Opening the black box: an open-source release of Maxent

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Maxent is a self-contained Java application for species distribution modeling (SDM) based on occurrence records (locations where the species has been found) together with environmental variables such as rainfall and temperature for a surrounding study area (Phillips et al. 2006, Phillips and Dudík 2008). Since performing well in a comparison of species distribution modeling methods (Elith et al. 2006), it has been widely used: Google Scholar reports more than 6000 citations for Phillips et al. (2006) at the time of writing. Until now the software source code has been owned by AT&T, but the application has been freely available and hosted online by Princeton Univ. (<www.cs.princeton.edu/%7Eschapire/maxent>).

Despite documentation of the underlying mathematics, the software has sometimes been referred to as a black box, since the underlying source code was not available. The source code is now released under the MIT open-source licence, and we invite interested developers to use and contribute to the code. The geospatial community has been a leader in open source and free software development (Bocher and Neteler 2012) and many in the ecology, evolution, and environmental science communities have called for increased openness as not only an ethical imperative but also a necessity to answer key pressing questions about global change (Wolkovich et al. 2012). The Maxent application will henceforth be hosted by the Center for Biodiversity and Conservation (CBC) at the American Museum of Natural History, at <https://biodiversityinformatics.amnh.org/open_source/maxent>, extending the role that the CBC has played in fostering the development of Maxent and hosting the New York Species Distribution Modeling Discussion Group for the past 15 yr.

In addition to the Java source code, we announce a new R package, maxnet (<https://CRAN.R-project.org/package=maxnet>; ver. 0.1.2, <https://github.com/mrmaxent/maxnet>, authored by SJP), which implements Maxent using the glmnet package for regularized generalized linear models. We discuss the implications of the IPP formulation in terms of model inputs and outputs, treating occurrence records as points rather than grid cells and interpreting the exponential Maxent model (raw output) as an estimate of relative abundance. With these two open-source developments, we invite others to freely use and contribute to the software.
in terms of ‘features’ (environmental variables such as temperature, and simple functions of those variables such as quadratic terms), and require that the mean of each feature should match the sample mean. This formulation is equivalent to maximizing the likelihood of a parametric exponential distribution (Phillips et al. 2004). More recently, it was noted that the exact same maximum likelihood exponential model can be obtained from an inhomogeneous Poisson process (IPP) (Aarts et al. 2012, Fithian and Hastie 2013, Renner and Warton 2013). This development is important for Maxent users, as it yields new interpretations of model inputs and outputs, and allows the use of other software packages for fitting Maxent models. Here we give a very brief overview of the IPP formulation, following Fithian and Hastie (2013); note that in following their notation, some of the same symbols (e.g. \( \lambda \)) are used differently from previous papers describing Maxent.

An IPP is a widely-used model for a random set \( Z \) of points falling in some domain \( D \) (Cressie 1993, Diggle 2003). To apply it to species distribution modeling, we can use the set of occurrence records for \( Z \), while \( D \) is the geographic study area. The IPP can be defined by an intensity function \( \lambda \) which assigns a non-negative real-valued intensity \( \lambda(z) \) to each point \( z \) in \( D \). It can be thought of as indexing the likelihood that a point (here, an occurrence record of the species) falls at or near \( z \). We can define a probability density over the domain \( D \) by:

\[
p_z(z) = \frac{\lambda(z)}{\int_D \lambda(z) dz}
\]

where the denominator simply makes \( p_z(z) \) sum to 1. An IPP with intensity \( \lambda \) is defined as an independent and identically distributed (i.i.d.) sample from \( p_\lambda \), whose size (number of points) is a Poisson random variable with mean \( \int_D \lambda(z) dz \).

Warton and Shepherd (2010) suggested modeling the occurrence records for a species as arising from an IPP whose intensity \( \lambda(z) \) is a log-linear function of a vector of real-valued features \( x(z) \):

\[
\lambda(z) = \exp(\alpha + \mathbf{b}^T x(z))
\]

The coefficient \( \alpha \) is essentially a normalizing constant, giving no information about the species’ distribution – its maximum likelihood value simply ensures that \( \int_D \lambda(z) dz \) equals the total number of occurrence records. Conditioned on the number of occurrence records, the likelihood of the IPP is the same as Maxent’s likelihood, since \( p_z \) is exactly Maxent’s exponential distribution. The maximum likelihood values of the coefficient vector \( \mathbf{b} \) are therefore exactly the same as those given by Maxent. This equivalence still holds true when using regularization (as is done by the Maxent software), by which a penalty term (Phillips et al. 2004, Elith et al. 2011) is added to the log likelihood to penalize larger values of the coefficients and thereby produce a simpler model.

**Implications for model inputs**

While the IPP model can be defined for a finite discrete domain (such as a regular grid), it is perhaps most natural for a continuous \( D \); for SDM, this means that occurrence records are considered to be points (with zero area) in geographic space rather than sites or quadrats of some non-zero area. The IPP then models the process of drawing some point locations randomly from the locations of all individuals of the species (leaving aside complications due to sample selection bias; Phillips et al. 2009, Fithian and Hastie 2013, Renner et al. 2015). Hence, it models occurrence records as being obtained with probability proportional to the local abundance of the species. This contrasts with Phillips et al. (2006), who outlined an idealized data model in which the domain \( D \) is a finite grid of equal-sized cells, with occurrence records corresponding to grid cells randomly selected from those occupied by the species. In this latter case, a grid cell with a single individual is considered as likely to have an occurrence record as a grid cell in which the species is very abundant; the difference between the two data models is more pronounced for larger grid sizes. Given the realities of biological sampling, the truth surely lies somewhere between these two extremes, and depends strongly on the data-collection methods used in the field (Renner et al. 2015). For example, the density of records derived from incidental sightings will likely be strongly affected by local abundance; in contrast, presence-only data sets of occurrence records from intensive sampling of transects will not distinguish between areas with a few individuals truly present per transect versus those with many.

For the IPP model, we expect to have more occurrence records in areas and environmental conditions where the species is abundant. However, care should be taken when multiple records lie close together, since co-located or nearby records are often an artifact of spatially auto-correlated sampling (for example, records may be clustered around a research station). For these reasons, the occurrence records may need to be thinned (Boria et al. 2014, Aiello-Lammens et al. 2015) to better match the IPP’s assumption of independent samples. Note that this particular issue of clustered sampling is separate from that of spatially biased sampling (Fithian et al. 2015) and it may be necessary to apply both thinning and bias correction to the same dataset (Sylrett et al. 2013).

Additionally, the primary goal of SDM is often to model and understand the environmental conditions inhabited by the species, rather than simply its geographic distribution. Both for this use and to better estimate the geographic distribution, it is important that (to the degree possible) the occurrence data represent a random sample of suitable conditions in \( D \). In addition to consideration of sampling biases (see above), this requires a careful choice of the study area \( D \) – see for example Renner et al. (2015) and discussion of environmental equilibrium and noise assumptions of Anderson (2013).

**Implications for model outputs**

The IPP model gives an estimate \( \lambda(z) \) of the intensity of occurrence records at or near the point \( z \). If the sampling effort is unbiased (an unlikely assumption – see Reddy and Dávalos 2003), this is also an estimate of the relative abundance of the species: i.e. it is linearly proportional to the average number of individuals per unit area at or near \( z \).
The proportionality constant \( c \) equal to the ratio of the true abundance of the species to that predicted by the model cannot be determined from occurrence records alone (Fithian and Hastie 2013). Rather, some independent measure or estimate of total population size is required to estimate \( c \) and hence absolute abundance. Maxent models (derived from occurrence records) have indeed been found to show correlation with independently measured local abundance (VanDerWal et al. 2009, Weber et al. 2016). We note, however, that although a linear relationship is theoretically predicted between \( \lambda(z) \) (Maxent’s ‘raw’ output format) and local abundance, a nonlinear (but still monotonic) relationship is predicted for transformed outputs such as the logistic transform used by VanDerWal et al. (2009).

From relative abundance to probability of presence

The interpretation of Maxent as an IPP allows Maxent’s ‘raw’ output format to be used directly as a model of relative abundance. However, many SDM uses call for models of probability of presence. Additionally, maps made from raw output do not often match ecologists’ intuition about the (potential or realized) distribution of their study species. For these reasons, Maxent’s default output scaling is a model of probability of presence, with an important caveat. Consider a quadrat within the domain \( D \), and assume the environmental conditions are constant within the quadrat. The IPP estimates the species’ absolute abundance in the quadrat as a Poisson variable with the following mean:

\[
P_{\text{mean}} = e^\alpha A \exp(\beta x(z))
\]

where \( A \) is the area of the quadrat. The probability of presence of the species in the quadrat is the probability that there is at least one individual there, which according to the Poisson distribution is:

\[
P_{\text{presence}} = 1 - \exp(-e^\alpha A \exp(\beta x(z)))
\]

thus yielding a Bernoulli generalized linear model whose link function is termed a complementary log-log (cloglog) link (Fithian et al. 2015). Note, however, that this derivation relies on the species’ presence or absence at nearby sites being independent. Therefore, it may not be appropriate when species distributions (including patterns of abundance) exhibit spatial dependence beyond that owing to spatial autocorrelation of the utilized predictor variables. For example, positive autocorrelation of individuals occurs for flocking birds and for plants with limited dispersal abilities, and negative autocorrelation for territorial mammals. Note that the IPP literature includes methods to detect spatial dependence (such as Ripley’s \( K \)-function) and to incorporate it into the model (e.g. using area-interaction processes) at the cost of increasing modeling complexity (Renner et al. 2015).

Because of the above derivation, a cloglog transform appears to be most appropriate for estimating probability of presence, and Maxent ver. 3.4.0 now uses it by default. The previous default (a logistic transform, Phillips and Dudik 2008) is now available as an option. For both transforms, the entropy \( H = -E_\lambda(\ln(p_\lambda)) \) of the probability distribution \( p_\lambda \) is used as a constant offset to the linear model; specifically, the new cloglog transformation estimates probability of presence as:

\[
P_{\text{presence}} = 1 - \exp(-\exp(H)p_\lambda(z))
\]

Note that this estimate is appropriate for some quadrat size, but we cannot say explicitly what that size is, since it depends on the (unknown) \( c \) (this is the important caveat mentioned at the beginning of this section). At best, we can define the quadrat size implicitly: consider a point \( z \) whose log probability under \( p_\lambda \) equals the mean log probability, i.e. \( \ln(p_\lambda(z)) = E_\lambda(\ln(p_\lambda)) \). Such a point could be called a ‘typical’ location of the species, as its predicted log abundance is average among all points where individuals of the species are found. The predicted probability of occurrence in a quadrat centered at such a typical point \( z \) is \( 1-1/e \approx 0.632 \), corresponding to a predicted abundance of one individual per quadrat. This is similar to Maxent’s logistic output, which gives a predicted probability of occurrence of 0.5 for such a location. In general, the cloglog transformed output is somewhat greater than the logistic one (Fig. 1), especially at higher values. The main effect of using the cloglog rather than the logistic transform is that areas of moderately high output (yellow and orange in Fig. 2 left) are more strongly predicted (relatively warmer colors in Fig. 2 right). We emphasize that the use of entropy as an offset is somewhat arbitrary, but has the advantage of being scale independent (for example, it would not be affected by changing units from meters to kilometers) and produces output values (and hence mapped predictions) with good visual discrimination across the same range of values (0–1) for all species. Importantly, whenever more is known about the species, such as its absolute abundance at some sites or its total population size, the use of entropy as an offset can be avoided by deriving an estimate of \( c \) and therefore the probability of presence for quadrats of any given size. This is analogous to using additional information about the

**Figure 1.** Comparison of logistic and cloglog transforms of Maxent output. For simplicity, no constant offset is shown in the transforms. A constant offset (such as the entropy of \( p_\lambda \), as described in the text) would shift both curves to the left or to the right, depending on its sign.
Maxent as infinitely-weighted logistic regression (IWLR): the maxnet package

Because Maxent is an IPP, standard generalized linear modeling software can be used to fit Maxent models via Poisson regression (Renner and Warton 2013), or even more conveniently, using standard logistic regression (Fithian and Hastie 2013). Specifically, the latter authors showed that the coefficients $\beta$ of the Maxent or IPP model can be fitted via a weighting process they call infinitely-weighted logistic regression (IWLR). The idea is to fit a logistic model to occurrence records (with response variable $y = 1$) and background data (points chosen randomly from the domain $D$, with response variable $y = 0$). This process yields coefficients $\beta$ for an exponential model, and has been used in studies of resource selection by animals (Manly et al. 2002), but may not produce the same values of the coefficients as Maxent. The novel contribution of Fithian and Hastie (2013) was to give a large weight $W$ to all the background data and to show that the limit (as $W$ tends to infinity) of the resulting vector of logistic regression coefficients equals the Maxent (and IPP) coefficients. This allows Maxent (and IPP) models to be fitted using standard GLM software.

Table 1. Comparison of performance of Maxent models with varying choices of feature classes and output transforms, for a reference data set of occurrence records of 226 species, and presence/absence data for model evaluation (Elith et al. 2006). Maxent feature classes are abbreviated as ‘l’ (linear), ‘q’ (quadratic), ‘p’ (product), ‘t’ (threshold) and ‘h’ (hinge). Results are shown for analyses run with random background pixels, as well as for those implementing a target-group background (Phillips et al. 2009). The AUC statistic measures area under the receiver operating characteristic curve, while COR measures the correlation between model output and 0/1 evaluation data representing observed absence/presence.

<table>
<thead>
<tr>
<th>Feature classes</th>
<th>Output scaling</th>
<th>Study with these defaults</th>
<th>Random background</th>
<th>Target-group background</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lqpt</td>
<td>Cumulative</td>
<td>Elith et al. 2006</td>
<td>0.7220 0.1989</td>
<td>0.7534 0.2368</td>
</tr>
<tr>
<td>Lqpth</td>
<td>Logistic</td>
<td>Phillips and Dudík 2008</td>
<td>0.7282 0.2110</td>
<td>0.7575 0.2447</td>
</tr>
<tr>
<td>Lqph</td>
<td>Raw</td>
<td></td>
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<td>0.7593 0.2404</td>
</tr>
<tr>
<td>Lqph</td>
<td>Logistic</td>
<td></td>
<td>0.7296 0.2125</td>
<td>0.7593 0.2465</td>
</tr>
<tr>
<td>Lqph</td>
<td>Cloglog</td>
<td>Present paper: Maxent</td>
<td>0.7296 0.2120</td>
<td>0.7593 0.2479</td>
</tr>
<tr>
<td>Lqph</td>
<td>Cloglog</td>
<td>Present paper: maxnet</td>
<td>0.7271 0.2100</td>
<td>0.7587 0.2490</td>
</tr>
</tbody>
</table>

Figure 2. A Maxent model for the brown-throated three-toed sloth Bradypus variegatus using the logistic transform (left) and cloglog transform (right). Occurrence data from Anderson and Handley (2001); for details on predictor variables, see Phillips et al. (2006).
new R package for fitting Maxent models (maxnet, available at <https://CRAN.R-project.org/package=maxnet>) does just this – leveraging the glmnet R package (Friedman et al. 2010) to fit an \( l_1 \)-regularized logistic regression model with a large weight \( W \). A weight of \( W = 100 \) is used by default, in contrast to a weight of 1 for occurrence records.

Instead of upweighting background points, we may equivalently downweight presence points (Renner et al. 2015). In addition, the intercept term (\( \theta \), above) can be manipulated by choosing the background weights based on the area of the study region, so that the resulting IPP is scaled in units of occurrence records per unit area (Renner et al. 2015). Given the area of the study region, this weighting scheme could easily be used with maxnet, though it would not affect any of the standard output formats (raw, cloglog etc.) since none of them use \( \alpha \).

There is a variety of R packages available for fitting point process models (Renner et al. 2015), so why introduce another? The novel contribution of maxnet is to implement all the derived feature classes (especially hinge features) and default tuned regularization values of the Maxent Java application, so that Maxent models can be fitted natively and easily in R. The package is brief – about 200 lines of code implementing feature classes and regularization parameters, model fitting, predicting from a model, and plotting of response curves. Additionally, it provides some simple use examples based on the *Bradypus variegatus* brown-throated three-toed sloth data set from Phillips et al. (2006). The purpose of the package is to replicate the behaviour of the Maxent Java application by using the equivalence with IPPs; this complements Renner et al. (2015), who show (Supplementary material Appendix 1 section 6) how to adjust default settings in the Maxent application in order to fit an IPP.

When run on the data set of Elith et al. (2006), maxnet has similar performance to the Maxent Java application. Small differences are likely due primarily to different implementations of hinge features and different random choices of background data. In order to limit computation time, the maxnet implementation of hinge features uses 50 hinge features per environmental variable by default, with evenly spaced knots, in contrast to Maxent which may use one knot per unique value of the environmental variable. The scripts used to run maxnet on that data set appear in the Supplementary material Appendix 1, along with further examples of usage.

**A change in default feature classes**

Both the previous and current releases of Maxent allow the use of quadratic, product (or interaction), threshold (or step-function) and hinge (piecewise linear) features, in addition to the original environmental variables (linear features). The default selection of feature classes for use in the model depends only on sample size, though \( l_1 \)-regularization forces many coefficients to zero. Given enough occurrence records (80+), all of the derived feature classes were previously considered by the model. Version 3.4.0 differs by omitting threshold features by default (although they are available as an option), since this appears to improve model performance generally and results in models that are smoother and simpler, and hence likely to be more realistic. Avoiding use of threshold features makes a small but useful improvement to the performance of Maxent (Table 1) on the data set of Elith et al. (2006). The differences in AUC and COR are similar to differences within the three groupings of modeling methods in Elith et al. (2006), but smaller than differences among groupings. Apparently hinge features, which were introduced to Maxent later than threshold features (Phillips and Dudik 2008), are best used as a replacement for threshold features rather than as a complement. Hinge features provide at least as much flexibility in the fitted response to predictor variables as threshold features, while tending to reduce over-fitting to the training data. The scripts used to run Maxent with various settings for Table 1 appear in the Supplementary material Appendix 1. Unfortunately, the data set of Elith et al. (2006) is not yet publicly available, but if and when it is publicly released, a link to it will be added to the AMNH web site, so that the values in Table 1 can be easily replicated.

We emphasize that the settings used in the analyses reported in Table 1 are merely defaults, and the best choice for other data sets may be different (Merow et al. 2013, Radosavljevic and Anderson 2014). We have also found that product features barely improve average performance on the data set of Elith et al. (2006) (not shown), and could usually be omitted in order to make simpler and more easily interpreted models. Importantly, avoiding product features enables the use of the Explain tool to interactively explore model predictions (Elith et al. 2010, Renner et al. 2015).

**Future directions**

Species distribution models based on Maxent and IPP remain an active area of research, as new methods are developed to accommodate the challenging nature of occurrence data and species distributions (Fithian et al. 2015, Merow et al. 2016). The open-source release of the Maxent Java code, together with the maxnet R package, will facilitate the work of others in improving the science of modeling species distributions. Similarly, we hope that it will facilitate the practical and public use of Maxent for mapping and preserving biodiversity, as done by the Atlas of Living Australia (<www.ala.org.au/>).

The IPP perspective on Maxent input requirements and interpretation of model outputs should provide new direction for research regarding studies of population abundance. One conclusion is that under certain assumptions regarding the occurrence data, Maxent’s raw (exponential) output can be interpreted as a model of relative abundance (Renner et al. 2015). A natural question arising from this is whether in practice, raw output indeed better correlates with local abundance than logistic output (as used by VanDerWal et al. 2009). This should also inform meta-analyses of relationships between SDM output and abundance and other measures of population performance (Weber et al. 2016).

The IPP model also offers new insights into spatial dependence for Maxent models, along with some tools for
detecting spatial trends in residuals (Renner et al. 2015). When we use the IPP intensity to infer a Poisson distribution for abundance within a quadrat (Eq. 3) and thereby determine probability of presence therein, we make a strong independence assumption, namely that presence of the species at nearby points within the quadrat is conditionally independent given the predictor variables. This assumption may often be violated on fine spatial scales, for example because individuals in close proximity interact through competition, reproduction, etc., and disturbances such as fire impose spatial signatures on species’ patterns of distribution (including abundance). Outstanding questions include: how important is this violation in practice when using IPP/Maxent for modeling abundance or probability of presence from occurrence data? In what circumstances should modelers resort to more complex variants of IPPs (such as Gibbs or Cox processes; Renner et al. 2015) to explicitly model spatial dependence? Similar issues arise when modeling abundance from count data: patterns of occurrence and abundance may be affected by different processes, resulting in excess zeroes in the abundance data (Wenger and Freeman 2008). This is likely related to the finding that Maxent models predict a ‘potential/maximal abundance’, which may not be attained at all sites (VanDerWal et al. 2009). Zero-inflated models are often used in place of simpler Poisson models when modeling abundance from count data that exhibit excess zeroes (Barry and Welsh 2002). Perhaps similar ideas can be applied to occurrence data.

The maxnet R package encodes feature classes and regularization defaults in order to fit the same models as the Maxent Java application, opening up new ways to better integrate Maxent modeling with the wide variety of visualization and analysis tools available in R. Future contributions to maxnet could facilitate this integration, for example by contributing code and/or a vignette that links maxnet with the dismo package or the ENMeval package (Muscarella et al. 2014) which manage data preparation, modeling and evaluation for SDM. A test suite would be added on the data set of Elith et al. (2010) and thereby generate new open-source software resources and tools. And innovate towards improvement of the software, and to generate new open-source software resources and tools.

to Maxent or acknowledge its use, cite this Software note as follows, substituting the version of the application that you used for ‘version 0’:


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**References**


