

Do Ecological Niche Models Accurately Identify Climatic Determinants of Species Ranges?

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ABSTRACT: Defining species' niches is central to understanding their distributions and is thus fundamental to basic ecology and climate change projections. Ecological niche models (ENMs) are a key component of making accurate projections and include descriptions of the niche in terms of both response curves and rankings of variable importance. In this study, we evaluate Maxent's ranking of environmental variables based on their importance in delimiting species' range boundaries by asking whether these same variables also govern annual recruitment based on long-term demographic studies. We found that Maxent-based assessments of variable importance in setting range boundaries in the California tiger salamander (*Ambystoma californiense*; CTS) correlate very well with how important those variables are in governing ongoing recruitment of CTS at the population level. This strong correlation suggests that Maxent's ranking of variable importance captures biologically realistic assessments of factors governing population persistence. However, this result holds only when Maxent models are built using best-practice procedures and variables are ranked based on permutation importance. Our study highlights the need for building high-quality niche models and provides encouraging evidence that when such models are built, they can reflect important aspects of a species' ecology.

Keywords: *Ambystoma californiense*, Maxent, percent contribution, permutation importance, recruitment, salamander demography.

A species' fundamental niche can be thought of as the set of environmental conditions under which it can persist (Hutchinson 1957). Identifying this set of environmental conditions has played a major role in predicting the geographic distributions of species, informing one of the primary aims of ecology (Walter 1985; Woodward 1987; Ellenberg 1988). The traditional method for identifying these environmental conditions has been a physiological approach in which population growth rates are measured along experimentally manipulated gradients (Maguire 1973; Tilman 1977; Tilman

and Wedin 1991). Given the large number of environmental factors than can simultaneously influence population growth rate, the number of experiments needed to measure all aspects of the niche and thus define its n -dimensional hypervolume can quickly become intractable (Schoener 2009). As a result, ecological niche modeling, which takes advantage of the rapidly growing body of accessible museum locality data and geographic information system-based climate layers, has become increasingly important in ecological and conservation-related research (Guisan and Zimmermann 2000).

Given the correlative nature of ecological niche models (ENMs) and the coarse scale of their input variables (usually averaged over square-kilometer grid cells) relative to traditional field studies, there have been legitimate questions raised as to what, if anything, ENMs really tell us about an organism's environmental niche requirements. This has led to a series of recent studies testing ENM outputs against field-based population parameters as a strategy for biological validation. Many of these studies have found that habitat suitability, the most basic ENM output, is positively correlated with population abundance (VanDerWal et al. 2009; Oliver et al. 2012; Martínez-Meyer et al. 2013) and negatively correlated with habitat marginality (Soley-Guardia et al. 2014). A few studies have gone a step further and demonstrated a positive correlation between habitat suitability and measures of fitness such as crop yield, maximum plant height, reproductive output, and survival (Buckley et al. 2010; Thuiller et al. 2010; Brambilla and Ficetola 2012; Estes et al. 2013). In both cases, the correlation between model outputs (usually using Maxent) and field demography suggests that ENMs reflect underlying ecological facets of species and may, therefore, be useful for making biological predictions across a range of past and future ecological conditions.

Some ENMs also provide a ranking of environmental variables based on their importance in delimiting the projected environmental niche, or range, of a species. If these rank-

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ings reflect the true underlying biological factors that limit the distribution of species rather than correlations with those factors, then this output should be particularly important for predicting the effects of past and future climate change on a species distribution. Climate change projection models that use only a subset of layers tend to statistically outperform those using all layers when projecting species distributions into new environments (Rödger et al. 2009). This is presumably because overfitting with variables that do not actually limit the niche of a species can lead to inaccurate predictions of presence/absence when projecting niche models into a new time or place. As a consequence, many studies that project ENMs into new environments use that subset of the standard set of 19 Bioclim layers (Hijmans et al. 2005) believed to be most important in defining the niche of a focal species (Elith et al. 2010; Milanovich et al. 2010; Ponce-Reyes et al. 2013). Although reasonable in principle, researchers often lack the ecological knowledge necessary to make well-informed choices about the most important variables (but see Austin and Van Niel 2010), resulting in somewhat arbitrary, albeit restricted, sets of environmental layers. An alternative approach to avoid overfitting is to tune model settings by imposing penalties for the introduction of additional parameters to the ENM (i.e., regularization/lasso) or by identifying those with the best performance on independent data or the best balance of complexity and explanatory ability (Anderson and Gonzalez 2011; Radosavljevic and Anderson 2014).

Maxent (Phillips et al. 2006) has emerged as the most popular presence-only ENM algorithm (Elith et al. 2006). In this study, we use an empirical, ecological ground-truthing approach to determine whether Maxent accurately identifies biologically important variables in setting the range limits of an endangered salamander in California. We compare the climatic variables that govern temporal variation in juvenile recruitment at monitored sites over two decade-long field studies to the climatic variables that limit the spatial distribution of the species at its range boundaries as predicted by Maxent models. Our study system is the California tiger salamander (*Ambystoma californiense*; CTS), an endangered amphibian that inhabits vernal pool grasslands in Central California (Searcy and Shaffer 2011). These grasslands are much warmer and drier than the forest habitats that most amphibians occupy (Searcy et al. 2013), and the species appears to exist at or near its physiological limits. Since CTS is already living at the margins of its environmental tolerances and is a listed species at the federal and state levels, there is legitimate concern that even slight climate change will push it over a demographic threshold, resulting in populations that are no longer self-sustaining. Recent ENM projections have validated this concern (Wright et al. 2013).

Because we have more than a decade of detailed field demographic data from multiple sites to draw on, we can con-

fidently identify both the climatic variables that determine juvenile recruitment within years and those that Maxent identifies as the most important in setting the species' range limits. Our reasoning is that if these two approaches to defining the climatic niche concur, it provides compelling evidence that the rankings of environmental variables provided by Maxent are biologically meaningful and justifies their use in identifying variables for climate change projections. In addition to this analysis of the commonality of variables, we also examine the shapes of the response curves, asking whether they agree with the directions of the correlations identified between the demographic and climatic data. We also explore the differences in variable ranking using percent contribution versus permutation importance and the extent to which incorporating several recently suggested refinements to Maxent modeling impacts these results. Finally, we use the resulting information to generate new projections for the effects of climate change on the endangered California tiger salamander case study.

Methods

Biological and Climatic Data

Field data were collected from the Jepson Prairie Preserve (JPP; Solano County, CA) and the Hastings Natural History Reservation (HNHR; Monterey County, CA). Both sites were the subjects of decadal field studies of *Ambystoma californiense* breeding and recruitment across a wide range of environmental conditions. Drift fences were constructed at the shorelines of two natural playa pools at JPP (Olcott Lake: 33 ha; Round Pond: 3 ha) and one artificially enhanced stock pond at HNHR (Blomquist Pond: 0.07 ha). All three ponds are seasonal and used by breeding CTS. The drift fence at Blomquist Pond was checked daily from December 1991 to June 1997, while those at JPP were similarly checked daily during the metamorph emergence period (early May to mid-July) from 2005 to 2013. The total number of metamorph CTS captured each year at each pond was tabulated, and these recruitment numbers (log transformed) are the basis of all further analyses. We have 9 years of recruitment data from both Olcott Lake and Round Pond and 6 years of recruitment data from Blomquist Pond. For additional ecological details, including trapping procedures, see Trenham et al. (2000), Searcy and Shaffer (2011), and Searcy et al. (2014).

Weather data for both JPP and HNHR were obtained from nearby (within 17 km) weather stations. Weather stations differed from study ponds by 1.5 km or less in distance from the coast and by 31 m or less in elevation. Raw weather data were used to calculate the 19 Bioclim variables (Hijmans et al. 2005) for each year that recruitment data were available. For the purposes of these calculations, each

year was considered to run from October 1 to September 30 (equivalent to the “water year” given California’s Mediterranean climate). This ensured that none of the quarters for which climate metrics were calculated were divided between years. It also matches well with the activity patterns of CTS, since the earliest breeding migrations start in November (Searcy and Shaffer 2011), and the last metamorphs emerge in August (Trenham et al. 2000).

Analysis

Each Bioclim variable was used in a separate ANCOVA model to predict recruitment. Each model used number of metamorphs as the response variable, pond (Blomquist, Olcott, Round) as the categorical variable, and one of the 19 Bioclim variables as the covariate. The R^2 value for each of these models was used as a measure of how well a climate variable correlates with CTS recruitment. We also used corrected Akaike information criterion (AICc) to select the multivariate model that best predicted recruitment, offering the model terms for all 19 Bioclim variables after pond had been fixed in the model as a blocking term.

We developed two models for CTS using Maxent (Phillips et al. 2006). One used basic Maxent procedures, with background points selected randomly from a geographic extent based on a political unit (California) rather than a biologically defined region (Anderson and Raza 2010) and the default regularization multiplier. The second, informed model used target group background to correct for sampling bias (Phillips et al. 2009) by choosing background points from locations where other amphibians and reptiles have been collected (records accessed through VertNet). These localities have a sampling bias very similar to the CTS localities used to train the models, since both sets are similarly restricted to areas that researchers or environmental consultants were able to access. The region from which these background points were drawn included all known CTS localities plus a 74-km buffer around those points; we chose 74 km because it is the distance between two currently occupied distinct population segments (Santa Barbara and Central) and, thus, is a minimum distance that CTS dispersed during their evolutionary history (Searcy and Shaffer 2014). For this informed niche model, we also used model selection to pick the regularization multiplier (Warren and Seifert 2011). Both models were trained using the 19 Bioclim variables at a 30-s resolution (downloaded from WorldClim; Hijmans et al. 2005) and the 1,627 CTS localities recorded by VertNet, the California Natural Diversity Database, or surveys conducted by the Shaffer Lab and the East Bay Regional Park District (Searcy and Shaffer 2014). Locality data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.667g2> (Searcy and Shaffer 2016).

As part of its output, Maxent ranks the environmental layers used to train the ENM based on their relative importance in model formulation. To do so, it employs two metrics: (1) percent contribution, which measures the increase in likelihood associated with modeling rules based on each environmental variable and then divides this by the total gain in likelihood to calculate the percent of the total gain associated with each variable (Phillips 2011), and (2) permutation importance, which randomizes the values for each environmental variable between the presences and background points in order to make that variable uninformative and then measures the resulting drop in area under the curve (AUC; ability to separate known presences from background points). The bigger the drop, the more important that variable was in the overall quality of the model (Phillips 2011). Although not analyzed here, a final metric that could be used to rank environmental layers is the sum of the λ weights associated with modeling rules based on that variable. This would be distinct from percent contribution, because λ weights can be adjusted both up and down during the iterations of model formation (Phillips et al. 2006). Percent contribution keeps track of all of these adjustments, while the final λ weights would consider only the net (rather than the gross) change in the weights during the iterative process.

We regressed three different measures of variable importance produced by Maxent against the R^2 values from the recruitment models: permutation importance from the basic model, percent contribution from the informed model, and permutation importance from the informed model. (We also analyzed percent contribution from the basic model, but it does not present any novel insights, and we do not consider it further.) We considered these regressions a test of whether the same climatic variables that govern recruitment also limit geographic range. Since recruitment is an important element of population growth rate, and since having a positive population growth rate determines whether a species can persist at a given locality, there is good reason to expect that the same or similar causative factors should drive recruitment and range limits.

To delve deeper into the Maxent models, we looked at the response curves that plot predicted habitat suitability against each of the climate variables. Essentially, we wanted to know if the form of the relationship that Maxent predicted between habitat suitability and each of the climate variables is the same as that between CTS recruitment and each of those variables. We analyzed our recruitment data using only linear terms, so we extracted from the response curves their underlying linear form. We did this using the nonmarginal (i.e., univariate) response curves, since they provided the most accurate comparison to our recruitment data, where we were limited in our degrees of freedom and could not include the 18 other Bioclim variables as covariates (for the marginal

response curves, see figs. A1, available online). The first step in this process was to record the predicted habitat suitability corresponding to the climatic conditions experienced in each of the years that we collected recruitment data. We then performed a linear regression between these habitat suitability scores and each of the climate variables that had shown significant linear relationships to the recruitment data. If the direction (positive/negative) of the relationship between the habitat suitability scores and the climate variables was the same as that between the climate variables and the recruitment data, then we considered this to be a sign of further agreement between the two approaches. Our method for calculating these correlations guaranteed that the response curves were analyzed over the same range of climatic variation as were the recruitment data. Thus, if the response curves generally increased over a certain set of values and then generally decreased over a different set of values, our method calculated the trend over the same range of climatic conditions that was used to analyze the recruitment data. It also guaranteed that the significance of the correlations between climate and habitat suitability and between climate and recruitment would be analyzed with the same number of degrees of freedom (one for each cohort of metamorph CTS in the field data).

We also used Maxent's ranking metrics to select a subset of the Bioclim variables to be used in training new niche models for projection into future climate scenarios to determine how well these projections agreed with changes in recruitment predicted by the demographic data. For each of these new niche models, we used the six Bioclim variables that were ranked highest by the associated metric (table A1; tables A1, A2 available online). Six training variables is near the lower end of the number generally used in future climate projections (Hijmans and Graham 2006; Rödder 2009; Elith et al. 2010; Kearney et al. 2010; Milanovich et al. 2010; Ponce-Reyes et al. 2013). The informed approach (target-group background, biologically defined extent, and model selection) was used when generating three of these models (variable rankings based on R^2 , permutation importance from the informed model, and percent contribution from the informed model). The basic approach was used when using variable rankings based on permutation importance from the basic model.

Each model was projected into seven different future climate scenarios based on the global climate models BCC-CSM1-1, CCSM4, GISS-E2-R, HadGEM2-AO, IPSL-CM5A-LR, MRI-CGCM3, and NorESM1-M (downloaded from WorldClim). For all seven scenarios, we ran predictions for 2070 (based on a 20-year mean from 2061 to 2080) using the highest greenhouse gas emission prediction (RCP8.5). Up to 2014, global emissions were tracking or exceeding the RCP8.5 prediction, making it the currently most realistic prediction of future change (Fuss et al. 2014) and an accurate

test of potential stress due to climate change (Kriticos et al. 2012). We then calculated a consensus projection for each model by averaging the projections from the seven future climate scenarios.

Models were compared based on average change in predicted climatic suitability across the CTS range estimate that was used to train the models (localities plus 74-km buffer). Field (Searcy and Shaffer 2011) and genetic (Fitzpatrick et al. 2010) studies have shown that individual CTS sometimes migrate ~ 2 km/year, suggesting that the 74-km buffer built into our range estimate provides a reasonable level of range shift potential for the species over the next several decades. To calculate average change in predicted climatic suitability, we first averaged the consensus suitability in 2070 across all of the pixels included in the range. We then averaged the current suitability across all of the pixels in the range and took the difference between these two values. This difference is the predicted change in habitat suitability for CTS by 2070. We also calculated this difference for each of the seven future climate scenarios individually and used these values to generate a confidence interval for each overall mean value.

As a final step, we contrasted these predicted changes in climatic suitability with a set of predicted changes in mean recruitment. We extracted the projected change in each Bioclim variable between now and 2070 at each of the 1,627 known CTS localities for each of the seven future climate scenarios. We then averaged across the 1,627 localities to generate the mean expected change in each Bioclim variable over the range of CTS and calculated the variance around this due to the seven future climate scenarios. Finally, we evaluated the percent change in recruitment predicted by all of the significant ANCOVA models based on these expected changes in each of their associated Bioclim variables.

Results

CTS Recruitment

A total of 2,380 metamorphs were captured at Blomquist Pond (1992–1997), 4,449 at Round Pond, and 11,573 at Olcott Lake (both 2005–2013). Sizes of individual cohorts varied between 116 and 707 at Blomquist Pond (Trenham et al. 2000). In 2007, Olcott Lake and Round Pond both produced zero metamorphs, while in the most productive year (2006), Round Pond and Olcott Lake produced 2,716 and 3,412 metamorphs, respectively.

Six of the 19 Bioclim variables had significant correlations with CTS recruitment (table 1). Of these six, BIO12 and BIO13 were both highly correlated with BIO16 ($r > 0.8$), and BIO12 (annual precipitation) stood out as the most highly correlated with annual metamorph recruitment. The

Table 1: Significant predictors of California tiger salamander (CTS) recruitment

Bioclim variable	Est. \pm SE	R^{2a}	P^b
BIO2 ^c	-.13 \pm .05	.28	.017
BIO6 ^c	.071 \pm .027	.28	.016
BIO12 ^d	.00089 \pm .00019	.53	<.001
BIO13 ^d	.0016 \pm .0006	.27	.019
BIO16 ^d	.0012 \pm .0004	.33	.007
BIO19 ^d	.0012 \pm .0005	.22	.042

Note: Each of the 19 Bioclim variables was used to predict CTS recruitment in an ANCOVA model where pond was the categorical variable and the Bioclim variable was the covariate. These six variables had significant correlations with CTS recruitment: BIO2 (mean diurnal range), BIO6 (minimum temperature of coldest month), BIO12 (annual precipitation), BIO13 (precipitation of wettest month), BIO16 (precipitation of wettest quarter), and BIO19 (precipitation of coldest quarter).

^a R^2 values include the variance explained by the pond term (only 3.2%).

^b P values are for the Bioclim term alone.

^c Measured in tenths of a degree Celsius.

^d Measured in millimeters.

best multivariate model for CTS recruitment based on AICc was

$$\ln(\text{metamorphs} + 1) = -0.15 \times \text{BIO2} + 0.15 \times \text{BIO8} \\ + 0.00052 \times \text{BIO12} \\ - 0.042 \times \text{BIO17},$$

where BIO2 is mean diurnal range (difference between daily maximum and minimum temperatures), BIO8 is mean temperature of the wettest quarter (both measured in tenths of a degree Celsius), BIO12 is annual precipitation, and BIO17 is precipitation of the driest quarter (both measured in millimeters). This relatively simple model explains 82% of the variance in CTS recruitment. The inclusion of both BIO8 and BIO12 in the multivariate model indicates that warmer minimum temperatures are positively correlated with CTS recruitment independent of their association with periods of rainfall, at least over the range of temperature and rainfall in our analysis.

Maxent Model Performance

All Maxent models did a good job of differentiating known localities from background points ($0.87 \leq \text{AUC} \leq 0.93$). When variable importance in predicting CTS range limits was measured based on permutation importance from the informed model, the correlation with variable importance in predicting CTS recruitment was highly significant ($P < .001$; fig. 1A). This indicated a strong concordance between spatial and temporal approaches to defining the climatic niche of CTS. The same concordance was not seen when variable importance in predicting CTS range limits was measured based on percent contribution or using a less biologically informed Maxent model (fig. 1B, 1C).

The correlations between predicted habitat suitability and the six Bioclim variables that were significantly related to recruitment were all highly significant ($P < .01$). For the two temperature-related variables, the correlations were in the same direction for both recruitment data and habitat suitability (positive for minimum temperature of the coldest month [fig. 2A, 2B], negative for mean diurnal range [fig. 2C, 2D]). For the precipitation-related variables, the correlations were in the opposite direction (positive for recruitment, negative for habitat suitability). This is illustrated only for annual precipitation (fig. 2E, 2F) but is virtually identical for the other three precipitation variables, all of which are highly correlated across the range of CTS ($r > 0.97$ for all pairwise correlations).

The projected changes in habitat suitability for CTS from its current range to that in 2070 for each model are detailed in figure 3 and table 2. All four models indicate decreases in average habitat suitability. In all cases, the variable most responsible for this decrease in habitat suitability is a winter minimum temperature variable, based on visual examinations of the most dissimilar variable plots and determination of which variable is assigned the largest geographic space (i.e., the variable that is expected to change the most between now and 2070 over the geographic space being considered; Elith et al. 2010). For the model based on percent contribution from the informed model, that variable is BIO8 (minimum temperature of the coldest quarter). For the other three models, which do not include BIO8, the variable is BIO6 (minimum temperature of the coldest month). This result may seem counterintuitive, since the demographic data indicate that recruitment is positively correlated with winter minimum temperatures, which are projected to increase due to climate change. However, the Maxent models indicate that habitat suitability increases with winter minimum temperature up to a certain point ($\sim 3^\circ\text{C}$) and then decreases. By 2070, winter minimum temperatures are projected to surpass 3°C across much of the range of CTS (see "Appendix" for additional discussion). In contrast, the ANCOVA models relating CTS recruitment to climatic conditions predict either no change or an increase in CTS recruitment between the present and 2070 (table 3). These conflicting results are largely due to the ANCOVA models being based on linear relationships, while the Maxent models indicate that many aspects of the climatic niche are non-linear in form.

Discussion

These results demonstrate a striking concordance between spatial and temporal approaches to identifying the niche and suggest that one can extract biologically (as opposed to simply statistically) meaningful niche parameters from Maxent models. This is best seen in figure 1A, which shows

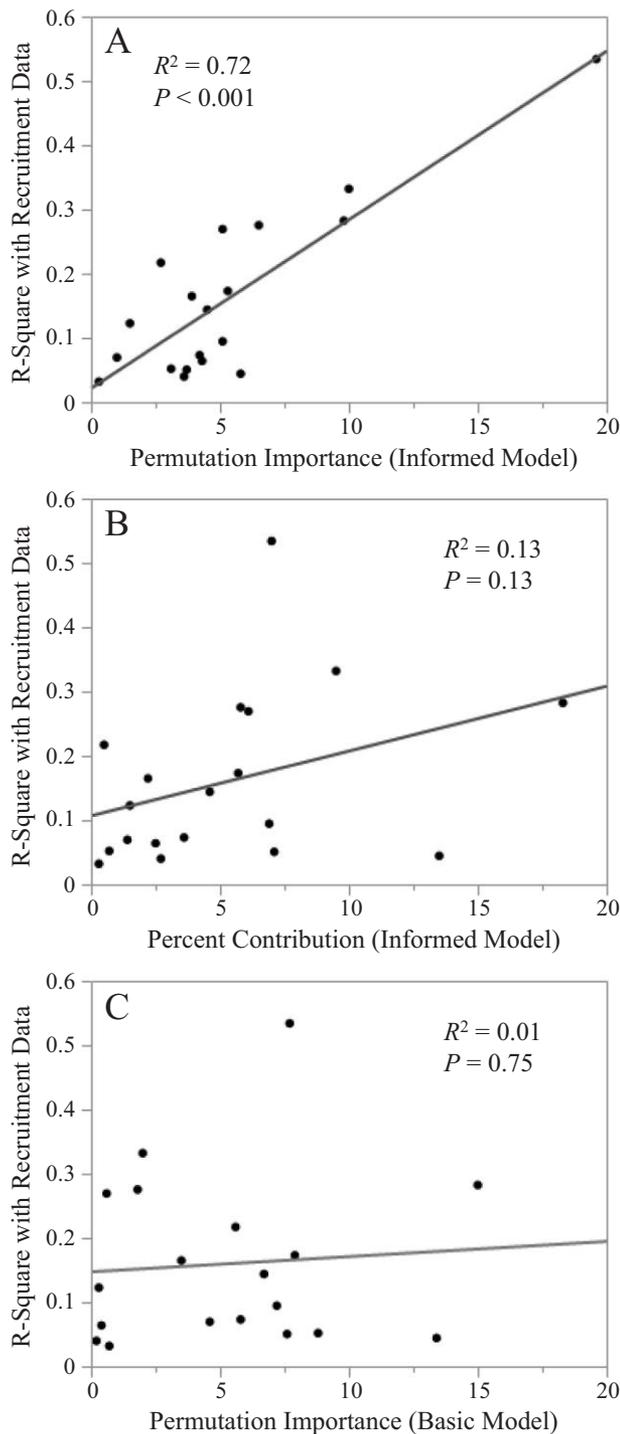


Figure 1: Correlations between variable importance in predicting California tiger salamander (CTS) recruitment and variable importance in predicting CTS range limits. The circles in each panel are the 19 Bioclim variables. The value each Bioclim variable is assigned on the Y-axis is always the R^2 value from the ANCOVA model relating it to CTS recruitment. Each panel shows the linear correlation between this measure of variable importance in predicting CTS recruitment and a different measure of variable importance in predicting

the highly significant correlation between the climatic variables that govern temporal variation in recruitment as measured in the field and the variables identified by Maxent as important in shaping range boundaries. Most pond-breeding amphibians have boom and bust years (Pechmann et al. 1991), and it may follow that the same climatic variables that control the gradient between successful and poor recruitment years would also define the species' range boundaries, since a species can persist only in areas where boom years occur at a sufficiently high frequency. Our observation that Maxent can accurately identify these key ecological variables is very encouraging, since the long-term recruitment data necessary to identify a species' response to climate will not be available for most taxa. Our results indicate that Maxent's ranking of environmental variables can provide important insights into a species' basic ecology that are otherwise very difficult to obtain.

However, the strength of this result depends on both the ranking metric and methodology used in building the Maxent model. We found that permutation importance provides a much more accurate ranking than percent contribution. There has previously been disagreement as to which of these metrics is most informative. Phillips (2011) has argued for permutation importance, since percent contribution depends on the particular path taken to get to the optimal model. If environmental variables are correlated, there will be multiple paths to the same model, rendering the percent contributions unstable. Alternatively, Halvorsen (2013) has used simulation results to argue for percent contribution, although these simulations were based on mostly uncorrelated environmental variables. Perhaps because it is listed first in the Maxent output, most studies looking at variable importance have opted to use percent contribution (Blach-Overgaard et al. 2010; Millar and Blouin-Demers 2012; Warren et al. 2014). Our results indicate permutation importance is a better option. Even though ours is only a single case study, given that climatic variables are almost always highly correlated, we suspect that the majority of studies would benefit from using permutation importance. However, ENM studies that use principal component analysis to generate independent environmental variables (e.g., Afkhami et al. 2014) might expect to see the opposite result.

Our results also indicate that several refinements of the default Maxent modeling process increase the biological

CTS range limit: permutation importance from the informed Maxent model (A), percent contribution from the informed Maxent model (B), and permutation importance from the basic Maxent model (C). When variable importance in predicting CTS range limits is measured based on permutation importance from the informed Maxent model, the relationship is highly significant ($P < .001$), even when the outlier at the upper right of the panel (BIO12) is removed ($R^2 = 0.48$, $P = .002$). The correlation is not significant when the other measures of variable importance in predicting CTS range limits are used.

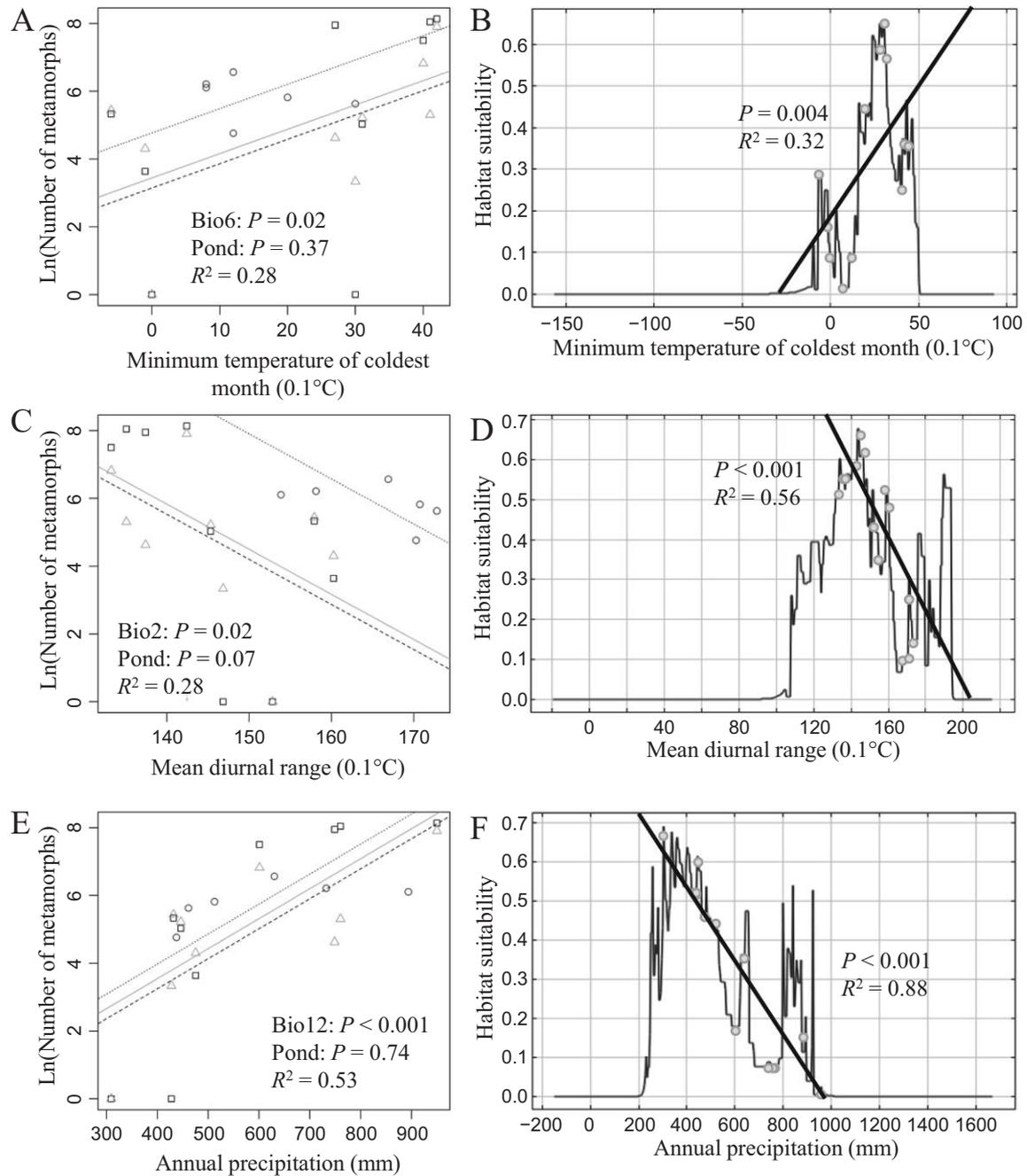


Figure 2: Linear responses of metamorph recruitment and habitat suitability scores to the three most important independent climatic variables. Responses are in agreement for minimum temperature of the coldest quarter (both positive) and mean diurnal range (both negative) but disagree for annual precipitation (one positive, one negative). A, C, E, Correlations between number of metamorphs recruited in a given year and three different Bioclim variables. Each panel illustrates the results of an ANCOVA model with pond as the categorical term (circles, dotted line = Blomquist Pond; squares, dashed line = Olcott Lake; triangles, solid line = Round Pond). B, D, F, Correlations between predicted habitat suitability based on the informed model and three different Bioclim variables. Correlations are based on the particular values for those Bioclim variables that were experienced during the years when recruitment data was collected (illustrated by gray dots). Each panel is mapped on top of the nonmarginal response curve for that Bioclim variable. A, B, BIO6 (minimum temperature of the coldest quarter). C, D, BIO2 (mean diurnal range). E, F, BIO12 (annual precipitation).

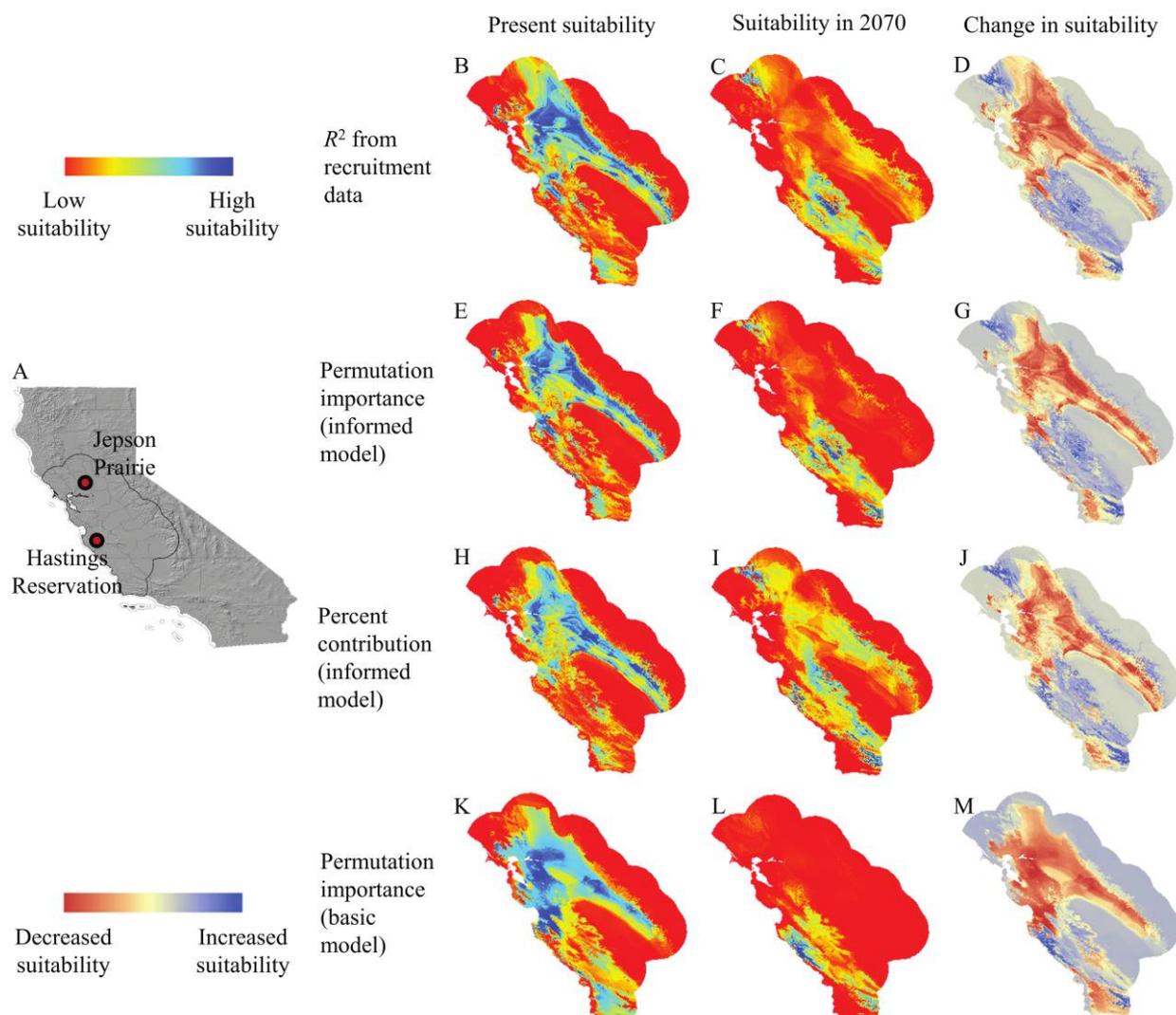


Figure 3: Changing climatic suitability for California tiger salamander (CTS). A, Hillshade map of California illustrating the region modeled using the informed approach (black outline) relative to county boundaries (gray lines). Red circles show locations of study sites where recruitment data were collected. Each niche model was built using six environmental layers that are ranked highest by a different metric (see table A1): R^2 from recruitment data (B–D); permutation importance from informed model (E–G); percent contribution from informed model (H–J); permutation importance from basic model (K–M); logistic suitability scores, which can be interpreted as probability of finding the focal species (Phillips and Dudík 2008; but see Royle et al. 2012) in the present (B, E, H, K) and projected suitability scores in 2070 (C, F, I, L), where for both, blue and red values represent high and low suitability, respectively (see upper color bar); and projected change in suitability between current climate and 2070 (D, G, J, M), where blue values represent areas where suitability is predicted to increase, and red values represent areas where suitability is predicted to decrease (lower color bar). Generally, climatic suitability is projected to increase in high-elevation areas and decrease in low-elevation areas. Pairwise comparisons of all maps in the same column based on Schoener's D are given in table A2 (Schoener 1968; Warren et al. 2008).

realism of the model. Most of these are simple to implement. For example, accounting for sampling bias through the use of target-group background (Phillips et al. 2009) is straightforward now that museum localities for closely related or ecologically similar taxa are available from the Global Biodiversity Information Facility. Selecting the appropriate regularization multiplier is similarly straightforward and can be

automated with ENMTools, SDMtools, or ENMeval (Warren et al. 2010; Brown 2014; Muscarella et al. 2014), although this substantially increases processing time. The only modeling refinement that requires increased knowledge of the focal species is using a biologically informed extent (Anderson and Raza 2010). There are no clear guidelines for this process, and it is very species specific, but by incorporating

Table 2: Predicted change in mean habitat suitability by 2070 for four different Maxent models

Model	Current mean suitability ^a	2070 mean suitability (95% CI) ^b	Projected change in suitability (95% CI) ^c
R^2 with recruitment data	.197	.083 (.044 to .122)	-.113 (-.152 to -.074)
Permutation importance (informed model)	.175	.055 (.034 to .076)	-.121 (-.142 to -.100)
Percent contribution (informed model)	.178	.085 (.035 to .135)	-.093 (-.143 to -.043)
Permutation importance (basic model)	.197	.027 (.011 to .043)	-.171 (-.187 to -.155)

Note: Models are each based on the six Bioclim variables in table A1.

^a Suitabilities are the mean habitat suitability over the range of California tiger salamander (localities plus 74-km buffer).

^b Future suitabilities are based on seven possible climate scenarios, so the mean and 95% confidence interval (CI) are calculated based on these seven possible outcomes.

^c Overlaps for all models except that based on permutation importance in the basic model, which predicts a more extreme decrease in mean habitat suitability than the other three models.

data on dispersal distance (measured or inferred), obvious barriers to dispersal, and ranges of potential competitors/predators, it should be possible to make substantial improvements for many taxa (Barve et al. 2011; Anderson 2013).

The comparison between the climate-recruitment correlations and the response curves produced by Maxent may appear to call into question the generality of these results. While the forms of the correlations and response curves were qualitatively similar for some variables (temperature), they were markedly different for others (precipitation). A clearer understanding of these results, and why these correlations can be in opposite directions in some cases, will require similar analyses from other field validation studies. In our case study, CTS respond differently to individual years that have above-average rainfall than they would to a predicted long-term increase in mean rainfall across years. At the demographic level, an individual year with above-average rainfall causes a longer breeding-pond hydroperiod (Searcy et al. 2015) and thus allows more larvae to reach the size necessary to metamorphose (fig. 2E). A long-term increase in mean rainfall, on the other hand, causes habitat suitability to decrease (fig. 2F), presumably because it is associated with a transition from the vernal pool grasslands that CTS favor (Searcy et al. 2013) to a more forested and less ecologically appropriate habitat type. In both cases, rainfall is identified as important, but differences in the timescale of rainfall shifts leads to different demographic and range-level outcomes.

This apparent contradiction is also due to our approximation of the response curve for annual precipitation as linearly decreasing (fig. 2F) for the years of our demographic sampling. In reality, the response curve is hump-shaped. Thus, Maxent's identification of annual precipitation as the most important climatic variable in defining the niche of CTS is due to both the probabilities of CTS presence increasing over low annual precipitation values and the probabilities of CTS presence decreasing over high annual precipitation values. Clearly, a full assessment of the quality of Maxent's response curves will require a system for which much more demographic data are available (e.g., Buckley et al. 2010),

ideally spanning the same or similar range of climatic regimes as the relevant Maxent models, or a system that is tractable for an experimental approach under replicated laboratory conditions. Our data indicate that Maxent does reliably retrieve biologically informative rankings of variable importance, and exploration of the similarity in functional form is an important area for further empirical study.

Climate Change Projections

The variable ranking based on permutation importance provides both insight into the variables that best define a species' niche and a useful subset of variables to be used for downstream ENM projections. The projection based on permutation importance from the informed model was closer to the projection based on R^2 with recruitment data than either of the other two projections (table 2). The projection based on R^2 with recruitment data currently represents our best estimate of the effects of climate change on CTS, given that it is based on accurate population demographic data. How-

Table 3: Projected changes in California tiger salamander (CTS) recruitment by 2070

Bioclim variable	Mean change in Bioclim variable (\pm SE) ^a	Projected % change in CTS recruitment (\pm SE) ^b
BIO2	-.05°C (\pm .12°C)	+7 (\pm 15)
BIO6	+2.9°C (\pm .4°C)	+680 (\pm 30)
BIO12	+3.9 cm (\pm 2.4 cm)	+3.5 (\pm 2.2)
BIO13	+1.9 cm (\pm .8 cm)	+3.1 (\pm 1.3)
BIO16	+4.2 cm (\pm 2.0 cm)	+5.2 (\pm 2.4)
BIO19	+3.5 cm (\pm 2.2 cm)	+4.3 (\pm 2.7)

Note: BIO2: mean diurnal range, BIO6: minimum temperature of coldest month, BIO12: annual precipitation, BIO13: precipitation of wettest month, BIO16: precipitation of wettest quarter, BIO19: precipitation of coldest quarter.

^a Mean change expected across the 1,627 CTS localities.

^b Derived by substituting the expected change in the Bioclim variable into the ANCOVA model described in the corresponding row of table 1. Standard errors (SE) are calculated based on the variation in the seven future climate scenarios.

ever, for most species, the decadal investment in field recruitment data necessary to build a projection using this approach is not feasible. The projection based on permutation importance from the informed model, on the other hand, can be generated for any species and appears to serve as a reasonable proxy for our test CTS case study. Finally, the only projection that is significantly different (based on nonoverlapping confidence intervals) from the best projection built using the recruitment data is the projection based on the basic model (table 2). This again emphasizes the importance of the model refinements and strongly suggests that they should be incorporated in ENM projections.

The implications of these ENM projections for CTS are not encouraging. All four projections show a significant decrease in habitat suitability relative to the present (table 2), with losses particularly concentrated in areas of low elevation and along the Pacific coast (fig. 3). These regions include the two distinct population segments that are in the gravest danger of extinction and are listed as endangered under the US Endangered Species Act (Santa Barbara and Sonoma Counties). Losses in these areas would be particularly harmful to CTS, since they encompass much of the species' genetic diversity (Shaffer et al. 2004). Areas where habitat suitability is projected to increase include the central Coast Range and the Sierran foothills. Fortunately, these areas include large tracts of relatively protected federal land (e.g., Los Padres National Forest, Mendocino National Forest, Sierra National Forest) that could constitute a refuge for the species. However, virtually all of the central coast region currently contains a hybrid swarm of native and invasive salamander genotypes that are viewed as a potent threat to native CTS (Riley et al. 2003; Ryan et al. 2009; Fitzpatrick et al. 2010). Climate change thus may promote the persistence and spread of nonnative genotypes and higher-fitness hybrids (Johnson et al. 2010; Ryan et al. 2013; Searcy et al. 2016), decreasing the fraction of the range occupied by pure CTS populations. The area where increased habitat suitability is most likely to benefit pure CTS populations is the Sierran foothills. Many other species have already begun shifting upward in elevation along the west slope of the Sierra Nevada (Moritz et al. 2008), and we may expect to see this in CTS as well.

Biological Realism in the Models

The relationships between recruitment and climate that we discovered make a great deal of sense given the life history of CTS and, particularly, its very strong reliance on high-rainfall years. Four of the six climate variables that were significantly correlated with recruitment were measures of rainfall (table 1). In addition to its direct effect on recruitment by providing an extended larval development period, rainfall also increases the number of breeding females; the

best predictor of number of CTS metamorphs is biomass of breeding females, and the best predictor of number of breeding females is rainfall (Trenham et al. 2000). We also found a positive correlation between recruitment and winter minimum temperatures. While increased temperature has not been shown to have an effect on the number of breeding females in CTS, it has been associated with the number of breeding females in two close relatives, *Ambystoma maculatum* (Sexton et al. 1990) and *Ambystoma talpoideum* (Semlitsch 1985). The final correlation we uncovered was a negative correlation with mean diurnal range. This is interesting given that salamanders reach their highest species richness in the Appalachian Mountains of North Carolina (Petranka 1998), which have a temperate maritime climate characterized by cool summers, mild winters, and generally overcast weather (Köppen 1936). These characteristics are all associated with a low diurnal range, suggesting that this type of climate may be important in predicting climate impacts on salamanders more generally.

Future Directions

While the demographic and ecological niche modeling approaches employed in this study agreed quite closely on which climate variables are most important in shaping the niche of CTS, they disagreed on the projected effects of climate change. The ENM approach (table 2) predicted decreases in habitat suitability across the majority of the range of CTS, while the demographic projection represented in table 3 predicted slight increases (or in the case of one variable, large increases) in recruitment by 2070. This raises the question of which approach is more reliable. The attraction of the demographic approach is that it is much more concrete. While based on correlations rather than experimental manipulations, it still shows that numbers of actual animals varied in a systematic way with variation in climatic regimes across years. The ENM approach has a less direct biological connection to the population dynamics of CTS, given the complexity of the models and the assumptions regarding the equilibrium distributions on which they are based (Anderson 2013). However, the advantage of the Maxent models is that they are derived from a much larger pool of data (mean climatic conditions at all 1,627 CTS occurrence localities), while the demographic models are limited to the climatic conditions experienced during the 15 years in which field data were collected. What we wish to emphasize here is that the approaches are not mutually exclusive and, in fact, may both be providing accurate projections at different temporal scales (Dormann et al. 2012). The demographic models represent the response of CTS to climatic variation between individual years around the current mean climate, while the Maxent models represent the response of CTS to variation in the climatic means themselves. Thus, in the

short term, we may expect CTS to respond to climate change according to the demographic models. In the longer term, however, as the entire community composition begins to gradually shift in response to change in mean climatic conditions, we may see the predictions of the Maxent models borne out. If we are correct about this, then the pace of range shifts currently being predicted based on Maxent models are an exaggeration, although the magnitude of the final shifts may be an accurate representation of the severity of the ecological effects of anthropogenic climate change.

Determining whether this proposed reconciliation of the two modeling predictions is accurate will clearly require many additional studies across a wide range of taxa. These will be most informative if studies are carried out in species where even larger demographic data sets covering a wider range of climatic conditions are available (e.g., Buckley et al. 2010) or in species that are much more tractable to experimental manipulation so that many replicate populations can be raised under factorially manipulated climatic conditions (Dormann et al. 2012). However, even if this level of experimentation is not possible, studies that compare ENM outputs to independently collected ecological data are essential for validating ENM predictions and, thus, moving the field forward. Ecological niche models are clearly a vital tool in our effort to confront our future under climate change, and we need to continually improve our modeling methodologies and understanding of which model outputs are biologically informative.

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Recently metamorphosed California tiger salamander (*Ambystoma californiense*). Recruitment is measured as the number of such individuals emerging from the breeding ponds each year. Credit: Christopher A. Searcy.