A SPECIES DISTRIBUTION MODEL FOR GUIDING OREGON SPOTTED FROG (*RANA PRETIOSA*) SURVEYS NEAR THE SOUTHERN EXTENT OF ITS GEOGRAPHIC RANGE

HUMBOLDT STATE UNIVERSITY

by

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ABSTRACT

A SPECIES DISTRIBUTION MODEL FOR GUIDING OREGON SPOTTED FROG (*RANA PRETIOSA*) SURVEYS NEAR THE SOUTHERN EXTENT OF ITS GEOGRAPHIC RANGE

Luke Alexander Groff

The Oregon Spotted Frog (*Rana pretiosa*), endemic to the Pacific Northwest, was once considered widespread in complex, warm water wetlands. Over 70% of historic populations are thought to be extirpated with range-wide habitat loss exceeding 90%. Using Maxent, I developed a series of Species Distribution Models (SDMs) to identify suitable habitat and predict the distribution of *Rana pretiosa* toward the southern extent of its geographic range. These SDMs were generated from two sets of spatial data: a set of occurrence points and a suite of environmental variables. Occurrence data included all verified populations within the study area. Environmental variables, used to characterize habitat associated with recognized populations, included variables derived from climatic, topographic, land cover and soil datasets. Three unique SDMs were averaged to produce a single distribution map that predicts and ranks suitable habitat across the species' southern range. I used the averaged output from the SDMs, along with aerial, topographic and National Wetlands Inventory imagery, to identify optimal survey sites within the Klamath and Pit river hydrographic basins. I surveyed 18 sites repeatedly and investigated an additional 44 sites. I attempted to focus my efforts on private land, as most preceding surveys in this region were conducted on public land. While I did not

detect *Rana pretiosa* in California, I documented two individuals at a previously unrecognized site in Klamath County, Oregon. This detection is significant because it represents the species' most northern point of occurrence in the Wood River and because only eight extant populations are currently recognized within the Klamath River hydrographic basin.

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INTRODUCTION

Effective management of a species, particularly one that is rare or threatened, requires accurate knowledge of its geographic distribution. As such, species distribution models (SDMs) have become increasingly popular and are being used for a variety of ecological applications (Guisan and Thuiller 2005). Generally, SDMs use presence/absence data with a suite of environmental variables to estimate statistical relationships between a species and its habitat. Most commonly, SDMs have been used to direct biological surveys aimed at identifying unrecognized populations or areas of distribution (Rebelo and Jones 2010; Jiménez-Valverde *et al*. 2008; Bourg *et al*. 2005; Greaves *et al*. 2006; Raxworthy *et al*. 2003); estimate species' responses to environmental perturbations, including climate and land use changes (Ficetola *et al*. 2010; Milanovich *et al*. 2010; Pauly *et al*. 2008; Preston *et al*. 2008; Thomas *et al*. 2004); predict potential range extensions of alien species (Hinojosa-Díaz *et al*. 2009; Wang *et al*. 2009; Ficetola *et al* 2007; Giovanelli *et al*. 2007); test evolutionary hypotheses (Peterson 2003; Graham *et al*. 2004); and identify high-priority conservation areas (Goldberg and Waits 2009; Hanna *et al*. 2007; Ferrier *et al*. 2004).

A variety of methods are available to model species distributions. Certain SDMs require species presence and absence data, while others require only presence data and use background data as pseudo-absences. Further, because individual SDMs employ different statistical approaches, model performance is influenced by sample size (i.e., number of occurrence records), species characteristics and spatial scale (Wisz *et al*. 2008

Pearson *et al*. 2007; Hernandez *et al*. 2006; Stockwell and Peterson 2002). Numerous comparative studies have evaluated the performance of different SDMs (Tsoar *et al*. 2007; Elith *et al*. 2006; Segurado and Araújo 2004; Brotons *et al*. 2004), but the appropriate choice is dependent on multiple factors (e.g., sample size, species rarity, size of species' geographic range, spatial scale, user preference). I chose to use Maximum Entropy Species Distribution Modeling (Maxent) to estimate the potential distribution of the Oregon Spotted Frog (*Rana pretiosa*) across the southern portion of its geographic range. Maxent is a machine-learning process that uses a statistical mechanics approach and requires only presence data, along with a suite of environmental variables relevant to the focal species' distribution. While considered a novel SDM, Maxent has consistently been shown to outperform established modeling methods (Tarkhnishvili *et al.* 2009; Kumar *et al.* 2009; Ortega-Huerta and Peterson 2008; Elith *et al*. 2006), especially when constrained by a low number of occurrence records (Benito *et al*. 2009; Wisz *et al*. 2008; Papes and Gaubert 2007; Pearson *et al*. 2007; Hernandez *et al*. 2006).

Rana pretiosa is endemic to the Pacific Northwest and historically occupied a geographic range between southwestern British Columbia and northern California. The species is considered a "Candidate for Federal Listing" by the U.S. Fish and Wildlife Service, "Endangered" in Washington, "Sensitive-Critical" in Oregon, a "Species of Special Concern" in California, and "Red-listed" in British Columbia (Pearl and Hayes 2004; Haycock 2000). Museum specimens and historic records describe 62 historic populations across its range, of which only 13 remain (Cushman and Pearl 2007;

Haycock 2000). Thus, 79% of known historic populations have been extirpated and the historic range has shrunk by more than 90% (Cushman and Pearl 2007; Hayes 1997).

Today, *R. pretiosa* is found in relatively few, small, disjunct populations in British Columbia, Washington and Oregon. The species has not been detected in California since 1918, but assertions that it is extirpated from the state are speculative and unverified. Populations may have remained unrecognized due to limited knowledge of habitat, site remoteness or restricted access to privately owned land. Prior surveys were concentrated almost exclusively on public land; private property remains mostly unexplored in the study area. The potential for unrecognized populations becomes especially plausible after considering that an extant population is located less than seven miles north of the California border. Increased scientific attention has resulted in the detection of 18 new populations (Haycock 2000; Haycock 1998; Hayes 1997; McAllister and Leonard 1997), but efforts aimed at identifying unrecognized populations in northern California are entirely lacking. For this reason, I used Maxent to estimate the potential distribution of *R. pretiosa* in southern Oregon and northern California, and subsequent to model generation and evaluation, conducted surveys at locations predicted to provide highly suitable habitat.

Aspects of *R. pretiosa's* ecology facilitate distribution modeling and the selection of environmental variables. For example, it has been demonstrated that SDM accuracy is improved when the focal species is rare, restricted to a small geographic range and possesses an affinity for wetlands (Franklin *et al*. 2009; McPherson and Jetz 2007). *Rana pretiosa* is restricted to complex, aquatic habitats measuring 4 hectares or larger (Pearl and Hayes 2004; Hayes 1994). Accordingly, variables pertaining to hydric environments were an obvious choice to incorporate into the models. Lastly, SDMs tend to be more accurate and have better predictive power when generated for specialist, rather than generalist, species (Elith *et al*. 2006; Brotons *et al*. 2004). This is because specialist species are restricted to a specific set of habitats, which are better described by environmental variables because such habitats correspond with smaller value ranges. Specifically, *R. pretiosa* is the only amphibian in the Pacific Northwest that requires large, complex, warm water wetlands with emergent vegetation and permanent water.

The objectives of this study were to: (1) generate a SDM for *R. pretiosa* to predict areas of suitable habitat near the southern extent of its geographic range, (2) determine the environmental variables that most influence the estimated distribution of *R. pretiosa*, and (3) conduct *R. pretiosa* surveys at areas predicted to be highly suitable for the species. To accomplish these objectives, I developed a series of SDMs that identify and rank suitable habitat. These models incorporated relevant environmental variables and all known *R. pretiosa* occurrence records (n = 17) within the study area. The SDMs were used to facilitate the site selection process related to the third research objective, surveying for unrecognized populations. Detection of *R. pretiosa* at any unrecognized locality, particularly near the species' southern range limit, would be important for the conservation of the species.

MATERIALS AND METHODS

Study Area

This study was designed to estimate the distribution of *R. pretiosa* habitat across the southern portion of its geographic range in northern California and south-central Oregon. The study area encompassed Lassen, Modoc, Shasta and Siskiyou Counties in California, and Jackson, Klamath and Lake Counties in Oregon (Figure 1). While I concentrated my field efforts within the Klamath and Pit River hydrographic basins, I did not constrain modeling to these drainages because I wanted to evaluate the presence of suitable habitat at adjacent areas positioned within different hydrographic basins.

Figure 1. Historic *R. pretiosa* distribution in Oregon and California indicated with diagonal hatching. Project study area, shown in gray, is located in northern California and southern Oregon, USA.

The Klamath River runs for approximately 423 km through southern Oregon and northern California and has a hydrographic basin that encompasses 40,468 km^2 (USGS 2007). The Klamath River system is partitioned into lower and upper sub-basins that differ in landforms and climate. For example, the lower Klamath sub-basin is generally characterized by confined channels and steep gradients in mountainous terrain, while the upper sub-basin is defined by poorly-confined channels and shallow gradients across an area best described as a large graben (Gannett *et al*. 2007). Climatic conditions change from temperate, near the Pacific Ocean, in the lower sub-basin to semiarid in the upper sub-basin which, in turn, influences a progressive vegetation change. Vegetation associations in the lower sub-basin grade from humid, coniferous forests dominated by coast redwood (*Sequoia sempervirens*) to mixed coniferous-deciduous forests dominated by Douglas-fir (*Pseudotsuga menziesii*) and big leaf maple (*Acer macrophyllum*). In contrast, conditions in the upper sub-basin support dry, coniferous forests dominated by ponderosa pine (*Pinus ponderosa*) and shrub-steppe grasslands consisting mostly of western juniper (*Juniperus occidentalis*) and Great Basin sagebrush (*Artemisia tridentata*; Gannett *et al*. 2007). The major tributaries of the upper Klamath sub-basin are the Wood, Williamson, Sprague and Sycan rivers; the Shasta, Scott, Salmon and Trinity rivers constitute the primary tributaries of the lower Klamath sub-basin.

The Pit River is the longest tributary of the Sacramento River and is located entirely in California. At 507 km long, the Pit River is longer than the Klamath River, but its hydrographic basin, which covers 11,199 km^2, is less than one-third of that of the Klamath's (Hyatt 1933). The Klamath and Pit rivers are two of only three rivers to penetrate the Cascade Mountains (the third is the Columbia River). Despite its hydrologic connection to the Sacramento-San Joaquin River system, much of the Pit River is physiographically connected to the western fringe of the Great Basin Province (Hyatt 1933). As a consequence, some similarities exist between the upper and lower sub-basins of the Pit River and the upper and lower sub-basins of the Klamath River. The lower sub-basin contains relatively well-confined serpentine canyons, whereas much of the upper sub-basin is less confined, includes several broad valleys and is characterized by perennial springs and ancient lakebeds (Hyatt 1933). Moreover, the climatic gradient is reflected in vegetation associations that change from shrub-steppe grassland and dry forest associations in the upper sub-basin, to mixed deciduous-coniferous, oak and chaparral associations in the lower sub-basin. Major tributaries of the upper sub-basin include the North and South Forks of the Pit River and Ash Creek. Fall River, Burney Creek and Hat Creek constitute the primary tributaries of the lower sub-basin.

Oregon Spotted Frog Locality Data

I obtained information for all known, verified *R. pretiosa* localities (n = 17) within the study area from Marc Hayes, a Senior Research Scientist with the Washington Department of Fish and Wildlife. Hayes gathered most data pertaining to extant populations via surveys conducted throughout the 1990s (Hayes 1994; Hayes 1997; Jennings and Hayes 1994), but the most recently discovered locality was identified by Michael Parker (Southern Oregon State College) in 2003. Hayes also inspected museum collections to verify the accuracy of historic records. The occurrence records were used as the dependent variable in the modeling process and consisted of three presumably extirpated localities in California, as well as six presumably extirpated and eight extant localities in Oregon (Figure 2). The California localities were positioned in both river basins and constitute the oldest regional records, dating from 1898 to 1918.

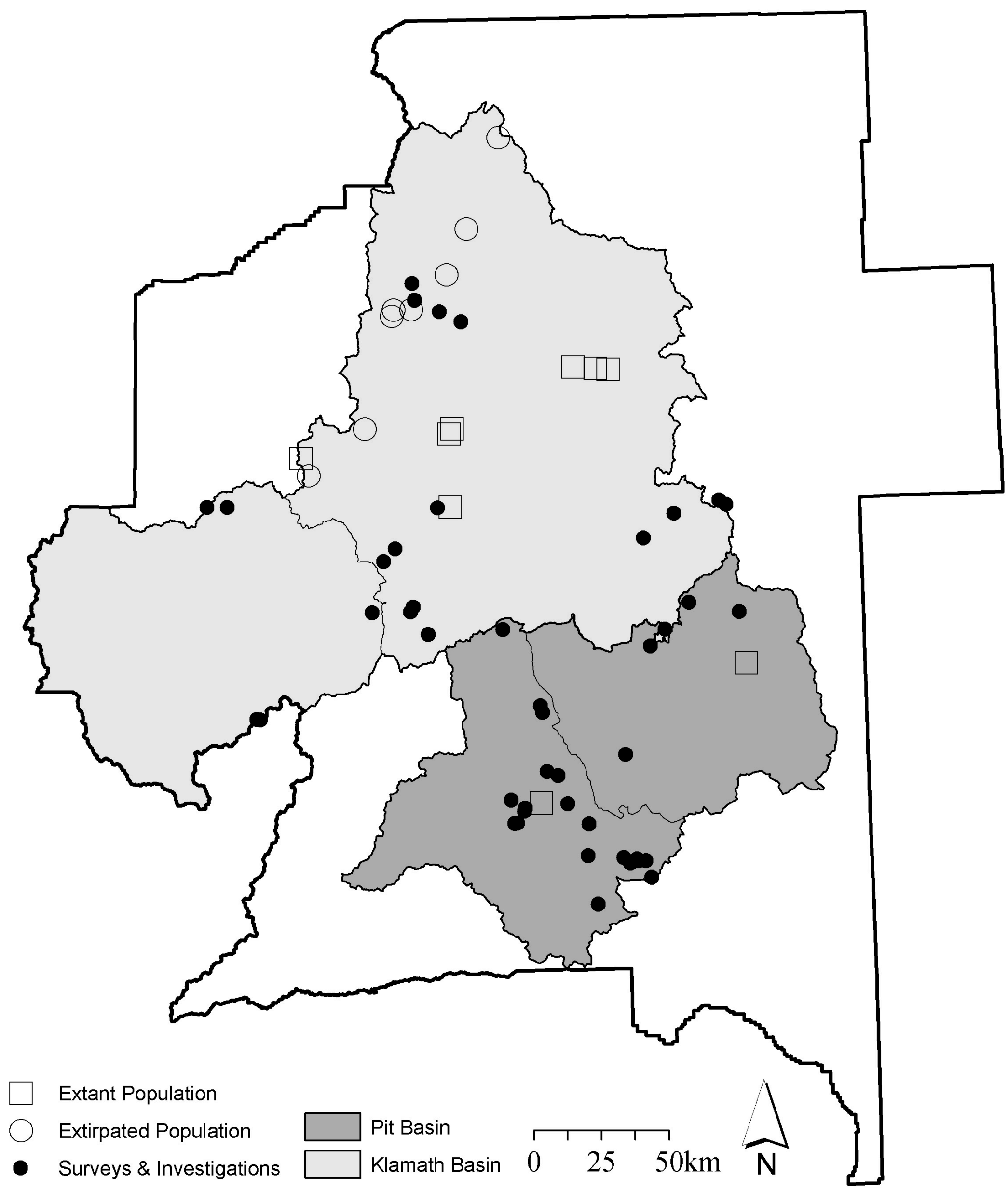

Figure 2. Detail of study area in northern California and southern Oregon, USA. Klamath River hydrographic basin indicated with light gray shading and Pit River hydrographic basin indicated with dark gray shading. Upper and lower sub-basin divisions shown within the respective basin. Unfilled circles and squares denote extant and presumably extirpated *R. pretiosa* populations, respectively. Survey and investigation sites designated with black-filled circles. Due to the close proximity of certain sites, some symbols may represent more than one location.

Environmental Variables

I collected a suite of 25 environmental variables from various sources to use in the SDMs (Table 1). These variables, which served as potential predictors of *R. pretiosa* habitat, were used to describe climatic, topographic, land cover and soil conditions. Four variables, derived from the 2001 National Land Cover Dataset (NLCD), were used to describe aquatic habitat. These variables included the proportion of woody wetland, emergent herbaceous vegetation, open water and aquatic habitat diversity within 2.79 km, which represents the maximum-recorded dispersal distance for the species (Cushman and Pearl 2007). Further, I derived a categorical soil moisture variable from the State Soil Geographic Database (STATSGO2), which was incorporated to help delineate aquatic habitats. Elevation data were obtained from the National Elevation Dataset (NED) and used to constrain model predictions, as the species is not known to occur within the study area at elevations below 1,004 m or above 1,605 m. Lastly, I incorporated 19 bioclimatic variables from the WorldClim dataset to describe temperature and precipitation patterns associated with the occurrence records. These variables were interpolated from observed data and were representative of the time period between 1950 and 2000.

To justify the inclusion of all locality records in my SDMs, I compared the means and 95% confidence intervals of presumably extirpated and extant *R. pretiosa* populations for each continuous variable. The soil moisture and wetland complexity variables represent ordinal, or categorically ranked, variables and were thus excluded from this analysis. If the confidence intervals overlapped, I considered the variation between the presumably extirpated and extant populations to be insignificant. If the confidence intervals did not overlap, I considered this evidence that the variation between populations was significant.

Table 1. Environmental variables described by original spatial resolution, as well as source and reference information.

Environmental Variables	Original Resolution	Source	References
Elevation	1 arc-sec (~30m)	National Elevation Dataset (NED); www.seamless.usgs.gov	Gesch *et al*. 2002; Gesch 2007
Emergent herbaceous veg. Woody wetland Open water Wetland complexity	1 arc-sec (~30 m)	2001 National Land Cover Dataset (NLCD); www.mrlc.gov	Homer *et al*. 2004
Soil moisture	-	State Soil Geographic (STATSGO2) Database; www.soildatamart.nrcs.usda.gov	Soil Survey Staff 2008
Annual mean temperature Mean diurnal range Isothermality Temperature seasonality Max. temperature of warmest month Min. temperature of coldest month Temperature annual range Mean temperature of wettest quarter Mean temperature of driest quarter Mean temp. of warmest quarter Mean temperature of coldest quarter Annual precipitation Precipitation of wettest month Precipitation of driest month Precipitation seasonality Precipitation of wettest quarter Precipitation of driest quarter Precipitation of warmest quarter Precipitation of coldest quarter	30 arc-sec (~1 km)	WorldClim bioclimatic database; http://www.worldclim.org	Hijmans *et al*. 2005

(-) Dash indicates source data was obtained in vector format

Modeling Procedure

Maxent estimates species' ranges by calculating the most uniform distribution (i.e., maximum entropy) given the constraint that the expected value of each environmental variable closely matches the empirical average of the occurrence data (Phillips *et al*. 2006). Importantly, Maxent generates a probability distribution across the entire study area, allowing for comparisons between different regions. These distribution values are typically very small, since they must sum to one, over the entire study area. Maxent also estimates each variable's contribution to the SDM via a jackknife analysis of the gain. Gain is a unitless statistic that assesses how well the predicted distribution fits the occurrence data compared to a uniform distribution.

I used ArcGIS 9.3 (ESRI, Redlands, CA) to format the occurrence records and environmental variables for use in Maxent. First, I reprojected all digital data to the Universal Transverse Mercator (UTM Zone 10) coordinate system using the North American Datum of 1983 (NAD83). I also converted all STATSGO2 vector soil layers to raster format. For each environmental variable, I mosaiced all input rasters for a specific variable into a single raster dataset, and if necessary, resampled it to one arc-second (~30 m) resolution. All resulting raster layers were clipped to the study area boundary. I chose to use one arc-second resolution data because *R. pretiosa* is associated with complex habitats and NLCD detail would have been sacrificed at lower resolutions.

Notably, the NLCD and STATSGO2 layers were transformed to better reflect the habitat requirements of *R. pretiosa*. For instance, I created three layers to represent the three aquatic classes identified in the NLCD: open water, woody wetlands and emergent herbaceous vegetation. I transformed all cells in each layer, using the Focal Statistics and Raster Calculator tools, to express the proportion of the respective aquatic class within a 186 × 186 cell neighborhood. This neighborhood incorporated all cells within 2.79 km of the focal cell and represented the maximum dispersal distance documented for the species (Cushman and Pearl 2007). Further, I created a fourth layer from the NLCD to address wetland complexity. Cell values in this layer represented the number of aquatic classes (i.e., 0-3) within the same 186 × 186 cell neighborhood. Lastly, because *R. pretiosa* is exclusively associated with aquatic environments, the STATSGO2 layer was reclassified using three soil moisture classes: non-hydric, partially hydric and completely hydric. The entire study area encompassed 104,802,905 cells, equivalent to approximately 94,304 km^2.

I used Maxent version 3.3.1 (http://www.cs.princeton.edu/~schapire/maxent/) to create three SDMs, which incorporated the 17 occurrence localities and a unique subset of environmental variables (Table 2). In accordance with Phillips *et al*. (2004), I used linear, quadratic and hinge features to generate each model and maintained other settings as default. The Max_Full model incorporated all 25 environmental variables. The Max_3% model incorporated the six variables that contributed greater than three percent to Max_Full; the contribution of these variables represented more than 90% of the total contribution of all variables. I then calculated Pearson correlation coefficients (r) for all pairs of quantifiable variables (i.e., NED, NLCD and WorldClim) using 1,195 random cells (Table 3). When r was equal to or greater than the absolute value of 0.7 per variable pair, I discarded the variable that contributed least to Max_Full. Consequently, the

Max_Cor model incorporated 11 variables: four NLCD derived variables, NED, STATSGO2 and five uncorrelated WorldClim variables. Lastly, I averaged the output from all three models to produce a single predictive SDM, Max_Avg, to help guide *R. pretiosa* surveys.

Table 2. Estimated percent contribution of each environmental variable per SDM. Bolded values indicate the three most contributing variables to each SDM.

Environmental Variables	Max_Full	Max_3%	Max_Cor
Elevation	3.8	1.1	1.5
Emergent herbaceous vegetation	**30.4**	**36.8**	**32.8**
Woody wetland	2.6	-	3.1
Open water	**24.6**	**26.7**	**25.6**
Wetland complexity	0.8	-	0.9
Soil moisture	**19.8**	**21.8**	**21.0**
Annual mean temperature	0	-	-
Mean diurnal range	5.4	5.3	5.6
Isothermality	1.7	-	1.4
Temperature seasonality	0	-	0
Max. temperature of warmest month	0.8	-	-
Min. temperature of coldest month	0	-	-
Annual temperature range	0	-	-
Mean temperature of wettest quarter	2.3	-	-
Mean temperature of driest quarter	0	-	-
Mean temperature of warmest quarter	0.6	-	-
Mean temperature of coldest quarter	0.2	-	-
Annual precipitation	0	-	-
Precipitation of wettest month	6.1	8.4	7.1
Precipitation of driest month	0.1	-	-
Precipitation seasonality	0.2	-	-
Precipitation of wettest quarter	0	-	-
Precipitation of driest quarter	0	-	-
Precipitation of warmest quarter	0.4	-	0.9
Precipitation of coldest quarter	0	-	-

Table 3. Correlation analysis results; top number is Pearson correlation coefficient (r), bottom number is P value and bolded values indicate r values with an absolute value equal to 0.7 or greater.

	Elev.	Wet.	Veg.	Open	WW	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10	W11	W12	W13	W14	W15	W16	W17	W18
Wet.	-0.08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Veg.	0.02	0.24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.34	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Open	-0.05	0.20	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.02	0.00	0.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WW	-0.08	0.20	0.08	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.00	0.00	0.00	0.90	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
W1	**-0.92**	0.13	-0.03	0.08	0.09	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.00	0.00	0.18	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
W2	-0.22	0.05	0.08	0.04	-0.02	0.28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.00	0.01	0.00	0.04	0.24	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
W3	-0.37	-0.10	-0.05	-0.14	-0.05	0.17	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.00	0.00	0.02	0.00	0.01	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
W4	-0.02	0.12	0.10	0.17	0.04	0.24	0.62	-0.57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.33	0.00	0.00	0.00	0.03	0.00	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
W5	**-0.80**	0.14	0.02	0.12	0.08	**0.92**	0.58	0.06	0.56	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.00	0.00	0.24	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-
W6	**-0.90**	0.06	-0.07	0.02	0.09	**0.88**	-0.14	0.31	-0.21	0.64	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.00	0.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
W7	-0.03	0.11	0.10	0.12	0.00	0.19	**0.87**	-0.25	**0.92**	0.55	-0.29	-	-	-	-	-	-	-	-	-	-	-	-
	0.18	0.00	0.00	0.00	0.86	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-
W8	**-0.72**	0.03	-0.07	0.03	0.05	**0.79**	0.10	0.19	0.07	0.67	**0.76**	0.01	-	-	-	-	-	-	-	-	-	-	-
	0.00	0.10	0.00	0.11	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.60	-	-	-	-	-	-	-	-	-	-	-
W9	**-0.86**	0.14	-0.01	0.11	0.09	**0.98**	0.36	0.04	0.41	**0.96**	**0.79**	0.34	**0.76**	-	-	-	-	-	-	-	-	-	-
	0.00	0.00	0.58	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-	-	-	-	-	-
W10	**-0.85**	0.14	-0.01	0.11	0.09	**0.98**	0.38	0.02	0.44	**0.97**	**0.77**	0.37	**0.75**	**0.99**	-	-	-	-	-	-	-	-	-
	0.00	0.00	0.78	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-	-	-	-	-
W11	**-0.92**	0.09	-0.06	0.04	0.08	**0.96**	0.08	0.31	-0.04	**0.78**	**0.97**	-0.08	**0.80**	**0.89**	**0.88**	-	-	-	-	-	-	-	-
	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-	-	-	-
W12	-0.32	-0.03	-0.10	-0.07	-0.03	0.26	-0.51	0.33	-0.67	-0.06	0.57	-0.69	0.29	0.14	0.10	0.47	-	-	-	-	-	-	-
	0.00	0.14	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-	-	-
W13	-0.40	-0.02	-0.09	-0.07	-0.02	0.32	-0.49	0.36	-0.65	-0.00	0.63	-0.68	0.33	0.19	0.15	0.53	**0.99**	-	-	-	-	-	-
	0.00	0.28	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.93	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-	-
W14	0.61	-0.17	0.01	-0.08	-0.00	-0.69	-0.44	-0.38	-0.13	-0.65	-0.52	-0.25	-0.50	-0.67	-0.66	-0.66	-0.16	-0.19	-	-	-	-	-
	0.00	0.00	0.66	0.00	0.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-	-
W15	-0.49	0.03	-0.06	-0.05	-0.02	0.37	-0.27	0.50	-0.60	0.10	0.62	-0.54	0.27	0.24	0.20	0.55	**0.84**	**0.88**	-0.40	-	-	-	-
	0.00	0.19	0.01	0.01	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-	-
W16	-0.38	-0.03	-0.09	-0.07	-0.03	0.30	-0.49	0.36	-0.66	-0.02	0.61	-0.68	0.32	0.17	0.13	0.51	**0.99**	**0.99**	-0.19	**0.88**	-	-	-
	0.00	0.16	0.00	0.00	0.16	0.00	0.00	0.00	0.00	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-
WC1	0.46	-0.14	-0.05	-0.13	-0.06	-0.61	**-0.71**	-0.02	-0.66	**-0.79**	-0.24	**-0.72**	-0.36	-0.68	**-0.70**	-0.42	0.46	0.41	0.68	0.19	0.42	-	-
	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-
W18	0.61	-0.14	-0.01	-0.10	-0.04	**-0.74**	-0.63	-0.17	-0.47	**-0.82**	-0.44	-0.54	-0.46	**-0.77**	**-0.77**	-0.61	0.15	0.09	**0.83**	-0.18	0.11	**0.89**	-
	0.00	0.00	0.50	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
W19	-0.39	-0.02	-0.09	-0.06	-0.03	0.33	-0.46	0.36	-0.63	0.02	0.63	-0.66	0.33	0.21	0.17	0.53	**0.99**	**0.99**	-0.22	**0.88**	**0.99**	0.38	0.06
	0.00	0.28	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Elev.:	Elevation	WW:	Woody wetland	W4:	Temperature Seasonality	W8:	Mean Temp. Wettest Quarter	W12:	Annual Precipitation	W16:	Precipitation Wettest Quarter
Wet.:	Wetland complexity	W1:	Annual Mean Temperature	W5:	Max. Temp. Warmest Month	W9:	Mean Temp. Driest Quarter	W13:	Precipitation Wettest Month	W17:	Precipitation Driest Quarter
Veg.:	Herbaceous emergent	W2:	Mean Diurnal Range	W6:	Min. Temp. Coldest Month	W10:	Mean Temp. Warmest Quarter	W14:	Precipitation Driest Month	W18:	Precipitation Warmest Quarter
Open:	Open water	W3:	Isothermality	W7:	Temperature Annual Range	W11:	Mean Temp. Coldest Quarter	W15:	Precipitation Seasonality	W19:	Precipitation Coldest Quarter

Model Evaluation

Model evaluations are necessary to test the predictive performance of SDMs. Typically, modelers randomly partition the occurrence dataset into training and testing subsets; however, the small number of *R. pretiosa* occurrence records within the study area did not allow for this approach because each locality was likely to provide unique and valuable information to the SDM. For this reason, I explicitly followed Pearson *et al.*'s (2007) jackknife, or leave-one-out, evaluation technique, facilitating use of all locality records in the final model. This approach required each *R. pretiosa* locality be removed once from the dataset and a model be generated with the remaining $n - 1$ localities. Each model was then assessed by its ability to classify the excluded locality as suitable according to two thresholds: the lowest presence threshold (LPT) and a fixed threshold. The LPT was set to reflect the lowest probability value associated with any one *R. pretiosa* locality and the fixed threshold was set at 10%. The former approach defined areas at least as suitable as any locality used in generating the model, whereas the latter approach was more liberal, defining the upper 90% of all probability values as suitable. Finally, I used the pValueCompute program provided by Pearson *et al*. (2007) to test whether model predictions were superior to a random assignment of excluded localities. To summarize, I generated 102 evaluation models to account for the two thresholds and 17 occurrence records used in each of the three SDMs.

I also evaluated each SDM by determining whether or not the respective model predicted suitable habitat in the appropriate regions of the study area. While all known populations within the study area are positioned within the Klamath and Pit river hydrographic basins, I intentionally modeled a much larger region (i.e., study area) to assess the ability of each SDM to constrain its predictions. Specifically, I calculated the percent of all low, moderate and high suitability predictions within the Klamath and Pit river drainages. Further, I calculated the percent of all low, moderate and high suitability predictions within the upper Klamath and Pit river sub-basins, where aquatic channels are less-confined, more gently graded and better suited for *R. pretiosa*.

Survey Efforts

I used the output from the Max_Avg model to select survey sites within the Klamath and Pit river hydrographic basins. I restricted the site selection process to these drainages because they contain all extant and historic *R. pretiosa* populations within the study area. I was able to further limit the site selection process after consulting with USDA Forest Service biologists (Redwood Science Laboratory, Arcata, CA). In particular, I excluded Lassen Volcanic National Park, the Thousand Lakes Wilderness and portions of Klamath National Forest because exhaustive Cascade Frog (*Rana cascadae*) surveys previously conducted in these areas would have also detected *R. pretiosa* (Figure 3). Both publicly and privately owned sites were selected and prioritized according to the models' suitability predictions; however, I attempted to focus on private lands, as they are less likely to have been previously surveyed. I first narrowed the Klamath and Pit river hydrographic basins to regional clusters possessing the highest probability values. I next consulted aerial, topographic and National Wetlands Inventory (NWI) data to identify specific sites within these clusters possessing adequate *R. pretiosa* habitat. For example, presence of springs, large bodies of water, emergent vegetation, hydrological connectivity and complex aquatic systems are favorable site characteristics for the species (Watson *et al*. 2003; Germaine and Cosentino 2004; Pearl and Hayes 2004; Chelgren *et al*. 2006; Cushman and Pearl 2007). Additionally, I received expert advice from biologists familiar with the region (personal communications: M. Hayes, Washington Department of Fish and Wildlife, 600 Capital Way North, Olympia, WA 98501; Maria Ellis, Spring Rivers Ecological Sciences, P.O. Box 153, Cassel, CA 96016). To obtain landowner contact information, I cross-referenced the selected sites with GIS parcel layers and ParcelQuest (http://www.parcelquest.com/), an online source for California parcel data and maps. I then mailed letters to two timber companies and more than 50 private landowners, as well as phoned all appropriate agencies, asking for permission to access the selected sites. I received survey permission from both timber companies, eight private landowners and all agencies.

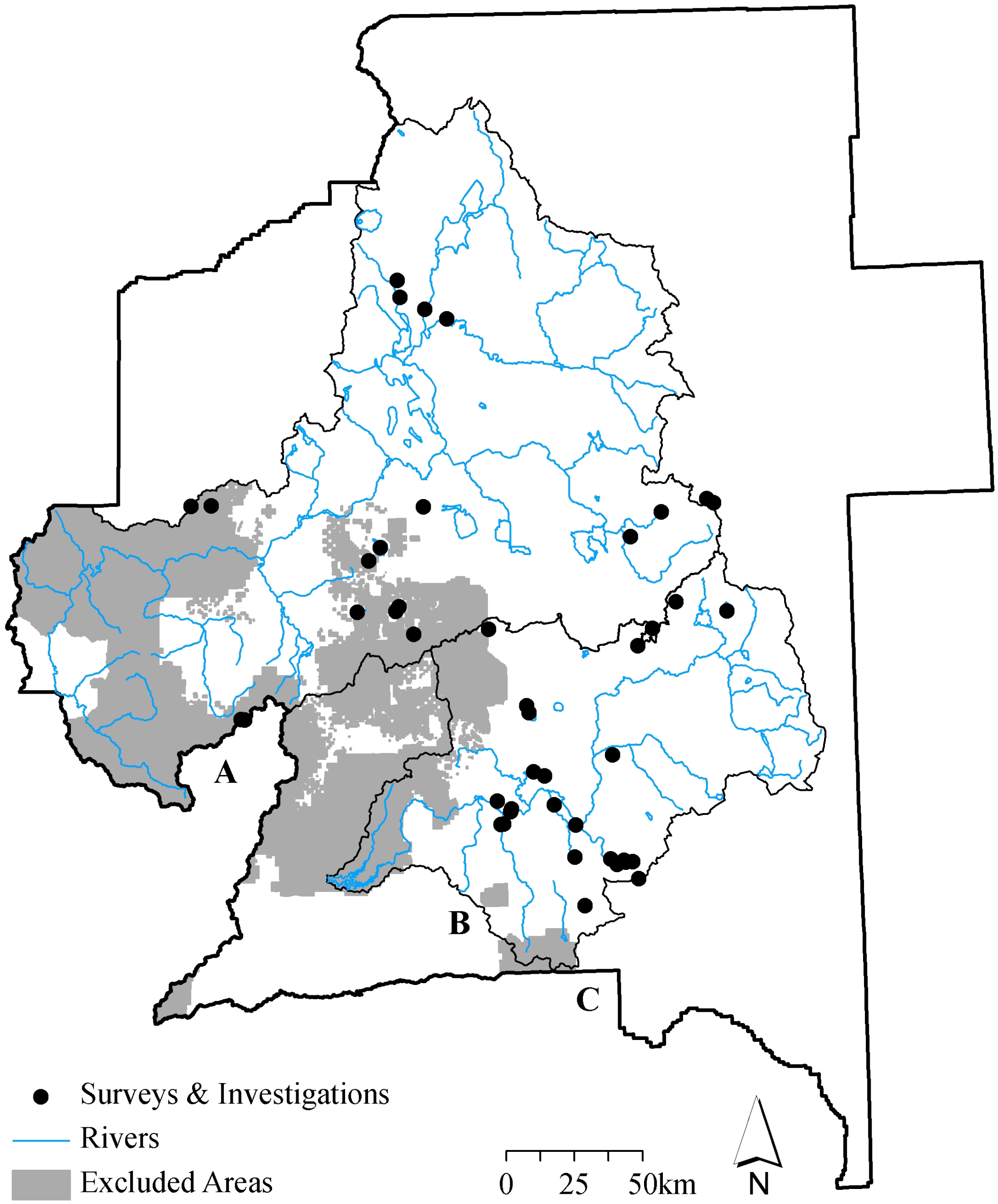

Figure 3. Detail of study area in northern California and southern Oregon, USA. Major rivers of Klamath (top) and Pit (bottom) river hydrographic basins shown in blue. Areas excluded from surveys shown in gray, including A) portions of Klamath National Forest, B) Thousand Lakes Wilderness, and C) Lassen Volcanic National Park. Survey and investigation sites designated with black-filled circles. Due to the close proximity of certain sites, some circles may represent more than one survey location.

I conducted *R. pretiosa* surveys between 2 April and 17 August 2010. I visited a total of 44 sites, 21 of which were privately owned (Table 4). Twenty-six of these sites were investigated, but either not surveyed or surveyed only once and rejected as unsuitable. Many of the rejected sites did not hold water throughout the year, a necessary element for sustainable *R. pretiosa* populations (Germaine and Cosentino 2004). Other reasons for rejection included the presence of predatory non-native fishes, a lack of hydrologic connectivity and complexity, and inadequate size (Watson *et al*. 2003; Pearl and Hayes 2004; Chelgren *et al*. 2006; Cushman and Pearl 2007). The remaining sites (*n* = 18) were surveyed three times throughout the field season with different methodologies that corresponded with the targeted life stage. For example, field efforts in April and May were focused on egg mass detection and primarily included visual encounter surveys (VES) in shallow, vegetated areas. I focused on detection of adults and larvae during the remainder of the field season and conducted VES in all appropriate habitats. Additionally, dipnet surveys were conducted where visibility was low (e.g., high turbidity, vegetation). VES and dipnet surveys were performed between 10:00 and 16:00 h to optimize detection, as *R. pretiosa* is most detectable during the warmest part of the day (personal communication: M. Hayes, Washington Department of Fish and Wildlife, 600 Capital Way North, Olympia, WA 98501).

Table 4. Surveyed and investigated sites with descriptive information.

Site Name	Private Owner	No. of surveys	Approximate location	Reasons for unsuitability
Ash Creek Wildlife Area	-	3	41°09'35", -121°03'55"	-
Antelope Creek Ranch	Michalak	1	41°34'13", -121°55'39"	1
Ashurst Lake	-	1	40°44'52", -120°57'48"	3
Bar-D-Bar Ranch	Rickert	1	41°05'40", -121°21'53"	2, 3
Baum Lake	PG&E	0	40°56'16", -121°32'47"	1
Beaver Creek	-	2	40°49'30", -121°14'23"	3
Bickford Meadow	Bickford	3	40°55'50", -121°13'57"	-
Bickford Reservoirs	Bickford	1	40°59'56", -121°19'29"	2
Big Carmen Lake	Timber Products Co.	3	41°17'32", -122°41'20"	-
Big Jack Lake	-	1	40°48'17", -120°59'16"	3
Big Lake	-	3	41°06'30", -121°24'46"	-
Collier Mem. State Park	-	3	42°38'43", -121°51'35"	-
Crystal Lake	PG&E	3	40°56'12", -121°33'33"	-
Devil's Gate Ranch	Jones	3	41°38'48", -122°00'21"	-
Donomore Meadow	Timber Products Co.	1	41°59'55", -122°54'26"	2, 4
Duncan Reservoir	-	0	41°31'10", -120°56'42"	1, 2, 3
Old Fish Hatchery	PG&E	3	40°59'15", -121°30'39"	-
Fort Creek	Crater Lake Resort	1	42°41'07", -121°58'17"	5
Grass Lake	Fruit Growers Supply	3	41°38'44", -122°10'32"	-
Grouse Creek Lake	Timber Products Co.	3	41°17'25", -122°40'24"	-
Indian Tom Lake	-	0	41°59'30", -121°52'45"	1, 2
Jacks Lake	-	1	40°48'39", -121°01'34"	2, 3
J.F. Kimball State Park	-	3	42°44'28", -121°58'54"	-
Juniata Lake	-	3	41°48'52", -122°07'23"	-
Little Jacks Lake	-	1	40°48'17", -121°01'06"	3
Long Lake	-	1	40°47'50", -121°03'20"	3
Love WRP	Love	3	42°36'41", -121°45'48"	-
McDonagh property	McDonagh	1	41°59'57", -122°49'01"	2
Medicine Lake	-	0	41°34'59", -121°35'52"	1
Meiss Lake Wildlife Area	-	3	41°51'27", -122°04'14"	-
Mosquito Lake	Sierra Pacific Industries	3	41°19'39", -121°26'10"	-
Orr Lake	-	3	41°39'44", -121°59'32"	-
Poisson Lake	-	0	40°39'46", -121°11'59"	3
Raker/Thomas Reservoirs	-	0	41°37'33", -120°32'53"	3
Renner Lake	-	0	41°59'56", -120°37'29"	2, 4
Reservoir C	-	0	41°39'42", -120°46'17"	1, 2, 3
Reservoir F	-	0	41°34'29", -120°52'43"	1, 2, 3
Sibley Lake	-	0	41°59'05", -120°35'35"	3, 4
Soldier Creek Ponds	PG&E	1	41°00'52", -121°34'21"	2
Steel Swamp	Tule Lake Bass Masters	0	41°52'50", -120°57'52"	1, 3
Straylor Lake	-	1	40°48'58", -121°05'02"	3
Tom Wolfen Springs	PG&E	3	40°58'40", -121°30'53"	-
Weed Valley	-	0	41°57'36", -120°49'35"	3
Whitehorse Flat Reservoir	Sierra Pacific Industries	3	41°18'17", -121°25'36"	-

(-) dash indicates site is publically owned
1: fish stocked on-site
2: lack of suitable *R. pretiosa* habitat
3: non-permanent hydroperiod
4: outside Klamath and Pit river drainages
5: incidental site, not re-visited

Most sites were very large and would have required a significant time investment to survey completely. As such, I concentrated my efforts on the perimeter of each site and walked transects through appropriate habitat when time allowed. While I listened for vocalizing males during all surveys, formal aural and nocturnal surveys (e.g., eye shine) were not conducted due to the large size and restricted access associated with most sites. Further, the species' nocturnal activity is generally restricted to a brief period following sunset during the warmest portion of the summer and vocalizations are not often heard, as males typically produce quiet calls from underwater (personal communication: M. Hayes, Washington Department of Fish and Wildlife, 600 Capital Way North, Olympia, WA 98501).

RESULTS

Model Predictions

All SDMs predicted similar core areas of suitable habitat, but the geographic extent and degree (i.e., suitability class) of suitability differed, albeit slightly, between each (Figure 4; see Appendix A – D for greater detail). The percentage of total area predicted per suitability class was similar between models (Table 5). The greatest discrepancy occurred between Max_Cor and the other SDMs, with Max_Cor predicting more suitable habitat, although most of this increase fell within the low suitability class. Overall, Max_3% and Max_Cor produced more fragmented distributions with notable differences in the extent and degree of predictions compared to Max_Full. For example, Max_3% and Max_Cor predicted a much greater extent of low and moderate suitability habitat in areas outside the Klamath and Pit river hydrographic basins. Variation was also noted between the Max_3% and Max_Cor predictions. For instance, Max_Cor predicted a greater extent of low suitability habitat near the southwest corner of the study area. Moreover, Max_Cor predicted a higher degree of suitability at areas just north of the Pit River's upper sub-basin, while Max_3% predicted a higher degree of suitability at areas near the southeast corner of the study area.

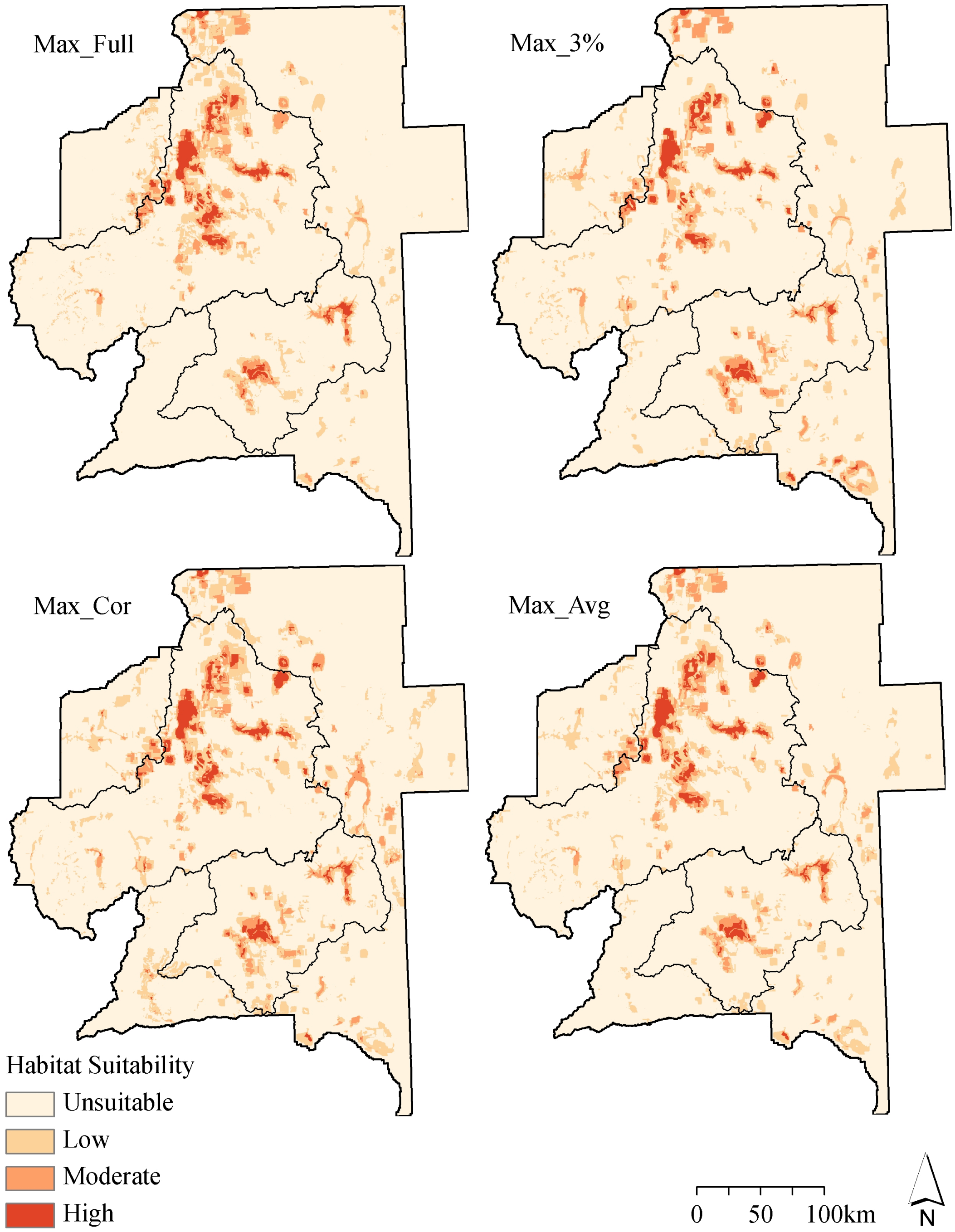

Figure 4. Predicted distributions of *R. pretiosa* in northern California and southern Oregon, USA. Habitat suitability values presented in four classes: unsuitable (0-0.07), low (0.08-0.27), moderate (0.28-0.56), high (0.57-1.00). Classification breaks derived using Jenks Natural Breaks (i.e., Jenks Optimization) classification method averaged across all SDMs.

Table 5. Percent of study area predicted by each SDM according to four habitat suitability classes: unsuitable (0-0.07), low (0.08-0.27), moderate (0.28-0.56), high (0.57-1.00). Classification breaks derived using Jenks Natural Breaks (i.e., Jenks Optimization) classification method averaged across all SDMs.

SDM	% of study area			
	unsuitable	low	moderate	high
Max_Full	87.8	7.6	3.1	1.6
Max_3%	87.6	7.3	3.5	1.6
Max_Cor	83.7	10.9	3.6	1.8
Max_Avg	86.3	8.7	3.4	1.6

Variable Contributions

According to Maxent's jackknife tests of variable importance, the NLCD and STATSGO2 derived environmental variables were most influential for all SDMs (Table 2). Emergent herbaceous vegetation contributed the most information to each model, followed by open water and soil moisture, respectively. Of the bioclimatic variables, precipitation of wettest month, mean diurnal temperature range, and mean temperature of wettest quarter were the greatest contributors. Further, each SDM's jackknife test showed that emergent herbaceous vegetation produced the highest gain when used in isolation, suggesting this variable contributed the most useful information. The jackknife test for Max_3% also showed that emergent herbaceous vegetation reduced the gain more than any other variable when omitted, suggesting this variable contributed the most information not garnered from other variables (i.e., low correlation). The jackknife tests for Max_Full and Max_Cor showed soil moisture to reduce the gain more than any other variable when omitted from the models.

The confidence intervals for 26% (6/23) of the tested environmental variables were disjunct, or did not overlap, and, accordingly, represented significant differences between the presumably extirpated and extant *R. pretiosa* populations (Table 6). The six variables were obtained from the WorldClim dataset, derived from precipitation data and included: annual precipitation, precipitation of wettest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter and precipitation of coldest quarter. Despite this variation in precipitation, the locality records associated with the presumably extirpated populations were still incorporated in all SDMs. This is because much of the variation was attributed to the two most southern *R. pretiosa* occurrence records. Particularly, all precipitation variable values associated with the Alturas and Fall River Mills populations, which constitute the only occurrence records in the Pit River hydrographic basin, were consistently much lower than those associated with the other seven presumably extirpated populations. I believe this variation is due to regional climatic differences between the Klamath and Pit river drainages, rather than habitat differences between the presumably extirpated and extant populations. Further, because I concentrated my survey efforts in northern California, I considered the Alturas and Fall River Mills occurrence records extremely valuable to the model generation process, as they represent two of California's three verified populations.

Table 6. Means and 95% confidence intervals for all continuous environmental variables segregated by presumably extirpated and extant *R. pretiosa* populations. Bolded values indicate disjunct, or non-overlapping, confidence intervals. Variable units and derivation described with footnotes.

Environmental Variables	Extirpated Populations		Extant Populations	
	Mean	95% C.I.	Mean	95% C.I.
Elevation [1]	1273.80	(1187.70, 1359.90)	1371.70	(1268.00, 1475.40)
Emergent herbaceous vegetation [2]	0.09	(0.01, 0.17)	0.20	(-0.06, 0.45)
Woody wetland [2]	0.00	(0.00, 0.00)	0.00	(0.00, 0.01)
Open water [2]	0.08	(0.00, 0.17)	0.01	(0.00, 0.02)
Wetland complexity [3]	-	-	-	-
Soil moisture [4]	-	-	-	-
Annual mean temperature [5]	77.56	(69.13, 85.99)	66.13	(59.83, 72.42)
Mean diurnal range [6]	165.00	(153.39, 176.61)	155.00	(149.00, 161.00)
Isothermality [7]	44.89	(42.95, 46.83)	44.25	(43.66, 44.84)
Temperature seasonality [8]	6751.00	(6551.00, 6951.00)	6525.00	(6455.20, 6594.80)
Max. temp. of warmest month [5]	290.11	(277.24, 302.98)	272.25	(263.37, 281.13)
Min. temp. of coldest month [5]	-74.22	(-81.65, -66.79)	-73.75	(-81.03, -66.47)
Temperature annual range [9]	364.10	(349.89, 378.33)	346.00	(337.54, 354.46)
Mean temp. of wettest quarter [5]	-0.11	(-7.46, 7.24)	-7.13	(-12.73, -1.52)
Mean temp. of driest quarter [5]	164.11	(154.57, 173.65)	150.88	(144.49, 157.26)
Mean temp. of warmest quarter [5]	166.11	(156.24, 175.98)	152.00	(145.49, 158.51)
Mean temp. of coldest quarter [5]	-5.78	(-13.31, 1.75)	-12.75	(-18.84, -6.66)
Annual precipitation [10]	**451.90**	**(339.80, 563.90)**	**651.80**	**(607.30, 696.20)**
Precipitation of wettest month [10]	**71.78**	**(50.10, 93.45)**	**112.50**	**(104.33, 120.67)**
Precipitation of driest month [10]	8.00	(6.12, 9.88)	10.50	(8.89, 12.11)
Precipitation seasonality [11]	**50.22**	**(43.59, 56.85)**	**62.00**	**(61.11, 62.89)**
Precipitation of wettest quarter [10]	**194.20**	**(134.90, 253.60)**	**313.00**	**(292.72, 333.28)**
Precipitation of driest quarter [10]	**40.11**	**(34.38, 45.84)**	**51.63**	**(49.14, 54.11)**
Precipitation of warmest quarter [10]	48.11	(42.37, 53.86)	55.38	(52.48, 58.27)
Precipitation of coldest quarter [10]	**179.80**	**(125.30, 234.30)**	**283.25**	**(265.33, 301.17)**

(-) Dash indicates variable is expressed in ordinal scale and not applicable for analysis
[1] m
[2] proportion of respective wetland class within 2.79 km of focal cell
[3] number of wetland classes within 2.79 km of focal cell
[4] non-hydric, partially hydric or completely hydric
[5] °C * 10
[6] mean of monthly (maximum temperature – minimum temperature)
[7] (mean diurnal range - temperature annual range) * 100
[8] standard deviation * 100
[9] maximum temperature of warmest month – minimum temperature of coldest month
[10] mm
[11] coefficient of variation

Model Evaluation

All SDM evaluation models produced moderately high prediction success rates (i.e., low omission rates) and were statistically significant when compared to a random assignment of the excluded localities. In fact, all SDM evaluations resulted in identical prediction success rates. Each evaluation model, using both the LPT and fixed threshold of 10%, successfully predicted 71% ($P \leq 0.000098$) of all *R. pretiosa* localities.

Each SDM produced predictions consistent with the known geographic distribution of *R. pretiosa* and successfully constrained its predictions to the appropriate regions of the study area. Specifically, 73% of the Max_Full, 65% of the Max_3% and 63% of the Max_Cor low, moderate and high suitability predictions fell within the Klamath and Pit river hydrographic basins. This is impressive considering that these drainages encompass less than 48% of the study area. Further, a substantial portion (60%, 47% and 46%, respectively) of the Max_Full, Max_3% and Max_Cor low, moderate and high suitability predictions fell within the upper Klamath and upper Pit river sub-basins, where habitat is better suited for the species. The upper Klamath and upper Pit river sub-basins represent only 22% and 7% of the study area, respectively.

Survey Efforts

Of the 44 sites investigated during the field season, 18 were surveyed repeatedly. While *R. pretiosa* was not detected in California, two individuals were documented at a previously unrecognized site in Klamath County, Oregon. Specifically, two adult females were detected at the same location on 20 May 2010, approximately 535 m from the headwaters of the Wood River. These individuals were identified as *R. Pretiosa* by their intense, seemingly superficial, reddish-orange venter coloration, as well as the upturned position of their eyes, lack of groin mottling and extensive webbing between the second, third and fourth digits of their hind limbs (Figure 5; Dunlap 1955; McAllister and Leonard 1997).

The detection location was situated privately owned property along the periphery of the Wood River and was characterized as having an unconsolidated substrate, little emergent vegetation and a water depth of approximately 13 cm. Water temperature measured 13° C at the detection location and 8° C at the headwaters. NWI Mapper (www.fws.gov/wetlands/Data/Mapper.html) described seasonally and temporarily flooded emergent, forested and shrub-scrub habitat within 400 m of the detection site; however, these areas appeared mostly dry during survey visits. The body size (i.e., snout-vent length) and mass of the two animals measured 62 and 65 mm, and 30 and 23 g, respectively.

Figure 5. Representative photographs of one *R. pretiosa* female detected near the headwaters of the Wood River in Klamath County, Oregon, USA. Photographs show identifying characteristics of the species, including venter coloration, upturned eyes and extensive webbing between digits of rear foot.

DISCUSSION

Model evaluations showed that all SDMs were successful in predicting the excluded *R. pretiosa* localities; however, the geographic extent and degree of predicted habitat varied among models. For instance, Max_3% and Max_Cor predicted much more liberal distributions when compared to the restricted distribution produced by Max_Full. Liberal distributions are advantageous in certain situations, such as when predicting range expansions or attempting to discover unrecognized populations. While Max_Full predicted the greatest percent of low, moderate and high suitability habitat within the Klamath and Pit river hydrographic basins, as well as the upper Klamath and Pit river sub-basins, the more liberal predictions produced by Max_3% and Max_Cor were considered valuable for identifying survey locations in northern California. As such, Max_Avg was generated to incorporate the variation of each SDM and was used to help guide field surveys. Max_Avg proved useful in predicting suitable habitat, as *R. pretiosa* was detected at one unrecognized location within the upper Klamath sub-basin. This detection is significant because it represents the species' most northern point of occurrence in the Wood River and because only eight extant populations are currently recognized within the Klamath River hydrographic basin. Due to known seasonal movements (Watson *et al*. 2003) and non-detection of other *R. pretiosa* individuals, the natal site of the detected frogs is likely located some distance from where they were found. *Rana pretiosa* has been recorded at specific wetlands along the Wood River, but these sites are located approximately 29 km downstream (16 km straight-line distance) from the point of detection. The maximum dispersal distance recorded for the species is 2.79 km (Cushman and Pearl 2007). Thus, further investigation is needed to determine where the detected frogs dispersed from.

All SDMs showed emergent herbaceous vegetation to be the most influential variable, followed by open water. These variables are appropriately indicative of *R. pretiosa* habitat, as oviposition sites are associated with the previous year's emergent herbaceous vegetation and open water is generally associated with permanent hydroperiods (Licht 1971; McAllister and White 2001; Germaine and Cosentino 2004; Pearl and Hayes 2004). These findings are in agreement with Watson *et al.* (2003), who determined low to moderate degrees of emergent vegetation (25-50%) to be the most important feature of *R. pretisoa* microhabitat and a necessary requirement for the completion of the species' life cycle. Emergent vegetation provides concealment, shade and resting platforms and may be associated with remnant pools during hot, dry periods. Open water is generally associated with deeper pools, which provide foraging and concealment opportunities, and greater sun exposure, which is important for embryonic development and invertebrate-supporting plant primary production (Watson *et al.* 2003).

False-positive predictions, or sites that were predicted to be highly suitable but did not yield *R. pretiosa* detections, should not be viewed as failures or be included in model validations (Pearson *et al*. 2007). Non-detections may be attributed to factors not accounted for by the model, such as biotic interactions, geographic barriers, dispersal limitations, geologic history and human influences (Peterson 2001; Anderson *et al*.

2003). Specific factors I believe to be potentially contributive to the non-detection of *R. pretiosa* in California include the presence of non-native fishes and American bullfrogs (*Lithobates catesbeianus*), as well as unsuitable hydroperiods. At minimum, of the 18 sites surveyed three times, nine contained predatory non-native fishes, eight contained *L. catesbeianus* and six contained both. Additionally, because *R. pretiosa* is a primarily aquatic species, permanent water is required; however, the SDMs did not account for hydroperiod, as the complete NWI dataset for the study area was not available in digital format at the time of modeling. While I am confident of my survey protocol and efforts, the possibility exists for the species to be present, but not detected, at any individual site. This is because most sites were very large and complex and the project was subject to personnel and time constraints.

The suitability predictions generated by any SDM should be interpreted with care (Phillips *et al*. 2006). One reason for this is because the occurrence localities, more than likely, do not represent the full range of environmental variables pertinent to the species. Second, inherent biases are typically present in occurrence datasets for rare species. For example, historic records are likely to be spatially autocorrelated because specimens were generally collected near camps, roads and other easily accessible sites. Third, the suite of variables used in most SDMs do not account for all factors deterministic of the species' distribution. For instance, 59% (26/44) of sites predicted to be moderately or highly suitable were deemed unsuitable after an initial investigation for reasons that include stocking of non-native fishes, lack of suitable *R. pretiosa* habitat, and non-permanent hydroperiods (Table 4). Limiting factors relevant to the distribution of *R. pretiosa*, but not incorporated in the SDMs include human and succession-related habitat losses, hydrologic alteration, exotic predators and vegetation, livestock management and population isolation (Haycock 2000). Consequently, it is important to recognize that the predictions generated do not represent actual distributional limits, but rather regions having similar environmental conditions as the occurrence record dataset (Pearson *et al*. 2007).

My research was limited in several ways. First, I was unable to incorporate derived variables from the NWI dataset because, at the time of model generation, the complete study area was not in digital format. Second, privately owned land was not adequately explored during this study. I initially intended to concentrate my survey efforts on private property, but was unable to obtain access permission from most private landowners. Lastly, I recognize the temporal deviations associated with the spatial data. This is most relevant for the NLCD and WorldClim datasets because they represent dynamic processes. The NLCD and WorldClim variables correspond with 2001 and 1950-2000 data, respectively; however, the oldest historic *R. pretiosa* record dates back to 1898. I recognize this as a model limitation, but believed it more important to incorporate all verified, known *R. pretiosa* occurrence records than use only temporally congruent data. While successful models have been generated with fewer than 17 occurrence records, predictive ability is greatly increased with additional records (Pearson *et al*. 2007; Hernandez *et al*. 2006; Stockwell and Peterson 2002).

Future modeling of *R. pretiosa* habitat or distribution could be improved by accounting for the limitations of my research. For example, the NWI dataset is now available in digital format for the entire study area and should be incorporated to account for wetland hydroperiod. Future modeling should also investigate differences between modeling with extirpated and extant versus only extant populations, as well as alternative spatial resolutions (e.g., 3 and 30 arc-seconds), as species-environment relationships can yield different distribution patterns when examined at different spatial scales (Guisan and Thuiller 2005). Moreover, future field efforts aimed at identifying new *R. pretiosa* populations should focus on areas predicted to be highly suitable by all SDMs, but which were not investigated because of logistic constraints and uncooperative landowners. These areas include portions of the Pit River, near Springs Valley, and Rising River, near Hat Creek Valley, in California, as well as Sycan Marsh, Lake of the Woods and portions of the Sprague River in Oregon. I strongly suggest that both public and privately owned property in these regions be investigated for the presence of *R. pretiosa* prior to any habitat alteration or manipulation, including the stocking of non-native fishes.

In conclusion, SDMs produce intuitive, spatially referenced predictions that cannot be derived from occurrence records alone (Pearson *et al*. 2007). As demonstrated, my SDMs were successful at identifying suitable *R. pretiosa* habitat in northern California and southern Oregon and proved valuable for directing survey efforts aimed at detecting unrecognized areas of occurrence; however, my results also have important conservation, habitat restoration and population management implications. For instance, all SDMs identified similar core areas of suitable habitat, as well as distribution gaps, which are critical information for effective management and conservation of any species. These core habitat areas, which encompass the occurrence localities, deserve focused scientific attention (e.g., investigations, surveys) and represent the best areas for species-specific conservation actions. Further, my models could be used to assess the suitability of potential sites prior to allocating limited resources to relocation and repatriation efforts, such as those at Fort Lewis Military Base in Washington (Adams *et al*. 1998) and Dilman Meadows in Oregon (Chelgren *et al*. 2006). The time, effort and money expended with such undertakings are substantial, but could likely be reduced and chances for success enhanced with the aid of my SDMs. Lastly, this modeling approach could also be applied to other aquatic-dependent anurans or be used to better understand the distribution of *R. pretiosa* in other parts of its range.

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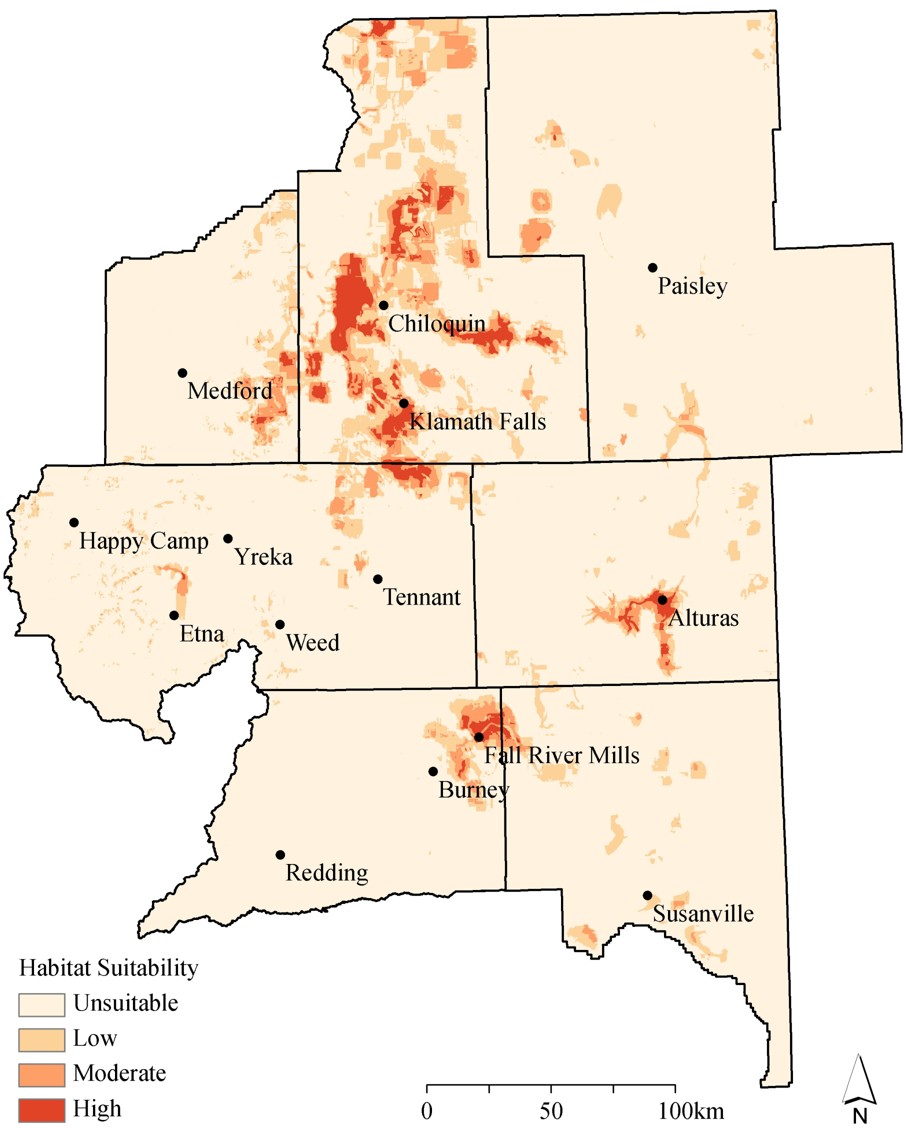
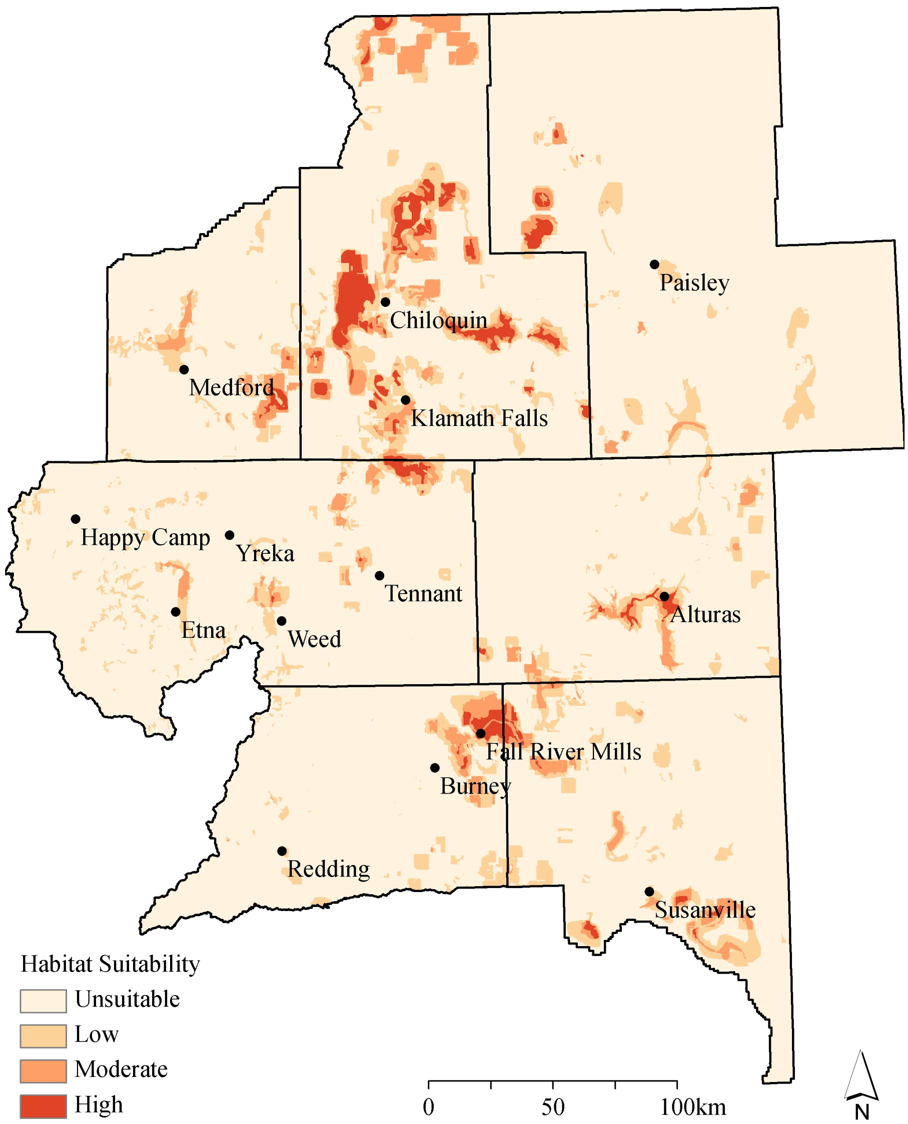
APPENDICES

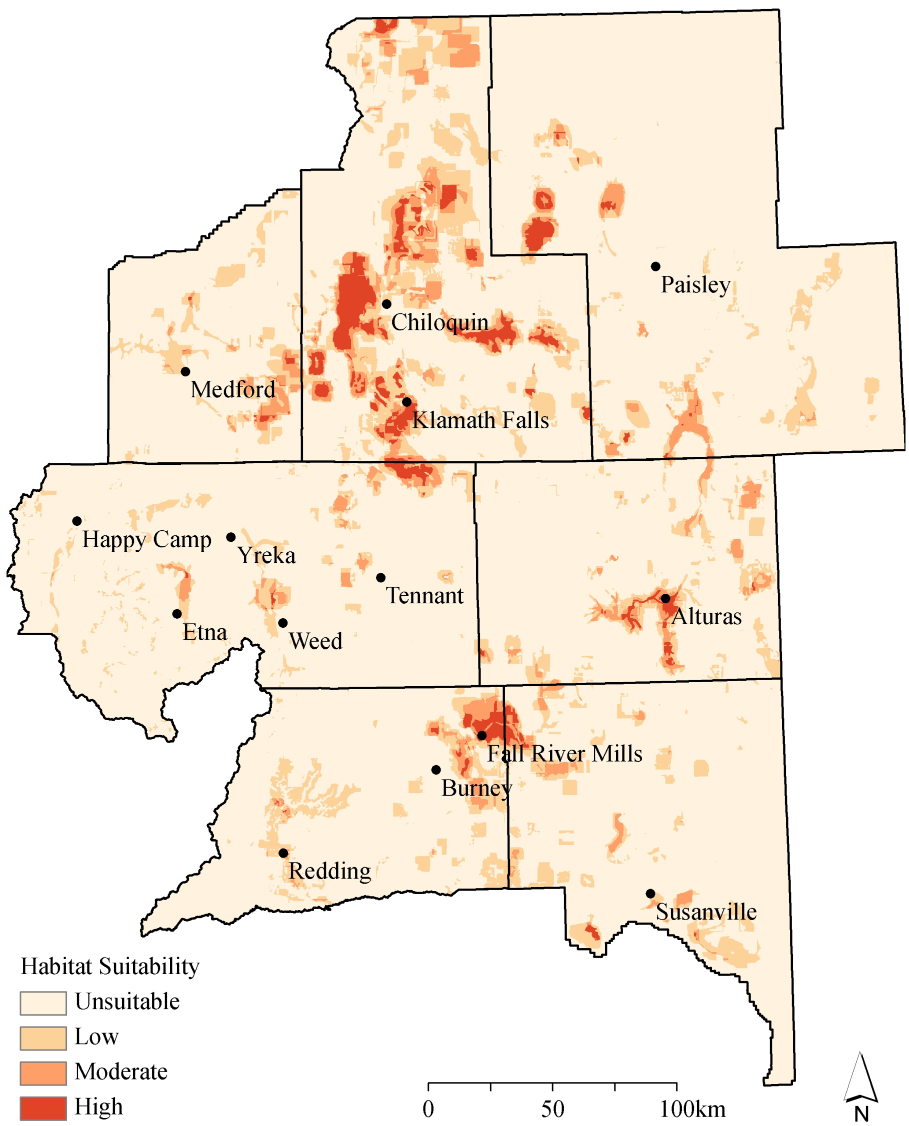
Appendix A. Max_Full predicted distribution of *R. pretiosa* in northern California and southern Oregon, USA. Habitat suitability values presented in four classes: unsuitable (0-0.07), low (0.08-0.27), moderate (0.28-0.56), high (0.57-1.00). Classification breaks derived using Jenks Natural Breaks (i.e., Jenks Optimization) classification method averaged across all SDMs.



Appendix B. Max_3% predicted distribution of *R. pretiosa* in northern California and southern Oregon, USA. Habitat suitability values presented in four classes: unsuitable (0-0.07), low (0.08-0.27), moderate (0.28-0.56), high (0.57-1.00). Classification breaks derived using Jenks Natural Breaks (i.e., Jenks Optimization) classification method averaged across all SDMs.



Appendix C. Max_Cor predicted distribution of *R. pretiosa* in northern California and southern Oregon, USA. Habitat suitability values presented in four classes: unsuitable (0-0.07), low (0.08-0.27), moderate (0.28-0.56), high (0.57-1.00). Classification breaks derived using Jenks Natural Breaks (i.e., Jenks Optimization) classification method averaged across all SDMs.



Appendix D. Max_Avg predicted distribution of *R. pretiosa* in northern California and southern Oregon, USA. Habitat suitability values presented in four classes: unsuitable (0-0.07), low (0.08-0.27), moderate (0.28-0.56), high (0.57-1.00). Classification breaks derived using Jenks Natural Breaks (i.e., Jenks Optimization) classification method averaged across all SDMs.