BIODIVERSITY RESEARCH

Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern

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ABSTRACT

Aim Ecological niche models are increasingly being used to aid in predicting the effects of future climate change on species distributions. Complex models that show high predictive performance on current distribution data may do a poor job of predicting new data due to overfitting. In addition, model performance is often evaluated using techniques that are sensitive to spatial sampling bias. Here, we explore the effects of model complexity and spatial sampling bias on niche models for 90 vertebrate taxa of conservation concern.

Location California, USA.

Methods We used Akaike information criterion (AICc) to select variables and tune Maxent's built-in regularization parameter (β) to constrain model complexity. In addition, we incorporated several estimates of spatial sampling bias based on interpolations of target group data. Ensemble forecasts were developed for future conditions from two emission scenarios and three climate change models for the year 2050.

Results Reducing the number of predictors and tuning β resulted in a reduction in the number of parameters in models built with sample sizes greater than approximately 10 occurrence points. Reducing the number of predictors had a substantially higher impact on the relative prioritization of different grid cells than did increasing regularization. There was little difference in prioritization of habitat when comparing models built using different spatial sampling bias estimates. Over half of the taxa were predicted to experience >80% reductions in environmental suitability in currently occupied cells, and this pattern was consistent across taxonomic groups.

Main Conclusions Our results demonstrate that reducing the number of correlated predictor variables tends to decrease the breadth of models, while tuning regularization using AICc tends to increase it. These two strategies may provide a reasonable bracketing strategy for assessing climate change impacts.

Keywords

Climate change, conservation, maximum entropy, model complexity, niche modelling, sampling bias, species distribution modelling.

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INTRODUCTION

Ecological niche models (ENMs) are applied to conservation problems ranging from predicting range shifts under climate change (e.g. Araújo *et al.*, 2006; Lawler *et al.*, 2009) to predicting colonization by introduced species (e.g. Mandle *et al.*, 2010; Rodda *et al.*, 2011). The methods used to build ENMs are developing rapidly (Elith & Leathwick, 2009) and have

become a standard tool for ecologists and conservation biologists. Although current methods have limitations, they are often the best tools available for making conservation decisions without detailed ecological and physiological data. Here, we explore the effects of two critical aspects of ecological niche modelling, model complexity and spatial sampling bias, on a data set composed of 90 vertebrate taxa in California.

California has the highest levels of wildlife biodiversity and endemism in the USA (Parisi 2003), with 157 terrestrial vertebrates listed as threatened or endangered under the California Endangered Species Act (CDFG 2011). To reduce additional state listings, California also recognizes species of special concern (SSC) to help focus research and management on at-risk taxa that are not currently listed. Several criteria contribute to designation as an SSC, including current or historic population declines or range contractions that would probably lead to state listing in the future (Comrack et al., 2008). Forthcoming assessments of species status in California will incorporate climate change impacts (e.g. R.C. Thomson, A.N. Wright & H. B. Shaffer, unpublished data), and recent reports (Shuford & Gardali, 2008) have been updated with climate change supplements (Gardali et al., 2012). To augment these assessments, we built ENMs for a set of terrestrial vertebrate SSC to predict shifts in environmental suitability across the state. For the purposes of this manuscript, we address only those aspects of suitability related to the included climatic variables, and as such, any mention of 'suitability' should be interpreted only with respect to those variables. Many non-environmental factors can impact the suitability of habitat for species, but our goal here is to examine the effects of climate specifically.

A key issue with modelling responses to climate change is that we do not fully understand how models made under current conditions will transfer to future conditions. The most commonly used methods (e.g. Maxent, Phillips et al., 2006) can fit arbitrarily complex models to explain the relationship between environmental variables and species occurrence data. However, an excessively complex model will often be extremely specific to the input data and will perform poorly when extrapolating. Warren & Seifert (2011) explored the use of sample-size-adjusted Akaike information criterion (AICc) for Maxent models to address overfitting. This approach does not control model fit directly, but rather uses AICc to choose appropriate settings for Maxent's built-in regularization.

Because the number of parameters in a Maxent model may not accurately estimate the degrees of freedom (Hastie et al., 2009), AICc may excessively penalize overparameterization. Simulation work has shown that AICc tends to choose models that better estimate environmental suitability and prioritization of environmental variables, and that are more transferable to future climate scenarios, than those chosen by maximizing the area under the receiver operator characteristic curve (AUC; Warren & Seifert, 2011). This suggests that either the imprecision in estimating degrees of

freedom by counting parameters from Maxent models is not sufficient to result in underparameterized models, or underparameterized models outperform models that are more complex. In contrast, a recent empirical study (Cao et al., 2013) examining the impact of information criterion-based model selection on ENMs found that AICc-based models tended to overestimate species richness compared to survey data, which may be due to underparameterization. Although these results are interesting and deserve further exploration, we feel that the suggestion that ENMs should correctly estimate species richness is predicated on the assumption that they are attempting to predict presence and absence of species, rather than the environmental suitability of habitat. As there are many non-environmental processes that can prevent a species from occurring in suitable habitat, and as we are not attempting to model those processes, we do not see these results as problematic for our application of AICc. Further, we note that the Cao et al.'s (2013) study only examined the performance of models under the same conditions used to construct them. As overfit models often perform well under training conditions but poorly when transferred, we do not see the results of the Cao et al.'s study as necessarily relevant to model performance in this study. Ideally, evaluation of the relative merits of information criterion-based approaches and AUC would involve comparison of the different models to estimates of climatic suitability from independent physiological data, but that falls considerably outside of the purview of this study.

Here, we use AICc as an alternative to cross-validation for model evaluation. Maxent users typically withhold a random subset of data from model construction and then quantify the ability of the model to predict those known occurrences using AUC. Although intuitive, this procedure has been criticized by several authors (e.g. Lobo et al., 2008; Peterson et al., 2008; Jiménez-Valverde, 2011). It has also been shown that AUC may overestimate model quality if test and training data are subject to similar sampling biases (Veloz, 2009). Spatial sampling bias is generally believed to be pervasive in species occurrence data, which were typically not sampled with uniform probability across the landscape. This may severely reduce the utility of AUC for evaluating niche models. An additional problem arises when incorporating spatial sampling bias into the construction of Maxent models: removing the effects of bias may reduce AUC scores on both training and test data when presence-only data are used for model validation (Phillips et al., 2009; Hijmans, 2012) even when the model better infers species' environmental tolerances. For these reasons, AUC is expected to be an unreliable indicator of model quality, or of the effects of incorporating sampling bias estimates, when using presence-only data.

We used AICc to select variables and set model complexity, incorporated multiple estimates of spatial sampling bias and averaged across several climate models and emissions scenarios to create ensemble forecasts of environmental suitability for 90 California SSCs. We predicted that models built using AICc and taking sampling bias into account would

have fewer parameters and be less specific to the training data, which should improve transferability to future climate conditions (Warren & Seifert, 2011). We discuss patterns of shifting environmental suitability and explore the effects of modelling decisions on these projections, highlighting the changes that are seen with different approaches. As this is to date the largest study using AICc on ENMs using real data, and one of very few studies to examine the effects of multiple bias estimates, these comparisons should provide general guidance on strategies for future modelling efforts.

METHODS

Species data

We focused exclusively on data from California. We obtained occurrence points from the Museum of Vertebrate Zoology at UC Berkeley via the Arctos interface (http://arctos.database.museum/SpecimenSearch.cfm). Ninety terrestrial vertebrate taxa that have been designated as SSC since 1994 were modelled: 22 birds, 42 mammals, 12 non-avian reptiles (hereafter, reptiles) and 14 amphibians (see Appendix S1 in Supporting Information). Taxa were chosen based on data availability, with an average of 48 data points used for each species. For each sampling group (birds, mammals, reptiles, amphibians), 10,000 occurrence points from non-modelled species in the same group were obtained for estimating sampling bias. If fewer than 10,000 occurrences were available, we used all available points.

Environmental data and model complexity

For each species, we used AICc to choose predictors and to tune model complexity. The inclusion of different variables can have large effects on model outputs (Rödder *et al.*, 2009; Synes & Osborne, 2011). Some researchers advocate choosing variables based on known relationships between environment and physiology (e.g. Kearney *et al.*, 2008; Rödder *et al.*, 2009). However, as such data are frequently unavailable, alternative methods are often necessary. A common approach is to use all 19 Bioclim variables (Hijmans *et al.*, 2005) because global coverages are available at a high resolution. However, strong correlations often exist between these variables, and models fit using correlated variables can behave erratically when they are transferred to a scenario in which correlations differ. Using a subset of the Bioclim variables can reduce collinearity and the risk of overfitting. In addition, Maxent has a regularization procedure (L-1 regularization) that balances model fit and complexity (Phillips *et al.*, 2006). However, the default settings for the regularization multiplier (β) are based on empirical tuning (Philips and Dudik 2008), which may not be appropriate for all systems (Warren & Seifert, 2011). Our procedure for tuning β and selecting predictors is as follows.

Environmental layers at a resolution of 30 arc seconds were obtained from Worldclim (Hijmans *et al.*, 2005) and

trimmed to California using ArcGIS (ESRI, 2006). For each species, we built a set of initial models with all 19 Bioclim variables plus slope and with β varying from 0 to 15 in increments of 0.2, resulting in 76 models per species. For each species, we retained the model with the lowest AICc score from the initial set (hereafter, the starting model). From each starting model, we calculated the Maxent contribution scores for each environmental variable. We used these scores in conjunction with the spatial correlations between the variables calculated using ENMTools (Warren *et al.*, 2010, Appendix S2) to select a final set of environmental variables. First, variables with contribution scores <5% in the starting model were discarded. Then, the variable with the highest score was retained and added to the final variable set. All other variables that were correlated with this saved environmental variable at Pearson correlation coefficient >0.70 were deleted. This process was repeated until all variables were either moved to the final set or deleted.

Another set of models was then built to determine the optimal value of β. For each species, models were built using their species-specific set of variables and β values again varying from 0 to 15 in increments of 0.2. We used AICc to select the best model and used the β value from this best model in all subsequent analyses. The end result of this two-stage process was a species-specific set of environmental layers and β value. All other Maxent settings were left at their default values.

Estimating spatial sampling bias

Maxent compares conditions at presence sites to the conditions at background localities where presence has not been documented. Phillips *et al.* (2009) suggested selecting background data from points where similar taxa have been documented (the 'target group background' method), so that similar sampling biases are present in the occurrence and background data sets. While this method may improve inference, it carries a risk of also factoring out some of the biology we are attempting to estimate. Additionally, using target group points as background data precludes the possibility of sampling background data from areas that might be sampled but that are unsuitable for the entire target group. In a hypothetical case in which data collection was completely unbiased, a model constructed using this approach will estimate the aspects of the focal species' environmental associations that distinguish it from other members of the group, rather than those that distinguish suitable from unsuitable habitat. This could prove problematic in cases in which environmental tolerances are conserved across the target group and species boundaries are primarily set by competition, as it would lead to underestimation of the species' niche and increased errors of omission.

As an alternative, Maxent allows users to provide a grid of sampling probabilities, and samples grid cells for background data in proportion to those probabilities. This allows continuous estimates of sampling probability and may be less

specific to target group biology. We explored three methods of constructing spatial sampling bias estimates from target group data: density, distance and behaviour. These bias models were built from target group data, but as they are interpolations from that data, we expected them to be less severely affected by the problems outlined above. For comparison, we also built models with a no-bias layer.

For the density method, we used ArcMap (ESRI, 2006) to estimate the relative density of sampling in each grid cell. This estimate allows interpolation, so that a grid cell that has no samples in the occurrence data, but that is adjacent to a grid cell containing presence data for another species from the target group, has some probability of being sampled for background data. The distance method is similar, but uses the distance from the centre of each grid cell to the nearest occurrence for the target group. The behavioural method of estimating sampling bias is based on the idea that there are geographic factors that affect the probability of biologists sampling a given locality. Models of target group occurrences were built in Maxent using slope, altitude, proximity to roads, proximity to fresh water and land management status as predictors. These layers were derived from data from the Cal-Atlas Geospatial Clearinghouse (atlas.ca.gov). Bias estimates were incorporated into model construction using Maxent's FactorBiasOut command.

For each combination of species and bias estimate (density, distance, behavioural and unbiased), 100 bootstrap replicates were performed. Bootstrap was chosen over 'delete 1' and 'delete D' jackknife procedures because 'delete 1' jackknife estimates of some statistics are known to be unreliable when distributions of those statistics are not smooth (Efron & Tibshirani, 1994, pp. 148–149), and because both jackknife procedures would have required separate regularization steps due to changes in sample size.

Estimating current and future environmental suitability

After ENMs were constructed for the four bias treatments, models were projected onto combinations of two emission scenarios (A2 and B2) and three climate change models (CCCMA, CSIRO and HADLEY) for the year 2050 (Hijmans et al., 2005). The final model projection for 2050 for each species therefore consists of 24 sets of 100 projections for 2050 (4 sampling bias estimates, 2 emissions scenarios, 3 climate models, 100 replicates). For each species, we constructed average suitability grids for each estimate of sampling bias, and then an overall average across all estimates of sampling bias for each future scenario and model. Additionally, a grand mean projection for 2050 was constructed by averaging across all combinations of bias estimate, emissions scenario and climate model.

One of the expectations both of reducing overparameterization and of factoring out sampling bias is that models will become less specific to the input data, resulting in a decrease in differences between suitability scores at suitable and unsuitable sites. To measure this, we used Levins' inverse concentration measure of niche breadth (Levins, 1968) as adapted for ENMs (Mandle et al., 2010; Warren et al., 2010). This metric ranges from 0, where all cells are given equal suitability scores, to 1, where only one cell contains a non-zero suitability score. Reducing parameters and incorporating bias were both expected to increase breadth.

To compare predictions of environmental suitability, we used the relative rank (RR) metric of Warren & Seifert (2011). We choose this metric instead of the Pearson correlation coefficient because it is based on ranking of habitat patches and is therefore more informative when the item of interest is the relative prioritization of habitat rather than the precise suitability value assigned to them. While there are other rank-based methods for measuring correlation (e.g. Spearman's rank correlation), these methods are computationally much more intensive for ENMs, particularly when the number of grid cells is large.

RESULTS

Changes in environmental suitability

Average patterns of environmental suitability are shown by taxonomic group in Figure 1. For the SSC taxa in this study, the most environmentally suitable areas of the state are concentrated along the coast from the San Francisco Bay south, and much of this habitat is predicted to remain highly suitable, or increase in suitability, in 2050 (Fig. 1, map of key areas Appendix S3). Areas showing the greatest reductions in environmental suitability include a region east of the San Francisco Bay into the Central Valley, a portion of the central San Joaquin Valley along the eastern foothills and parts of the southern Coast Ranges, Transverse Ranges and the Klamath Mountains. The greatest improvements in environmental suitability are in the Mojave and Colorado deserts and the Peninsular Ranges.

Amphibian environmental suitability is currently greatest along the coast, in the Sierra Nevada and parts of the northern mountains. The greatest predicted reductions in amphibian suitability are in the Central Valley, around the San Francisco Bay and in the central Coast Ranges between San Francisco and Santa Barbara. The greatest potential improvements for amphibians are in parts of the Great Basin Desert, the Peninsular Ranges of southern California and parts of the Klamath Ranges in the north. Mammals currently have highest suitability in the San Joaquin Valley and inner coast ranges, and south from Los Angeles to the Mexican border both along the coast and in the Peninsular Ranges. Mammals are predicted to experience the most severe decreases in environmental suitability in the Klamath Mountains and Modoc Plateau in the north, and the southern San Joaquin Valley and central and southern Coast Ranges farther south. The Mojave and Colorado deserts are predicted to increase in environmental suitability for mammals. Areas of highest environmental suitability for birds are tightly concentrated
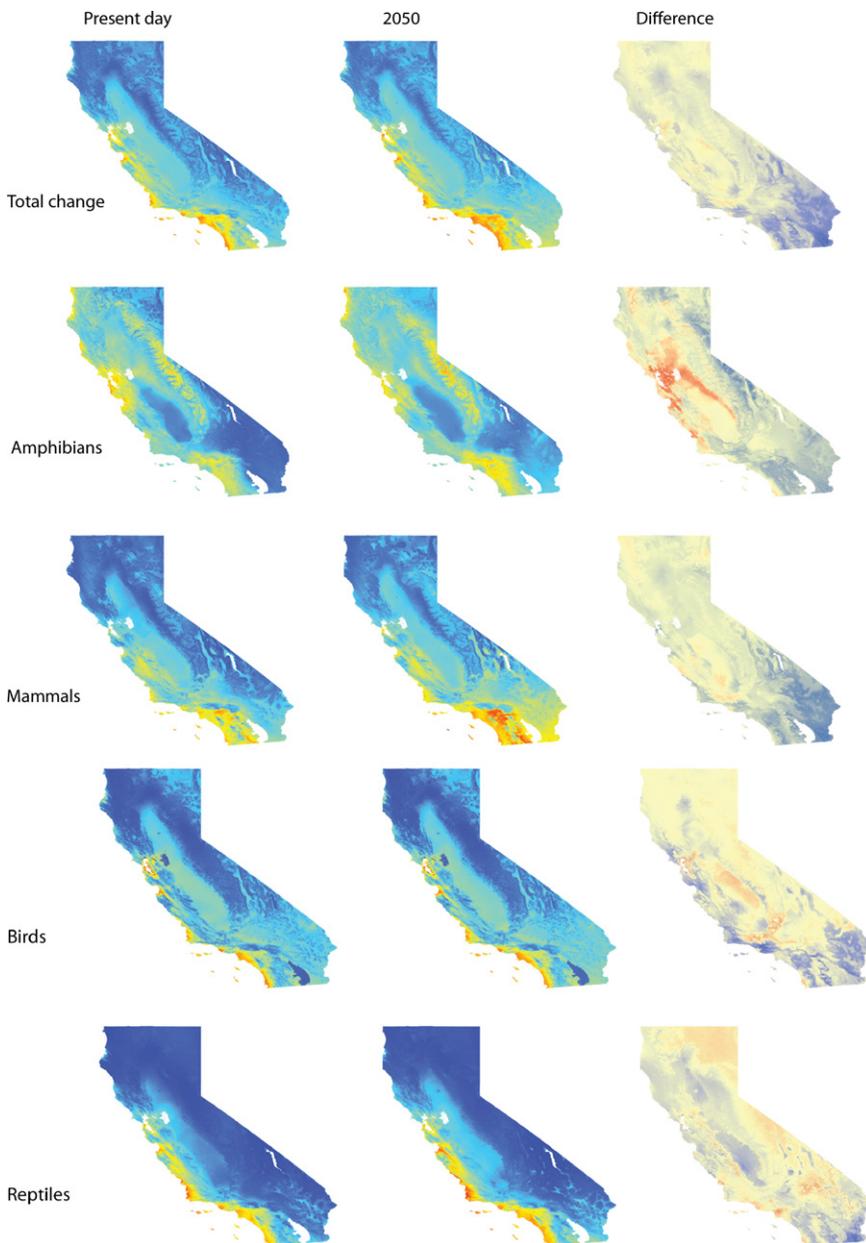
Present day   2050   Difference

Figure 1 Present and future predictions of environmental suitability by taxonomic group. Species suitability estimates were averaged across all bias estimates. Aggregate suitability scores were obtained by summing models across all species within each group, so the upper bound differs across sampling groups. In the left and centre columns, warmer colours (red) represent areas that are more suitable (or suitable for more species), whereas cooler colours (blues) are less suitable for that group. In the right column, red areas are those where habitat is projected to deteriorate with climate change, while blue areas are projected to improve with respect to that group. The intensity of coloration is proportional to the amount of change. Future projections and amount of change are based on models averaged across all combinations of bias estimate, climate model and emissions scenario.

along the coast, with greatest reductions predicted around the San Francisco Bay, the San Joaquin Valley and the Transverse Ranges. Environmentally favourable bird habitat is predicted to increase along parts of the coast, the Peninsular Ranges and the southern Mojave and Colorado deserts. Reptile habitat is most suitable along the coast from San Francisco to the Mexico–US border, and the greatest increase in environmental suitability is in the Colorado Desert and, to a lesser extent, the San Joaquin Valley and Peninsular Ranges. Environmental suitability for reptiles is expected to decrease in the Great Basin Desert, the Transverse Ranges, the Los Angeles basin, the Mojave Desert and the western rim of the San Joaquin Valley.

The percentage of currently occupied grid cells predicted to decrease in suitability for each taxonomic group is shown in Figure 2. Two-thirds of all taxa (60/90) are predicted to have more than half of currently occupied cells decline in environmental suitability, with 27/60 of these taxa experiencing reductions in suitability in all currently occupied cells. Nine taxa show increases in suitability in all currently occupied cells. Results for individual taxa are shown in Appendix S4.

Spatial sampling bias

Ecological niche model breadth was similar between each method for incorporating sampling bias and the no-bias default in both the present and 2050 projections (paired *t*-tests, $P > 0.3$ for all comparisons, Fig. 3), indicating that the effect of incorporating sampling bias on the smoothness of the geographic distribution of suitability scores was not strong. The inclusion of sampling bias estimates had a fairly

Figure 2 Change in suitability at currently occupied localities. For each species, the estimated change in suitability between the present (averaged over all bias estimates) and future (averaged over bias estimate, climate model and emissions scenario) were calculated at all occurrence points used in model construction. Species (bars) are grouped by taxonomy, while the y-axis represents the percentage of currently occupied grid cells that are predicted to become unsuitable.
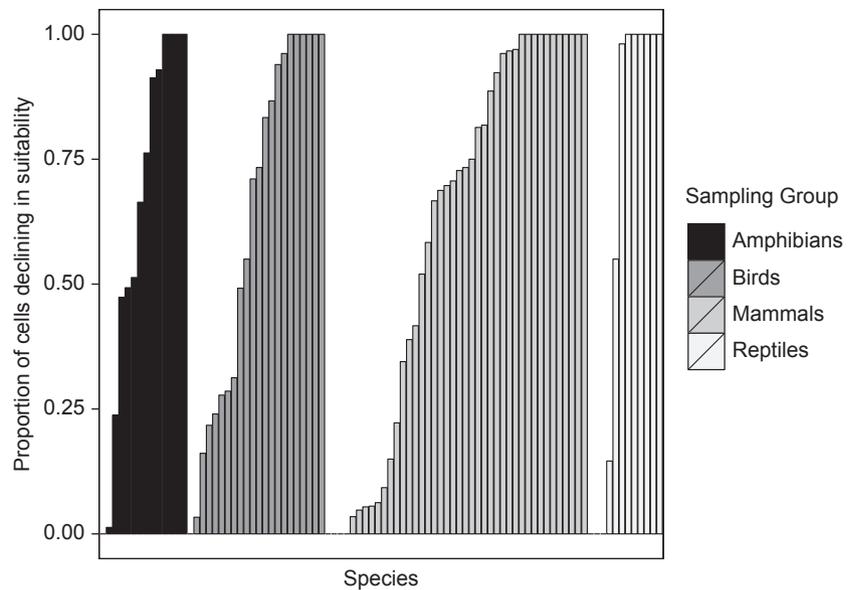
weak effect on the relative prioritization of suitable habitat. The average RR metric comparing models built using the density method to those built with no bias was >92%, while the distance method was 98% and the behavioural method was 97%.

Model complexity and environmental variable reduction

Of the 20 environmental layers used to build initial models, on average 5.27 ± 2.23 SD were selected for species-specific models (range: 1–9 layers retained, Appendix S5). Reducing the variable set from the initial 20 resulted in approximately halving niche breadth under present conditions (Fig. 4a). Among the layers that were most consistently included in the reduced models, BIO3 (isothermality) occurred in at least 50% of species-specific models for all groups except reptiles, and BIO15 (precipitation seasonality) occurred in at least 50% of species-specific models for all groups except mammals. Ectotherms (reptiles and amphibians) included BIO4 (temperature seasonality) and slope in at least 50% of models, while endotherms (birds and mammals) had BIO11 (mean temperature of the coldest quarter) in at least 50% of models.

Reducing complexity by discarding variables and tuning β resulted in fewer parameters for models built with more than approximately 10 data points (Fig. 4b). There was no effect of sample size on the best β value (Fig. 4c). Models built using default regularization and the full variable set on average produced geographic predictions of environmental suitability that were concentrated in a much narrower geographic area than those with fewer predictors and AICc-selected β (Fig. 3). This effect is primarily due to the change in regularization, as a comparison between the full and reduced variable sets with default regularization demonstrates that reducing the variable set tends to decrease ENM breadth
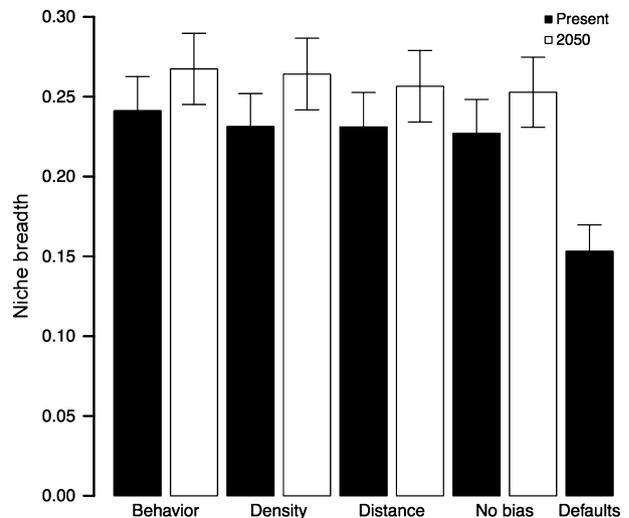

Figure 3 Average ecological niche model (ENM) breadth across all species as a function of bias estimate and model complexity. All models were created using species-specific tuning of the regularization multiplier (β) and a species-specific set of environmental layers (see text). No significant differences were detected between bias estimates, nor between any bias estimate and the default 'no-bias' estimate, either in the present or in future projections. In contrast, models built using Maxent defaults (no-bias estimate, full variable set, regularization multiplier (β) = 1) demonstrated much lower ENM breadths (far right). Error bars indicate one standard error.

(Fig. 4a), while AICc-tuned regularization on average tends to increase ENM breadth (Fig. 4d). The RR metric comparing the trimmed variable set to the default set was 88% ±5 SD averaged across taxonomic groups (range: 69–96%), while the average RR in comparisons of default and AICc β models using the reduced variable set was 94% ±6 (range: 68–100%). Taken together, these results indicate that

reducing the variable set has a larger effect on the relative prioritization of habitat patches than does overall model complexity (i.e. change in β multiplier), while tuning model complexity has a comparatively larger effect on the breadth of the inferred model.

DISCUSSION

This study addresses two complementary goals in species management with niche modelling. First, we present the largest study to date measuring the effects of using AICc to tune Maxent regularization on empirical data, and one of the few studies that measures the effects of different estimates of spatial sampling bias. Second, we explore the projected impacts of climate change in 2050 on a suite of 90 special concern vertebrate species across California.

Given the difficulties with assessing model quality in the presence of sampling bias (Phillips *et al.*, 2009; Veloz, 2009), the present study cannot determine which bias estimate or complexity level produces the most accurate models. However, these results do suggest some generalities regarding dif-

ferent modelling strategies. Removing correlated environmental predictors decreases breadth, creating models that tend towards errors of omission compared to models built with a larger variable set. In contrast, increasing regularization increases breadth, with a resulting increased tendency towards errors of commission. Neither is necessarily preferable, and the two strategies may be useful as a partial strategy for assessing uncertainty. We anticipate that the positive relationship between number of predictors and niche breadth seen here would not generally hold for uncorrelated predictors; increasing the number of potential limiting factors will generally reduce niche breadth.

Reducing the number of predictors had a substantially higher impact on the prioritization of different grid cells than did increasing regularization. Inclusion of sampling bias estimates had a statistically non-significant effect. Model complexity had a substantially larger effect both on model breadth and on estimates of suitability, suggesting that less complex models may provide less extreme estimates of the effects of future climate projections on species distributional envelopes.
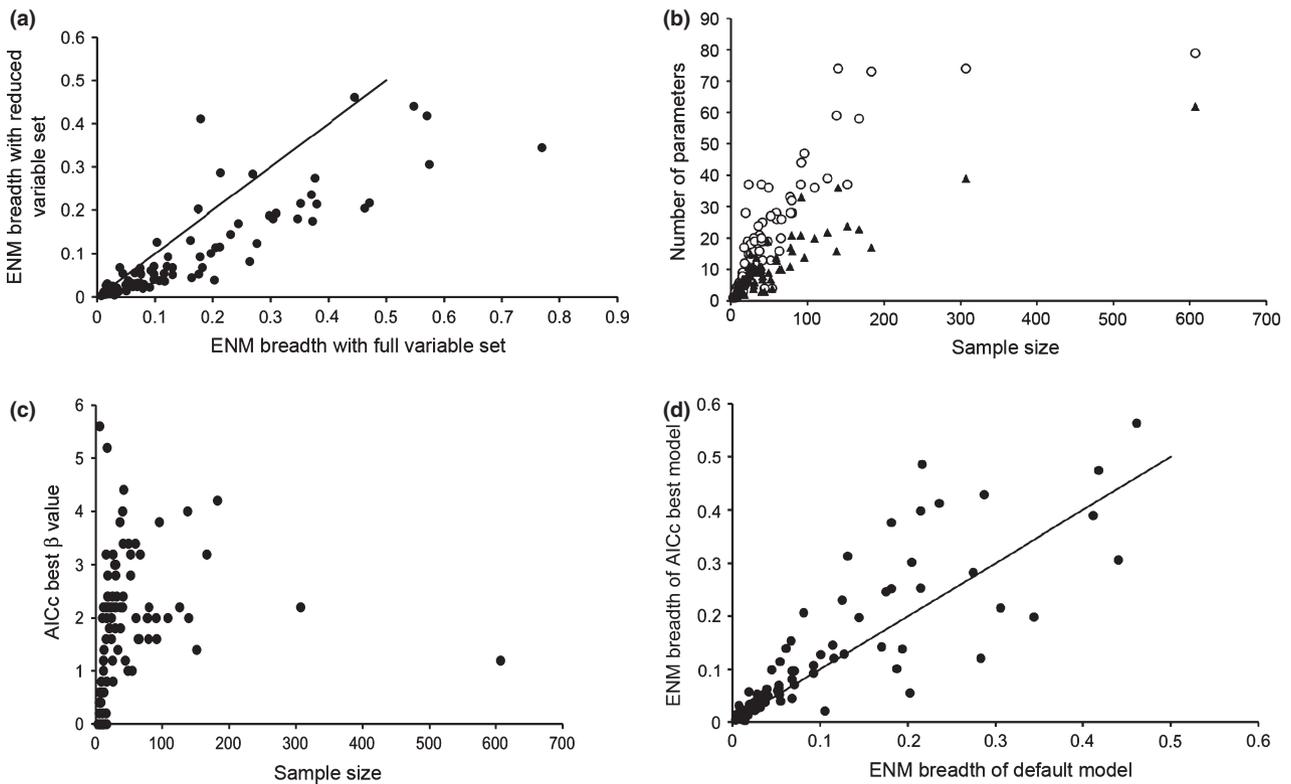

Figure 4 Panel (a) shows the present-day ecological niche model (ENM) breadth using full and reduced environmental variable sets. Each point represents a single species. The dark line shows a 1:1 relationship. Panel (b) gives sample size and number of parameters for models constructed using default and Akaike information criterion (AICc) regularization. Open circles are models with default regularization multiplier (β) values; filled triangles are models with the AICc best β values. While default and AICc models are quite similar at lower sample sizes (N < approximately 10), AICc tends to favour much simpler models with larger sample sizes. In panel (c), regularization multiplier (β) value chosen by AICc is given as a function of sample size. AICc generally selects models with higher β than the Maxent default (β = 1) when N > 25, but there is a considerable variation in the optimal β value selected for any given sample size. Panel (d) shows the effects of AICc model selection on ecological niche model breadth. Each point represents a single species. The dark line shows a 1:1 relationship.

However, the results were fairly similar across all modelling approaches. The strength and repeatability of the effects seen here may in part be a function of the study region. Given its topographic and ecological complexity, much of California is unsuitable habitat for many of the species modelled, and the magnitude of this variation may obscure some of the subtler effects that we examined; models and decisions made at a finer scale may be more seriously affected by model complexity and bias estimates. Regardless, these results suggest that optimal modelling approaches should be chosen with the application of the models in mind. Models biased towards errors of commission (i.e. including estimates of sampling bias, increasing regularization) might be favoured when the goal is to broadly identify areas where a species may occur, while models biased towards errors of omission (i.e. reducing the number of predictors, using less strict regularization) might be favoured when the price of protecting an unsuitable area is high.

Caution should be used when inferring a biological basis for the inclusion of variables from Maxent models. The AICc procedure has previously been shown to produce models that outperform Maxent defaults at selecting the true relative importance of variables for simulated species (Warren & Seifert, 2011), but overall performance in this respect was still relatively poor. This does not imply that the included variables are biologically unimportant, but rather that the possibility of spurious correlations is high and that variables should be examined in the context of the biology of individual species. The inclusion of BIO3, BIO4 and BIO15 in many of our models may in large part be due to the coastal distribution of many of the modelled species; BIO3 and BIO15 exhibit high values near coastal areas and lower values inland in California, while BIO4 is negatively correlated with BIO3 ($r^2 = -0.88$). Similarly, the suitability of habitat for most ectotherms tended to decrease with slope, but given the distribution of slope values in California, this may simply indicate that most species are either restricted to or completely absent from high elevations.

We used ENM breadth and the RR metric to evaluate the differences between models. An alternative approach is to apply thresholds for predicted presence and adopt a metric that is based on the proportion of grid cells occupied or the proportion of grid cells for which the predictions of two models agree. We did not apply thresholds here for several reasons. First, predictions of range contraction and expansion may be substantially affected by choice of threshold (Nenzen & Araujo, 2011). Second, predictions of presence and absence can be misleading for species with low prevalence, small sample size and/or gradual responses to environmental gradients (Bean *et al.*, 2011; Meynard & Kaplan, 2011), and SSC tend to have low prevalence and small sample sizes. Finally, our choice of the RR metric means that patterns seen without the application of thresholds should be indicative of the patterns seen with thresholds, as long as thresholds with the same biological interpretation can be chosen across modelling approaches.

The future of SSC in California

The taxa included in this study on average showed highest current suitability along the coast from the centre of the state south. SSC taxa tended to be concentrated along the coast, largely due to risks imposed by urbanization and high human impacts (Appendix S6, see Machado *et al.*, 2003). A critical question for management is whether climate change is likely to be an additional stressor in these habitats. In many cases, the answer is yes, with most taxa experiencing reductions in suitability of some currently occupied habitat. Despite taking steps to reduce overparameterization of models, over half of the taxa were predicted to experience >80% reductions in suitability in currently occupied cells (Fig. 2). Mammals had the greatest numbers of taxa showing little to moderate (0–20%) decreases in future suitability, a pattern driven largely by bats in southern California.

Reductions in suitability do not necessarily mean that species cannot persist in these areas, and our analyses do not include dispersal or adaptation. We therefore recommend focused monitoring within the areas of greatest predicted decrease to determine how species respond to climate change. Based on the current distribution of the SSC taxa expected to suffer 100% declines in environmental suitability, particularly sensitive areas are the San Francisco Bay region, including the Santa Cruz Mountains and the Bay Delta, the eastern San Joaquin Valley, the eastern slope of the central Sierra Nevada, the Tehachapi Mountains, the eastern slope of the Peninsular Ranges, and along the Mojave River. For many species and communities, monitoring in these regions would be particularly productive to gain a sense of on-the-ground effects of climate change.

The broad range of geographic distribution and life history characteristics represented in our data set make it difficult to generalize about factors influencing threat level. For example, almost all of the taxa expected to experience rangewide reductions in environmental suitability across California had very small ranges, occupying <10% of the state (e.g. several Bay Area endemics). However, other taxa with similarly small ranges were predicted to have no decreases in environmental suitability (Appendix S4). Future studies that quantify the relationship between life history and risk would be useful to augment the approach taken here.

It is important to note that the current study only examines changes in suitability due to climate change, while other factors have significant impacts on habitat quality. Comparing the distributions of suitable habitat for all SSCs (Fig. 1) to the distribution of habitat currently deemed to be in poor condition (Appendix S6), we note that much of the suitable habitat for SSCs in Figure 1 is located in the Bay Area and densely occupied areas of southern California, which are also the regions of poor habitat condition driven most strongly by urbanization. This suggests that habitat condition may be one of the most important factors causing species to require designation as SSCs. As we do not consider habitat condition in the analyses presented here, our projections almost certainly

underestimate overall changes in suitability and provide an overly optimistic view of future range predictions.

Our predictions may be pessimistic for taxa that have ranges that extend outside of California. These taxa may occupy habitat that is not represented in our study region, leading to an underestimation of the breadth of species' tolerances. Future studies should evaluate the effect of setting the extent of the study area (Anderson & Raza, 2010; Barbet-Massin *et al.*, 2010). The distance and density methods for estimating sampling bias may somewhat address this issue with respect to drawing background data, as they will cause Maxent to preferentially draw pseudoabsence data from areas where sampling of the target group is most intense. While this may include areas that are not close to occurrences of the target species, it will serve to exclude areas that are not close to, or were not sampled for, any species in the target group. Conversely, our predictions do not take into account other potential climate change impacts such as sea level rise and levee failure, vegetation shifts, changes in wildfire, snowpack and stream hydrology and thus may underestimate risk for some taxa (PRBO 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of taxa.

Appendix S2 Correlations among the 19 Bioclim variables and slope.

Appendix S3 Key to areas of California referenced in the text.

Appendix S4 Predicted changes in environmental suitability in currently occupied cells.

Appendix S5 Environmental variables retained in AICc best model for each taxon.

Appendix S6 Habitat condition index.

BIOSKETCH

Dan Warren is a postdoctoral researcher at The Australian National University, working with Marcel Cardillo and Lindell Bromham. His interests include evolution, ecology, biogeography and conservation biology.

Author Contributions: Models were constructed by D.L.W. and S.N.S. *Post hoc* analyses were conducted by A.N.W. and D.L.W. A.N.W. and D.L.W. led the writing of the manuscript, with significant contributions by H.B.S.

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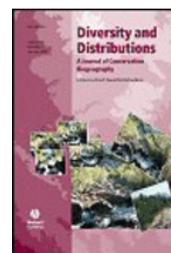
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Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern

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