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Review

Use of Maximum Entropy Modeling in Wildlife Research

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Abstract: Maximum entropy (Maxent) modeling has great potential for identifying distributions and habitat selection of wildlife given its reliance on only presence locations. Recent studies indicate Maxent is relatively insensitive to spatial errors associated with location data, requires few locations to construct useful models, and performs better than other presence-only modeling approaches. Further advances are needed to better define model thresholds, to test model significance, and to address model selection. Additionally, development of modeling approaches is needed when using repeated sampling of known individuals to assess habitat selection. These advancements would strengthen the utility of Maxent for wildlife research and management.

Keywords: habitat selection models; maxent; species distribution models; wildlife; maximum entropy

1. Introduction

Factors that influence species distributions and habitat selection are of great importance to researchers and managers of wildlife. For example, wildlife agencies are often tasked with establishing hunting quotas for game species and must rely on information about habitat potential and wildlife distributional patterns to help establish these quotas; wildlife managers and researchers are frequently tasked with delineating current and potential distributions of endangered species to establish protected areas; while in other regions, invasive species are expanding their ranges into new areas requiring rapid identification of these areas to slow down or eliminate this invasion. There is a constant need for alternative and presumably more effective methods for assessing these distributional patterns.

Traditionally, analyses have been conducted with presence-absence data (e.g., logistic regression, discriminant function analysis). However, absence data is often unavailable (e.g., museum specimen collections). Additionally, absence data is difficult to verify given the potential for a species to be present at a site but not observed resulting in substantially biased wildlife–habitat relationships [1,2]. However, a number of new approaches (e.g., BIOCLIM, DOMAIN, GARP, Maxent) have been developed over the last decade that utilize only presence locations, thereby eliminating the need for true absence locations. Several recent studies comparing up to 16 of these approaches indicated that maximum entropy (Maxent) modeling performed as well or better than the other approaches [3–5]. As such, a recently developed Maxent program [5] should be a very useful tool for delineating species distributions and habitat associations. In the following sections, I will: 1) describe how the Maxent method works, as well as output features associated with the most current version of Maxent software [6], 2) describe strengths and potential weaknesses of the Maxent approach for wildlife research, and 3) indicate areas for needed research and development to increase the utility of Maxent for wildlife research and management practices.

2. What is Maxent?

Maxent is based on a machine learning response that is designed to make predictions from incomplete data. This approach estimates the most uniform distribution (maximum entropy) of sampling points compared to background locations given the constraints derived from the data [5,7,8]. The maximum entropy algorithm is deterministic and will converge to the maximum entropy probability distribution [5]. Therefore, the resultant output represents how much better the model fits the location data than would a uniform distribution [5,7]. Maxent has the added advantage of allowing the use of both continuous and categorical variables.

Maxent is prone to overfitting, resulting in predicted distributions that are clustered around location points. Therefore, a relaxation component, called regularization, has been added to Maxent to constrain the estimated distribution thereby allowing the average value of each sampled variable to approximate its empirical average but not equal it. This regularization component can be adjusted for each sampling area. However, recent simulations have indicated that default settings perform as well as adjusted settings [9].

2.1. Model output

Maxent provides output data in raw, cumulative, and logistic formats [9]. Raw values are the primary output for Maxent. However, these raw values are not intuitive, and because they must sum to 1, are often very small for each data point thereby making interpretation difficult. The cumulative format is scale independent with scores for locations equal to the probability of finding the species of interest at that site plus all others with equal or lower probabilities. Scores range from 0–1 [5]; therefore, output is more easily interpreted when projected into a geographic information system (GIS) although these projections are not necessarily proportional to the probability of occurrence. As such, the logistic format is currently recommended given that it provides estimates of the probability of occurrence as predicted by included environmental variables [9]. This means that large differences in derived output values will correspond better with large differences in suitability. As with the cumulative format, logistic output ranges from 0–1. Therefore, the logistic format allows for easier and potentially more accurate interpretation over the other approaches. All output types can be imported into a GIS to map probability distributions. It should be noted that the raw, cumulative, and logistic formats are monotonically related; all sites will be ranked in the same order when using ranked based statistics such as AUC (see Section 2.3), but will perform differently when using statistics that involve the actual values (e.g., correlations) [9].

2.2. Variable response

In most cases, it is important to know how each variable influences the presence of the modeled species and, subsequently, which variables have the greatest influence on the model and in what manner these variables influence species occurrence. Variable importance can be determined in two ways. First, Maxent provides the percent contribution of each variable to the final model [10,11]. This is a heuristic approach to model importance in which the contribution values are determined by the increase in gain in the model provided by each variable [11]. Caution must be used when employing this method as strong collinearity can influence results by indicating more importance for one of two or more highly correlated variables.

An alternative method for assessing variable importance is the jackknife approach [11,12]. This approach excludes one variable at a time when running the model. In so doing, it provides information on the performance of each variable in the model in terms of how important each variable is at explaining the species distribution and how much unique information each variable provides. This can point out highly correlated variables, thereby allowing the user to determine if percent contribution values are likely to be skewed due to these correlations.

It is also important to know in what manner each variable influences species distributions. For example, is a species more likely to be found closer to water, at sites with greater annual precipitation, or at lower elevations? Because Maxent is an exponential model, the probability assigned to a location is proportional to the exponential of the selected combination of variables, thus allowing construction of response curves to illustrate the effect of selected variables on probability of use [10–13]. These response curves consist of a chart with specified metrics for the variable in question represented on the x-axis and the predicted probability of suitable conditions as defined by the logistic output when all other variables are set to their average values over all other presence locations along the y-axis [11]. Upward trends for variables indicate a positive association, downward movements represent a negative relationship, and the magnitude of these movements indicates the strength of these relationships. These response curves are also highly influenced by strong collinearity. Therefore, caution must be exercised when interpreting these curves if strong collinearity is present.

2.3. Model evaluation

As with any modeling approach, the fit or accuracy of the model should be tested to determine the relevance of the model. This primarily has been done in two ways: 1) through receiver operating characteristic (ROC) plots, and 2) through defined thresholds. The ROC plot is a plot of sensitivity and 1–specificity, with sensitivity representing how well the data correctly predicts presence, whereas specificity provides a measure of correctly predicted absences [14]. To develop a ROC plot, a certain percentage of the data is selected for training data; the other portion is used for test data. A good model is defined by a curve that maximizes sensitivity for low values of the false-positive fraction [4]. The significance of this curve is quantified by the area under curve (AUC) and has values that typically range from 0.5–1.0. Values close to 0.5 indicate a fit no better than that expected by random, while a value of 1.0 indicates a perfect fit. It is possible to have values less than 0.5; this indicates that a model fits worse than random [15]. The AUC is a ranked approach for assessing model fit that determines the probability that a presence location will be ranked higher than a random background location [5]. These random background locations serve as pseudo-absences for all analyses in Maxent.

Another approach involves selecting thresholds to establish sites that are considered suitable or unsuitable for the species of interest. These thresholds are established by maximizing sensitivity while minimizing specificity [5,14]. The proportion of sites that are correctly classified as suitable locations can be compared to the proportion of unsuitable sites to determine the accuracy of the model. The difficulty with this binary approach is selecting the appropriate threshold (see Section 4.2). Additionally, because this approach categorizes locations into presence or absence, you lose the ability to differentiate between varying probabilities within these classes, although this may be preferable for practical scenarios where presence-absence maps are desired (e.g., delineating preservation areas).

3. Strengths of Maxent

3.1. Sampling effort

In addition to the benefit of needing only presence locations, Maxent also appears to be less sensitive than other approaches to the number of presence locations required to develop an accurate model [3–5]; in some cases only five locations were required to develop a useful model [4,16] although >30 locations are recommended [17]. As with any modeling approach, more locations will likely result in a more precise and accurate model. However, the added benefit of additional locations appears to plateau at 50 [4] (but see [16]). The reason for Maxent's relative insensitivity to sample size appears to be driven by its regularization procedure which compensates for overfitting when using only a few locations.

The relatively small number of locations required for accurate model construction is a very beneficial aspect of the Maxent approach as there is often a lack of reliable locations available for mapping the distribution of many species. However, caution should be used when interpreting these models as the accuracy of the model can be strongly influenced by bias in sampling effort [4,16–18]. For example, all documented locations of a particular species may have been observed along roads, as this was the area where it was most easy to detect them even though they may utilize many areas far from roads. This resulting model may not accurately define all areas that this species uses. However, Phillips *et al.* [18] showed that targeting background locations from areas where locations were sampled, even if location sampling was biased toward a specific area, could counter this sample-selection bias. Regardless, when developing models with a small number of locations, the resultant distribution should be defined as areas that have similar environmental conditions where the species is known to occur rather than to define the species environmental requisites throughout their range [16]. In fact, the greatest utility of models constructed from very few location sites may be to point out areas where future survey efforts should be focused [17].

3.2. Spatial error of location data

A common concern when using location data is the accuracy associated with the location. For example, many museum specimens have location data that is relatively general. Obviously, at some point, spatial error will influence model results. However, Maxent does not appear to be strongly influenced by moderate spatial error associated with occurrence data, as location errors up to 5 km appear to have no impact on model performance [19]. Additionally, you should not conduct analyses with location data that are less precise than available environmental data [19]; if this situation occurs, environmental data should be converted to the precision of the location data. However, the fact that Maxent is relatively insensitive to errors in location data further increases its utility for assessing habitat use and distributional patterns.

3.3. Mapping feature

Maxent also produces distribution maps that illustrate the likelihood of finding the species of interest in a particular area [11]. These maps can be constructed to represent the probability of finding a particular species in a given area (e.g., black bear, *Ursus americanus*, den sites [10]) or to indicate whether a species is likely to be present or absent in a given area (e.g., Javan slow loris, *Nycticebus javanicus*, locations [20]). For the former, the logistic output is typically used to represent the probability of occurrence, while for the latter, a defined threshold is used to indicate if a species is likely to be found (defined as present or absent) in a given area. Both methods can be incorporated into a GIS, thereby making rapid assessments of important areas easy to discern.

4. Potential Weaknesses of Maxent

4.1. Transferability

One potential problem with Maxent deals with the ability to transfer findings from within a sampled area to unsampled areas. This transferability issue could be a major problem given that composition of environmental variables often varies across a species occupied range. Therefore, if a species entire range is not sampled, or if a species range is expanding over time (*i.e.*, invasive species), constructed models may inadequately define this range, as well as inadequately define which variables are important to the species of interest. Initial research suggested that Maxent may not adequately account for transferability issues between sampled and unsampled areas [21]. However, this observed difference was likely more representative of a bias in sampling distribution rather than a transferability issue [22]. Ultimately, the accuracy of any model is heavily influenced by the sampling distribution. If the distribution is heavily skewed, the resultant model is less likely to accurately predict the given species distribution. As already pointed out (see Section 3.1), if the sampling distribution is expected to be strongly biased, background locations can be targeted from heavily sampled areas to provide unbiased results [18].

4.2. Model evaluation

Perhaps one of the biggest obstacles to be overcome by Maxent pertains to model evaluation and subsequent model selection. After all, just because a model can be built does not mean that it is informative. Several approaches have been used to assess the significance of developed models although it is unclear which is most appropriate and if they can assist in model selection. As mentioned previously (see Section 2.3), AUC's are developed from ROC plots to provide a ranked approach for assessing differences in species distributions for developed models compared to a random distribution. A binomial test of omission (known areas of presence predicted absent) can then be used to test whether or not this difference is significant [5], and provides some information on the usefulness of the model (*i.e.*, AUC: >0.9 = very good; AUC: 0.7–0.9 = good, AUC: <0.7 = uninformative [23]).

A similar approach assesses the correlation between the predicted value from a presence and pseudo-absence location [3]. This correlative approach has the benefit of assessing the actual difference observed between presence and pseudo-absence locations rather than just the ranked difference seen in the AUC approach. However, results from correlations are similar to results from AUC [3]. Therefore, AUC values are typically reported.

The mean deviance per observation is a good complement to AUC as it represents the magnitude of deviation of the fitted values from the observations [24]. Deviance is affected by the calibration of the model and must be interpreted with reference to this calibration. However, proper calibration is not likely given the lack of true absence data. Therefore, deviance should not be used independently, but rather in combination with additional model evaluation methods [24].

Null models have recently been proposed for testing model fit [25]. This approach compares AUC scores from the developed model to AUC scores from 1,000 null models using randomly generated presence locations equal to the number used in the developed distributional model. This allows the development of a frequency histogram with which to compare the AUC scores from the actual model to the null models. One-sided 95% CI's are used to test for significance, as there is only interest in if the model performs better than random, not if it performs worse than random. This approach has the added advantage of using all data points rather than having to separate data into training and test categories [25].

Kappa [3,26,27] and jackknife statistics [16,20,27] are also used to test models. Kappa is a chance corrected measure of agreement that is commonly used in ecological studies that use presence-absence data [28]. The kappa index considers both omission and commission (areas of absence predicted present) errors thereby resulting in a less biased measure of predictability. However, kappa tends to respond to the prevalence of a species in a unimodal fashion [29]. A similar approach called the true skill statistic has been developed that is not dependent on prevalence, and as such, may be more appropriate than kappa [29]. The jackknife procedure uses a "leave-one-out" approach in which 1 location is removed from the sample pool (n). Then a model is constructed with the remaining n–1 localities. This is repeated n times so that each variable is left out of the model construction process 1 time. The performance of each model is then assessed based on its ability to predict each location left out (see [16] for a full description of this approach). The jackknife approach is effective when sample locations are ≤25, although use of this method with larger sample sizes can create overoptimistic estimates of predictive power [16].

Both kappa and the jackknife approaches rely on threshold values to predict presence-pseudo-absence locations. Threshold values differ for each model and are selected to provide a desired balance between omission and commission [4,14]. Where this threshold is applied is determined from ROC plots and is selected at the discretion of the modeler. For example, when dealing with endangered species, the modeler may want to maintain zero omission error while identifying the minimum predicted area. However, if the modeler is interested in identifying any possible area that a species *might* use, then they would want to minimize commission error [16]. Once a threshold has been identified, locations can be classified as suitable or unsuitable for the species of interest.

4.3. Model selection

Model evaluations provide information regarding whether a model can predict distributions that are different than random. However, they provide little information for selecting the best model out of a subset of potential models (*i.e.*, model selection). Such comparisons are important in selecting a parsimonious model that accurately predicts species distributions and habitat use, as simpler models are more intuitive and provide a more realistic set of habitat components that can be managed for wildlife. There are only two published attempts that I am familiar with that addressed this topic. One involved the use of a critical ratio test that compared the most general model (*i.e.*, containing all variables) to more parsimonious models [10,13]. This approach used AUC scores and associated SE's to derive a Z-score to determine if competing models were different [30]. Following this approach, all possible combinations of variables were modeled and subsequently ranked according to AUC scores. The model with the highest AUC score for each subset of variables (*i.e.*, one-variable model, two-variable model, etc., up to the full model) was selected and compared to the most general model to determine if these two models differed. If there was a difference, the more general model was selected; if not, the most parsimonious model was used given the greater ability to interpret simpler models and manage fewer variables.

An alternative model-selection approach used the jackknife test to assess the importance of predictor variables [12]. Following this approach, the least important predictor variable from the full model was determined and dropped from subsequent models. Then a new model was constructed with all predictor variables except the previously dropped variable. The weakest of the remaining variables was again determined using the jackknife test and was dropped from subsequent models. This procedure was continued until only one variable remained. Ninety-five percent confidence intervals were then constructed for the training gain values (a measure of the likelihood of samples) associated with each of these subsequent models (n = number of predictor variables). The most parsimonious model that exhibited overlap in confidence intervals (*i.e.*, not statistically different) with the full model or the model with the highest training gain was selected as the best model [12].

5. Needed Advancements in Maxent

Maximum entropy is a rapidly evolving machine learning process that could become a very useful tool for wildlife researchers. However, it is still a relatively new method that has not yet been fully developed. In particular, I feel several aspects need to be more explicitly addressed to increase Maxent's utility in wildlife research. These include: 1) developing protocol for selection of appropriate threshold values, 2) developing methods for model selection, and 3) developing methods for dealing with habitat selection when using repeated sampling of known individuals.

5.1. Threshold development

The selection of an appropriate threshold level is a common concern when converting model output into suitable and unsuitable areas as no general method for establishing these thresholds has been developed [5,27,30]. Many approaches have been used when dealing with presence-absence data [26]. Unfortunately, threshold selection is less clear when dealing with presence-only locations as there is no way to balance false-positive and false-negative predictions [16]. Nonetheless, commission errors tend to decrease while omission errors subsequently increase as the threshold increases [4,14]. As such, threshold levels are typically selected to minimize the error term that is most detrimental to the model objectives (e.g., [16,20,31,32]). However, this still involves the somewhat arbitrary selection of a threshold level; a more consistent or more clearly defined selection approach would provide greater consistency in model output and is worthy of further investigation.

5.2. Model selection

Developing methods for model selection would also have great utility for wildlife research, particularly when trying to discern which variable or combination of variables has the greatest influence on the distribution of the species of interest. Many variables that are included in full Maxent models often have little known influence on distributional patterns [10,12,13]. Their elimination from distributional models would simplify the management of the species of interest and may increase the generality of the model over a broader area by decreasing the potential for overfitting the model. The critical ratio test and jackknife procedure described in Section 4.3 provides one possibility for assessing model fit. Alternatively, it may be possible to compare distributional maps from competing models to test for differences in model fit. This approach has been implemented for distributional maps using single variables within GARP [33], although I am not aware of a similar comparison using Maxent, nor of the validity of using this approach with multivariate models.

The development of an information-theoretic (e.g., Akaike's Information Criterion [AIC]) approach for Maxent might provide the greatest utility for model selection. The information-theoretic approach weights model fit with the number of variables included in the model to provide a relativized score for each model [34]. These models are then ranked to determine the best approximating model based upon a combination of explanatory power and parsimony. Elith and Leathwick [24] used a Deviance Information Criterion (DIC; essentially the Bayesian equivalent to AIC [35]) score to assess the importance of model type, sampled regions, and biological groups on AUC scores when using a generalized linear mixed model for multivariate adaptive regression splines (MARS). A similar approach may be possible with competing Maxent models thereby allowing the determination of the best competing model, although research is needed to assess the utility of this or a similar information-theoretic approach for model selection.

5.3. Repeated sampling of known individuals

Most initial studies using Maxent have focused on delineating species distributions (Table 1) rather than on determining important habitat characteristics for the species of interest. However, Maxent provides a powerful tool to assess habitat use as well. Traditionally, habitat studies have been based on associations between any number of ecological variables and wildlife locations. Maxent is well equipped to assess these relationships given that current technology has yielded high resolution environmental and climatic coverages that are readily accessible for comparison to species locations. However, in situations where you have repeated sampling from the same individual, usually determined through marked or radiotelemetered individuals, the individual may need to serve as the replicate in analyses rather than each specific location, particularly if locations are not independent or if the number of locations is not relatively equivalent among sampled individuals. In such situations, it may be inappropriate to build a habitat-use model for a given species by combining all locations for all individuals sampled without weighting these locations in some manner to account for the number of locations observed for each individual, as well as the total area used by each individual. For situations like this, a different approach is needed to model habitat use.

Table 1. Studies involving wildlife that have used maximum entropy modeling to relate distributional patterns to stated objectives.

Reference	**Species**	**Location**	**Objective**
[16]	Geckos (*Uroplatus* spp.)	Madagascar	Predict species distributions
[10]	American black bear (*Ursus americanus*)	North-central Colorado, USA	Assess denning habitat
[36]	Bush dog (*Speothos venaticus*)	Central and South America	Evaluate quality of protection and direct research effort through species distributions
[32]	Little bustard (*Tetrax tetrax*)	Central Spain	Model seasonal changes in distribution
[12]	Sage grouse (*Centrocercus urophasianus*)	Southern Oregon, USA	Predict and map nesting habitat
[37]	Brown-backed bearded sakis (*Chiropotes israelita*) Black uakaris (*Cacajao* spp.)	Western Amazon, Brazil	Model geographical distributions and fundamental niches
[38]	Cuban treefrog (*Osteopilus sepentrionalis*)	Caribbean and Gulf of Mexico	Assess potential distribution of invasive species
[20]	Asian slow lorises (*Nycticebus* spp.)	Southeast Asia	Assess threats and set conservation priorities through species distributions
[13]	Mule deer (*Odocoileus hemionus*) Gemsbok (*Oryx gazella*)	South-central New Mexico, USA	Assess habitat use

One proposed method is to build a model for each sampled individual by using its home range to serve as the source of background data for the model [39]. Once models are constructed for each individual, the percent contribution of each variable in each model could be compared across all sampled individuals using a Kruskal–Wallis test [40] to assess which variables were most important in determining the distributional patterns. These selected variables could then be used to construct a final model to assess their relative impact on this model, how they influenced distributional patterns, and to map distributions throughout the study area. However, the appropriateness of this approach has not been rigorously tested. Such information could greatly increase the utility of Maxent modeling for assessing important habitat characteristics for a multitude of wildlife species.

6. Conclusions

Maxent modeling has proven to be very effective at determining habitat use and species distributions for a variety of species and localities (Table 1). Because it relies only on presence data, it lacks many of the complications associated with presence-absence analytical methods [5]. Maxent modeling has frequently outperformed a number of other approaches that rely on presence-only data [3–5], it is relatively insensitive to spatial errors associated with location data [19], and it can produce useful models with as few as five locations [4,16]. As with all modeling approaches, Maxent is influenced by heavily biased sampling distributions, although this bias can be reduced by targeting background locations from sampled areas [18]. However, Maxent is still a relatively new method that has not yet been fully developed. Therefore, further advances are still needed to: 1) develop a general method for establishing threshold levels, 2) develop methodology for selecting the best approximating model, and 3) establish protocol for assessing habitat selection based on repeated sampling of individuals. Addressing these aspects should further increase the utility of Maxent modeling for wildlife research.

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