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USING ECOLOGICAL NICHE MODELS TO DIRECT RARE AMPHIBIAN SURVEYS: A CASE STUDY USING THE OREGON SPOTTED FROG (*RANA PRETIOSA*)

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Abstract.—Rare amphibian species pose significant survey challenges because of their limited distributions and cryptic behavior. Using the Oregon Spotted Frog (Rana pretiosa) as a case study, we developed ecological niche models (ENMs) to guide surveys across the southern extent of the species' geographic distribution and assess the species' presence in California, where some regard it as extirpated. We used MAXENT to generate three ENM variants with 17 verified localities and a unique subset of environmental variables describing land cover, soil, topography, and climate. We applied jack-knife analyses to evaluate the estimates produced by each ENM. All ENMs predicted similar core areas of suitable habitat, but the spatial distribution of each suitability class differed among models. Land cover, particularly emergent herbaceous vegetation, and soils-derived variables most influenced all ENMs. Model evaluations produced moderately high prediction success rates (71%). We generated a consensus model using all ENM variants to facilitate survey site selection, and investigated 44 sites predicted as moderately and highly suitable between 2 April and 17 August 2010. Based on initial on-site evaluations, we repeatedly surveyed 18 of these sites. We detected R. pretiosa at one previously unrecognized locality in Oregon. We show that ENMs generated from small datasets are useful for directing exploratory surveys for rare amphibians, and that variables derived to correspond with a species' ecology can contribute disproportionately to ENMs.

Key Words.—amphibian; California; distribution; ecological niche modeling; Maxent; Oregon; Oregon Spotted Frog; Rana pretiosa

INTRODUCTION

Effective species conservation, particularly for at-risk taxa, requires accurate knowledge of geographic distributions. In the case of rare species, obtaining this information can be challenging because species detection is positively associated with abundance, complicating efforts to obtain accurate geographic distribution data. Ecological niche models (ENMs) and species distribution models (SDMs) have become increasingly important tools for refining distribution-based data (Guisan and Zimmermann 2000; Guisan and Thuiller 2005). Though now used in diverse applications that range from estimating species' responses to environmental perturbations (Preston et al. 2008; Milanovich et al. 2010) to identifying high-priority conservation areas (Hannah et al. 2007; Goldberg and Waits 2009), the power of these models lies in their ability to elucidate robust potential distribution estimates from occurrence data (Loiselle et al. 2003). For this reason, ENMs can greatly focus exploratory surveys, making them a potentially useful tool for the study and conservation of rare amphibians.

ENMs estimate a species' potential distribution, or abiotically suitable area, in geographic space by modeling the existing fundamental niche of that species in environmental space (Peterson et al. 2011; Anderson 2012). A species' potential distribution is that geographic area where, in the absence of competitors and other negatively interacting species, and given unlimited dispersal ability, the abiotic environment is favorable to the species (Peterson et al. 2011). In contrast, SDMs estimate a species' realized range, or occupied distributional area, in geographic space without first estimating the species' fundamental niche in environmental space or potential distribution in geographic space (Peterson et al. 2011; Anderson 2012).

ENMs hold great potential as a conservation tool, but certain approaches may be poorly suited for facilitating exploratory amphibian surveys. Commonly, ENMs incorporate a standard suite of coarse-resolution environmental variables (e.g., elevation, climate-derived variables) and omit finer-resolution landscape and habitat variables (e.g., forest cover, wetlands, biotic factors; Trumbo et al. 2012). Topography or climate may drive the geographic distribution of a species (Baselga et al. 2012), but habitat features often define a species' presence within that range (Mazerolle and Villard 1999; Guerry and Hunter 2002; Van Buskirk 2005). Further, amphibians are frequently less mobile than other vertebrates, and may be patchily distributed. Thus, finer-resolution models may be necessary to focus survey efforts.

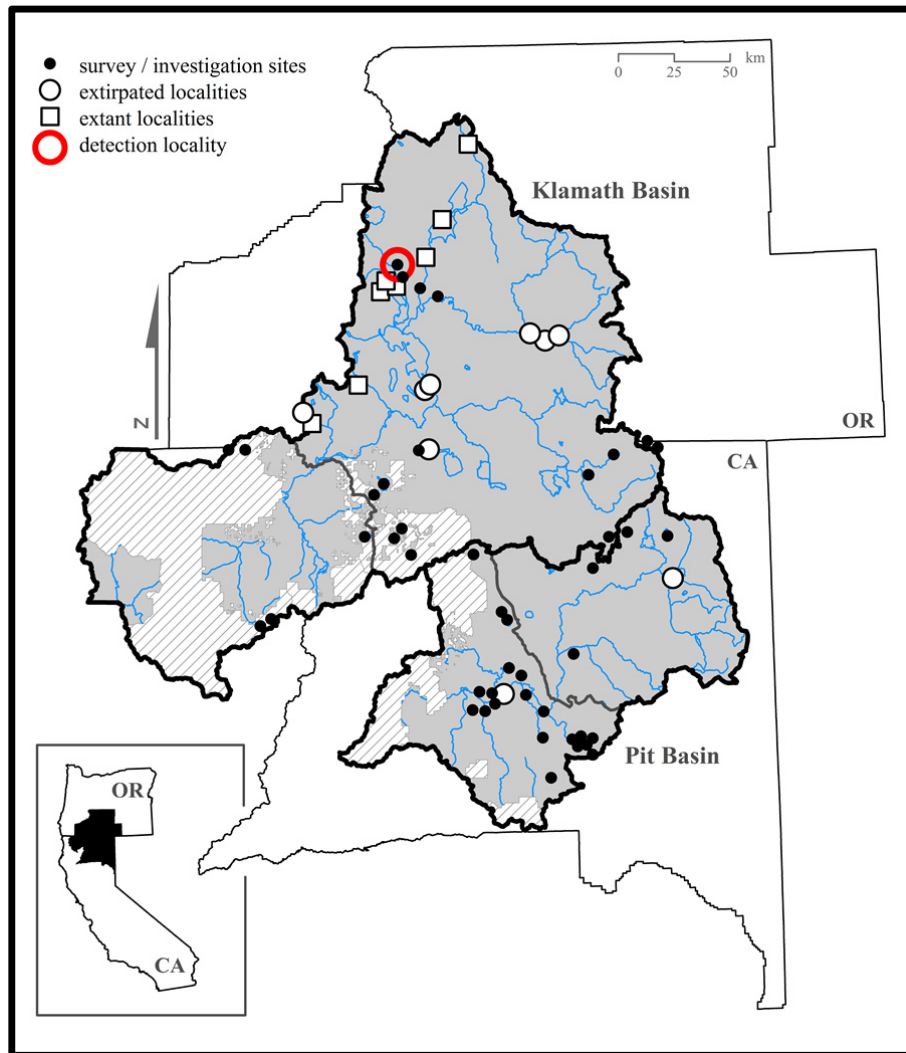While numerous ENM approaches exist, we judged Maximum Entropy (MAXENT) to be most suitable for

FIGURE 1. Inset map shows study area location in California and Oregon, USA. Klamath and Pit River hydrographic basins are indicated with gray shading and bold, black outline; upper and lower sub-basin boundaries delineated with dark gray lines. Blue lines represent rivers and major streams. Diagonal hatching represents areas excluded from the survey site selection process. Due to the proximity of a few sites, some symbols were shifted as to not be masked by others.

developing predictive distribution models for rare amphibians. MAXENT is a machine-learning method that generates estimated distributions from presence data and suites of environmental variables (Phillips et al. 2004, 2006; Phillips and Dudík 2008). Other modeling approaches, such as generalized linear models, generalized additive models, and classification and regression trees, require absence data, which are typically unavailable for rare amphibians. One work-around for this issue, as used by another ENM approach called GARP (Genetic Algorithm for Rule-set Production), is to randomly select pseudoabsence localities from the study area (Stockwell and Peters 1999). However, this approach may produce false absences (i.e., false negatives) that may bias model results (Chefaoui and Lobo 2008; VanDerWal et al. 2009). Alternatively, MAXENT uses background data, or a collection of randomly selected points, to convey

the distribution of covariates in the study area (Elith et al. 2011). Moreover, MAXENT has been shown to perform well when compared to established modeling techniques (Elith et al. 2006; Ortega-Huerta and Peterson 2008; Tarkhnishvili et al. 2009), particularly when constrained by few localities (Pearson et al. 2007; Wisz et al. 2008; Benito et al. 2009), as is characteristic of rare amphibians. Not only has MAXENT been successfully applied to different taxa (Pearson et al. 2007; Rebelo and Jones 2010; Sehgal et al. 2011), but it was recently used to identify suitable habitat in Chile for the critically endangered Darwin's Frog (*Rhinoderma rufum*) using only 19 occurrence localities (Bourke et al. 2012).

Our overarching aim was to assess the utility of MAXENT in guiding surveys aimed at identifying unrecognized populations of a rare amphibian, the

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FIGURE 2. Representative photographs of one *R. pretiosa* female detected along the Wood River in Klamath County, Oregon, USA. Photographs show identifying characteristics of the species, including venter coloration (upper left), upturned eyes (lower left and center), and extensive webbing between digits of rear foot (upper right). (Photographed by Luke Groff).

Oregon Spotted Frog (*Rana pretiosa* Baird and Girard, 1853). Endemic to the Pacific Northwest, *R. pretiosa* historically ranged from southwestern British Columbia to northeastern California, but is now absent from 70–90% of its historic range (Hayes 1997; Cushman and Pearl 2007). The species is listed as Vulnerable by the International Union for Conservation of Nature (IUCN. 2013. IUCN Red List of Threatened Species. Available from http://www.iucnredlist.org [Accessed 26 July 2013]), Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2011), and threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2014). Knowledge of *R. pretiosa* distribution across the southern extent of its geographic range, from Oregon's Klamath Basin south, is extremely limited; only 17 verified localities are known, nine of which no longer support the species (Fig. 1). The eight localities where *R. pretiosa* is extant within this area are located in Oregon (Cushman and Pearl 2007). The species' presence in California is known only from three historic records, with the most recent being from 1918 (Hayes 1997). Consequently, our first objective was to develop ENMs to estimate the potential distribution of *R. pretiosa* across the southern extent of its geographic range with a focus on northern California, where some consider this species extirpated (Pearl and Hayes 2004; Cushman and Pearl 2007; Pearl et al. 2009). However, such an assertion is speculative because the detection of the species may have been constrained by limited knowledge of habitat under range margin conditions, site remoteness, or limited access to private lands. While the potential for the species to be present in California but remain undetected for 95 years seems unlikely, an extant population was detected in 2003 < 12 km north of the California border (Parker 2009). Our second objective was to use predictions of these ENMs to guide exploratory surveys in an attempt to detect unrecognized populations. Because *R. pretiosa* is currently known from so few localities, the discovery of even one previously unrecognized locality would be important for its conservation.

MATERIALS AND METHODS

Study species.—*Rana pretiosa* (Fig. 2) is a habitat specialist that requires complex, permanent warm water wetlands > 4 ha in size with low emergent vegetation (Hayes 1997; Watson et al. 2003; Pearl and Hayes 2004). Wetland complexity is important because the species uses different aquatic habitats across seasons and life stages. Shallow areas with stable water levels are used for egg deposition and larval development; somewhat deeper water is used by juveniles and adults during dry periods; and vegetated, ice-covered, shallow areas are used by juveniles and adults during cold wet periods (Watson et al. 2003). Our modeling efforts were facilitated by the species' habitat associations and relatively small geographic distribution. Models generated for specialists, rather than generalists, tend to have greater predictive power,

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and model accuracy has been shown to improve when the focal species has a small geographic range (Segurado and Araújo 2004; Elith et al. 2006; McPherson and Jetz 2007).

The geographic range of *R. pretiosa* overlaps with those of two other native ranid frog species. *Rana pretiosa* can be readily distinguished from the Cascade Frog (*R. cascadae*) by its intense, superficial reddish-orange venter coloration, and it can be discriminated from the Northern Red-legged Frog (*R. aurora*) by its lack of sharp groin mottling, more upturned eyes, and extensive webbing between the second, third, and fourth digits of its hind limbs (Dunlap 1955; McAllister and Leonard 1997).

Study area.—Our study area encompassed the Klamath and Pit River hydrographic basins because all known populations, extirpated and extant, across the southern extent of the species' geographic range occur within these drainages (Fig. 1). However, we modeled a larger area, defined by county boundaries, so as to assess the potential distribution of *R. pretiosa* in adjacent hydrographic basins. The Klamath and Pit systems are each partitioned into lower and upper sub-basins that differ in landform, climate and, thus, suitability for *R. pretiosa*. For instance, the lower sub-basins are characterized by confined channels and steep grades, while the upper sub-basins are less confined and exhibit more gradual grades. The upper sub-basins are likely more suitable for *R. pretiosa*, as their topography better facilitates the presence of large wetlands. This is reflected by the distribution of the species' known occurrence records (Fig. 1).

Species locality data.—We used all verified *R. pretiosa* localities within the study area (n = 17) to generate each ENM. Of these localities, 14 are located in Oregon and three are located in California. *Rana pretiosa* is thought to be extirpated from nine localities; six of these are located in Oregon's upper Klamath sub-basin and one is located in each of California's upper Klamath, upper Pit, and lower Pit sub-basins (Fig. 1). We obtained most locality data from surveys conducted during the 1990s (Hayes 1994, 1997; Jennings and Hayes 1994), but also inspected museum collections to verify the accuracy of historic records. We incorporated the localities representing extirpated populations not only because

TABLE 1. Environmental variables described by original spatial resolution, source, and reference. A dash (-) indicates the source data were obtained in vector format; thus, it is inappropriate to describe original resolution. Bioclimatic variables were resampled to spatially match the 1 arc-sec environmental variables (see Materials and Methods: model approach).

Environmental variable	Original resolution	Source	Reference
Elevation	1 arc-sec (~30 m)	National Elevation Dataset http://datagateway.nrcs.usda.gov	Gesch et al. 2002; Gesch 2007

Land cover
  Emergent herbaceous vegetation
  Woody wetland
  Open water
  Wetland complexity
	1 arc-sec (~30 m)	2001 National Land Cover http://mrlc.gov	Homer et al. 2004

Soil moisture	-	State Soil Geographic Database (STATSGO) http://soildatamart.nrcs.usda.gov	Soil Survey Staff 2008

Climate
  Annual mean temperature
  Mean diurnal range
  Isothermality
  Temperature seasonality
  Maximum temperature of warmest month
  Minimum temperature of coldest month
  Temperature annual range
  Mean temperature of wettest quarter
  Mean temperature of driest quarter
  Mean temperature 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://worldclim.org	Hijmans et al.2005

so few occurrence records are known within our study area, but also because these localities help to better approximate the species' fundamental niche. Omission of these localities may misrepresent or constrain the ecological tolerances of *R. pretiosa*, and thus bias the estimate of its potential distribution (Peterson et al. 2011).

Environmental variables.—We considered 25 environmental variables in our ENMs that describe land cover, soil, topography, and climate (Table 1). Because *R. pretiosa* is almost entirely aquatic in habit and is thought to require complex wetlands, we derived four variables from the 2001 National Land Cover Dataset (NLCD; Homer et al. 2004) to describe aquatic habitat: woody wetland, emergent herbaceous vegetation, open water, and wetland complexity. We also derived a categorical soil moisture variable from the State Soil Geographic Database (STATSGO2; Soil Survey Staff 2008) to help delineate aquatic habitats. We used elevation data obtained from the National Elevation Dataset (NED; Gesch et al. 2002; Gesch 2007) to constrain the estimated potential distribution of *R. pretiosa* to appropriate elevations. This species and *R. cascadae* are similar in appearance (McAllister and Leonard 1997), use similar habitats (Brown 1997), and occupy similar geographic distributions within our study area (Stebbins 2003). However, *R. pretiosa* and *R. cascadae* populations typically segregate by elevation, and are known to co-occur in only three areas (Dunlap 1955; Green 1985). All *R. pretiosa* localities within our study area are associated with elevations less than 1,605 m, whereas *R. cascadae* typically occupies higher montane habitats (Brown 1997). The remaining 19 variables, all bioclimatic and derived from the WorldClim database, describe temperature and precipitation. These variables were interpolated from observed data and summarize the period 1950–2000 (Hijmans et al. 2005). Amphibian distributions are known to be influenced by temperature and precipitation (Daniels 1992; Soares and Brito 2007; Qian 2010) and extreme values (e.g., precipitation of driest month, minimum temperature of coldest month) are likely more influential than value ranges or averages.

We used ArcGIS 9.3 (ESRI, Redlands, California, USA) to format the locality data and environmental variables for use in MAXENT. Using the NEAREST resampling algorithm, we resampled all bioclimatic raster layers to one arc-second (approx. 30 m) resolution to match that of the other variable raster layers. This technique did not improve the accuracy of the bioclimatic layers, rather it partitioned each layer's cells into smaller cells and assigned the original cell value to each partition. We chose one arc-second resolution because *R. pretiosa* is associated with complex habitats (Pearl and Hayes 2004) and lower resolutions would have sacrificed NLCD detail. The NLCD and STATSGO2 layers were transformed to better reflect the species' habitat requirements.

Specifically, we created three raster layers to represent three aquatic classes identified in the NLCD: open water, woody wetland, and emergent herbaceous vegetation. We transformed all cells in each layer 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, reflecting the species' maximum recorded dispersal distance (Cushman and Pearl 2007). Further, we 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 (McAllister and Leonard 1997), we reclassified the STATSGO2 layer according to three soil moisture classes: non-hydric, partially hydric, and completely hydric.

To verify whether we could effectively include localities in our ENMs from which *R. pretiosa* had been extirpated, we compared the mean ($\bar{x}$) and 95% confidence interval (CI) between localities associated with extirpated and extant populations for each continuous variable. The soil moisture and wetland complexity variables represent ordinal variables and were excluded from this analysis. We considered variation between localities associated with extirpated and extant populations to be insignificant if the CIs overlapped, whereas we judged variation between locality types to be significant if the CIs did not overlap.

Model approach.—We used MAXENT version 3.3.1 (Phillips et al. 2004, 2006) to estimate the potential distribution of *R. pretiosa* across the southern portion of its geographic range. MAXENT estimates species' distributions by calculating the most uniform distribution (i.e., maximum entropy) given the constraint that the expected value of each environmental variable matches the empirical average of the locality data (Phillips et al. 2006). Importantly, MAXENT generates a probability distribution for habitat suitability (based on an index) across the study area (Elith et al. 2011), allowing comparison of suitability estimates among regions. MAXENT can also estimate each variable's contribution to the ENM via a jack-knife 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 (Elith et al. 2011).

We generated three ENMs, which incorporated 17 localities and a unique subset of the environmental variables described previously. Following the approach of others, we used linear, quadratic, and hinge features to generate each model and maintained other settings as default (Phillips et al. 2004; Pearson et al. 2007). These settings included the parameter values associated with MAXENT'S L_1 regularization process, which determined how closely the modeled distributions matched the empirical mean of the
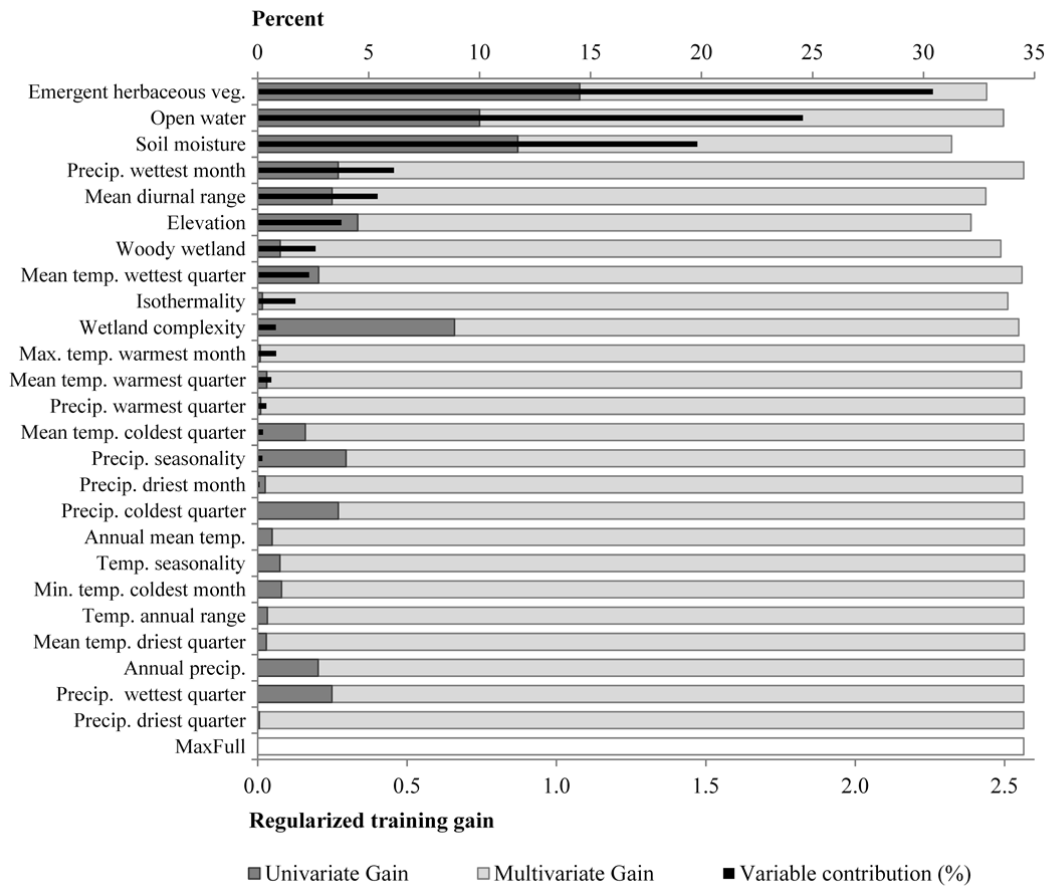
FIGURE 3. Gain and percent contribution of all environmental variables used to generate the MaxFull ecological niche model (ENM). Dark gray bars represent the univariate model gain calculated when each variable by itself is used to generate a model. Light gray bars represent the multivariate gain calculated when all variables but the respective one is used to generate a model. Black lines represent the estimated percent contribution of each environmental variable to the MaxFull ENM. The open bar (bottom) represents the multivariate gain calculated with all variables.
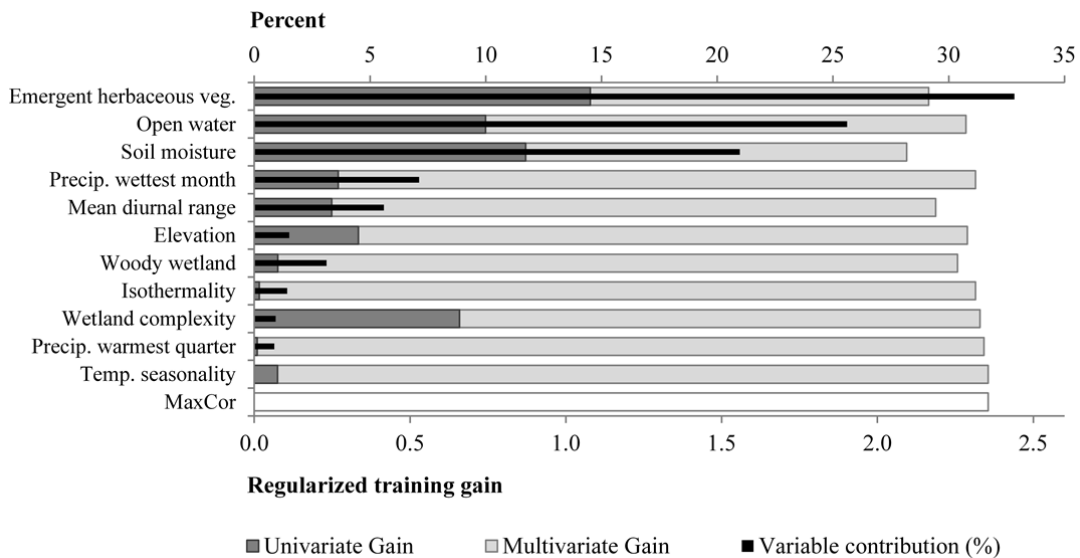

FIGURE 4. Gain and percent contribution of all environmental variables used to generate the MaxCor ecological niche model (ENM). Bars and lines as in Fig. 3 (except applied to MaxCor ENM).

locality data (Warren and Seifert 2011). The schema used to name the ENMs pertains to the environmental variables incorporated in the respective model. The MaxFull ENM incorporated all 25 environmental variables (Fig. 3). Many of these variables were correlated; however, MAXENT is known to perform relatively well with correlated datasets (Elith et al. 2011). Next, we calculated Pearson product-moment correlation coefficients (r) for all pairs of quantifiable variables (i.e., NED, NLCD and WorldClim) using 1,195 random cells. When $r \geq |0.7|$ for any variable pair, we discarded the variable that contributed least to MaxFull. The remaining 11 uncorrelated variables were incorporated in the second ENM variant, MaxCor. These variables included four NLCD-derived variables, NED, STATSGO2, and five WorldClim variables (Fig. 4). The third ENM variant, Max3%, incorporated the six variables that contributed > 3% to MaxFull (Fig. 5); these variables represented 90.1% of the total contribution to MaxFull. Next, we classified the logistic predictions produced by each ENM according to four suitability classes: unsuitable, low, moderate, and high. We derived classification breaks for each ENM using the Jenks Natural Breaks (i.e., Jenks Optimization) classification method (Jenks 1967) available in ArcGIS, and then averaged these break values across ENMs. This allowed us to homogenize the break values so that comparisons could be made across ENMs. Finally, we created a consensus model to combine the three ENMs, which identified the low, moderate, and high suitability areas predicted as such by at least two ENMs. This technique is akin to that of the consensus or ensemble approach (Araújo et al. 2005; Araújo and New 2007), which incorporates variability from multiple models and identifies commonly predicted areas.

Model evaluation.—We used a jack-knife evaluation technique (Pearson et al. 2007) to test the ENMs because the dataset was too small to partition into training and testing subsets, and each locality was likely to provide unique, valuable information. This approach required each locality be removed once from the dataset and a model be generated with the remaining 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, which was set at 10% (Pearson et al. 2007). The LPT is a conservative approach, defining suitable habitat as that with probability values equal to or greater than the lowest probability value associated with any one occurrence locality. The fixed threshold is less restrictive, defining suitable habitat as that with probability values greater than the lowest 10% of all probability values. Finally, we used the pValueCompute program (Pearson et al. 2007) to test whether model predictions were superior to a random assignment of excluded localities. We generated 34 evaluation models for each ENM, with each locality evaluated at both thresholds.

Survey effort.—We used the consensus model to select survey sites primarily within the Klamath and Pit hydrographic basins. We excluded Lassen Volcanic National Park, the Thousand Lakes Wilderness, and portions of Klamath National Forest from the site selection process (Fig. 1). Exhaustive *R. cascadae* surveys were previously conducted in these areas by U.S. Forest Service biologists (Karen Pope, pers. comm.; see also Fellers et al. 2007 and references therein), which would likely also have detected *R. pretiosa* if present.

Publicly and privately owned sites were selected and prioritized according to the suitability predictions of the consensus model. However, we attempted to focus our survey efforts on private lands, as they were less likely to have been previously surveyed. We first narrowed the Klamath and Pit hydrographic basins to regional clusters of high and moderate suitability
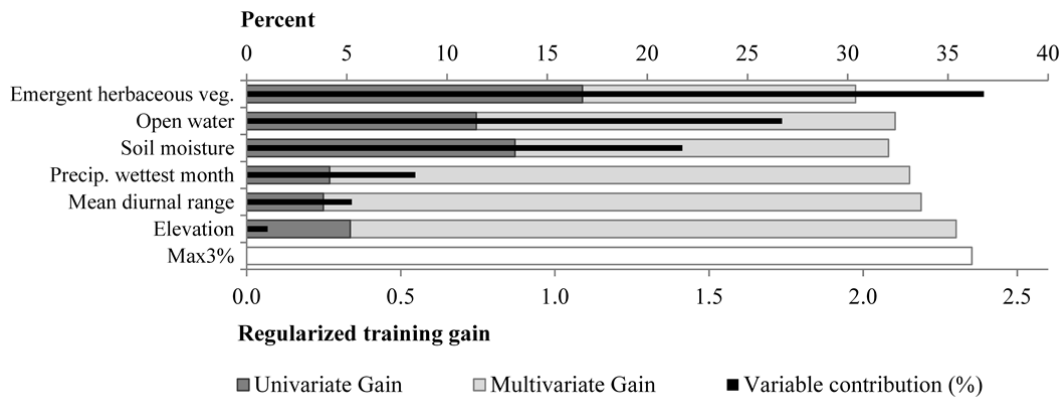

FIGURE 5. Gain and percent contribution of all environmental variables used to generate the Max3% ecological niche model (ENM). Bars and lines as in Fig. 3 (except applied to Max3% ENM).
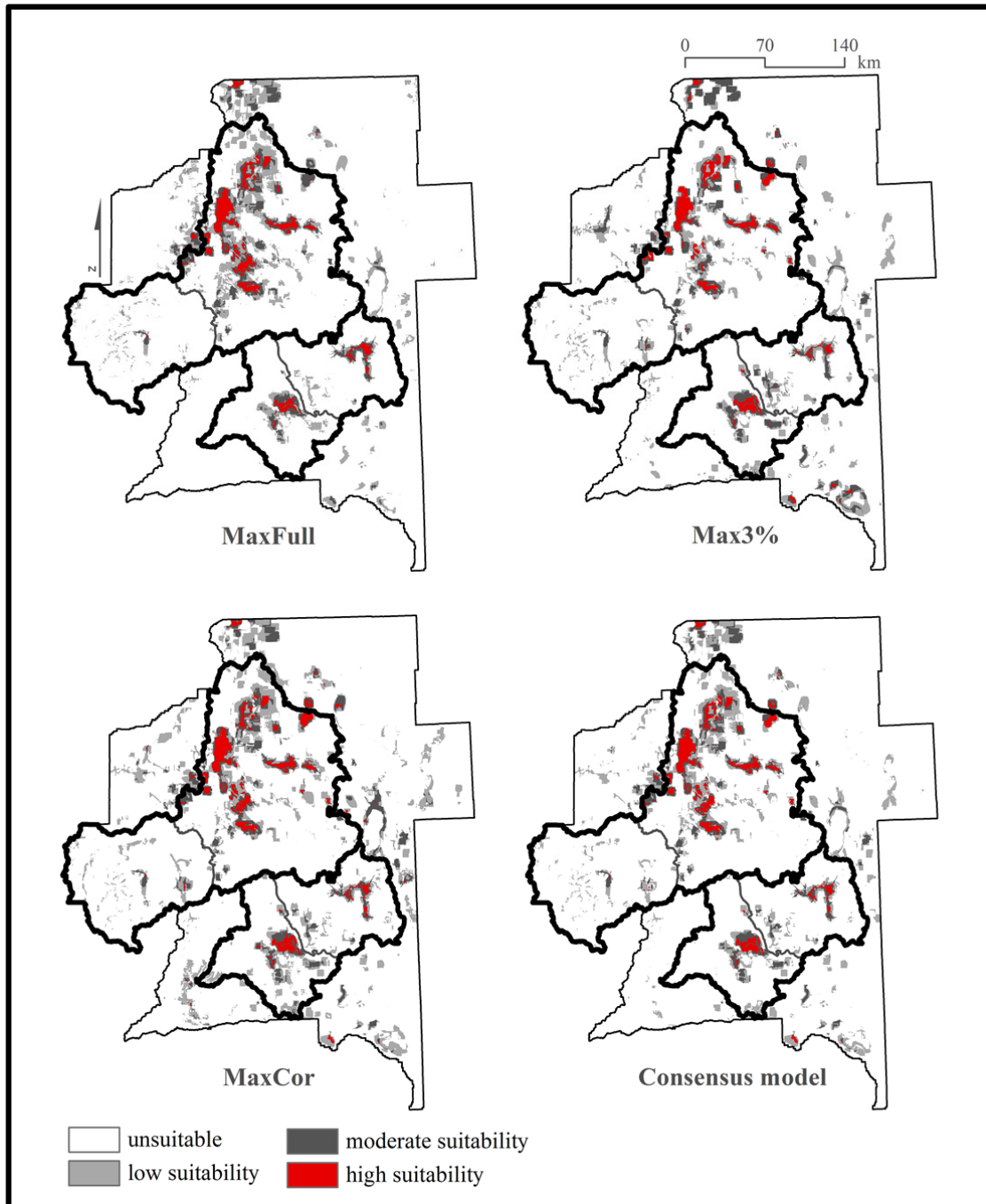
FIGURE 6. Estimated potential distribution of *R. pretiosa* across northeastern California and south-central Oregon, USA produced by MaxFull, Max3%, MaxCor, and the consensus model. Klamath (above) and Pit (below) River hydrographic basins indicated with bold, black outline; upper and lower sub-basin boundaries are delineated with gray lines. Habitat suitability values are partitioned into four classes: unsuitable, low suitability, moderate suitability, and high suitability (see Materials and Methods: Model approach).

predictions. We then used aerial imagery, topographic maps, and National Wetlands Inventory (NWI) data to identify specific sites within these clusters that apparently possessed favorable *R. pretiosa* habitat, including the presence of springs, bodies of water ≥ 4 ha, emergent vegetation, hydrologic connectivity, and complex aquatic systems (Germaine and Cosentino 2004; Pearl and Hayes 2004; Cushman and Pearl 2007). We contacted two timber companies, 66 private landowners, and all appropriate agencies asking for permission to access selected sites. We received permission from both timber companies, eight private landowners, and all agencies.

We investigated 44 sites between 2 April and 17 August 2010, 21 of which were privately owned. Twenty-six of these sites were investigated, but not surveyed (n = 10) or surveyed only once (n = 16), and consequently rejected as unsuitable. A site was considered unsuitable if at least two of the following criteria were observed: lack of permanent water, presence of predatory non-native fishes, lack of hydrologic connectivity and complexity, and inadequate size (Pearl and Hayes 2004; Chelgren et al. 2006; Cushman and Pearl 2007). Remaining sites (n = 18) were each surveyed three times. Field efforts in April and May 2010 were focused on egg mass detection and primarily comprised visual encounter surveys (VES) in shallow, vegetated areas. We used VES and dipnet surveys to detect adults and larvae during the remainder of the field season. Many sites were very large (> 40 ha) and, as such, we concentrated our efforts in suitable habitat along the perimeter of each site.

RESULTS

Model predictions.—All ENMs predicted similar core areas of suitable habitat, but the spatial distribution of each suitability class differed between the models (Fig. 6). The percent of study area predicted per suitability class was similar between models (Table 2). The greatest discrepancy occurred between MaxCor and the other ENMs, with MaxCor predicting more low suitability habitat. Overall, Max3% and MaxCor produced more fragmented and scattered distributions than MaxFull. For example, Max3% and MaxCor predicted a greater distribution of low and moderate suitability habitat in areas outside the Klamath and Pit hydrographic basins. The Max3% and MaxCor models also differed in their predictions. For instance, MaxCor predicted a greater distribution of low suitability habitat near the southwest corner of the study area. Moreover, MaxCor predicted a higher degree of suitability at areas north and northeast of the upper Pit sub-basin, while Max3% predicted a higher degree of suitability near the southeast corner of the study area.

Each ENM produced predictions consistent with the known geographic distribution of the species. Approximately 73% of the MaxFull, 65% of the Max3%, and 63% of the MaxCor low, moderate, and high suitability predictions, respectively, fell within the Klamath and Pit hydrographic basins; by comparison, these drainages encompass less than 48% of the study area. And while the upper Klamath and upper Pit sub-basins collectively represent only 29% of the study area, they contained 60% of the MaxFull, 47% of the Max3%, and 46% of the MaxCor low, moderate, and high suitability predictions.

Environmental variable contribution.—According to the jack-knife analyses of variable importance, the NLCD and STATSGO2-derived environmental variables most influenced all ENMs (Figs. 3–5). Based on each ENM's percent contribution estimates, emergent herbaceous vegetation provided the most information to each model (> 30%), followed by open water (> 24%) and soil moisture (> 19%), respectively. This metric may be influenced by highly correlated environmental variables. However, the same pattern of variable importance holds true when assessing univariate and multivariate model gain. For each ENM, jack-knife analyses revealed that emergent herbaceous vegetation produced the highest gain when used in isolation (i.e., univariate model), indicating this variable contributed the most useful information. For the Max3% model, emergent herbaceous vegetation also reduced the gain more than any other variable when omitted (i.e., multivariate model), indicating this variable contributed the most information not garnered from other variables (i.e., low correlation; Fig. 5). For MaxFull and MaxCor, soil moisture reduced the gain more than any other variable when omitted (Fig. 3 and 4, respectively).

Comparisons of the variables associated with extirpated and extant populations revealed considerable similarity between the two datasets. The CIs overlapped for 74% (17/23) of the continuous environmental variables, suggesting that variation between extirpated and extant populations was not significant for these variables. However, the CIs were disjunct for the remaining six variables, all of which were precipitation-linked bioclimatic variables: annual precipitation, precipitation of wettest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, and precipitation of coldest quarter. Despite this variation, we elected to incorporate the localities associated with the extirpated populations because these variables

TABLE 2. Percent of study area predicted by each ecological niche model (ENM) according to four habitat suitability classes: unsuitable, low suitability, moderate suitability, and high suitability (see Materials and Methods: model approach).

ENM	Percent of study area			
	unsuit.	low	moderate	high
MaxFull	87.8	7.6	3.1	1.6
Max3%	87.6	7.3	3.5	1.6
MaxCor	83.7	10.9	3.6	1.8
Consensus	86.6	8.5	3.2	1.7

contributed very little (≤ 8%) to any ENM (Figs. 3–5). Further, this variation is likely driven by extreme values associated with the two southernmost localities, reflecting regional precipitation differences rather than habitat differences between the localities associated with extirpated and extant populations. Because we concentrated our survey efforts in northern California, we considered these localities valuable, as they represent two of California's three verified occurrence records.

Model evaluation.—All ENM 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. All ENM evaluations produced identical success rates, predicting 71% ($P \leq 0.001$) of localities at both the LPT and 10% fixed thresholds. This corresponds with a 29% omission rate. Five localities were consistently excluded by all ENMs at both thresholds; these localities represent populations that are presumed extirpated, positioned along the fringe of the species' regional distribution, or both.

Survey efforts.—While we did not find *R. pretiosa* in California, we did detect two individuals at a previously unrecognized site in Klamath County, Oregon (Fig. 1). On 20 May 2010, we observed two adult females on private land along the margin of the upper Wood River (Fig. 2). These individuals were positively identified by their venter coloration, upturned eyes, lack of groin mottling, and extensive hind limb webbing (Dunlap 1955; McAllister and Leonard 1997). Prior to our study, *R. pretiosa* was known from other wetlands along the Wood River, but these sites are located approx. 29 river-km downstream (16 km Euclidean distance) from our detection point, well beyond the maximum dispersal distance recorded for the species (Cushman and Pearl 2007).

DISCUSSION

We have demonstrated that ENMs generated at fine resolutions can be a useful tool for directing exploratory surveys for rare amphibian species for which few localities are known. Using the consensus model to direct our survey efforts, we detected *R. pretiosa* at one previously unrecognized location within Oregon's upper Klamath sub-basin. This detection is significant because it represents the species' northernmost point of occurrence in the Wood River. Furthermore, *R. pretiosa* is currently recognized as extant at only nine localities within the Klamath hydrographic basin, and this is the southernmost basin known to be occupied by the species (Christopher Pearl, pers. comm.). Our analysis revealed that variables derived to correspond with a species' ecology can contribute substantially to ENM

performance. In particular, emergent herbaceous vegetation was the most influential variable in all ENMs, followed by open water. These variables correspond with habitat characteristics thought to be important to sustain *R. pretiosa* populations. Specifically, emergent vegetation is used for oviposition, thermoregulation, and predator avoidance; and open water is generally associated with deep, permanent water bodies, which are used for overwintering (McAllister and White 2001; Germaine and Cosentino 2004; Pearl and Hayes 2004). Our results also agree with Watson et al. (2003), who determined that 25–50% emergent vegetation was the most important feature of *R. pretiosa* microhabitat and a necessary requirement for the completion of the species' life cycle.

Our model set included a comprehensive (MaxFull), a parsimonious (Max3%), and an uncorrelated variant (MaxCor). Each produced a unique distribution. For example, MaxFull produced the tightest distribution, clustered around known localities, and predicted the greatest percent of moderate and high suitability habitat within the Klamath and Pit hydrographic basins, as well as within the upper Klamath and Pit sub-basins. However, tightly clustered distributions may be disadvantageous in certain situations, such as when predicting range expansions or attempting to detect unrecognized populations. For this reason, we also valued the more widely distributed predictions produced by Max3% and MaxCor. Ecological niche models generated with fewer variables, such as Max3% and MaxCor, are subject to fewer constraints and may predict a greater area of suitable habitat (Phillips et al. 2006). Thus, a trade-off exists between identifying potential occurrence areas and limiting distribution estimates to facilitate survey efforts.

We generated the consensus model, which incorporated the estimate produced by each ENM, because we believed each model provided unique and potentially valuable information. For example, the site at which we detected *R. pretiosa* was predicted as highly suitable by MaxFull and MaxCor, but only moderately suitable by Max3%. Survey efforts based solely on Max3% may not have identified this detection site. Further, while the spatial distribution of each suitability class differed among models, the percent of moderate and high suitability habitat varied by only 0.5% and 0.2%, respectively. Thus, field efforts were not burdened by incorporating the more widely distributed predictions produced by MaxCor and Max3%.

While we did not detect *R. pretiosa* in California, false-positive predictions, or sites that were predicted to be highly suitable but did not yield detections, should not be viewed as failures (Pearson et al. 2007). Non-detections may be attributed to factors not accounted for by the model, such as species detection and rarity, biotic interactions, geographic barriers, population isolation, dispersal limitations, range contraction, geologic history, and human influences

(Peterson 2001; Anderson et al. 2003). However, the waterbodies investigated and surveyed in northeastern California did not appear suitable for *R. pretiosa*. Non-native species, hydrologic alteration, and non-permanent hydroperiods were routinely documented; as a result, 59% (26/44) of our sites were rejected as unsuitable after the initial investigation or first survey. Of the 18 sites surveyed three times, nine contained predatory non-native fishes, eight contained non-native American Bullfrogs (*Lithobates catesbeianus*), and six contained both. The negative effects of these introduced predators on amphibian populations are well documented (Kats and Ferrer 2003; Pearl et al. 2004; Eby et al. 2006). *Rana pretiosa* and *L. catesbeianus* are known to successfully co-exist long-term only in Washington's Glenwood Valley (Joseph Engler and Marc Hayes, unpubl. report). Many of the sites we visited were hydrologically altered (e.g., dammed, diked) and devoid of vegetated shallows, a habitat requirement of *R. pretiosa* (Germaine and Cosentino 2004). And because *R. pretiosa* is primarily aquatic, it requires permanent water. However, many sites proved to have ephemeral water sources, albeit with long hydroperiods, and offered no nearby permanent aquatic refugia.

We recognize that temporal discrepancies exist in our dataset. This is most relevant for variables that represent dynamic processes. Specifically, the NLCD-derived variables contributed 58–64% to each model and correspond with 2001 data, while the bioclimatic variables contributed 13–18% and correspond with 1950–2000 data. However, the oldest historic *R. pretiosa* locality record dates back to 1898. While successful models have been generated with fewer than 17 occurrence records, predictive ability is greatly increased with additional records (Hernandez et al. 2006; Pearson et al. 2007). We considered it more important to incorporate all verified, known localities than use only temporally congruent data if, as in our case, no problematic asymmetry exists between the localities associated with extant and extirpated populations for variables that contribute importantly to the models.

We also recognize that our decision to use MAXENT'S default regularization parameter values may have produced models that overfit the input data (Anderson and Raza 2010; Peterson et al. 2011; Warren and Seifert 2011). This is suggested by the 29% omission rate and the fact that the ENMs' moderate and high suitability predictions are concentrated in areas that correspond with *R. pretiosa* localities, namely the upper Klamath and upper Pit sub-basins. However, little guidance was available for determining the appropriate level of regularization at the time we generated our models (Phillips and Dudík 2008; Warren and Seifert 2011). Further, we recognize that alternate methods of evaluating logistic predictions across ENMs may have produced dissimilar consensus models. Lastly, we recognize that MAXENT may produce indices not directly related

to the parameter of interest – the probability of occurrence – and that formal model-based inference requires a random sample of presence locations (Royle et al. 2012). However, our aim was not to develop a formally precise model, but rather one that would facilitate survey efforts by identifying areas most suitable for *R. pretiosa*. We are under no illusion that our limited locality dataset was random, but maintain the belief that our approach is useful for prioritizing sites when conducting exploratory surveys for rare amphibians.

Future *R. pretiosa* modeling efforts can be improved in several ways. First, the NWI dataset should be incorporated to account for the species' dependence on permanent water. We were unable to integrate hydroperiod or other NWI-derived variables because, at the time of modeling, the dataset was not available in digital format across our entire study area. Second, further efforts should be made to investigate privately owned land, as our survey efforts were hindered by our inability to access selected private lands. Privately owned land represents approximately 42% and 23% of the California and Oregon portion of our study area, respectively, with 62–65% of the ENMs' moderate and 69–72% of the ENMs' high suitability predictions corresponding with private ownership. Incongruously, only 12% of the private landowners we contacted granted survey permission. We believe privately owned land represents the best opportunity for detecting unrecognized populations of *R. pretiosa* in our study area because such a large proportion of the ENMs' moderate and high suitability predictions correspond with private lands and because we know of no other concerted effort to survey these areas. This is supported by the fact that all of the > 10 new *R. pretiosa*-occupied localities discovered within the last five years, including the one discovered during our surveys, have been on private lands (Marc Hayes, unpubl. data). Third, future modeling should also investigate the use of 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 (Wiens 1989; Guisan and Thuiller 2005; Guisan et al. 2007; Austin and Van Niel 2011). For example, models generated at 30 arc-seconds may produce estimates constrained to large wetlands, a suspected habitat requirement of *R. pretiosa*. Fourth, in light of recent studies, alternative regularization parameter values should be evaluated, since less regularization may produce better potential distribution estimates and, thus, produce more informative models. For example, Anderson and Gonzalez (2011) demonstrated that model performance can vary greatly according to the level of regularization specified, as well as be substantially improved with species-specific tuning. Warren and Seifert (2011) promote the use of information criterion approaches to setting regularization, as inappropriately complex or simple models may, among other things, exhibit a reduced

ability to infer habitat quality. Lastly, future field efforts aimed at identifying new populations should focus on areas predicted to be highly suitable by our ENMs, but which we did not have the opportunity to investigate, either because we could not obtain survey permission or, in two cases, because the sites were too large to effectively survey given the resources available.

Our modeling approach can be applied to other rare amphibian species or aquatic-dependent anurans or, with some caution, be used to better understand *R. pretiosa* distribution in other parts of its range. Our results also have important conservation, habitat restoration, and population management implications. For instance, all ENMs identified similar core areas of potentially suitable habitat and distribution gaps; this information is critical to understanding *R. pretiosa* habitat use and suitability. Further, our models could be used to assess the suitability of potential sites prior to relocation and repatriation efforts, as to avoid misusing limited conservation resources. While we did not detect *R. pretiosa* in California, the potential remains for the species to exist within the state. Focused surveys should continue, with concerted effort made to access privately owned land.

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