

National Environmental Science Programme



Modelling distributions of species under environmental change

A report to The Environmental Resources Information Network (ERIN), Australian Government Department of Agriculture, Water and the Environment (DAWE)

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Front cover: White bellied frog (Geocrinia alba). Photo: Adam Parsons

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Executive summary

The Department of Agriculture, Water and Environment has requested a review of their internal species distribution modelling practices used by the Environmental Resources Information Network, and last reviewed more than a decade ago. We have concluded that the current practices are still valid for the purpose of describing broad distributions of species across temporally static landscapes. The modelling can be improved upon with respect to treating survey bias and evaluating predictions, and we provide recommended methods to accomplish this. We also provide recommendations to accommodate landscape/climate change and species range shifts, albeit with more sophisticated and complex models that are more data-intensive. The highest-priority identified task is to implement automated analysis systems – currently underway in the Collaborative Species Distribution Project.

Section 1: Introduction

Within the Department of Agriculture, Water and Environment (DAWE), species distribution modelling (SDM) is used to identify species of national environmental significance which may potentially be impacted by development and to inform subsequent conservation planning decisions. These practices were last reviewed more than a decade ago, and despite advances in distribution modelling tools and approaches, have not been updated to reflect current best practice.

Conservation decisions rely on robust information about the current and future distributions of threatened species, which are used to inform policy, conservation and recovery planning, offsets, and environmental impact and strategic assessments. There is a need to identify modelling approaches that can be broadly and swiftly applied across thousands of species (including those with limited data), to provide robust distribution predictions that are suitable for particular applications under a range of future climate change scenarios. In DAWE, a precautionary approach is taken for species distribution modelling to consider all places that species might occur, as the distributions are primarily used to identify species of national environmental significance which may potentially be impacted by development. However, if the models do not adequately capture changes that are likely to happen to species' distributions under future conditions, the approach will not be as conservative as believed, as it is missing key processes driving distribution through time. Further, if the models are intended to inform conservation planning or recovery actions at finer scales, alternative procedures and methods may be required. These deficiencies will lead to mismatches between recommendations made by the department and threatened species' responses.

Using models that are fit-for-purpose to predict species distributions under future conditions and at varying scales will improve versatility and enable the department to appropriately advise stakeholders on how best to ensure preservation of threatened species into the future. This will likely impact each facet of the department's use of species distribution models: assessing impacts of development on threatened species, prioritising areas for conservation management and recovery plan actions, informing strategic assessments, and assessing invasive species mitigation strategies. These improvements to modelling distributions under future conditions and at varying scales will be explored here with a synthesis of best-practice methods, such as biophysical modelling, providing tangible guidelines for future work.

There was a pilot Collaborative Species Distribution Modelling (CSDM) project, led by researchers at Griffith University, to critique and standardise correlative SDM practice (focusing only on Maxent as a modelling method) which involved DAWE and several state agencies. Consequently, we will only report here on topics and items not extensively covered through the CSDM project to avoid unnecessary duplication of information. Because CSDM is a tool that operates on decisions made by an analyst, we discuss more broadly the topics relating to these choices. We also highlight any contemporary departures or omissions from the original recommendations of the report by Elith (2008), provide key literary references, and in applicable sections, some worked technical examples.

The aims of this report are to:

- 1. Review the current SDM practices used by the Environmental Resources Information Network (ERIN) of the DAWE with respect to contemporary practice;
- 2. Assess key modelling practices identified in the original report (Elith, 2008) and highlight any updates to original advice;
- 3. Identify limitations of current modelling practices to address multiple objectives and propose updates to existing modelling practices; and
- 4. Introduce new modelling operations that consider shifts in species ranges.

We will use a motivating case study throughout the report to demonstrate some of the introduced concepts -Greater Gliders (Petauroides volans), a nationally-listed vulnerable species, in the East Gippsland region of Victoria (Figure 1). These data were sourced from the Victorian Biodiversity Atlas (VBA) maintained by the Victorian Department of Environment, Land, Water and Planning (DELWP) and include presences, absences, and inferred absences (i.e. generated from observations of other arboreal mammal species).

Note, the Greater Glider is well studied and therefore the quality and quantity of observation records do not characterise many of the data-deficient threatened species for which DAWE models the distributions. Further, DAWE considers species distributions at the national-scale and must consider all available data across their whole range. We provide this example to illustrate some of the concepts discussed in the report.



Figure 1: Map of the East Gippsland region of Victoria. Species data are: presences (red circles), species absences (black triangles) and inferred species absences (blue squares). The road network is shown as light gray lines.

Section 2: Evaluation of current ERIN/DAWE SDM practices

The general processes used for modelling species distributions in correlative frameworks have not changed much over the past decade and the description in Section 3.2 of Elith (2008) is still applicable. To summarise some key points that will be relevant for this report:

- What is being predicted from the models is a subset of the environmental niche, not the entire fundamental or realised niches, of a species. This is because correlative SDM is not able to incorporate biotic factors such as dispersal or vital rates but see alternatives in Section 4 of this report.
- SDM uses environmental information, which is tied to geographical information, and this can lead to patterning due to spatial autocorrelation in environmental conditions. These patterns arise despite geographical patterning in the species observations but spatial information can be explicitly added to the modelling to address this issue.
- Features of species data that may degrade model quality are: insufficient sample size of observation points to capture major trends in the environmental space, co-dependent or duplicate observation points, inaccurate taxonomic identification, high uncertainty in spatial locations, large time lags between observation records and intended timespan of model predictions (e.g. change in habitat), and biased sampling (e.g. close to roads or towns).
- Features of predictor variables that may degrade model quality are: environmental variables not relevant to species ecology, inappropriate scale (i.e. resolution), and high correlation between predictors.
- Models are mathematical simplifications of data and will always contain error. Consequently, predictions made from models will have uncertainty which should always be represented wherever possible. Evaluation and refinement can reduce model error and uncertainty in predictions.
- Using presence-only data has theoretical and practical limitations for species distribution models. Presence/ absence and abundance data should be collected, archived in a suitable database, and used for modelling whenever possible.

2A. Choice of modelling method

Although several methods exist for performing correlative species distribution models, the choice of Maxent as a modelling method is still valid and applicable to the current SDM work being conducted at ERIN/DAWE. Maxent is freely available, computationally efficient, easy to use, and well-described in the ecological and SDM literature (Elith et al, 2011). In the past few years, there have been two notable changes to the Maxent software, however, these should not have any major implications for the outputs produced at ERIN/DAWE.

To improve its agreement with theoretical work, Maxent now uses the complementary log-log (cloglog) link as a default rather than the logistic link often found in generalised linear modelling. This provides a stronger theoretical justification for Maxent being essentially equivalent to an inhomogeneous point-process (Renner & Warton, 2013; Phillips et al, 2017). The response curves between the logistic (employed in past versions of Maxent) and the cloglog (default in the newest version of Maxent) functions are quite similar - lower predicted probabilities will be nearly indistinguishable (Figure 2). However, given that presence-only data is often opportunistic (i.e. collected without respect to systematic survey design), it can be envisioned as observation events arising randomly in both space and time. Further, this link assumes that binary data arise from the truncation of count data, which is often the case in ecological studies on species distributions. Spatially-duplicated observations (despite differences in time) are collapsed to single observations (regardless of initial data treatments) by Maxent and, therefore, the choice of this link function is appropriate. For more information on the relationships between count, presence-absence, and presence-background (or point) data in SDM, see Aarts et al (2012).



Figure 2: Differences in predicted habitat suitability between the cloglog (left panel) and logistic (center panel) transformation from a Maxent model trained on presence-only data, 10,000 randomly selected background points, and eleven environmental predictors at 500m resolution. The right panel shows the difference between the two.

One important caveat to using the cloglog link is that all points are assumed to be spatially independent which may not be realistic considering many species' patterns of distribution exhibit spatial dependence (e.g. flocks of birds or mobs of kangaroos). Methods (e.g. Ripley's K-function – see Figure 3) and software (e.g. Spatstat - Baddeley et al, 2015) exist to detect spatial dependence. Spatial dependence, if detected, can be corrected for, however, this adds complexity to the modelling process and may not be practical for ERIN. Given the large amount of species distributions required by ERIN, this is an area where automating modelling procedures can prove useful (see Section 2D).



Figure 3: Estimated Ripley's K for occurrence points. The dashed red line is what would be expected if the data had no spatial dependence – what Maxent assumes – and the solid black line indicates the patterning in the observations. A solid line above the dashed line indicates clumping and below the dashed line suggests dispersion. Ideally, the two lines should be coincident.

The questions articulated in the preceding phase will, in all likelihood, guide development of the program design itself. The other change in recent versions of Maxent is a disabling of the "threshold feature" option. This change has two justifications; first, omitting this type of feature generally improves model performance and produces smoother and simpler response curves – likely to be more realistic for biological systems (Figure 4). Second, "hinge features" work better as replacements, rather than complements, to "threshold features". Hinge features match threshold features with respect to flexibility in fitted responses to predictor variables but tend to reduce model over-fitting (Phillips et al, 2017).



Figure 4: Maxent model fitted response curves for likelihood of occurrence against minimum temperature of the coldest period (TEMPMINCP) with a) threshold feature disabled (default), and b) threshold feature enabled. Disabling the threshold feature results in a more easily interpreted variable.

Tracking and assessing modelling choices, as recommended by Elith (2008), is always important regardless of the modelling methods used. This appears to be captured via metadata in many steps throughout the ERIN/DAWE map update process. The newly established CSDM project aims to automatically record and summarise model parameters and deliver it to users via metadata. Although it is assumed that analysts have carefully thought about parameter choices for a model, we recommend reviewing all metadata about modelling choices and performing sensitivity analyses around parameters thought to contain high uncertainty.

2B. Considerations for input data

Treating and/or reducing sampling bias has been identified as a difficult area by ERIN/DAWE and strategies to reduce bias appear not to be incorporated into the current workflow. Presence-only data makes treating bias difficult and the information presented in Section M6c of Elith (2008) is still quite relevant today. Fourcade et al (2014) simulated four types of sampling bias in presence data based on splits and clustering and compared different treatment methods and Maxent model outputs. Some common methods for addressing sampling bias are spatial filtering (thinning occurrence points prior to modelling – as currently practised by ERIN) and bias files (additional layers added to the model).

Spatial filtering attempts to remove bias by thinning presence points based on interspatial proximity - i.e. observation records are removed to maintain some minimum spatial distance of separation (Figure 5). Given an adequate amount of initial records, this method has been shown to improve model performance (Boria et al, 2014). The choice of spatial separation distance between observations will depend on the heterogeneity of the study area and characteristics of the target species; sensitivity analyses can help identify useful values. Whilst this method is useful to incorporate into SDM, if additional data that quantifies the spatial biases are available, we recommend implementing these data as inputs into models. Note, these treatments have statistical motivations – primarily to avoid violating assumptions of independence in sampled data. The nature of ecological systems and small sample sizes make this very difficult (e.g. sedentary organisms with potentially very limited range and habitat). In these cases, we recommend assessing spatial patterns in the observations using methods such as kernel-density estimation or similar (see Baddeley et al, 2015), even if spatial treatment prior to modelling is not possible.



Figure 5: Occurrence points thinned to maintain a minimum 1000m separation distance.

Spatial layers can be used to characterise patterns of sampling effort, such as distance to roads or urban areas (Warton et al, 2013). These treatments are referred to as 'bias-predictor' or 'bias-corrected' methods. Both treatments use additional model predictors (Figure 6) to represent the assumed bias in the data and are therefore applied to all points (presence and background) in the modelling. The distinction arises in how the explanatory variables are treated during prediction. The bias-predictor method uses the values sampled from the spatial layers to fit the model and predict outcomes. Similarly, the bias-corrected method also uses the values sampled from the spatial layers to fit the model. However, once the model is fitted to the data, all values are set to a constant (typically, the mean value across all species occurrences or zero) in the bias layers before making predictions (Figure 7). Note, if bias layers are used in modelling, it is important to disallow interactions between bias-predictors and other environmental predictors in the models (i.e. create a purely "additive" model, see Warton et al, 2013). By default, Maxent uses several "features" (i.e. functional relationships between predictors) when fitting models. Therefore, attention should be paid to the feature settings used in Maxent if modelling with bias-predictors. Further, all environmental predictors should be screened for high amounts of correlations with bias-predictors as this will negate the effects of bias-correction. Habitat selection by a species may coincide with patterns in bias layers and therefore high correlation may be observed between environmental predictors (e.g. vegetation greenness) and bias layers (e.g. roads). In these cases it is up to the analyst to draw upon biological knowledge of the species and decide whether it is prudent to incorporate the bias correction methods. Alternatively, other environmental predictors can be selected for use or transformations can be made to environmental predictors to reduce correlations. Experimentation will be necessary and is recommended.



Figure 6: Sampling bias predictor indicating distance from towns or roads. Note, the distance values have been rescaled to be between zero and one and then inverted (i.e. values near one are closest to roads).



Figure 7: Differences in predicted habitat suitability between no use of bias-correcting environmental variables (left panel) and use of bias-correcting roads layer (center panel). Maxent model trained on presence-only data, 10,000 randomly selected background points, no interaction effects, and environmental predictors at 500m resolution. The right panel shows the difference between the two.

Inferred absence points (Figure 1), also known as "target-group background" can also be used to account for sampling bias. These are observations of similar species separated by a set spatial distance from, and assumed to have the same sampling biases as, target species occurrences. Whilst model predictions may be considered more robust using this method (Figure 8), they are still unable to differentiate between regions not sampled due to inaccessibility and regions where a species has low occurrence rates.



Figure 8: Differences in predicted habitat suitability from random background (left panel), and target background (center panel) selected from presences of other arboreal species at least one kilometre from greater glider observations. Maxent model trained on presence-only data, 1,955 randomly selected background points or target background points, and environmental predictors at 500m resolution. The right panel shows the difference between the two.

Presence-absence and count data for many surrogate species, thought to exhibit the same patterns of sampling bias, can also be used to correct for bias in presence-only SDM. Fithian et al (2015) used an Inhomogeneous Poisson Process (IPP) model with an added function representing the fraction of individuals near presence-only locations determined by the presence-absence data. This joint analysis of presence–absence and presence-only data obtains more precise and reliable estimates of species distributions, however, requires more sophisticated modelling methods and large amounts of data. Given the additional requirements, these methods may not be possible for ERIN at the current time. Further, as with many other modelling methods, spatial autocorrelation and errors in the data, and biased detection of presences/absences, can be problematic. Nevertheless, we recommend the collection and use of presence-absence (see Yackulic et al, 2013) and count data to augment further SDM work and for use in future alternative modelling methods.

Issues resulting from small sample size are also problematic for ERIN/DAWE. This is a common problem when modelling data-deficient species. As alluded to in Elith (2008), Maxent may produce reasonable models with small sample sizes (at least 15 records). However, the accuracy of these models is highly influenced by geographic range size and environmental tolerance of species. This highlights the importance of selecting a relevant boundary (extent) and resolution (cell size) to model and make predictions for and is discussed in more detail in Section 3 of this report. It is difficult to assign fixed numbers as guidelines for required observations given all of the complexities involved in modelling ecological systems. As a general rule, more observations used to train a model are better – provided they have been assessed for quality and spatial patterning.

The choice of feature classes and regularisation parameters influences the ability of Maxent to model species with low sample sizes (Shcheglovitova & Anderson, 2013). In cases where species occurrences are fewer than 80 records (most of the species modelled at ERIN), Maxent will reduce the number of feature classes used. Maxent "features" are derived from the environmental predictors and "feature classes" are the types of functional relationships of the predictors including: linear, quadratic, product, threshold, hinge, and categorical indicator. These relationships are analogous to fitting transformations on, and interactions between, predictors in generalised linear regression and are important to consider – especially when Maxent is choosing what to include and not include based on small sample sizes. The threshold numbers of presences at which Maxent uses different feature classes can be manually set in the software settings (Figure 9). For rare species, we recommend performing a sensitivity analysis on these parameters to determine optimal settings (see Merow et al, 2013).



Figure 9: Differences in predicted habitat suitability between limited feature classes (left panel - default for low sample sizes) and an adjusted threshold to enable the use all feature classes (center panel). Maxent model trained on 11 occurrence points, 10,000 randomly selected background points, and environmental predictors at 500m resolution. The right panel shows the difference between the two.

Other methods employ simulations of species presence and absence to determine minimum numbers of presence records required for various levels of species prevalence (van Proosdij et al, 2016). This can be difficult, however, as it requires prevalence (ratio of unoccupied to occupied cells in a landscape) to be known a priori which is not possible with presence-only data or presence-absence with unknown species detectability. Therefore, there are several assumptions to be made when simulating presence and absence data for a species and the high levels of uncertainty may render simulation methods poorly suited to applied ecological problems.

Surrogate species are sometimes used in ecological studies to provide missing information for data-deficient species. The level of detail can vary from a single value for a parameter (e.g. survival rate) to spatial and temporal data about species observations. Whilst surrogate species occurrences are more often used to correct for bias in SDM, they can also be used to increase sample sizes for rare species. This practice, however, comes with high uncertainty and many underlying assumptions, requires sophisticated knowledge of the target biological organisms (often not available for many threatened species - especially the more poorly known / recently discovered ones), and is rarely encountered in the literature. Organisms with strong host-dependent relationships, where one organism is difficult to survey, and consequently rare, may lend itself to this data-augmenting practice.

Ensemble approaches have also been used to account for rare species with low numbers of observations (Breiner et al, 2015). Ensemble modelling refers to fitting several small models, making predictions, and then averaging the predictions to produce a single output. Having an adequate number of samples relative to predictors is considered good statistical practice but this can be problematic for analysts having a large suite of biologically-relevant predictors but a small sample size, as in the case of rare species. Lomba et al (2010) used an ensemble approach to create a large number of bivariate (two predictor) models - spanning a large set of environmental predictors - from which the predictions were combined using a weighted average based on each model's performance (e.g. Figure 10).



Figure 10: Differences in predicted habitat suitability from a single Maxent model using all environmental variables (left panel) and an ensemble of 55 bivariate (two environmental variable) models (center panel). For the ensemble, predictions were aggregated from all models weighted by their performance (AUC). Models were trained on 11 occurrence points, 10,000 randomly selected background points, and environmental predictors at 500m resolution. The right panel shows the difference between the two.

Regardless of improvements in modelling data-deficient species, increasing the pool of relevant, high-quality observations will improve statistical power, and consequently, predictions from SDM. If any survey records exist outside of digital databases, we recommend prioritising the digitising and quality-controlling of these data. Metadata should also be catalogued to capture information such as uncertainties in spatial location and collection time - this is useful to assist with subsetting data to fit the intended purpose of modelling (see Section 3).

We will conclude this section on a final note about the number of background points required for modelling. A longstanding convention has been 10,000 background points, likely influenced by Phillips & Dudik (2008) or Barbet-Massin et al (2012) albeit a number not necessarily endorsed by the authors. This coarse rule is obviously flawed as it doesn't take into account the geographical extent or spatial resolution of a landscape - both of which influence the choice of background points. This had led some modellers to choose the number of background points as a percentage of the total number of grid cells. In the case of Maxent, which internally thins points to one per grid cell, it is worth considering how this thinning process would affect the distribution of background points. We recommend analysts perform sensitivity analyses on the choice of background point sample size and determine an optimal number. One method to determine the best number of background points is to use an iterative process fitting multiple Maxent models with identical parameterisations and input data with differing numbers of background points to determine a threshold above which the model output (predictive accuracy) does not change much (Figure 11). This analysis can be easily achieved by using automated methods (e.g. computer scripts).



Figure 11: Maxent model performance (AUC; in-sample validation) based on background sample size. The x-axis indicates both the total number of randomly-sampled background points and their percentage of total grid cells in the landscape (48,749). Models were trained on presence-only and environmental predictors at 500m resolution. In this case, background points that cover between 18 – 60% of the landscape grid cells produce similarly well-performing models.

2C. Model Evaluation

Elith (2008) describes different methods for model evaluation which include both automated (i.e. statistical analyses) and manual inspection of maps by experts. ERIN/DAWE have included peer review in their workflow - eliciting species experts to provide comment on predicted distributions – and validate their predictions with independent data for a small portion of species (dependent on data availability). This information is catalogued in detailed metadata for each species. Given that the intent of modelling is to make predictions about where species occur in the landscape, assessments of model fit to the data alone do not adequately identify model utility. Incorporating validation methods that are systematic and automated, if implemented correctly, could improve the applicability of SDM outputs.

Maxent offers three forms of replication to evaluate models; cross-validation, repeated subsampling, and bootstrapping. Bootstrapping and cross-validation both sample/split the data into information used to fit the model (training) and information used to compare to fitted model predictions (testing). Two major differences arise in the number of, and the overlap between, observations used to train and test models.

In bootstrapping, the sample size of both the training and test datasets are equal; species observations (presences and background) are sampled at random with replacement (i.e. unique observations can appear multiple times) to fit a model and make predictions. The predictions are then compared to the original dataset to estimate prediction error. This process is then repeated many times, resampling at random each time, and the results are averaged.

Cross-validation involves dividing the data into smaller subsets, fitting models to all but one subset, making predictions, and then comparing predictions to the subset of data not used for model fitting. This procedure is repeated to accommodate all subsets - in other words, all subsets are used in both model fitting and testing. Like bootstrapping, prediction error is averaged across all folds; unlike bootstrapping, there is never overlap in the subsets (i.e. each of the validation folds are distinct from the other training folds). K-fold cross-validation is a commonly used method for estimating the prediction error of species distribution models (Figure 12). K refers to the number of folds, or splits, in the data used to fit and test the models. It is generally accepted practice that specifying between five and ten folds satisfies tradeoffs between bias and variance, however, this is contingent upon a large enough sample size to accommodate the number of splits.

When using cross-validation, Merow et al (2013) suggest avoiding thresholding and only using metrics based on how well the model predicts presences (sensitivity) and Hijmans (2012) cautions that interpreting cross-validation results is only meaningful when "spatial sorting bias" has been addressed and/or results are calibrated with the results for a null model - albeit this advice is specific to presence-absence data.



Figure 12: Differences in predicted habitat suitability from a single Maxent model iteration (left panel) and 10-fold iterations where data is held-out and tests the model fit. For the 10-fold iterations, predictions were aggregated from all models (center panel), weighted by their performance (AUC). Models were trained on presence-only, 10,000 randomly selected background points, and environmental predictors at 500m resolution. The right panel shows the difference between the two. For this example, the differences in predicted values were slight; however, this may not always be the case and should be verified.

Spatial patterning in the data and unequal ratios of presence to background data (prevalence) between folds are two considerations when using cross-validation. Spatial patterning is common in ecological data because of species' behaviours and biotic interactions (Figure 13), however, also arises from the manner in which species observations are recorded (e.g. sampling close to roads or towns). In some SDM these spatial patterns are corrected for by modifying model parameters or inputs (see Dormann et al, 2013) but few studies address spatial patterning during evaluation. Prevalence should be consistent throughout all of the folds used for evaluation and naive selection of observation points for cross-validation often ignores this. This problem is compounded by presence-only data where assumptions are often made about the distribution of the background sample, and for which prevalence must be inferred.



Figure 13: Moran's I is a measure of correlation between values – often based on distance (in this case Euclidean). This plot indicates marginally high correlation in the model's residual error (perhaps from spatial autocorrelation in the predictor variables) at small distances between observations and decreasing correlation at larger distances.

Both considerations above can be addressed by using a technique known as "block" cross-validation (Roberts et al, 2017) which involves separating the data based on spatial, temporal, or relational characteristics. However, the analysis involved in defining the blocks can be laborious and may not add much value if modelling data is of high quality and other forms of bias treatment have been incorporated (Figure 14). Valavi and colleagues (2019) have developed software to assist with choosing blocks and describe some of the techniques involved. This software also assists analysts to determine how many observations should be used in developing the model, and how many observations should be reserved for evaluation (Figure 15). This development will easily integrate into the CSDM project which may make block cross-validation a more feasible option for incorporation into ERIN's SDM workflow.



Figure 14: Differences in predictions using 10-fold random cross-validation (left panel) and block cross-validation (center panel). Models were trained on subsets of presence and 10,000 randomly selected background points, and environmental predictors at 500m resolution. The right panel shows the difference between the two.



Figure 15: The 'BlockCV' software developed by Valavi and colleagues (2019) automatically determines the presence and background observations to be used in model fitting and evaluation based on a specified block size (right panel). A block size that minimises the effects of spatial autocorrelation in the environmental variables is also automatically determined by the software (inset panel).

Cross-validation can give an indication of uncertainty by using each model fitted to a subset of data to predict habitat suitability and then generating statistics on each cell in the stack of predicted rasters, such as the quantile ranges (i.e. 25th and 75th percentile values) or the differences between maximum and minimum predicted values (Figure 16).



Figure 16: Predictions using 10-fold random cross-validation (left panel) and uncertainty in predicted values represented by absolute differences in maximum and minimum habitat suitability values (right panel). Models were trained on subsets of presence and 10,000 randomly selected background points, and environmental predictors at 500m resolution.

Section 3: Modelling for conservation objectives

Modelling methods are often driven by data availability, resource provisions (e.g. computing power, expertise), and/ or administrative directives. Whilst these motivations may ensure efficiencies, and hopefully good modelling practices, they can also neglect alignment with management objectives. Villero et al (2017) discuss strategies to improve the connection between SDM and conservation practice, focusing on the decision context, modelling framework, and products for decision-making (model outputs). Importantly, all of these topics rely on robust methods of communication and feedback.

In the case of work done by ERIN, the current objective is to produce realistic and reliable spatial distributions of threatened species through modelling and prediction to support broadscale enforcement and regulatory operations at a national scale. The maps produced are referred to by, and featured in, species recovery plans which can be used as evidence to trigger referrals for actions with potentially negative environmental impacts. More importantly, the primary role is to underpin the spatial query tools for Environment Impact Assessments (e.g. Protected Matters Search Tool (external) and Wylie (internal)). With the exception of items noted in Section 2, we consider the current SDM operations and outputs to be acceptable for these purposes. However, the current data and methodologies employed by ERIN, or in the future CSDM platform, make predicting future distributions or range shifts extremely difficult (but see Section 4).

There are other potential uses of SDM outputs to inform environmental decisions. Examples include prioritising investments (Alagador et al, 2016), emergency response planning (Reside et al, 2019), biodiversity assessments (Araújo et al, 2019), and planning habitat critical to species survival. All of these activities would require additional procedures to be added to current SDM work conducted by ERIN. Whilst the maps ERIN produces may be used, to some degree, for the applications listed above, they are not promoted as the best models for purposes other than precautionary triggering of further investigations of potential impacts on Matters of National Environmental Significance (MNES) under the Environment Protection and Biodiversity Conservation Act (EPBC) Act .

The scale over which model data is fitted and predicted is important to consider when using SDM to assist conservation efforts. ERIN currently uses broad agro-climatic regions to assess and bound both the data used to fit models and prediction extents. Regardless of the modelling boundary chosen, if an area has not been consistently sampled, then accurate distributions are extremely difficult to ascertain. In areas of the landscape that are subject to high levels of disturbance, we recommend additional modelling and prediction be done at localised scales, and then compared to broader areas (Figure 17). Automated systems, such as the CSDM pilot project, would make these procedures less tedious. Note, more detailed SDM, and temporal change detection, may require much more data collection.



Figure 17: Differences in predicted habitat suitability between Snowy River National Park (local scale – left panel), East Gippsland (regional scale – center panel), and Southeastern Australia (broad scale – right panel) from a Maxent model trained on presence-only, 10,000 randomly selected background points, and 11 environmental predictors at 500m resolution. Note, models were fitted to species observations and environmental data that were contained within each respective boundary and then predicted to the local scale boundary for comparison.

Choosing a spatial resolution (the cell size of a projected raster layer) that is appropriate to capture the influence of microclimates on species is important, especially when assessing effects of climate change. Further, other threats such as fire and land use change may operate at different scales and it is important to accurately reflect their relative influences. Much SDM is performed using raster grids that have grid cells measuring one square kilometre - a common resolution for interpolated climate (e.g. Worldclim) or remote-sensed (e.g. MODIS) data. Statistical software that makes predictions directly to spatial outputs (i.e. raster grids), as opposed to sites, often requires all environmental predictor layers to match in scale, projection, and resolution. This requires an analyst to choose to resample all rasters to either the coarsest or finest resolution in the set of predictor layers. We caution against the assumption that one resolution is appropriate for all species and recommend choosing a resolution that will be most appropriate for the species and the management objective (Figure 18). Environmental predictors can be downsampled, through methods that consider other environmental data, to provide more relevant information (Lenoir et al, 2017). Bounding modelling and predicting to targeted areas for management may also provide data at spatial resolutions that are appropriate to the species and conservation objectives.



Figure 18: Differences in predicted habitat suitability between Maxent's model trained on presence-only 10,000 randomly selected background points, and 11 environmental predictors at 500m (left panel), and 1,000m (right panel), resolution.

Different conservation objectives (and modelling algorithms) require different baseline levels of input data. Guillera-Arroita et al (2015) describe the inferences possible with SDM using presence-only, presence-absence, and repeated presence-absence data. The authors also elaborate on several management objectives, including monitoring wildlife, prioritising invasive species management and estimating species richness, with respect to utility, and consequences, of modelling with each type of data.

Some conservation objectives, such as identifying climate refugia, require choosing environmental variables that more directly influence biotic processes (Williams et al, 2012). Summarising climate data to represent known or expected extremes (e.g. maximum period of low precipitation) may improve predictions (Morán-Ordóñez et al, 2018; e.g. Figure 19), however, should be carefully considered when used in combination with more generalised predictors that are potentially correlated.



Figure 19: AUC values for 197 models of mammal species using three predictor sets: AVG (long-term averaged climatic conditions), EXT (averaged short-term extreme weather conditions) and COMP (averaged short-term extreme weather conditions) and COMP (averaged short-term extreme weather conditions plus long-term average annual rainfall). The boxes indicate the 25th and 75th percentile interquartile ranges (median values shown as bold black horizontal lines) and error bars indicate approximately two standard deviations (95% confidence intervals). Figure taken from Morán-Ordóñez et al (2018) and shows that there are slight gains in model performance from using the extreme, and long-term weather conditions.

Explicitly incorporating species and habitat dynamics into SDM will be required for conservation objectives that involve ensuring the persistence of populations - methods are covered in detail in Section 4. Given range shifts and the potential failure to capture areas that are/may be critical to the survival of a species, an operational planning framework would be useful to incorporate into current ERIN modelling practices. This could involve a decision-tree that is used in parallel with information contained on a spreadsheet that summarises modelling objectives, data availability, resourcing requirements, and precedent case studies for a species. The decision framework should respond to variations in species characteristics and scale, and guide the analyst accordingly. For example, the analysis required for a wide-spread species with good biological data will be different than that of a poorly studied/observed species. Further, the scale of an analysis will depend on several factors including the availability of data, species characteristics (e.g. resiliency, dispersal), and threatening processes. No precedent case studies were discovered during this review, however, Guisan et al (2013) provides good guidance for incorporating the predictions of species distributions into conservation planning and is a good starting point for developing decision tools.

Section 4: Accounting for range shifts in species distributions

The need to characterise accurate range shifts in species distributions is a well-identified and researched problem. Despite known limitations, predicting range shifts via correlative SDM in relation to climate change projections has rapidly increased over the past decade. Three major challenges associated with current practice are dealing with the effects of niche truncation, model selection, and variance in model outcomes (Peterson et al, 2018).

The first challenge is based on biotic interactions and dispersal limitations, both implicit processes in correlative SDM. Although future predictions of distributions based on climate change may suggest range expansion or contraction due to suitable conditions, species (particularly rare or threatened) may be limited by other abiotic dispersal barriers such as topography or dependency on other species (e.g. host-dependent network relationships).

The second challenge is due to the recent methodologies incorporated in Maxent and other software to prevent over-fitting (i.e. balancing the bias-variance tradeoff). Albeit better than previous ad-hoc methods of adjusting model parameters and choosing the best performing model, there is still some discord between model performance and quality. It is recommended to first determine which models perform well when predicting to independent data, and once candidate models are chosen, then impose methods that aim to maximise model simplicity and complexity (see Merow et al, 2014b).

Lastly, whilst controlling for model uncertainty - when the aim is to predict species distributions in novel environments - is mostly methodological (e.g. choice of input data (Porfirio et al, 2014), modelling algorithm, or model parameters), it is also dependent upon the choice of climate scenario (representative concentration pathway, or RCP). Peterson et al (2018) demonstrated that the most important source of variation was in model parameters. This finding suggests that sensitivity analyses are an important addition to modelling operations, especially when predicting to novel environments, and cautions against mass processing of correlative SDM.

Given these limitations, we make several suggestions for ERIN to consider when incorporating climate change into a correlative SDM (e.g. Maxent) workflow.

- 1. Prioritising the use of environmental variables that are more directly related to a species (proximal) over variables that can be potentially confounded with other effects (e.g. topography) can reduce potential errors when extrapolating to novel environments. These decisions are often informed by biological knowledge of a target species, however, statistical tests can also be used for parameter selection by using information criteria (e.g. Zeng et al, 2016).
- 2. Assess the temporal scale over which the presence data and environmental predictors span (see Guevara et al, 2018). If models are fitted with species observations from before and after major disturbances (e.g. drought), but the environmental variables do not account for these events, there could be large errors in future predictions.
- 3. Weighting observation records based on assumed biases has been shown to improve model predictions and create more even spreads of future distributions (Elith et al, 2010). Treating bias is especially important when presence-background data is used to train models that extrapolate to future environments.
- 4. As predicting species distributions in future environments is highly uncertain, performing sensitivity analyses on model parameters is useful to identify, and potentially control for, sources of uncertainty.
- 5. Choose thresholds to transform predictions in future environmental conditions with caution. Nenzén & Araújo (2011) demonstrated that the choice of threshold can drastically affect species range expansions or contractions under future climate scenarios. The choice of thresholds will depend on the intended use of the model outputs and thus recommendations are difficult to make. Common choices involve maximising the sum of the sensitivity and specificity or using the lowest presence value but each may be more/less appropriate with respect to a conservation objective. See Liu et al (2013) for a good review of prediction thresholds.
- 6. Add a category titled 'future occur' which is defined as a broad environmental envelope or region within which a species may occur in the future based on range shifts. This category should include some measure of uncertainty; either as the range of predictions from models using a range of sensitive parameter values (item 4 above), or as a mean and standard error around predicted values.

Although correlative SDM have the ability to predict relative habitat suitability into the future, they fail to explicitly consider biological processes (e.g. dispersal limits, species interactions) or anthropocentric impacts (e.g. habitat modification, roadkill). In contrast, several process-explicit SDM techniques that incorporate population and habitat dynamics are available (Briscoe et al, 2019).

Occupancy dynamics models are able to incorporate the detection process in modelling species distributions. This is because they use repeated observations of species at sites to determine whether species are truly absent, or present and simply unobserved at the time of survey (false absence). This type of model is also able to predict changes in species distributions over time, or range dynamics. Simply put, these models consider two states (occupied or unoccupied) and transitions between states are based on probabilities of colonisation and local extinction (Figure 20). Freely available software packages, such as the statistical software R (R Core Team, 2020), can be used to fit these models as exemplified by a study on European crossbills (Kery et al, 2013). These models have limited ability to extrapolate to new areas and require structured input data but are useful for estimating extinction risks; however, perhaps not as well as phylogenetic models (Morlon, 2014).



Figure 20: Site occupancy dynamics under imperfect detection. Circles are the states of site occupancy and squares are the possible observations. Solid lines/arrows represent occupancy transitions and dashed lines/arrows indicate observations at each survey replicate. Figure taken from Kery et al (2013).

Biophysical models, also known as mechanistic niche models or eco-physiological models, use experimental firstprinciples of physiology to determine biological responses of species to environmental (often climatic) variables (Figure 21). For example, information may exist on how a species uses energy to thermoregulate based on their ecology and behaviour (e.g. activity and posture). This energy budget can be in surplus, allowing an organism to grow or produce offspring, in balance, or in deficit, resulting in reduced fitness and survival. Once models have been parameterised for a species, spatial and temporal distributions of climate data can indicate where species may thrive, perish, or redistribute (Kearney et al, 2010). Whilst these models have a tremendous ability to extrapolate to any area where climate data is available, they require specialised data to specify and fit, and can be computationally demanding (Cabral et al, 2017). Freely available software, NicheMapR - which runs in the statistical software R, has recently been made available to assist analysts with these models (Kearney et al, 2019).



Figure 21: A mechanistic niche modelling diagram. Heat, water and metabolic processes are a function of an organism's traits and the environments it experiences. The development and reproduction resulting from these individual-level processes affect population processes through vital rates (fertility, mortality), ultimately affecting distribution and abundance. Individual-level processes are further influenced by biotic interactions between species and within species. Figure taken from Kearney & Porter (2019).

Abundance dynamics models fit observed abundance data to simulated abundance data to verify the demographic and observation parameters used to build the simulation (Figure 22). Once these parameters are validated, they are then used to project future population abundances. This often involves a multiple step process. For example, Cabral & Schurr (2010) modelled the distributions of eight South African plant species by first simulating local population dynamics - based on demographic and dispersal parameters and a habitat suitability model - which resulted in spatially-explicit range dynamics (arrivals and departures in each grid cell across the landscape). A second model was then used to estimate the observation likelihood of individuals in each grid cell based on the simulations. Known species abundance data were used to validate the model predictions. These types of models can produce estimates of occurrence, extinction risk, and population size but have difficulty extrapolating to other environments. This is partly because of the correlative SDM which underpins the simulations. As with other modelling involving demographic parameters, reliable input data can be difficult to obtain.



Figure 22: The framework used to fit models of range dynamics to data on the spatial distribution of abundances. Figure taken from Cabral & Schurr (2010).

Demographic distribution (integral projection) models use environmental data to predict changes in vital rates – i.e. survival and fecundity (Figure 23). A population change parameter (lambda) is estimated from observed survival and reproductions of several life-stages of a species in a place (usually a grid cell). The lambda values can be above one, indicating growth in a population, or less than one, indicating a shrinking population. Lambda values are fitted to environmental variables in much the same way as species occurrences are fitted to environmental variables in correlative SDM. Similar to occupancy dynamics models, integral projection models require longitudinal data – in this case on individuals' survival, growth, and reproduction. These models offer insight into mechanistic processes occurring in species populations (Merow et al, 2014a), however, are difficult to extrapolate to new environmental conditions (Briscoe et al, 2019).



Figure 23: Workflow for Integral Projection Models (IPMs) in which demographic observations are linked to biological inference using linear regression. A relationship is first established between an individual's size in successive time intervals (panel a). The expected size at time t + 1 is then modelled using quadratic regression (red line) and the continuous regression functions are integrated to form a growth model (panel b). A discretised IPM kernel is derived from combining the growth model (panel c) with a survival and fecundity model and/or other environmental variables. IPMs are then projected across a landscape to produce a habitat suitability map (panel d). Figure taken from Merow et al (2014a).

Individual (agent) based models simulate dynamics of individuals based on rulesets which are then aggregated to populations. Each agent is an individual in a species population that interacts with other agents, biotic organisms, and the abiotic environment. As shown in Figure 24, where other simulation models operate in a top-down manner (e.g. vital rates are set at the population level), agent-based models simulate population changes arising from iterations between autonomous individuals (bottom-up). Once parameters are defined for a system, simulations can be extrapolated to other areas quite easily. Individual-based models have been around for several decades but have only recently featured in ecological studies (DeAngelis & Grimm, 2014). The high amount of data required to initially parameterise these models, and the unavailability of easy-to-use software, limits broader use.



Figure 24: The relationship between top-down and bottom-up approaches in ecological modelling. The top-down approach begins with conceptual ideas, applies state variable models and considers average individuals. The bottom-up approach begins with an individual-based model and 'theory' emerges from this approach if comparative computer experiments are performed. Figure taken from Grimm (1999).

Coupled SDM-population models – also referred to as spatially-explicit population models (SEPM) in the literature – link habitat suitability with other demographic (e.g. dispersal, vital rates) and landscape (e.g. clearing, climate) processes to simulate species persistence in space and time (Figure 25). Data on initial abundances of species – either observed/ surveyed or simulated – is required. Augmenting correlative SDM with population dynamics is not a new practice (see Akçakaya et al, 2004; Keith et al, 2008), and has been demonstrated to produce better forecasts of species distributions (Fordham et al, 2018). SEPM can be a useful extension to correlative SDM as they use predictions of occurrence or abundance as inputs to simulations. Manually combining model frameworks for all of the components required in SEPM (e.g. dispersal, growth, density dependence, biotic interactions) is possible (Merow et al, 2016), but software has been created to assist analysts to organise input data, streamline computations, and visualise results. Lurgi et al (2015) review several of these software in detail and Visintin et al (2020) have developed SEPM software that is freely available, highly customisable, and computationally efficient.



Figure 25: Spatially-explicit population modelling enables integration of spatial products from other modelling software, including climate, landscape, physiological and disturbance information to simulate changes in species abundance through space and time. These simulations require a habitat suitability layer, some initial abundances – either from existing data or simulated, and some information on vital rates (survival and fecundity) and dispersal characteristics for a species. Figure taken from Visintin et al (2020).

Section 5: Conclusions

Adopting the methods and recommendations outlined in this report will align ERIN's SDM procedures with current best-practice. It is understood that some of the required changes may be difficult due to staff limitations. It should be noted that many of the changes proposed in this report will have high "initial start-up costs" (especially the setup of automated processes), however, the long-term savings in time should provide adequate offsets. Additional benefits include increased quality and utility of SDM outputs produced by ERIN.

Although prioritising the recommendations in this report is a difficult task, we propose the following order:

- 1. Develop automated systems that are adequately parameterised for flexibility this is partially underway with the CSDM project for correlative SDM.
- 2. Expand existing databases to catalogue absences and abundance data, and digitise historic data. Further, provide a data repository with appropriate transfer and access agreements to receive unpublished/unlicensed data from researchers and Indigenous groups.
- 3. Develop decision-support systems which pre-empt automated modelling systems to ensure modelling efforts (and methods) are matched to conservation or regulatory objectives.
- 4. Incorporate methods to correct for sampling bias into existing operations.

Terminology used

Abiotic/biotic - used to differentiate non-living entities (abiotic) from living organisms or networks (biotic).

Bias-variance tradeoff - the balance between the simplicity and complexity of a model to maximise performance (fit to existing data) and generality (ability to predict to new data).

Fundamental/environmental/ecological niche - any environmental state that would allow a species to persist indefinitely.

Life stages - identified functional stages of development for a species (e.g. juvenile, subadult, adult).

Longitudinal data - data that track the same sample, or individual, over time and used for trend and state-based analyses.

Parameters - configuration variables that can either be estimated by a model given a specific set of data or specified to control the behaviour of a simulation.

Realised niche - portions of the fundamental niche where a species exists considering biotic interactions.

Sensitivity analysis - a technique used to understand how relative magnitudes of changes in model parameters change the performance or outputs of mathematical models.

Vital rates - a measurement of how fast vital statistics (births, deaths, growth rates) change for a species within demographic categories (age or sex).

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