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Field validation supports novel niche modeling strategies in a cryptic endangered amphibian

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Many studies employ ecological niche models (ENMs) to predict species' occurrences in undersampled regions, generally without field confirmation. Here, we use field surveys to test the relative utility of four potential refinements to the standard ENM approach: 1) altering model complexity based on AIC, 2) selecting background points from a biologically informed region, 3) using target-group background to account for sampling bias in existing localities, and 4) using many rangewide localities (global model) versus fewer proximal localities (local model) to construct geographically restricted range predictions. We used Maxent to predict new localities for the California tiger salamander Ambystoma californiense, an endangered species that often goes undocumented due to its cryptic lifestyle. We followed this with a field survey of 260 previously unsampled potential breeding sites in Solano County, CA and used the resulting presence/absence data to compare all factorial combinations of the four model refinements using a new application of the Kruskal-Wallis test for ENM outputs. Our field surveys led to the discovery of 81 previously undocumented breeding localities for the California tiger salamander and demonstrated that ENMs could be significantly improved by utilizing target-group background to account for spatial sampling bias and local models to focus model output on the subregion of the range being surveyed. Our results clearly demonstrate the potential for local models to outperform global models, and we recommend supplementing traditional Maxent global models that utilize all known localities with local models, particularly when species occupy geographically structured, heterogeneous habitat types. We also recommend using target-group background since the improvement we observed when including it in our models was significant and very similar to that documented by previous studies. Most importantly, we emphasize the importance of field verification to enable rigorous statistical comparisons among models.

Ecological niche models (ENMs) have been growing in popularity over the last decade, largely because they utilize two types of easily accessible data: 1) georeferenced locality data, often culled from museum collections (e.g. Global Biodiversity Information Facility), and 2) environmental GIS layers, which are being developed to describe the environment at any point on the earth's surface at increasingly finer resolution (New et al. 1999, 2002, Hijmans et al. 2005). ENMs are used for three main purposes (Halvorsen 2012): 1) ecological response modeling (ERM), which describes the relationship between species modeled suitability and specific environmental variables, 2) projective distribution modeling (PDM), which predicts the distribution of a species in either a time or geographic area different from where the data were originally collected, and 3) spatial prediction modeling (SPM), which predicts the probability of finding a species at a particular location as accurately as possible. Of these applications, the last is the least controversial, because it involves the fewest modeling assumptions and is also the most easily tested.

To test an ERM prediction requires physiological studies in which one tests the performance of the target

species while continually varying one of the environmental variables in question and keeping all other environmental variables constant. PDM predictions can be verified by either experimentally introducing the target species to localities in the new geographic area and monitoring performance, or waiting for a future time frame and observing whether the target species is capable of persisting in the projected range. Testing an SPM prediction is comparatively easy; one only has to visit a set of previously unsampled localities and determine whether or not the target species is present. By repeating this procedure across multiple localities, one can make a statistical statement about the fit of a model to the true species distribution and compare alternative models. Although this kind of model validation is relatively straightforward, there are few published examples of ground truthing SPMs. Rather, SPMs are usually tested with locality data drawn from the same survey that provided the data on which the model was originally trained. Even if these two sets of data consist of entirely unique localities, they will still be spatially correlated, because the same surveyor(s) collected both data sets, and thus both sets of localities are constrained to come from the general areas the surveyor(s) visited (Veloz 2009). This is a recognized problem, and attempts have been made to divide locality data in a more informed manner and avoid spatial correlation (Phillips 2008). These divisions are usually geographical and therefore run the risk that spatially distinct subsets of the target species are locally adapted and thus have different underlying ENMs. An alternative that we use in this study is to train the model(s) with known locality data and test them with new, independent field surveys.

Maxent (Phillips et al. 2006) has been an increasingly popular ENM algorithm since it was placed in the top tier of ENM algorithms by the most comprehensive comparison of ENM methods to date (Elith et al. 2006). When developing a Maxent model, there are many choices that the modeler must make, including: 1) the geographic area from which to sample background points, 2) whether the background points should be chosen at random or to account for sampling bias, and 3) whether to adjust the regularization parameter to select the appropriate model complexity. There is clear evidence that the geographic area from which background points are drawn has a large effect on the final model (VanDerWal et al. 2009, Anderson and Raza 2010, Giovanelli et al. 2010), but there are no clear operational guidelines on choosing the optimal area. It has generally been recommended that one choose a biologically informed area, which should be based on "species' dispersal ability, the topographic complexity of the region in question, and the distributional patterns of congeneric species'" (Anderson and Raza 2010). While most studies choose background points randomly, there is evidence that choosing them from localities where biologically similar species have been documented improves model performance (Phillips and Dudík 2008, Phillips et al. 2009). This approach is termed target-group background; it posits that restricting absences to localities that have been surveyed for similar taxa and failed to uncover the target species increases the realism of the pool of absence localities. Finally, most studies use the default regularization parameter set by Maxent, although there is evidence that a higher regularization parameter usually produces a more accurate model (Anderson and Gonzalez 2011), and that the appropriate regularization parameter can be chosen using AIC_c (Warren and Seifert 2011).

A key question that has not been previously addressed is whether ENMs provide a better prediction of a subregion of the target species' range if one uses all of the known localities for that species (here referred to as the 'global' approach) or only localities from that subregion (the 'local' approach). Addressing this question is a central element of the current study.

This question arose as we launched a study to predict the range of the endangered California tiger salamander *Ambystoma californiense* (CTS) within Solano County, CA. CTS once had a much wider distribution in California, but has lost at least 55% of its original range (Jennings and Hayes 1994) and shows a marked shift away from lower elevations (Fisher and Shaffer 1996). The species starts life as an aquatic larva, but spends over 95% of its postmetamorphic life underground (Trenham et al. 2000) in the burrows of California ground squirrels *Otospermophilus beecheyi* (Loredo et al. 1996) or Botta's pocket gophers *Thomomys bottae* (Trenham and Shaffer 2005). Postmetamorphic individuals are only active on the surface immediately after metamorphosis or on rainy winter nights (Loredo and Van Vuren 1996, Trenham et al. 2000). They are thus rarely observed, and most known localities come from larval breeding pond surveys. However, adult salamanders travel up to \sim 2 km from their natal/breeding ponds, and understanding the species' spatial distribution and habitat occupancy is an important component of regional conservation planning (Searcy and Shaffer 2008, 2011). The combination of its endangered status, exceedingly cryptic activity patterns, and importance as an umbrella for habitat management (Searcy and Shaffer 2011) suggests that accurate ENMs describing the distribution of CTS are an essential component of effective conservation planning.

In this study, we used Maxent to create 16 ENMs for the Solano County population of CTS. These models used all factorial combinations of four potential modeling refinements: 1) a biologically informed geographic extent (Anderson and Raza 2010), 2) target-group background (Phillips and Dudík 2008), 3) selecting the regularization parameter using AIC_c (Warren and Seifert 2011), and 4) using a local rather than global model. We focused on Solano County because the contained salamander metapopulation is geographically isolated north of the San Francisco Bay Delta near the northern limit of the species' range (Fig. 1), and because the county is actively developing a habitat conservation plan. We then conducted a countywide survey for new CTS localities to ground truth the resulting models. Using this new, independent set of presence/absence data we compared the fit of the 16 models to determine which ENM(s) provided the most accurate predictions. Our results, while specific to our study system, suggest several guidelines for model improvements that should have greater generality to other systems.

Methods

Niche modeling

We used 21 environmental layers in all of our niche models. These included the 19 Bioclim layers (Hijmans et al. 2005; <www.worldclim.org>), an elevation layer from the National Elevation Dataset (<www.nationalmap.gov>), and a potential vegetation layer including 54 vegetation types (Küchler 1976; <www.portal.gis.ca.gov/geoportal>). We downloaded the Bioclim layers at the highest available resolution (30 arc-second), and then resampled them down to a higher resolution (1 arc-second) to match the elevation layer. This was accomplished purely by partitioning existing cells, so no interpolation was required. The vegetation layer was originally a shapefile in a different datum, so we first georeferenced it using 10 control points and a cubic convolution algorithm and then converted into a raster of the appropriate resolution.

Our localities came from four sources: 1) HerpNet (a compendium of the herpetology collections of 53 worldwide museums), 2) the appendix to Shaffer et al. (2004), 3) surveys conducted by the East Bay Regional Park District, and 4) the UC Davis Herpetology Museum. The Shaffer et al. (2004) data set includes some localities which contain *A. californiensel/A. [tigrinum] mavortium* hybrids (Fitzpatrick and Shaffer 2007), and we only included ponds where the



Figure 1. Map of the California counties and all localities used in training the niche models. All localities were used to train the global model, while only the Solano localities (blue circles) were used to train the local model.

majority of the gene pool was from native CTS. Apart from these hybrids, CTS only co-occur with other ambystomatid salamanders in a handful of ponds in Santa Cruz County, giving us confidence that specimens within the range of CTS that were identified as CTS were identified correctly. To account for specimens georeferenced to localities outside the range of CTS, we eliminated all localities from counties in which CTS is not known to occur. We also removed four additional localities that are outside of the recorded range of CTS and we believe are in error: Bakersfield (Kern County), Davis (Yolo County), San Luis Obispo (San Luis Obispo County), and Tehachapi (Kern County). The resulting set of 590 training localities are in Supplementary material Appendix 1, Table A1. Niche modeling was conducted using Maxent ver. 3.3.3e. We created 16 niche models – all factorial combinations of our four potential model refinements (Table 1).

Surveys

We next downloaded a shapefile from the California Spatial Information Library (<www.atlas.ca.gov>) with all of the water bodies in Solano County to identify potential survey sites. After extensive landowner negotiations (most potential survey sites were on private land) we were able to determine presence/absence in 260 ponds, either through our own field surveys or those conducted by environmental consultants. Surveys were conducted from 2008–2011, always between 28 March and 13 May. Based on over a decade of extensive field work at Jepson Prairie in Solano County (Searcy et al. 2014) this is the time window during which we feel most confident that a lack of detection of salamanders can be interpreted as a true absence, since larvae are large enough to be efficiently sampled and have not begun to metamorphose.

Our sampling consisted of a minimum of four seine hauls per pond. Each seine haul was either ~25 m in length, or completely traversed the pond being sampled, and we used

Table 1. Description of the four potential ENM refinements tested in this study. All factorial combinations of these refinements were tested, yielding a total of 16 models.

	Standard approach	Potential refinement
Geographic extent	Region of California between 34.5 and 39.5°N and 118 and 123°W. This combines the two most common approaches to choosing a geographic extent: using political boundaries and choosing an arbitrary rectangle based on longitude and latitude.	Seventy-four kilometer buffer around all known California tiger salamander localities. Seventy-four kilometers is the largest gap within the current range of the California tiger salamander, and thus represents a distance we know California tiger salamanders would have been capable of dispersing over the course of their evolutionary history. ^a
Background points	Ten thousand randomly chosen background points, which is the default setting for Maxent.	Ten thousand target-group background points taken from HerpNet (i.e. localities where other amphibians and reptiles have been collected). ^b
Regularization parameter	Regularization parameter equal to one, which is the default for Maxent.	Regularization parameter chosen based on AIC _c using ENMTools 1.3.
Localities	Used all 590 localities from across the species' range (global approach).	Used only the 21 localities from Solano County (local approach).

^aWhen combining this refinement with the local approach, we used a different geographic extent. In these models, the geographic extent was a rectangle around the Solano County localities that stopped 5 km short of the nearest localities in other counties. All of this extent is within 74 km of the Solano County localities, and thus comprises an area that California tiger salamanders could have sampled over their evolutionary history. Also, 5 km is considered an upper-bound on the distance that California tiger salamanders can migrate from their breeding sites on an ecological time-scale, so this extent is presumably not being utilized by California tiger salamanders from other counties that may have similar climatic tolerances.

^bWhen combining this refinement with the geographic extent described in footnote ^a, we had to use additional sources for target-group background points in order to find 10 000 within the specified geographic extent. The additional sources we used were Calflora, CNDDB, FishNet, MaNIS, and ORNIS, which contain georeferenced localities for plants, listed species, fish, mammals, and birds, respectively. The decreased specificity from using these additional sources was more than made up for by the increased number of background points (i.e. the AUC for a model using background points from all of these sources was higher than for a model using only background points from HerpNet, but having fewer than 10 000).

a 5 m long seine with a 4 mm mesh. For each site, we also noted any pond characteristics that would prevent CTS from utilizing it as a breeding site even if they were in the neighboring terrestrial habitat. These pond characteristics included: short hydroperiod (< 90 d), presence of introduced predators, brackish water, any indication that at some point in the year the pond was part of a flowing watercourse, substantial amounts of emergent vegetation (> 10% of surface area), or an artificial substrate.

Model evaluation

Our original training data included 21 localities from Solano County. We excluded these sites when testing our 16 models, since models should not be tested with their training data. We also only used absences from ponds that lacked all six characteristics, identified above, that might deter CTS breeding from otherwise appropriate breeding sites. This made it more likely that our absences actually fell outside of CTS's environmental niche rather than being unoccupied due to local habitat features. Maxent's logistic output can be interpreted as the probability of presence (Phillips and Dudík 2008). To determine which of the niche models best predicted our survey results, we extracted the probability of salamander occurrence predicted by each model at each of our surveyed ponds. For each pond with salamanders present, these probabilities represent the probability of the model in question correctly predicting salamander presence. For each pond with salamanders absent, one minus these probabilities represents the probability of the model correctly predicting salamander absence.

To compare the models, we used two approaches. First, we used a Kruskal–Wallis test with each pond as a data point and the probability of each model making the correct prediction on presence/absence as the observed score (we also included a blocking term for locality in the model, since all models were applied to the same set of 119 breeding sites). We then compared all pairs of models using the Steel–Dwass method (Critchlow and Fligner 1991). Second, we compared the AUC scores of each model. The AUC scores used for model comparison were all calculated over this identical set of presence/absence localities, and therefore are statistically comparable.

To understand why certain models outperformed others, we examined the rules that each model produced to relate the different environmental variables to the probability of salamander presence. We evaluated both the models' relative ranking of the environmental variables, and, for a few of the most important variables, the shapes of the functions representing the probability of salamander presence. Maxent provides two different metrics for measuring variable importance: percent contribution and permutation importance. Percent contribution is the percent of the total variation explained by the model that resulted from iterations of the algorithm that involved rules based on the variable in question. Permutation importance is based on the loss in AUC that results from randomly permuting the variable in question. Halvorsen (2012) showed that metrics based on fraction of total variance explained (e.g. percent contribution) are more reliable than metrics based on AUC (e.g. permutation importance), so we based variable importance on percent contribution.

Results

Field results

Our field surveys detected 81 salamander presences and 178 salamander absences, but only 38 of these absences were from ponds that we categorized as having all of the appropriate local habitat features to support CTS breeding (Fig. 2). Of the 140 non-habitable ponds, our field teams surveyed 84 and we relied on reports from environmental consultants for the other 56. We took the conservative approach of automatically disqualifying the 56 ponds that we did not personally survey, since we did not have the opportunity to appropriately assess the local pond features. The remaining 84 ponds were disqualified for the following reasons: 39 had insufficiently long hydroperiods, 22 contained brackish water, 18 were inhabited by invasive predators, 8 contained abundant emergent vegetation, 7 were part of a seasonal watercourse, and 4 had an artificial substrate (Supplementary material Appendix 1, Table A2).

Model comparison

When comparing all 16 models, the Steel–Dwass method separated the models into two groups (Table 2). One group contained 12 models that performed equally well, while the second group contained four models that underperformed the first group. The group of 12 models included all eight of the local models and all four global models that utilized target-group background. While AUC did not order the models in exactly the same way as the Kruskal–Wallis test, it did place the same four models at the bottom of the ranking. The mean AUC of local models was 0.024 higher than the mean AUC of global models. Including target-group background, model selection, and a biologically informed geographic extent increased mean AUC by 0.036, 0.006, and 0.002, respectively.

Target-group background

Target-group background was the potential modeling refinement that yielded the greatest increase in mean AUC. In addition, all models that included target-group background were in the higher ranking group of models based on the Kruskal-Wallis test. To understand the difference between models with and without target-group background (Fig. 3A, B), we first examined the localities that target-group background was using as background points (Fig. 4). These localities were least dense in the Central Valley, denser in the Central Coast and Sierra Nevada, and most dense in the Bay Area. As a result, when using target-group background, environmental factors characteristic of the Central Valley were less penalized in the model building process because they may simply have been sampled less by biologists, while environmental factors characteristic of the Bay Area were penalized more. Percent contributions associated



Figure 2. Results of the countywide survey. Original presences (21), where California tiger salamanders were known to occur prior to the survey, are shown in yellow. New presences (81), where California tiger salamanders were discovered during the survey, are shown in green. Habitable absences (38), where California tiger salamanders were not found, but where all of the local habitat features appeared appropriate for breeding, are shown in purple. Non-habitable absences (140), where California tiger salamanders were not found, but where either the local habitat features could not be properly assessed, or where the local habitat features appeared inappropriate for breeding, are shown in red.

with temperature seasonality, vegetation, and annual precipitation were most strongly altered by this shift in background points. When using target-group background, the percent contribution of temperature seasonality and annual precipitation decreased by 15.6 and 4.1%, respectively. This released constraints that those layers had been placing on the model, allowing it to expand into drier, more seasonal areas, such as the Central Valley. Using target-group background increased the percent contribution of vegetation by 5.0%, and the constraints associated with this layer increased

Table 2. Ranking of the 16 niche models based on rank sums from the Kruskal–Wallis test. The types of model are either global (used all 590 localities) or local (used only the 21 Solano County localities), but all models were evaluated using the same set of 119 new localities. Parenthetical listing of the model improvements that were included range from none of the tested improvements to all three. Models with the same letter in the significance grouping column were not significantly different from each other based on a Kruskal–Wallis test. Models were compared over the combined set of new presences and habitable absences. AUC values over the same set of localities are also provided. They do not yield precisely the same ranking, but they do divide the two significance groupings similarly.

Model	Significance grouping	Rank-Sum	AUC
Global (all)	А	1144.57	0.8483
Global (target-group background + model selection)	А	1115.83	0.8668
Global (target-group background + geographic extent)	А	1113.5	0.8471
Local (target-group background)	А	1069.85	0.8635
Local (model selection)	А	1064.43	0.8419
Local (geographic extent)	А	1050.92	0.8558
Local (geographic extent + model selection)	А	1037.91	0.8359
Global (target-group background)	А	1036.5	0.8635
Local (target-group background + model selection)	А	1036.27	0.8681
Local (target-group background + geographic extent)	А	1026.83	0.8528
Local (none)	А	1011.54	0.8454
Local (all)	А	996.55	0.8255
Global (geographic extent + model selection)	В	741.69	0.8210
Global (model selection)	В	634.93	0.8086
Global (geographic extent)	В	594.71	0.7981
Global (none)	В	563.97	0.7430



Figure 3. Model comparison. For all panels, red circles represent absences and blue circles represent presences. Light shading represents areas with high modeled habitat suitability and dark shading represents areas with low modeled habitat suitability. (A) Average of the four global models that include target-group background. (B) Average of the four global models that do not include target-group background. (C) Average of the four local models that do not include target-group background. To see the effect of target-group background, compare panels (A) and (B). To examine the effect of local versus global models, compare panels (B) and (C).

predicted habitat suitability in riparian forests (characteristic of the Central Valley) and decreased predicted habitat suitability in mixed hardwood forests (characteristic of the Bay Area).

Local versus global

The other set of models that were uniformly placed in the higher group by the Kruskal–Wallis test were the local models. The local and global models have very different response curves for the two environmental factors with high percent contributions for both sets (elevation and precipitation of the driest quarter), and we think that this is the explanation



Figure 4. Distribution of pseudoabsences used in the models utilizing target-group background. 10 000 background points were used in the models, but for easier viewing a random subset of only 5000 are shown here. When using target-group background a much lower density of background points are taken from the Central Valley compared to the Bay Area. This is representative of the relative densities of museum specimens taken from each region.

for most of the differences between the two sets of models (Fig. 3B, C). Precipitation of the driest quarter makes a 35.2% and a 10.0% contribution to the local and global models, respectively. The response curve for the local models limits CTS occurrence to areas with less than 6 mm of rain during the driest quarter, while the response curve for the global models expands this to areas with up to 10 mm of rain during the driest quarter (Fig. 5A). The percent contribution of elevation to the local and global models is 17.6 and 7.0%, respectively. Again, the local model predicts a very narrow range of habitat suitability (limited to areas below 42 m elevation), while the global model predicts a much wider range of habitat suitability (including areas up to 1279 m). These wider ranges of predicted suitability cause the global models to predict CTS presence in the Cordelia Hills and Vaca Mountains, two high-elevation regions of Solano County that are nearer to the coast and receive moisture from fog even in the summer. CTS occur in very similar sets of hills less than 30 km distant on the south side of the San Francisco Bay Delta, but they do not occur in the Cordelia Hills or Vaca Mountains, which leads the local model to outperform the global model in Solano County (Fig. 5B).

Discussion

Our results clearly demonstrate the benefits of using both target-group background to correct for sampling bias and local data to predict local occurrence probabilities.



Figure 5. Differences between local and global models. For both panels, red circles represent absences and blue circles represent presences. (A) Precipitation of the driest quarter: green areas receive 5 mm of precipitation or less; orange areas receive 6 mm of precipitation or more. (B) Elevation: green areas are below 42 m; orange areas are above 42 m. Most presences are in the areas with 5 mm of precipitation or less during the driest quarter and in areas below 42 m. These are the areas favored by the local models.

We are reasonably confident that CTS in the Solano County metapopulation occupy a remnant habitat type that was once typical of the species as a whole, but has become rare as a result of agricultural and urban development and invasive species distributions in the Central Valley. Rangewide, CTS has shown a pronounced shift toward higher elevation site occupancy (Fisher and Shaffer 1996), although the species has persisted in low-elevation sites locally in Solano County, presumably leading to the superior performance of target-group background and local data. Whether this result is generalizable beyond our case study is an open, empirical question, but based on our interpretation of the models that utilized target-group background and local samples, we believe that the refined prediction probabilities that we found will be common to many other systems.

Importance of target-group background

Target-group background accounts for sampling bias of previous surveys by selecting background points from localities where closely related species have been recorded, or where species that require similar survey methods have been found (Phillips and Dudík 2008). This assures that background points are drawn from a pool of localities that biologists have actually visited and thus had the potential to observe and record the target species. Moreover, if biologists were recording closely related taxa, it is more likely that they would have recorded the target species if it was present, since many field biologists are trained to be broad taxonomic specialists (ornithologists, herpetologists, etc.). Similarly, if they were using survey methods that would have discovered the target species if present, then they may have been more likely to record it. In remote areas, this can be very important since there may be a limited number of places that biologists can access (e.g. near roads, towns, waterways, or airstrips).

We found this effect to be equally important in the well-sampled habitats of central California, where land conversion and private property rights can also severely limit access by biologists. Using informed background points appears to be correcting for the fact that open space with reasonable biodiversity is only present and accessible in certain parts of central California. CTS were not the only species extirpated from the floor of the Central Valley when it was converted to agriculture in the 1880s, and most museum collecting in the region did not begin until the early 1900s, leading to few museum specimens from the Central Valley. By incorporating this into the ENM, targetgroup background causes Maxent to allot lower penalties to environmental parameters characteristic of the Central Valley, since it correctly views them as undersampled. This is important for the global models, because the Greater Jepson Prairie Ecosystem (which encompasses 79% of the known CTS localities in Solano County) is typical of much of the former Central Valley habitat and allotting lower penalties to this type of habitat allows the global models to incorporate more of the Solano County range. This highlights an additional value of target-group background: it can correct for land use history in addition to correcting for sampling bias, as it was originally designed to do. Given that it can do both increases the probability that it will be useful in a wide range of ENM studies.

Local vs global approach

There are at least three possible interpretations for the enhanced performance of local models over global ones without target-group background. The first is that the Solano County CTS population is locally adapted to unique environmental conditions. The global models without target-group background predicted salamander occurrence in two hill regions (Cordelia Hills and Vaca Mountains) that contain a number of constructed cattle ponds where all local habitat features appear perfect for CTS breeding and that appear to be virtually identical to regions where CTS occur further south in the Bay Area and Coast Range. In addition, these hills form the edge of the fog bank during California's hot, dry summer, and thus receive more summer precipitation than the rest of Solano County. It is possible that the Solano County California tiger salamander population is locally adapted to the drier conditions further inland and cannot persist in the moister, more coastal hill habitat. In support of this interpretation, molecular data indicates that the Solano County CTS population is more closely related to CTS in the Sierran foothills, where it is even drier, than to the geographically proximate populations in the Bay Area (Shaffer et al. 2004).

A second interpretation for the success of local over global models without target-group background is that local idiosyncrasies of land use history shape species distributions, and that local models are better able to capture and predict such details than global models. In our study, the local models have a narrow elevation range focused on elevations between 0 and 42 m. In Solano County, 91% of the known CTS localities fall within this range, and most are located in the Greater Jepson Prairie Ecosystem (Witham 2006). This region is known for its alkaline, saline, and clay-rich soils that form an aquatard that collects water on the surface in large vernal pools, creating optimal CTS breeding habitat (Bates 1977). These soils are also infertile and, unlike most of the Central Valley which was leveled and plowed in the

1880s, have never been subject to intensive agriculture. This renders CTS habitat in Solano County unique compared to the rest of the currently occupied range, where most localities are now restricted to hilly areas and only 16% fall below 42 m. While they probably once lived throughout the lowlying floor of the Central Valley (as evidenced by relictual populations scattered across the Central Valley floor), most CTS populations have been extirpated from this area, and the species largely persists in a ring in the surrounding foothills (Fig. 1). This elevational shift is reflected in the higher elevation of current compared to historical museum localities (Fisher and Shaffer 1996). In Solano County, some of the hilly areas (e.g. Montezuma Hills) harbor the more productive soils and have been plowed, making it quite possible that they were home to CTS breeding populations prior to European agriculture, but that these populations have been extirpated within the last 150 yr. Thus, to some extent the pattern of land use in Solano County is the inverse of that in the rest of the range, lending a considerable advantage to the local models.

A third possibility for the success of the local models resides in the null expectation that the local models should simply perform better because of spatial autocorrelation. Since the local models are fit only to the Solano County localities, they should be more spatially correlated with those localities. If new salamander localities discovered by our survey are also spatially correlated with the previously known localities, then the local model will do a better job of predicting their distribution based on this autocorrelation. We tested this possibility with a null model that assigned a probability of salamander presence equal to the inverse of the distance to the closest known locality (Hijmans 2012). This null model had an AUC score very near the mean of our other models (0.847), and thus we cannot reject the possibility that spatial autocorrelation explains, or at least contributes to, the success of the local models. However, this does not mean that the local models are uninformative. Hijmans (2012), which emphasizes the necessity of making comparisons against null models, also acknowledges that for small, clustered ranges (like the Solano County CTS population), it will be impossible to distinguish a successful ENM from a null model, even when the range is actually driven by strict habitat requirements. All three interpretations thus seem to provide plausible explanations, and they are not mutually exclusive. A combination of all three may be driving the success of the local models.

Generality of results

This is the third study to evaluate target-group background with Maxent using presence–absence data (Phillips and Dudík 2008, Phillips et al. 2009), and the similarity of the results between the three indicates that using target-group background, or another form of bias correction, should become standard practice. The mean increase in AUC from using target-group background in our study (0.036) is very similar to the magnitude of model improvement observed in those other studies (0.031 and 0.029 in Phillips and Dudík (2008) and Phillips et al. (2009), respectively). Sampling bias in museum localities is almost certainly universal, and correcting for it in a biologically meaningful way should always bring the predicted range closer to the true range. Our results also indicate that target-group background can account for geographical variation in land use history and other possible anthropogenic disturbances in addition to accounting for sampling bias, which adds to its general utility.

The generality of our finding that local models outperform global models at predicting presence/absence data in a subregion of the target species' range is an empirical question that requires testing in other systems. However, our current interpretation is that local models will outperform global ones when a species' range consists of ecologically divergent subregions. For example, in the Coast Range habitat that defines the western portion of their distribution, CTS reach elevations up to 1200 m, while in the Sierra Nevada foothills 80 km to the east, they are limited to elevations below 500 m. A local model specific to either of these subregions would probably outperform a global model that pooled localities across both. Furthermore, as a California endemic, CTS has a more limited, and probably more ecologically homogeneous range than many other species. While a species with a relatively homogeneous range may fare better with a more inclusive global model, such taxa may be uncommon (Sork et al. 2010). Also, a subregion does not need to be very large or well sampled to benefit from a local ENM approach, since Maxent generates well-performing models with as few as 15 localities (Pearson et al. 2007). In our case, a subregion with 21 localities outperformed a global model with 590, a 28-fold difference.

We found no improvement from altering the regularization parameter based on model selection (selected regularization parameters varied between 0.4 and 4.8 (mean 1.8 ± 0.55 SE) and yielded an average increase in AUC of only 0.006). We also found no improvement from choosing a biologically reasonable geographic extent (average increase in AUC of 0.002), although we defined biologically reasonable extent based solely on dispersal distance, and there may be additional factors (e.g. dispersal barriers, presence of predators/ competitors) that limit the geographic range that a species is able to sample. We suspect that in general neither of these modeling refinements will be important for spatial prediction modeling (SPM). Model selection is meant to limit model complexity. This is probably important for ecological response modeling (ERM) because the goal is to analyze relationships with particular environmental variables and therefore functions characterized by fairly simple geometries ease the interpretation of models and have greater biological plausibility. It may also be important for projective distribution modeling (PDM; Anderson and Raza 2010), because the novel projection environment will often have novel combinations of variables that could be excluded by overly complex models that were not exposed to these combinations in the training data. For SPM, on the other hand, a complex model is less of a problem because all of the relevant variable combinations are present in the training data and the geometries of the fitted relationships are not critical as long as they model a close fit to the species distribution. The importance of choosing a biologically reasonable geographic extent with respect to SPM, ERM, and PDM is likely to be similar.

Conclusions

Our study illustrates how a local ENM, trained with a limited set of localities proximal to the area of interest, can outperform a global ENM trained with a much larger data set drawn from the entire species range when the goal is to understand and predict a species' distribution in a specific subregion of its range. It also illustrates the utility of target-group background, which can correct for geographical variation in land use history in addition to sampling bias in training localities. We confirmed these results with presence/absence surveys in our target region. Such field-based confirmation is rare, and gives us considerable confidence in our modeling results. It also allows us to assign statistical probabilities to our among-model comparisons. We recommend increased use of target-group background generally, and local models for local range and occupancy predictions. Finally, we emphasize the unique contributions that presence/absence data can make when new ecological niche modeling methods are being tested, and recommend fieldverified surveys as the best data type for model comparison and evaluation of model refinements.

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Supplementary material (Appendix ECOG-00733 at <www. ecography.org/readers/appendix>). Appendix 1.

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