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# Combined Use of Data From Avian Surveys Along the Pacific Crest Trail With Biodiversity Repositories to Model Habitat Suitability Throughout Northern California

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## Abstract

Models that describe species distributions are valuable in guiding management decisions. We compared and combined two avian datasets during the 2010 breeding season in northern California, USA. These datasets were a large-scale avian diversity survey from McGrann and Furnas (2016; 2018) and combined data from Biological Information Serving Our Nation (BISON) and Global Biodiversity Information Facility (GBIF). Our objective was to compare the utility of these two datasets, that employ separate field protocols, to model habitat use for the Black-headed Grosbeak, Hairy Woodpecker, and Yellow-rumped Warbler, three common forest birds in our study area that occupy distinctive habitat types. We also tested whether combining the datasets together would create a model with greater generality over the study area and determine if the data will create response curves that explain certain relationships between environmental characteristics and species occurrences. We found that fine-scale data along a single, albeit extensive, transect built models that predicted suitability well for the section of trail, but did not predict occurrences well for areas beyond the trail in two of the three species. We also found that data from Biological Information Serving Our Nation (BISON) and Global Biodiversity Information Facility (GBIF) did not have the sampling structure required for finer scale modeling and lacked observations in areas that may be critical for sampling, such as fire-impacted areas. By combining these two datasets, we produced models that captured the range of these species throughout the study area, and we created response curves that explained anticipated habitat associations for each species.

**Keywords:** BlueSpray, habitat suitability modeling, MaxEnt, passerines, woodpeckers

## Introduction

Birds are excellent indicators of environmental change because they rely on plant communities and the overall structure of vegetation to provide food, shelter, and breeding and nesting sites. Their distributions, therefore, will shift as a result of human land use change (Lee et al., 2004) and other factors such as fire or drought (Zimmerman, 1997). In an effort to conserve bird habitat, managers require tools to aid their decision-making processes, including spatial modeling tools (Tingley et al., 2009; Turner et al., 2016). In this study, we use a spatial modeling tool, MaxEnt, in a habitat suitability modeling procedure to select environmental characteristics that determine what habitat types are associated with specific avian species occurrences. It is important to create accurate habitat models to determine areas which may be crucial to establish as nature preserves that anticipate the effects of climate change and human land-use.

Habitat suitability models predict the spatial occurrence and distribution of a species based on measures of habitat suitability (Peterson et al., 2011), with elevation, topography, habitat type, precipitation, and temperature as common measures of habitat suitability (MacArthur, 1965; Hedley & Buckland, 2004; Odion et al., 2010; McGrann & Thorne, 2014; Asner et al., 2015; Kadmon et al., 2016; McGrann & Furnas, 2016). Habitat suitability models are represented as grid-based maps of the spatial distribution of estimated habitat suitability (Kimble, 2016). Habitat models have been created for many avian species, such as the species that we include in this study: Hairy Woodpecker (*Picoides villosus*) (Russell et al., 2007), Yellow-rumped Warbler (*Dendroica coronata*) (Price, 2000), and Black-headed Grosbeak (*Pheucticus melanocephalus*) (St-Louis et al., 2014).

MaxEnt is a spatial modeling tool that has been used in a wide variety of species distribution applications, including the mapping of phenotypic diversity in Hairy Woodpeckers (Klicka et al., 2011), modeling climate-induced shifts in the distribution of Warbler species (Ralston & Kirchman, 2013), and it has been applied in conservation planning by modeling habitat suitability for migratory birds, including the Black-headed Grosbeak (Seavy et al., 2012).

Habitat suitability models use species occurrence data, which are typically geographic locations where the species has been detected in the field using a standardized survey protocol that typically employs some randomized

sampling procedure. Ideally, data is collected via these same protocols across the entire study area of interest (Austin & Heyligers, 1989). However, in reality, most published species distribution studies employ very different survey protocols; it is rare to find that data is collected in a standardized manner across more than one study. It is for this reason that most biodiversity databanks and clearinghouses, such as Biological Information Serving Our Nation (BISON) and Global Biodiversity Information Facility (GBIF), offer a collection of existing datasets that may be biased due to the original purpose of the study (Barry & Elith, 2006).

Using a single modeling approach, we compared two datasets of avian species distributions that were collected using varying sampling designs and spatial coverage in northern California. Our analysis compared data collected using a large-scale avian diversity survey along the Pacific Crest National Scenic Trail in northern California (McGrann & Furnas, 2016; Furnas & McGrann, 2018), which we will, henceforth, call the PCT Data, and combined data from Biological Information Serving Our Nation (BISON) and Global Biodiversity Information Facility (GBIF), which we will call the GBIF-BISON Data. The PCT Data represents a study with a standardized methodology for point counts and automated recording units, while the GBIF-BISON Data obtains their data from contributors who have varying methods and data quality.

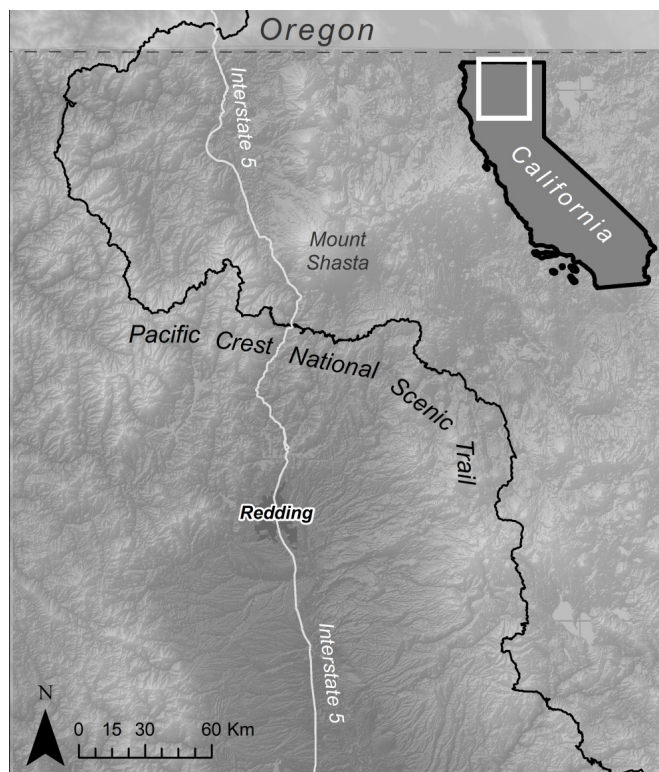
Our objectives were to test the generality of model predictions derived from each dataset and use these predictions to evaluate three hypotheses. Our hypotheses were: (1) the PCT Data will perform well for modeling the habitat associations of the species for areas near the trail but will decrease in performance with distance from the trail. (2) The GBIF-BISON Data, although composed of observations dispersed throughout the entire study area, will not be detailed enough to transfer to a finer scale analysis. (3) By combining these two datasets, which we will call the Combined Dataset, we can create a model that is fine-tuned to the scale of the analysis but that also generalizes well across our entire study area and creates parsimonious response curves by associating species occurrences with environmental characteristics. In order to test these hypotheses on the generality of model predictions, we felt it was best to compare model predictions for three relatively common and widespread species that also have distinctive niches, habitat associations, and life histories. We reference these species using a six-letter alpha coding system (Pyle & DeSante, 2003): (1) Black-headed Grosbeak (BKHGRO)

is a neotropical migrant. The species prefers a complex vegetation composition and structure with a mixture of hardwood and conifer trees (Williams & Koenig, 1980). (2) Yellow-rumped Warbler (YERWAR) is a year-round resident and elevation migrant and considered a habitat generalist, found in all elevations but with a preference for coniferous forests. Both BKHGRO and YERWAR also have close habitat associations with water (Kirkpatrick et al., 2009; Becker, 2013). (3) Also a resident, Hairy woodpeckers (HAIWOO) occur at higher elevations, and although abundant in green forests, they are particularly associated with recently burned areas. In burned forests, there is an abundance of snags, which yield wood-boring insects (Parker et al., 2006), an important food resource (Saab et al., 2019).

## Methods

### Study Region

We studied a region along the northern California portion of the PCT that extended from Bucks Lake Wilderness (39.907°N, -121.127°W) to the Oregon Border (42.005°N, -122.913°W) (Figure 1). Much of the southern and eastern portion of this section of the PCT lies with-



**Figure 1.** The PCT route where data was collected in 2010 by McGrann and Furnas (2016).

in the rain shadow of the Cascade Mountains, exhibiting drier conditions. The trail then turns west into the moister Klamath Mountains (McGrann et al., 2014). These conditions create a diverse climate that is predominantly forested, ranging from mixed hardwood/conifer forests at lower elevations to mixed conifer and subalpine forests at mid- to upper-elevations. Some portions of this section of the PCT, particularly further to the south and to the east, consist of semiarid sagebrush (*Artemisia tridentata*) and montane chaparral (Schoenherr, 1992).

### Occurrence Data

The PCT Data contains avian occurrence data for the year 2010 and was acquired from McGrann and Furnas (2016). The PCT Data was collected along the trail via fixed-radius (50 m) point-counts and automated recorders in a standardized method as described in detail in Furnas & Callas (2015), McGrann and Furnas (2016), and Furnas and McGrann (2018). BKHGRO was detected at 83 sites, YERWAR, 206 sites, and HAIWOO, 29 sites.

We downloaded data from GBIF and BISON for the year 2010 in the months of May, June, and July to match the timeframe of when surveys were completed for the PCT Data. These two databases both obtain occurrence data from data contributors such as Cornell lab of Ornithology, the eBird Observation Dataset, and the Great Backyard Bird Count. These two datasets were combined into a single dataset, which we call GBIF-BISON Data. For each species, the number of individual detections extracted from the GBIF-BISON Data for the study area included 84 for BKHGRO, 195 for YERWAR, and 101 for HAIWOO. The GBIF-BISON Data contains spatial bias due to an uneven method of sampling and may distort spatial models (Beck et al., 2014). Modeling was completed using the GBIF-BISON Data and the PCT Data separately and combined to cover a larger area for each species in the study area, which we call the Combined Dataset.

### Environmental Covariates

We tested 14 environmental covariates that we thought would be associated with habitat for the three avian species based upon the natural history and habitat requirements as described in Sousa (1987) and DeGraaf & Rappole (1995). We downloaded 8 variables from the Oregon State University's Landscape Ecology, Modelling, Mapping and Analysis (LEMMA) program, which obtain their data by integrating vegetation measurements from field surveys, mapped envi-



ronmental data, and Landsat Thematic Mapper (TM) imagery (30 m resolution) (Ohmann & Gregory, 2002; Landscape Ecology, Modeling, Mapping, 2020). The variables we selected were hardwood and conifer canopy cover, total canopy cover, quadratic mean diameter of all dominant and codominant trees (qmd\_dom), forest type based on the basal area of dominant tree species (Fortypba), vegetation class based on the canopy cover and basal area (vegetation class), and density of live trees and snags. The Fortypba layer contained 983 categorical values, but some modeling software, such as the Hyper-Envelope Modeling Interface Version 2 (HEMI2), require less than 255 categories, so we did the following process to reduce the amount into coarser scale. First, we extracted the Fortypba values to the survey sites and classified these as values from 1-98. The remaining values in the Fortypba layer were combined into coarser classifications based on the dominant tree species. At the end of this process, 141 categories were represented in the new Fortypba layer.

The remaining 6 covariates included in our models were distance from fire, distance from water, distance from bark beetle infestation, elevation (as surrogate for temperature), aspect, and slope. Distance from fire, water, and bark beetle infestations help measure habitat resources (e.g., food, cover, and nesting habitat) that may be important to a species. Elevation, aspect, and slope are characteristics of the terrain which can be associated with temperature or light exposure, which also influences vegetation. All covariates were converted to rasters of grid cells that represent the value of the covariate at on location in the landscape. We calculated a distance to fire raster (i.e., a grid of cells where the value assigned to each cell represents a distance value) by downloading fire polygons of mapped burned areas from the Monitoring Trends in Burn Severity data set (Eidenshink et al., 2009) and applying the Euclidian distance function in ArcGIS (version 10.7.1, Environmental Systems Research Institute, Redlands, CA). This resulted in a raster that calculated distance to the edge of the polygon where everything within the polygon was assigned a value of zero. Stream and river polylines were downloaded from the National Hydrography Dataset (1:24,000; Terzioti & Archuleta, 2020). Bark beetle infestation polygons were downloaded from the USDA Forest Service and were obtained via aerial “sketchmapping” (Schrader-Patton & Pywell, 2003). We used a similar approach to convert streams and rivers polylines into a distance to water raster and to convert bark beetle infestation polygons into a distance raster. Digital elevation maps (DEMs) were downloaded from the U.S. Geologic Survey (30 m resolution). Temperature decreases with

increasing elevation according to a known rate (i.e., the adiabatic lapse rate). Therefore, we considered elevation to be a surrogate covariate for temperature. From the DEMs, we also derived aspect and slope rasters, which represent a surrogate covariate for precipitation (Geroy et al., 2011; Phillips & Schümm, 1987). All rasters were scaled to 30 m to match the vegetation covariate raster cell size, clipped to the study area, and converted into ASCII files using ArcGIS.

We reduced the number of variables used to create the model by performing several steps. First, we analyzed the correlation between all the environmental variables using the Pearson correlation statistic (Appendix: R Script). Next, we used MaxEnt’s jackknife feature to evaluate each environmental variables contribution to each model (Elith et al., 2010). We removed variables that had less than 2% contribution and were highly correlated (i.e., a correlation coefficient  $> 0.7$ ), or did not impact the jackknife’s regularization training gain when removed. The regularization training gain is a measure between a random sample of the entire study area the species could inhabit and the environmental covariates correlated to the species occurrence (Elith et al., 2010).

### *MaxEnt*

We performed MaxEnt within the software BlueSpray (beta version 42, SchoonerTurtles, Arcata, CA), which calculates area under the curve (AUC) and the Akaike information criterion (AIC). AUC measured model performance by measuring a model’s discriminatory ability and represents the proportion of times the actual sample of presence locations has a larger estimated suitability than a random sample (Fielding & Bell, 1997). AIC attempts to balance predictive ability of the model with model complexity by providing an estimate of the relative “quality” among a series of competing models (Plant, 2012). Additionally, BlueSpray can perform Monte Carlo simulations within MaxEnt (Graham & Kimble, 2018). Monte Carlo simulations are a statistical method where the model is replicated a large amount of times with aspects of the model randomized with each replicate (Plant, 2012). Using the spatial coordinates of the bird occurrences and the set of covariates that we selected, which were selected based upon the criterion of at least 2% contribution to the model, we increased the regularization multiplier in the combined model by increments of 0.5 until we achieved the lowest AIC. A higher regularization multiplier smooths out the response curves to reduce the complexity of the models produced. To create the most parsimonious model and to be able to evaluate how the two datasets models compare for each species, we

used the best regularization parameter from the Combined Dataset to create models with only the PCT Data and only the GBIF-BISON Data.

#### *Model Selection and Evaluation*

Models were evaluated based on their AIC (Muscarella et al., 2014), delta Akaike information criteria ( $\Delta AIC$ ), and AUC. In order to assess whether the models are accurately predicting suitable habitat, we calculated the number of observed occurrences that fell within the predicted habitat suitability grid cells using the 10% logistic threshold MaxEnt calculated for each species. This 10% logistic threshold indicates probability value that is the minimum value for suitable habitat and it can assist in determining the generality of our models between datasets.

We also employed cross-validation to test the generality of our models across datasets and to evaluate model performance on the best model for each species with the lowest AIC. Cross-validation can be performed in MaxEnt. This process involves splitting a designated percent of occurrence locations into a training dataset, which is used to fit the model, and a testing dataset, which is used to test against the rest of the occurrence locations (Merow et al., 2013). A robust model would have little variation of predicted habitat among iterations (Kimble, 2016) and generally, models that over fit the data perform well on the training data and poorly on the test data. For the Combined Dataset, 70% of the data was used for training and 30% was used for testing. We performed cross-validation on the PCT Data where 100% of the data was used for training and used the GBIF-BISON Data for testing. We then reversed the process using 100% of the GBIF-BISON for training and used the PCT Data for testing. To assess whether the models are accurately predicting suitable habitat, we calculated how many of these occurrences fall within the 10% logistic threshold.

To further validate model robustness, we used Monte Carlo simulations to check for spatial uncertainty in the occurrence points and covariates. We injected error into each of the species models with the Combined Datasets using the Monte Carlo feature in BlueSpray (Graham & Kimble, 2018). We ran 80 iterations and evaluated the mean AIC, standard deviation of the AIC, mean AUC and standard deviation of the AUC. The DEM is noted to vary vertically up to 2.42 meters in the conterminous United States (Gesch et al., 2014). In the programming language Python, we calculated the standard deviation of error in the slope and aspect rasters by varying the amount of error in the DEM and taking the average standard deviation over 10 runs (Appendix: Python Script). We found that slope had an average standard error of 0.728 degrees and aspect varied by 56.91 degrees. Data from OSU LEMMA underestimates values (Bell et al., 2015), with most rasters seen to have reductions by 0.05. Bark beetle infestations had patch areas combined into a larger polygon (USDA, 2010), so there may be an overestimation. LEMMA also notes that their overall classification accuracy for 10 categories was 45% and that most misclassification errors were minor (Ohmann & Gregory, 2002). Monitoring Trends in Burn Severity map fires accurately that are greater than 1000 acres (Eidenshink et al., 2009). GPS average error is 0.715 meters (U.S. Department Of Defense, 2007).

#### Results

Six environmental covariates for BKHGRO, six for HAIWOO, and five for YERWAR contributed to explaining more than 2% of the variation in the MaxEnt model initially made for each species and were included in building these individual models for each species using the Combined Dataset (Table 1). These covariates appear to have a significant correlation with the occurrence locations of the species

**Table 1.** Environmental covariates selected for each species to build the habitat suitability models based on the MaxEnt Jackknife feature using the Combined Dataset.

Species	Environmental Covariates
BKHGRO	1) Forty pba 2) elevation 3) distance to bark beetle infestations 4) distance to fires 5) slope 6) distance to streams
HAIWOO	1) Forty pba 2) distance to bark beetle infestations 3) slope 4) hardwood canopy cover 5) distance to fires 6) aspect
YERWAR	1) Forty pba 2) slope 3) hardwood canopy cover 4) distance to fires 5) distance to streams

and were determined to be valuable in creating the habitat suitability models.

The best model for BKHGRO, based on the lowest AIC, had a regularization multiplier of 1.5 to produce smooth response curves that did not over fit the data. For HAIWOO, the regularization multiplier was 5.5. For YERWAR, the best regularization multiplier was 1. In the best model of the Combined Dataset for each species, the 10% logistic threshold MaxEnt calculated for each species was

0.33 for BKHGRO, 0.37 for HAIWOO, and 0.28 for YERWAR (Table 2).

The PCT Data and the GBIF-BISON Data had consistently higher AUC values than the Combined Dataset (Table 3). The Combined Dataset was lower in AUC by 2-3 units. When we performed cross-validation on the PCT Data or the GBIF-BISON Data, the AUC decreased to just over the random prediction line. When we performed cross-validation on the Combined Dataset, the AUC decreased slightly.

**Table 2.** Model parameters run for each bird species and their resulting AIC,  $\Delta$ AIC, and AUC.

Data	Bird Species	Software	Regularization multiplier	AIC	$\Delta$ AIC	AUC
Combined	BKHGRO	MaxEnt	1.5	10157	0	0.88
Combined	BKHGRO	MaxEnt	2	10159	2	0.87
Combined	BKHGRO	MaxEnt	1	10201	44	0.89
Combined	HAIWOO	MaxEnt	5.5	4782	0	0.75
Combined	HAIWOO	MaxEnt	6	4784	2	0.75
Combined	HAIWOO	MaxEnt	5	4785	3	0.76
Combined	HAIWOO	MaxEnt	4.5	4789	7	0.76
Combined	HAIWOO	MaxEnt	4	4796	14	0.76
Combined	HAIWOO	MaxEnt	3.5	4800	18	0.77
Combined	HAIWOO	MaxEnt	3	4825	43	0.78
Combined	HAIWOO	MaxEnt	2.5	4896	114	0.79
Combined	HAIWOO	MaxEnt	2	4968	186	0.80
Combined	HAIWOO	MaxEnt	1.5	4986	204	0.82
Combined	HAIWOO	MaxEnt	1	5110	328	0.83
Combined	YERWAR	MaxEnt	1	29863	0	0.80
Combined	YERWAR	MaxEnt	1.5	29866	3	0.79

#### *BKHGRO Habitat Suitability*

We found that covariates elevation, Fortypba, distance to bark beetle infestations, slope, stream distance, and fires contributed significantly to our model for BKHGRO habitat suitability (Figs. 2 & 3). BKHGRO appears to find close proximity to bark beetle infestations as more suitable; this species has been observed to prefer forests

impacted by beetle impacts (Fair et al., 2018; Mosher, 2011). BKHGRO most likely does not forage on the boring beetles but may instead feed on other insects located in areas impacted by bark beetles, since BKHGRO glean insects (Airola & Barrett, 1985) rather than drill for boring beetles. The species appears to favor elevations above 800 meters but below 1,100 meters, but our models indicate

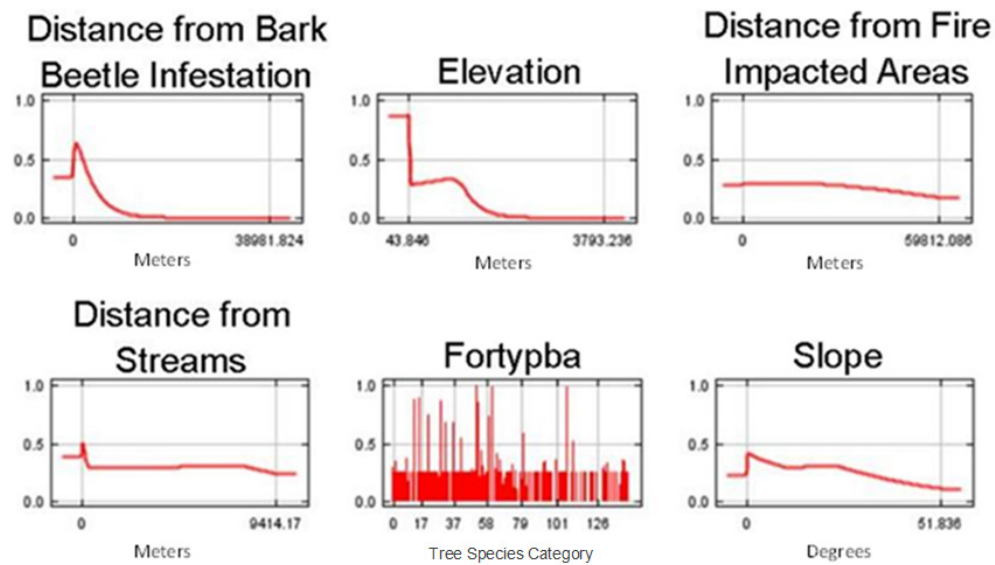


**Table 3.** Results of models created with the two datasets and the Combined Dataset. Cross-validation was performed against each of the models along with their AUC. For the logistic threshold, the number of occurrences that fall within the area selected by the model divided by the number of occurrences available by the dataset is provided.

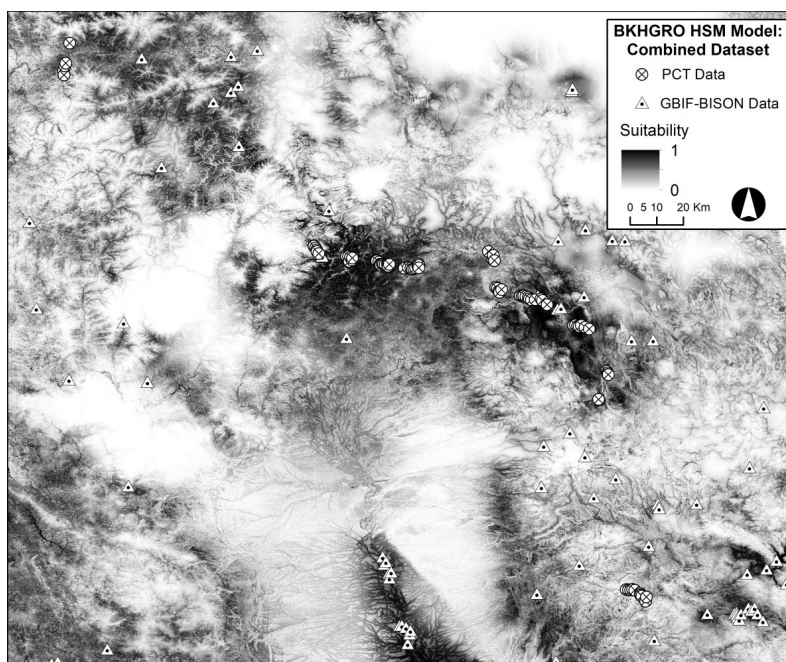
Bird Species	Data Used to Create Model	AUC	Data used for Cross-validation	Cross-validation AUC	Logistic Threshold for the PCT Data	Logistic Threshold for the GBIF-BISON Data
BKHGRO	PCT	0.95	GBIF- BISON	0.55	0.88	0.12
BKHGRO	PCT	0.91	PCT	0.85	0.85	0.30
BKHGRO	GBIF-BISON	0.91	PCT	0.56	0.23	0.88
BKHGRO	GBIF-BISON	0.90	GBIF- BISON	0.78	0.28	0.87
BKHGRO	Combined	0.88	Combined	0.83	0.93	0.88
HAIWOO	PCT	0.78	GBIF- BISON	0.57	1.00	0.83
HAIWOO	PCT	0.77	PCT	0.55	0.97	0.88
HAIWOO	GBIF/BISON	0.79	PCT	0.58	0.55	0.83
HAIWOO	GBIF-BISON	0.79	GBIF- BISON	0.77	0.59	0.89
HAIWOO	Combined	0.76	Combined	0.71	0.83	0.91
YERWAR	PCT	0.91	GBIF- BISON	0.51	0.85	0.24
YERWAR	PCT	0.91	PCT	0.88	0.83	0.25
YERWAR	GBIF-BISON	0.81	PCT	0.54	0.56	0.92
YERWAR	GBIF-BISON	0.82	GBIF- BISON	0.72	0.52	0.89
YERWAR	Combined	0.79	Combined	0.77	0.94	0.87

some suitability in lower elevations where occurrences were recorded in isolated forested habitats in the central valley as indicated by our Fortypba layer. We found higher suitability closer to burned areas. Suitability also peaks close to streams. BKHGRO has been noted to have a preference for a mixed hardwood/conifer plant community (Airola & Barrett, 1985) and Fortypba did confirm these

preferences showing a high affinity for white fir (*Abies concolor*), Ponderosa pine (*Pinus ponderosa*), California incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), Douglas fir (*Pseudotsuga menziesii*), California black oak (*Quercus kelloggii*), and canyon live oak (*Quercus chrysolepis*). This species appears to find slopes less than 30 degrees as more suitable.



**Figure 2.** BKHGRO response curves from MaxEnt with a regularization multiplier of 1.5 for each of the environmental covariates using the Combined Dataset.

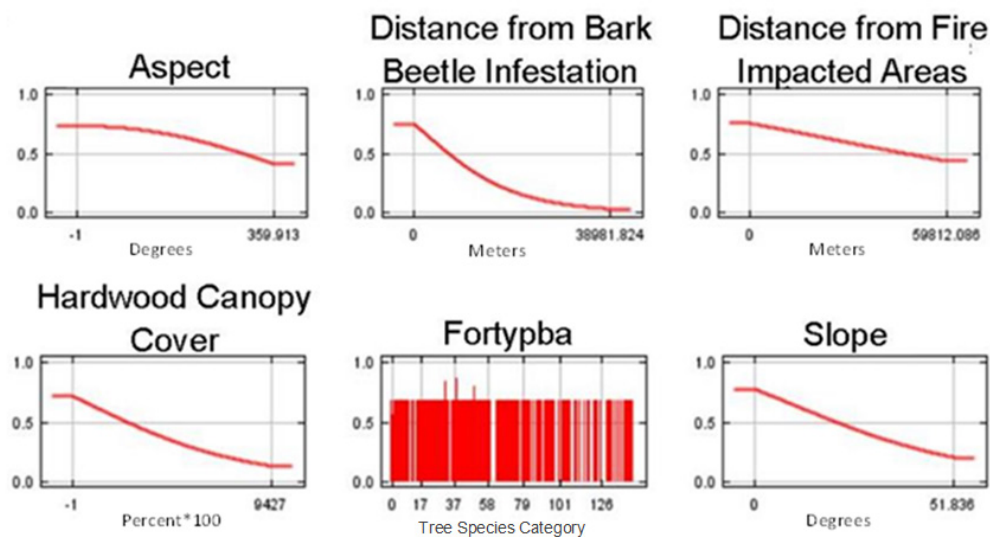


**Figure 3.** Habitat suitability model for the BKHGRO built from the Combined Dataset with a regularization multiplier of 1.5.

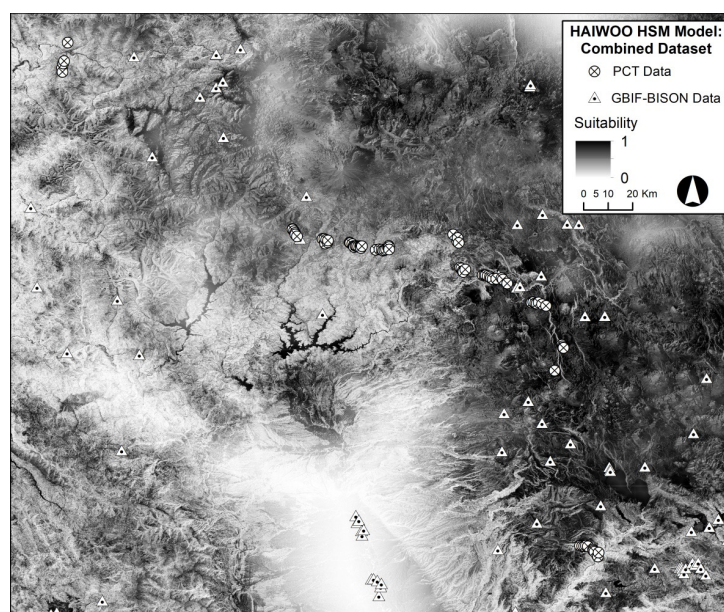
### HAIWOO Habitat Suitability

For HAIWOO, we found that the covariates of aspect, distance from bark beetle infestations, distance from fires, hardwood canopy cover, Fortypba, and slope contributed significantly to our model of habitat suitability (Figs. 4 & 5), where areas closer to bark beetle infestations and fire-impact-

ed habitat are considered more suitable. HAIWOO appears to prefer northwest facing slopes that are under 30 degrees. Areas with lower percentages of hardwood canopy, but greater percentages of conifer species, had higher suitability, including red fir (*Abies procera*), white fir, Jeffrey pine (*Pinus jeffreyi*), Ponderosa pine, white oak (*Quercus garryana*), and California black oak.



**Figure 4.** HAIWOO response curves from MaxEnt with a regularization multiplier of 5.5 for each of the environmental covariates using the Combined Dataset.



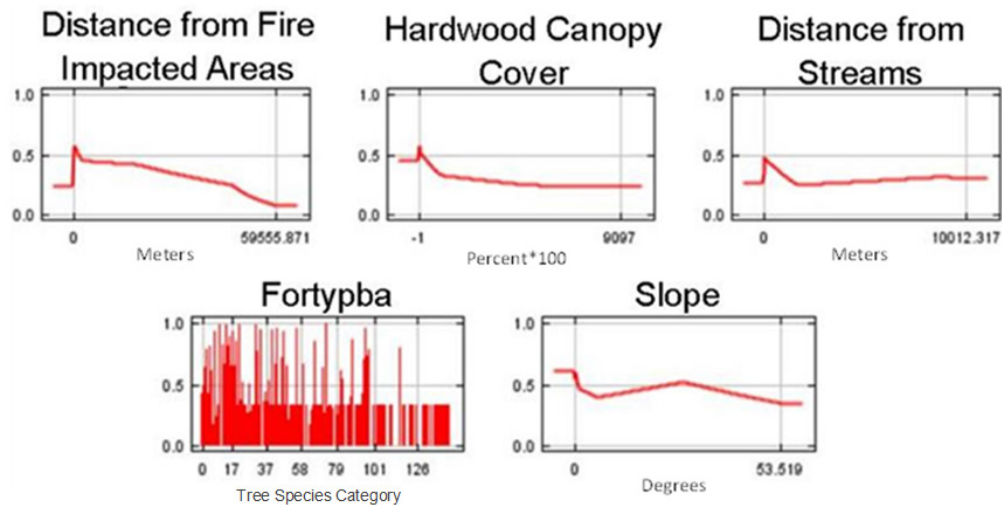
**Figure 5.** Habitat suitability model for the HAIWOO built from the Combined Dataset with a regularization multiplier of 5.5.



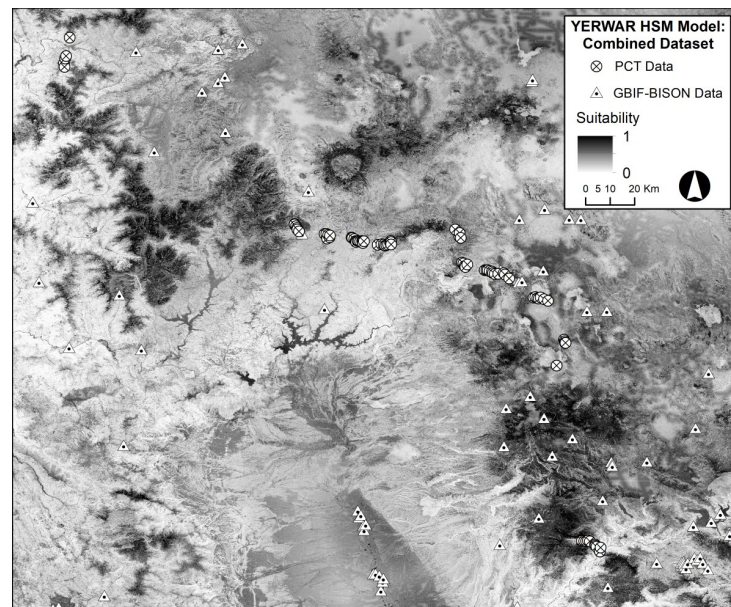
### YERWAR Habitat Suitability

For YERWAR, we found that the covariates of distance from fire impacted areas, hardwood canopy cover, distance from streams, Fortypba, and slope contributed significantly to our model of habitat suitability (Fig. 6 & 7). Our model also indicated higher suitability nearer to areas

impacted by fire. We found that suitability was greatest with little to no hardwood canopy cover. Areas nearer to streams have greater suitability than areas away from streams. Suitability was greatest in habitats dominated by coniferous trees, including white fir, red fir, California incense cedar, Jeffrey pine, sugar pine, Western white pine (*Pinus monticola*),



**Figure 6.** YERWAR response curves from MaxEnt with a regularization multiplier of 1 for each of the environmental covariates using the Combined Dataset.



**Figure 7.** Habitat suitability model for the YERWAR built from the PCT Data and GBIF-BISON Data combined with a regularization multiplier of 1.

Ponderosa pine, Douglas fir, mountain hemlock (*Tsuga mertensiana*), knobcone pine (*Pinus attenuate*), Brewer spruce (*Picea breweriana*), lodgepole pine (*Pinus contorta*), live oak, subalpine fir (*Abies lasiocarpa*), white oak, bitter cherry (*Prunus emarginata*), blue oak (*Quercus douglasii*), and Pacific silver fir (*Abies amabilis*). YERWAR appears to find slopes less than 30 degrees as more suitable.

#### Model Evaluation

With injected uncertainty into the best MaxEnt models for BKHGRO, the AIC increased by 58 and the AUC decreased by 0.03 from the original model. For HAIWOO, the AIC increased by 19 and the AUC decreased by 0.04. For YERWAR model, the AIC increased by 135 and the AUC decreased by 0.02.

#### Discussion

Our approach of combining complementary datasets derived from different methods in the field has resulted in habitat suitability models that are generalizable across our entire study area. Previous studies have also combined this PCT Data with data from another large-scale biodiversity monitoring program throughout northern California to model bird diversity-climate relationships (McGrann & Furnas, 2016; Furnas & McGrann 2018). In these studies, the PCT Data served to strengthen the multi-species occupancy models used for the analysis and to improve the representation of the remote, high-elevation habitats that were poorly sampled by the more extensive region-wide monitoring program. The models created with the Combined Dataset

**Table 3.** Monte Carlo results for injecting uncertainty into the model for BKHGRO.

Species		AIC Deviation		AUC Deviation
BKHGRO	10215	63.99	0.85	0.01
HAIWOO	4801	28.45	0.71	0.01
YERWAR	29998	84.20	0.78	0.01

performed at predicting the occurrences in all but one case with HAIWOO. In a similar approach, we used MaxEnt to create response curves that represent the expected habitat associations for each species across the entire study area beyond only the PCT. Further, we determined that our models were robust after injecting error into the observed data and the covariates and found the AUC only decreased by 0.02 to 0.04 points. Altogether, this indicates that our models are predictive of the actual spatial distribution of these species and of where these species might find suitable habitat across our entire study area. Our future research direction will include the use of these models to study how these species' habitats might be shifting due to drought, fire, or climate change, thus making our modeling approach useful to management decisions.

By combining the two datasets, we created a model that increased the ability to predict locations that included occurrences with a small reduction in AUC values. Although the AUC for the PCT Data was high, it did not predict occurrences well beyond the trail for YERWAR and BKHGRO, indicating that the PCT Data may be suitable for fine-scale

analysis on species distributions along this specific region of the trail. The PCT survey sites, due to the trail's design and the route chosen for the trail, may be biased towards higher elevations and other habitats disproportionately occurring along the trail, which was also reported by Furnas & McGrann (2018). It appears, from our analysis, that the PCT Data does not have enough predictive power to project to a larger area and requires additional data covering the broader range of environmental covariates throughout the study area. Yet, it would be cost prohibitive to apply more widely, across the entire study area, the intensive survey methods designed for application along this transect.

The GBIF-BISON Data has wider coverage of the study area but also has its own inherent biases. The AUC for the GBIF-BISON Data was slightly lower than the PCT Data overall, and it did not project well to the PCT Data. This can indicate that although GBIF-BISON Data may cover a larger area, it may not have the consistent and structured sampling design required for fine scale modeling. Additionally, data from these sources are generally biased towards roads (Ronen Kadmon, 2004) and contain surveyor bias as observers favor habi-

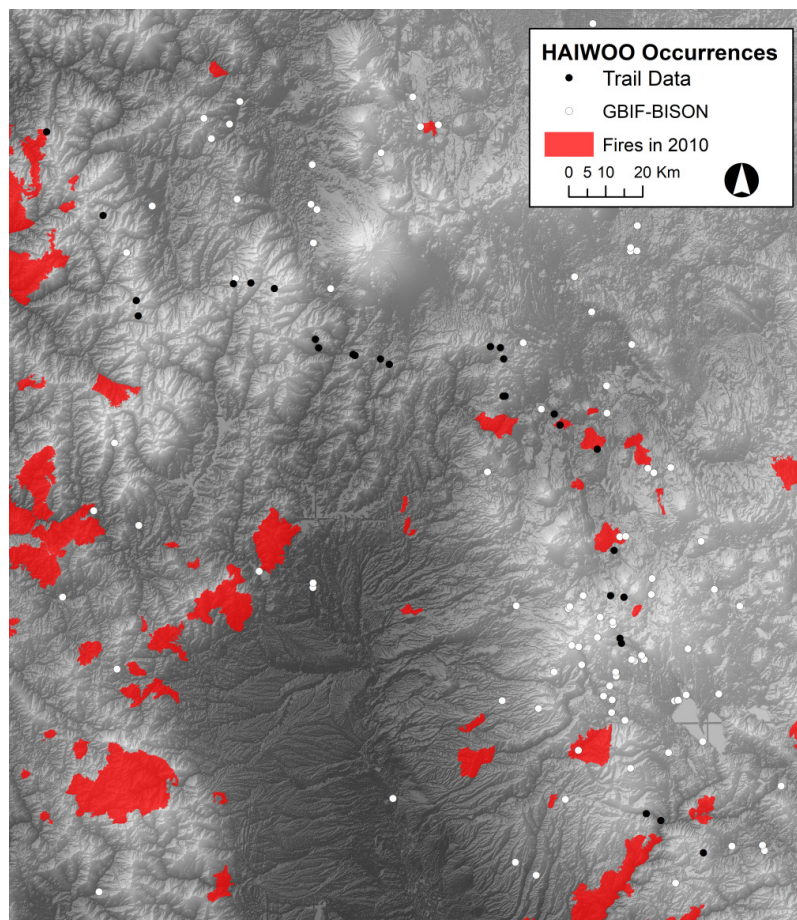


tats that are easier to access from roads or that are considered favorable for observing greater numbers of birds (Tulloch & Szabo, 2012). For example, we noticed that HAIWOO, which was expected to benefit from foraging in fire-impacted areas, was observed to have few occurrences within these areas (Figure 8). We suspect that observers who collected GBIF-BISON Data, chose to avoid burned forests. The GBIF-BISON Data, however, included some sampled areas at lower elevations, such as in the Sacramento Valley, where the PCT Data did not have any survey sites. The GBIF-BISON Data also had gaps, particularly in the remote and high-elevation wilderness areas, where the PCT Data was able fill in. Inclusion of the occurrences in the Sacramento Valley influenced the shape of the response curves, and the full range of the species was represented more appropriately.

#### *Habitat Associations for BKHGRO, HAIWOO, and YERWAR*

Response curves described well our anticipated habi-

tat associations for BKHGRO, HAIWOO, and YERWAR. Previous studies have documented BKHGRO in disturbed habitat near fires (Bagne & Purcell, 2011) and, more rarely, in high-elevation habitats (Wilson, 2013). As a canopy nester, it prefers nesting in close proximity to streams, which can act to moderate temperatures for the nest site (Becker, 2013). BKHGRO forage in a variety of habitats (Airola & Barrett, 1985) but within 2 km of a water source and readily use shrubs in early successional habitats (Gardali & Holmes, 2011). BKHGRO's affinity for shrubs may also lead to an affinity for a specific tree cover from the Fortypba layer (Pase, 1982), particularly at lower- to mid-elevation montane forests where a distinct shrub layer is commonplace in the understory. The response curves for the BKHGRO, when run with individual covariates, may suggest a bimodal response with distance to bark beetle infestations (Figure 8). They are found in bark beetle infested habitats (Mosher, 2011) where they may consume arthropods that follow a bark beetle infestation (Weslien &



**Figure 8.** Occurrences from HAIWOO and the zones of fire-impacted areas. Fire polygons from Monitoring Trends in Burn Severity (2009).

Schroeder, 1999), but also forage away from these infestations on other insects or seeds. When the distance to bark beetle infestations covariate is combined into the full model, it takes on a curve where close proximity to bark beetles is very suitable.

HAIWOO utilizes fire-impacted areas and forages on bark beetles (Saab et al., 2019), and we observed these habitats to have higher suitability. Since HAIWOO nest and forage in both snags or live conifer trees that may show signs of defoliation from bark beetles (Bull et al., 1986), lower amounts of hardwood canopy cover would have higher suitability. Slope and aspect may influence the woodpecker's choice of nest site, preferring cooler, moister areas (Bull et al., 1986). All the categories for tree species, from the Fortypba layer, showed some suitability, with only three tree species showing higher suitability. This could indicate that HAIWOO is a generalist, preferring many tree species for foraging and nesting.

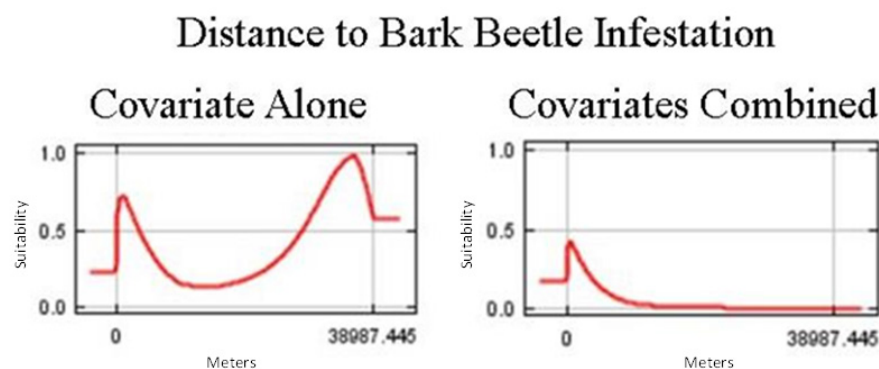
For YERWAR, high suitability was evident near, but not *within*, fire-impacted habitat, as the edge of this habitat may provide good forage for insects that are abundant on the edges of burned forests. We documented higher suitability in close proximity to streams; which is also documented by others (Kirkpatrick et al., 2009).

### Conclusions

We found that first identifying the trade-offs of each dataset, and deciding on whether to select the appropriate dataset, or combine both, was crucial in creating the best model to address our research questions and hypotheses. The PCT Data, derived from a transect survey protocol, may

be suitable for intensive sampling along environmental gradients and in describing climate-diversity relationship (the original purpose of the data) but not necessarily for extrapolation far beyond the trail itself. The intent of the original biodiversity study along the PCT was *not* to describe species distributions across a broader study area. Data from BISON or GBIF is beneficial for broad scale analysis but may leave out areas for fine scale analysis and these data may poorly represent more remote and high-elevation habitats. Also, the GBIF-BISON Data may not include the full range of the species and their habitats. If we use these models to generate fine-scale maps, we need to find additional datasets that capture more of the covariates required to model those areas, and combining datasets, habitat suitability models can be built that fill in spatial gaps and can more adequately inform management (Turner et al., 2016). Additionally, we found that BISON-GBIF underrepresented fire-impacted areas and throughout the region.

We provide a useful approach to modeling habitat suitability by combining an intensive transect survey with data sources from repositories such as BISON and GBIF. Overall, our models well characterized the suitability of habitat for these three bird species and demonstrated their utility. With well-developed models, managers can determine which habitats in their area are suitable and also track the overall response of avian diversity to drought, fire, climate change, or human land-use change. Future research directions should examine whether this modeling approach can track the response of birds, and their habitats, to these environmental changes.



**Figure 9.** Response curves for distance to bark beetle infestations with the covariate alone and combined in the full model. The covariate alone displays a bimodal response where the species is either very close to the infested area, or is further away. The covariate combined shows that areas near the infested habitat is more suitable.

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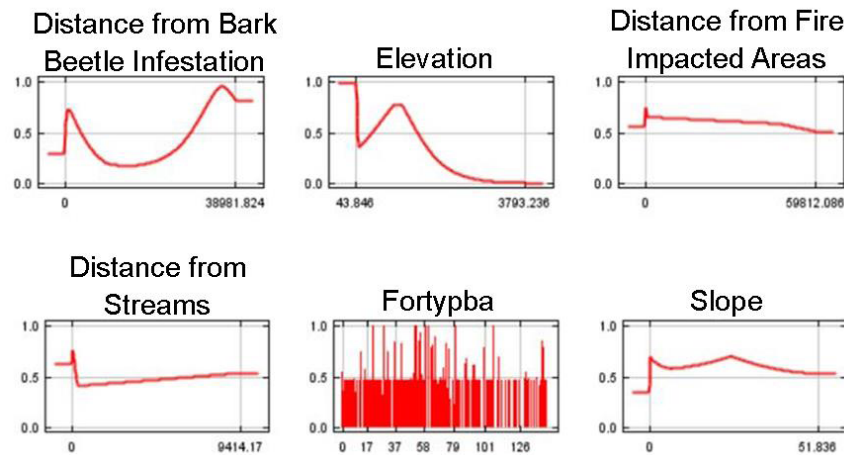


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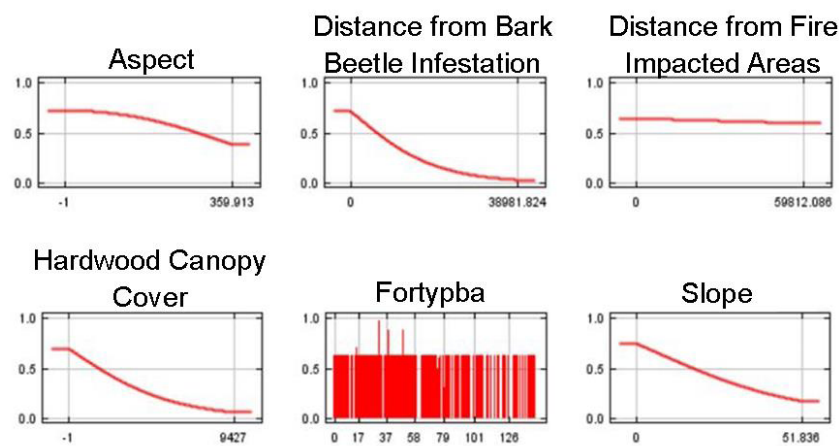
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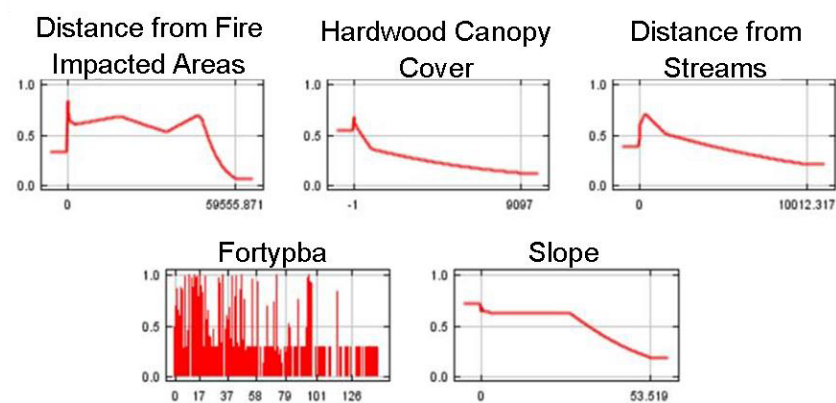
## Appendix



**Appendix figure 1.** BKHGRO response curves for the individual covariates.



**Appendix figure 2.** HAIWOO response curves for the individual covariates.



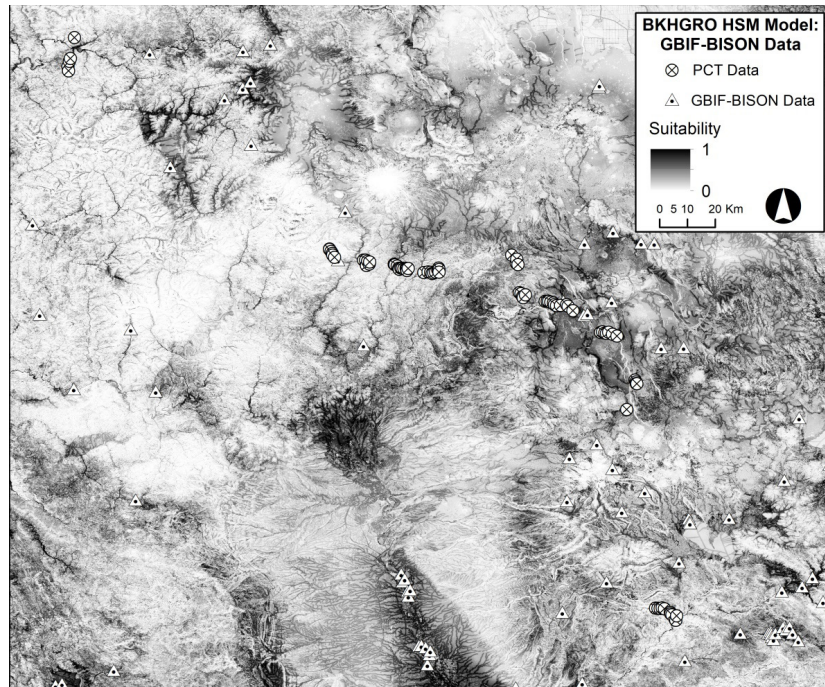
**Appendix figure 3.** YERWAR response curves for the individual covariates.

**Table 4.** Pearson correlation matrix produced in R (R code in the Appendix Section RCODE) of the correlation between environmental covariates. Covariates with a relationship above 0.7 were not used within the same model and prevent a potential reversal of the relationship within the model.

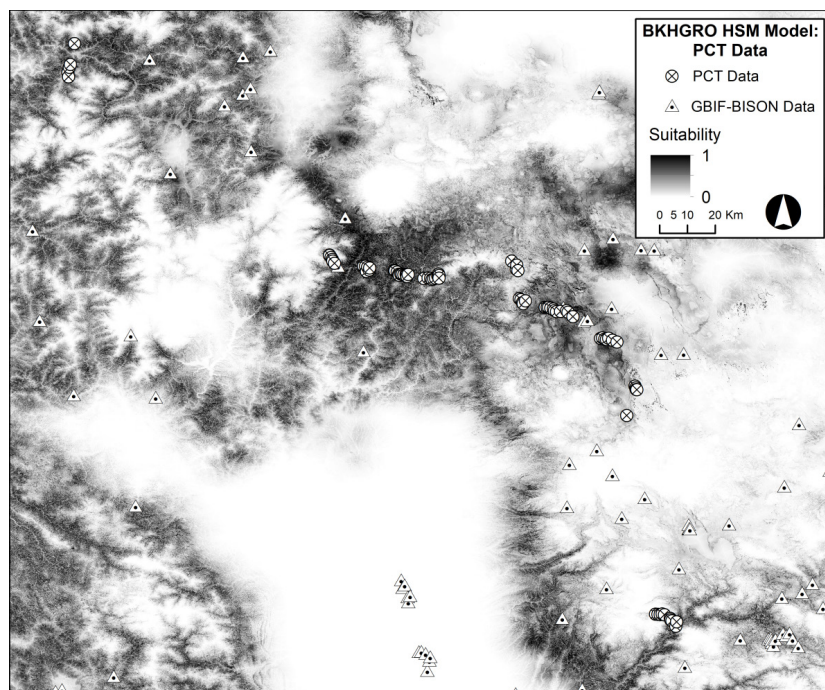
	Vegetation Class	Live Tree Density	Distance to Streams	Snag Density	Quadratic Mean Diameter of Dominant Tree Species	Hardwood Canopy Cover	Forest Type Based on the Basal Area of Dominant Tree Species
Vegetation Class	1.000	0.643	-0.315	0.157	0.638	-0.125	-0.223
Live Tree Density	0.643	1.000	-0.285	0.086	0.419	0.119	-0.194
Distance to Streams	-0.0315	-0.285	1.000	-0.152	-0.263	-0.100	0.122
Snag Density	0.157	0.086	-0.152	1.000	0.178	-0.122	-0.077
Quadratic Mean Diameter of Dominant Tree Species	0.638	0.419	-0.263	0.178	1.000	-0.162	-0.085
Hardwood Canopy Cover	-0.125	0.119	-0.100	-0.122	-0.162	1.000	0.390
Forest Type Based on the Basal Area of Fominant Tree Species	-0.223	-0.194	0.122	-0.077	-0.085	0.390	1.000
Distance to Fires	0.074	0.032	-0.248	-0.020	0.117	-0.031	0.015
Elevation	0.135	-0.017	-0.050	0.248	0.223	-0.653	-0.429
Conifer Canopy Cover	0.863	0.758	-0.354	0.150	0.624	-0.130	-0.236
Total Canopy Cover	0.763	0.780	-0.363	0.071	0.503	0.368	-0.041
Distance to Bark Beetle Infestations	-0.039	-0.049	0.078	-0.087	-0.051	-0.014	0.009
Aspect	-0.07	0.019	0.060	0.057	0.017	0.059	0.066
Slope	0.001	0.038	-0.354	0.143	0.096	0.262	0.170

**Table 4 Continued**

	Distance to Fires	Elevation	Conifer Canopy Cover	Total Canopy Cover	Distance to Bark Beetle Infestations	Aspect	Slope
Vegetation Class	0.074	0.135	0.863	0.763	-0.039	-0.007	0.001
Live Tree Density	0.032	-0.017	0.758	0.780	-0.049	0.019	0.038
Distance to Streams	-0.248	-0.050	-0.354	-0.363	0.078	0.060	-0.354
Snag Density	-0.020	0.248	0.150	0.071	-0.087	0.057	0.143
Quadratic Mean Diameter of Dominant Tree Species	0.117	0.223	0.624	0.503	-0.051	0.017	0.096
Hardwood Canopy Cover	-0.031	-0.653	-0.130	0.368	-0.014	0.059	0.262
Forest Type Based on the Basal Area of Dominant Tree Species	0.015	-0.429	-0.236	-0.041	0.009	0.066	0.170
Distance to Fires	1.000	0.203	0.070	0.040	0.436	-0.044	0.328
Elevation	0.203	1.000	0.074	-0.220	0.071	-0.064	-0.046
Conifer Canopy Cover	0.070	0.074	1.000	0.858	-0.080	0.013	0.021
Total Canopy Cover	0.040	-0.220	0.858	1.000	-0.080	0.027	0.135
Distance to Bark Beetle Infestations	0.436	0.071	-0.080	-0.080	1.000	-0.065	0.040
Aspect	-0.044	-0.064	0.013	0.027	-0.065	1.000	0.039
Slope	0.328	-0.046	0.021	0.135	0.040	0.039	1.000

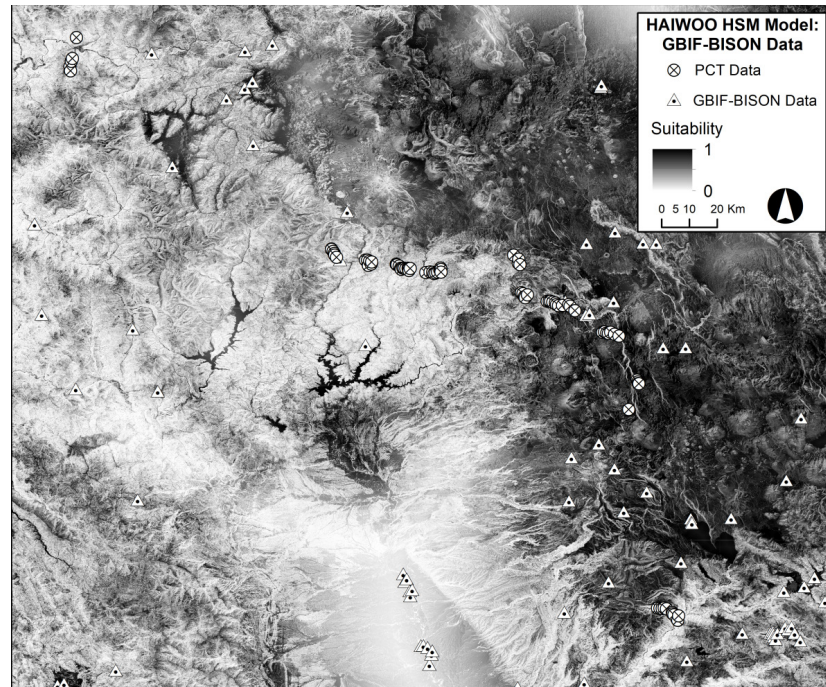


**Appendix figure 4.** BKHGRO habitat suitability model built from GBIF-BISON Data with regularization multiplier of 1.5.

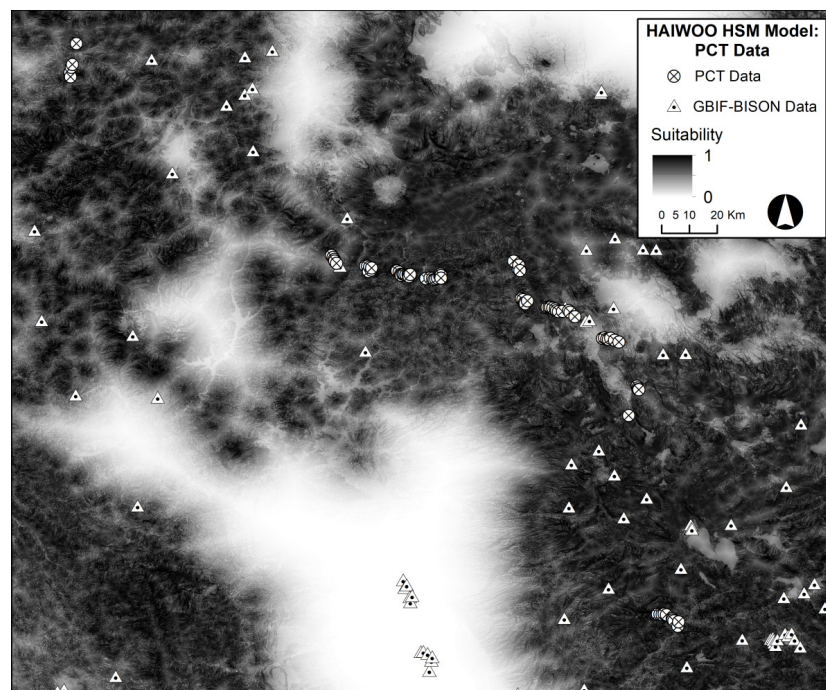


**Appendix figure 5.** BKHGRO habitat suitability model built from PCT Data with a regularization multiplier of 1.5.



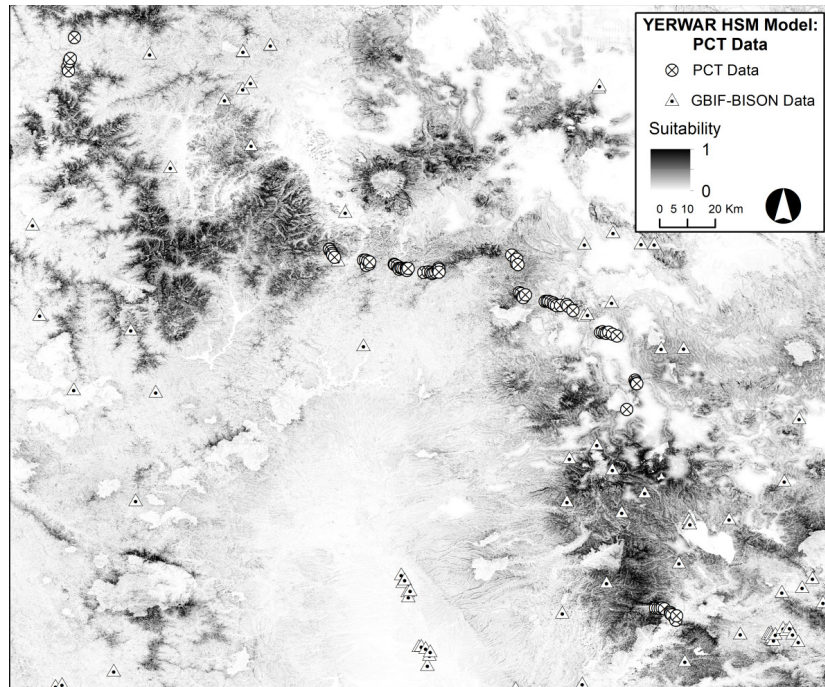


**Appendix figure 6.** HAIWOO habitat suitability model built from the GBIF-BISON Dataset with a regularization multiplier of 5.5.

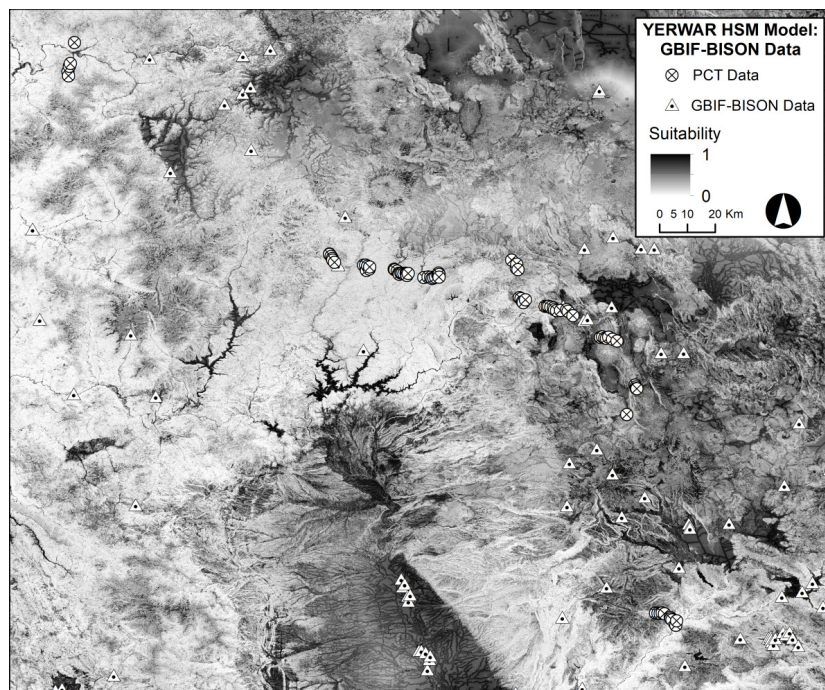


**Appendix figure 7.** HAIWOO habitat suitability model built from the PCT Data with a regularization multiplier of 5.5.





**Appendix figure 8.** YERWAR habitat suitability model built from the PCT Data with a regularization multiplier of 1.



**Appendix figure 9.** YERWAR habitat suitability model built from the GBIF-BISON Data with a regularization multiplier of 1.

**RSCRIPT**

```

# Finding the correlation between environmental covariates
#adding data to R
dat<-(read.csv("", head=T))
attach(dat)
# Assessing correlations from the 12th column to the end
cor(dat[,12:ncol(dat)], use="pairwise.complete.obs",method="pearson")
#####
####
# R script to compare the suitability values for all the occurrence records for BKHGRO
# Import the suitability comparison csv file
BKHGRO=read.csv("")
plot(BKHGRO$Point, BKHGRO$maxent_R_4, pch=21, bg="black", xlab="Occurrence Record Number", ylab="Habitat Suitability")
# Finding the mean value of suitability
mean(BKHGRO$maxent_R_4)
#####
####
# R script to compare the suitability values for all the occurrence records for HAIWOO
# Import the suitability comparison csv file
HAIWOO=read.csv("")
plot(HAIWOO$Point, HAIWOO$MaxEntR3, pch=21, bg="black", xlab="Occurrence Record Number", ylab="Habitat Suitability")
# Finding the mean value of suitability
mean(HAIWOO$MaxEntR3)
#####
####
# R script to compare the suitability values for all the occurrence records for YERWAR
# Import the suitability comparison csv file
YERWAR=read.csv("")
plot(YERWAR$Point, YERWAR$MaxEntR3, pch=21, bg="black", xlab="Occurrence Record Number", ylab="Habitat Suitability")
# Finding the mean value of suitability
mean(YERWAR$MaxEntR3)

```

**Python Script for calculating the standard error in the Aspect and Slope rasters**

```

import os
import sys

# Open source spatial libraries
import shapely
import numpy
import gdal
import math
import random

# SpaPy libraries
from SpaPy import SpaBase
from SpaPy import SpaPlot
from SpaPy import SpaVectors
from SpaPy import SpaView
from SpaPy import SpaReferencing
from SpaPy import SpaDensify

```

```

from SpaPy import SpaView
from SpaPy import SpaRasters
from SpaPy import SpaTopo
from SpaPy import SpaRasterVectors
# set the input to the path where the original files are

#InputPath="C:\\Projects\\ProjectsPython\\HollsPaper\\Elevation.tif"
#InputPath="C:\\Projects\\ProjectsPython\\HollsPaper\\Sampled.tif"
InputPath1="C:\\Projects\\ProjectsPython\\HollsPaper\\ProjectedDEM_NoMask.tif"

OutputPath1="C:\\Projects\\ProjectsPython\\HollsPaper\\Slope1.tif"
OutputPath2="C:\\Projects\\ProjectsPython\\HollsPaper\\Slope2.tif"
OutputPath3="C:\\Projects\\ProjectsPython\\HollsPaper\\Temp.tif"

# Load the initial DEM
TheDEM=SpaRasters.SpaDatasetRaster()
TheDEM.Load(InputPath1)

WidthInPixels=TheDEM.GetWidthInPixels()
HeightInPixels=TheDEM.GetHeightInPixels()

# Create the base slope raster with no error
TheSlope=SpaTopo.Slope(TheDEM,OutputPath1)

TheSlope=SpaRasters.SpaDatasetRaster()
TheSlope.Load(OutputPath1)

# Setup the StdDev variables
SumOfSquares=0
N=0

# Loop over and over to improve the StdDev
Index=0
while (Index<1):

    # Load the DEM
    TheDEM3=SpaRasters.SpaDatasetRaster()
    TheDEM3.Load(InputPath1)
    TheBand=TheDEM3.GetBand(0)

    Row=0
    while (Row<HeightInPixels):
        Column=0
        while (Column<WidthInPixels):

            Value=TheBand[Row][Column]

            Random=numpy.random.normal(0,2.42)

            Value+=Random

```

```

        TheBand[Row][Column]=Value

        Column+=1

    Row+=1

TheDEM3.SetBands([TheBand])
TheDEM3.Save("C:\\Projects\\ProjectsPython\\HollsPaper\\TempDEM.tif")

SpaTopo.Slope("C:\\Projects\\ProjectsPython\\HollsPaper\\TempDEM.tif",OutputPath2)

TheSlope2=SpaRasters.SpaDatasetRaster()
TheSlope2.Load(OutputPath2)

#
TheBand1=TheSlope.GetBand(0)
TheBand2=    TheSlope2.GetBand(0)

Row=0
while (Row<HeightInPixels):
    Column=0
    while (Column<WidthInPixels):

        Value1=TheBand1[Row][Column]
        Value2=TheBand2[Row][Column]

        if (Value1!=-9999) and (Value2!=-9999):
            SumOfSquares+=(Value1-Value2)**2
            N+=1

        Column+=1

    Row+=1

Index+=1

StdDev=math.sqrt(SumOfSquares/N)
print(StdDev)

```