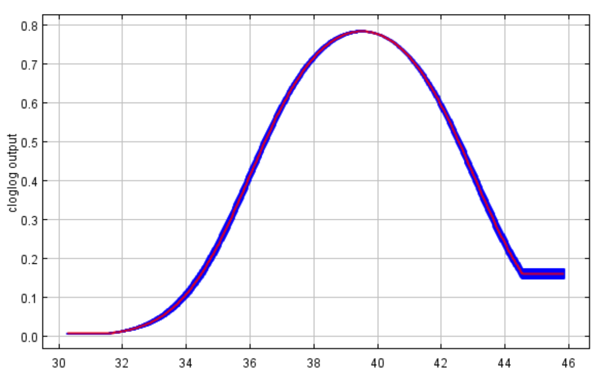


AGRICULTURAL LAND COVER PERCENTAGE

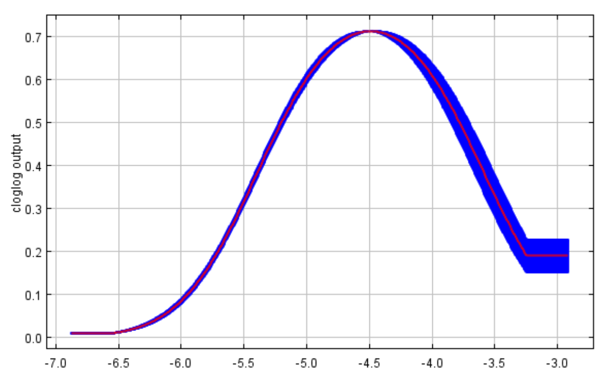


ELEVATION

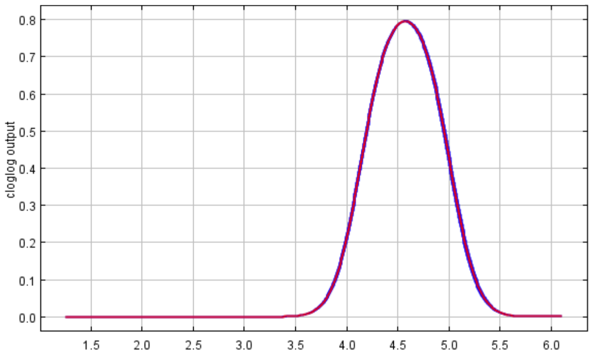
Region 4 Final Variable Response Curves



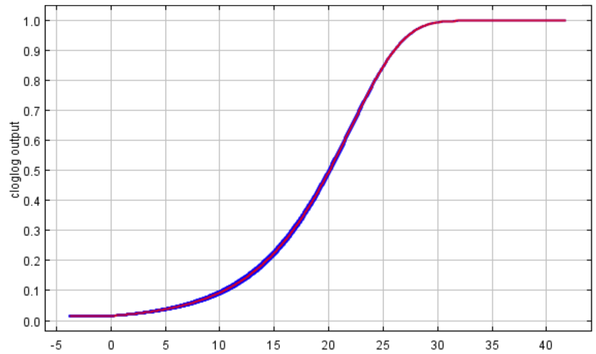
TEMPERATURE ANNUAL RANGE (BIO7)



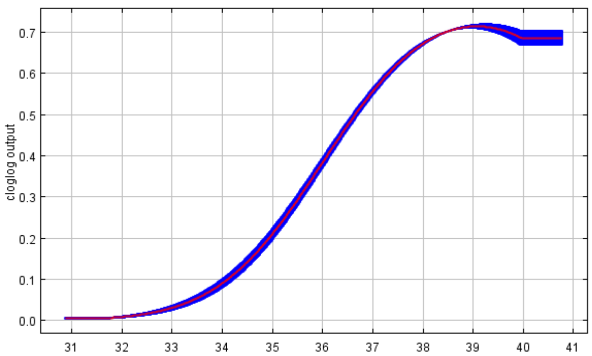
MEAN TEMPERATURE OF COLDEST QUARTER
(BIO11)



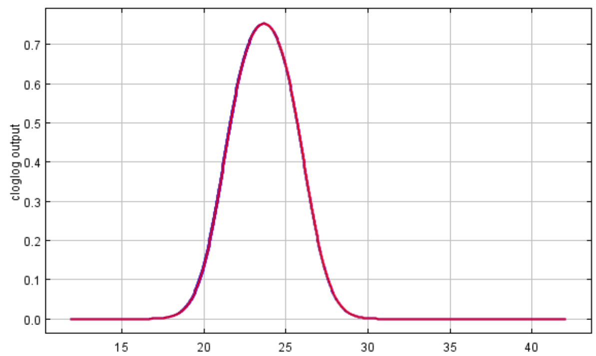
MEAN ANNUAL TEMPERATURE (BIO1)



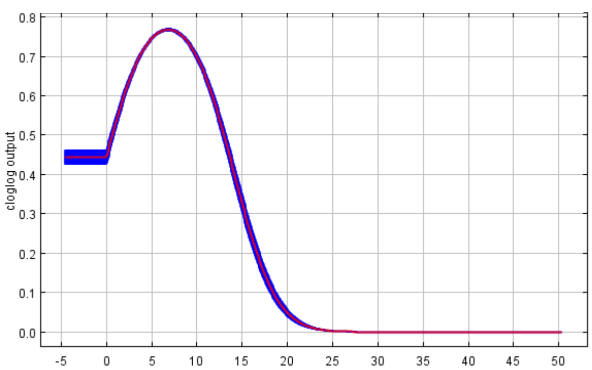
LITTER COVER PERCENTAGE



ISOTHERMALITY (BIO3)



PRECIPITATION OF DRIEST MONTH (BIO14)



SLOPE

Region 5 Final Variable Response Curves

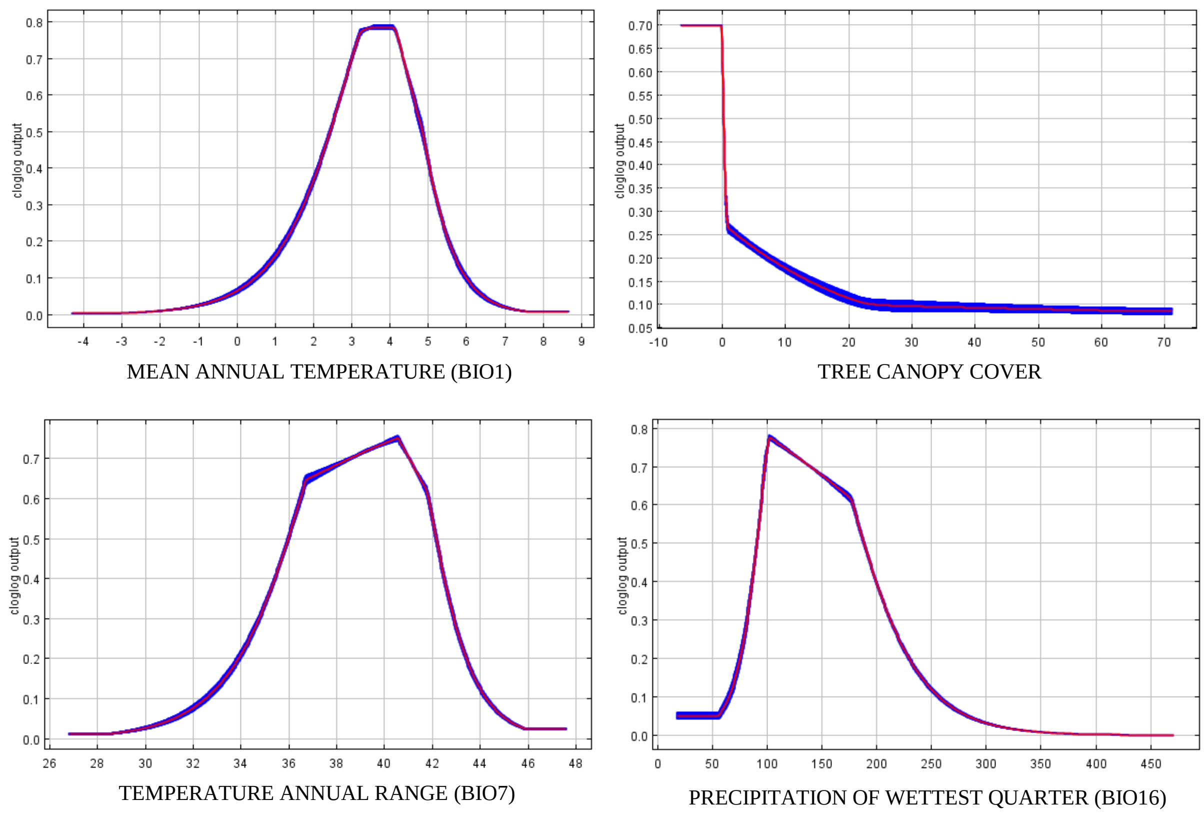
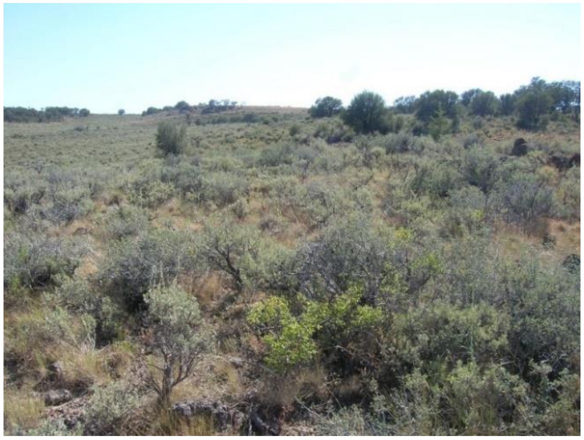


Figure S1. *Variable response curves for regional SDMs for pygmy rabbits across five regions in Idaho and neighboring states, USA. These curves represent the Maxent model results that only include a single variable (i.e., predicted suitability based on one variable and no interactions). Red lines represent the mean response of the replicate Maxent runs, and the blue lines are the mean value +/- one standard deviation.*

APPENDIX C: Supplemental Photographs

Region 1: Owyhee Desert



Region 2: Southern Desert

Region 3: Central Desert

Region 4: Bear Lake

Region 5: Salmon/ Lemhi