

Testing MaxEnt model performance in a novel geographic region using an intentionally introduced insect

Sutton, G. F.^{1†}; Martin, G.D.^{1,2}

¹ Center for Biological Control, Department of Zoology and Entomology, Rhodes University, Makhanda, 6140, South Africa

² Afromontane Research Unit and Department Zoology and Entomology, University of the Free State, Phuthaditjhaba, 9866, South Africa

Corresponding author † g.sutton@ru.ac.za

Abstract

Ecological models are important tools to support and guide the development and implementation of environmental policies and management programs. Species distributions models (SDM's), such as the popular MaxEnt software, are frequently used to guide conservation programmes, predict the potential distribution of invasive species, forecast the impacts of climate change and develop applied ecological research (e.g. biological control). Many applications of these models require that SDM's are transferred in either space and/or time. However, few studies to date have tested the transferability, and thus usefulness, of MaxEnt models using fully independent data. Moreover, numerous authors have raised concerns over how model complexity (controlled primarily by feature class and regularisation multiplier settings) may affect MaxEnt model transferability. In this paper, we evaluated the usefulness of MaxEnt models transferred in space using a native Australian insect, *Dasineura rubiformis* Kolesik (Diptera: Cecidomyiidae) that has been intentionally introduced as a biological control agent of the invasive plant, *Acacia mearnsii* De Wild (Fabaceae) in South Africa. MaxEnt models were developed using native-range records only (Australia) and projected over South Africa to identify the potential climatic suitability for the insect, using a range of model settings configurations. Model transferability was assessed using independent post-release data from South Africa. Our results demonstrated that MaxEnt scores were positively correlated with increased establishment rates for *D. rubiformis* in South Africa. MaxEnt model outputs and projections were relatively consistent, irrespective of the settings used. Despite MaxEnt having to extrapolate over much of South Africa, MaxEnt performance was higher than modelling climatic suitability as a function of whether models were in extrapolation or interpolation. Our study demonstrates that MaxEnt models can prove useful when transferred in space, however, users need to be aware of the effect of different model settings configurations and model extrapolation can have on model transferability and usefulness in applied ecological settings.

Keywords: Species distribution model, biological control, *Acacia*, *Dasineura rubiformis*, model complexity, model transferability

1. Introduction

Ecological models are important tools to support and guide the development and implementation of environmental policies and management programs (Addison et al., 2013; Schuwirth et al., 2019). For example, ecological models can be used for planning conservation programs (Guisan et al., 2013), predicting the establishment of invasive species (Martin et al., 2020), implementing biological control programmes (Mukherjee et al., 2021), or forecasting species responses to environmental change (Bocedi et al., 2014). Species distribution models (SDM's) are an example of ecological models that have become increasingly popular in recent years (Elith and Leathwick, 2009). SDM's typically take the form of correlative or mechanistic models that relate species presence/absences to environmental covariates to map habitats that may be suitable for a taxon (Elith et al., 2011). The Maximum Entropy Species Distribution Model (hereafter 'MaxEnt') (Phillips et al., 2017) is among the most popular methods for species distribution modeling and has been shown to perform well compared to alternative modeling algorithms (Elith et al., 2006). It uses maximum entropy to distinguish between environmental conditions where the focal taxon is present from environmental conditions at background locations where the taxons' presence is absent (or assumed absent) (Elith et al., 2011).

Despite its popularity, the usefulness of MaxEnt has been questioned when used to generate predictions for novel geographic regions (transferred in space) or time periods (transferred in time) from those for which the data used to build the model were collected (Blasi et al., 2021; Yates et al., 2018). To date, studies assessing transferability have produced contrasting results (Bahn and McGill, 2013; Capinha et al., 2018; Randin et

al., 2006). Model transferability has typically been assessed by cross validation, whereby a fraction of the data is withheld to calibrate the model (i.e. training data) and the remaining data is retained to validate the model (i.e. the testing data) (Wenger and Olden, 2012). However, cross validation may not provide an estimate of model transferability as a selected test sample may not provide an unbiased estimate of the full data set, and therefore may not reflect the heterogeneity that may exist in the underlying data in space or time (see Wenger and Olden, 2012). Ideally, a direct test of model transferability should use an independent dataset of species presence/absences and environmental covariates (Fielding and Bell, 1997; West et al., 2016). Unfortunately, very few studies, to date, have tested model transferability using independent datasets (e.g. Costa et al., 2010; Rebelo and Jones, 2010), which may have limited our understanding of how useful SDM's can be when transferred in space or time. Issues with model transferability may lead to misleading conclusions, which may hinder scientists abilities to address important ecological questions (e.g. where could an invasive species establish?, where should a conservation priority be translocated?) (Merow et al., 2013).

Model complexity can affect uncertainty of model transferability in space and time (Warren et al., 2014). Model complexity may be affected by numerous parameters, notably the feature classes and regularisation (beta) multiplier settings used to specify the MaxEnt model (Elith et al., 2011; Merow et al., 2013). MaxEnt allows users to specify combinations of different feature classes that modify the shape and complexity of species-environment functions. Moreover, MaxEnt uses a regularisation multiplier (a form of L_1 -regularisation) to balance model complexity with the model fit, penalising unnecessarily complex models (Merow et al., 2013). The default MaxEnt settings use all feature classes in model fitting except 'threshold' features (depending on sample size of training data) and a regularisation multiplier of 1 (Phillips et al., 2017). Several recent studies have highlighted the importance of species-specific tuning of feature classes and regularisation multipliers for optimising model complexity (Radosavljevic and Anderson, 2014;

Shcheglovitova and Anderson, 2013), with default settings often producing models that are overly complex, and thus, may perform poorly when transferred (Elith et al., 2011; Merow et al., 2013). Despite the potential implications, surprisingly few studies use user-defined feature class and regularisation settings (e.g. Sutton, 2019), and as such, little is known about how model settings configurations may influence model transferability (Low et al., 2021; Moreno-Amat et al., 2015).

In this study, we performed a retrospective assessment of the transferability of SDM's built using MaxEnt (Phillips et al., 2017). Here, we modelled the potential climatic suitability of an insect that is native to Australia, and that has been introduced into South Africa as a biological control agent. The insect, *Dasineura rubiformis* Kolesik (Diptera: Cecidomyiidae) was introduced into South Africa from Australia in 2013, to curb the spread of the invasive Australian *Acacia mearnsii* De Wild (Impson et al., 2013). Extensive field surveys have been performed in Australia (characterizing the native distribution of *D. rubiformis*) (Adair, 2004) and long-term post-release monitoring has been performed in South Africa to measure establishment rates of the insect, following experimental releases of the insect (Impson et al., 2021). As such, the availability of independent testing data from a separate continent to the data used to generate the models makes this an ideal study system for assessing the transferability of SDM's.

We built MaxEnt models for *D. rubiformis* using distribution records from its native distribution (Australia), and projected the resulting MaxEnt suitability rasters over South Africa. MaxEnt scores range from 0 to 100, whereby 0 represents regions predicted to be highly unsuitable and 100 indicating highly suitable regions. To test model transferability, we fit the MaxEnt scores as a covariate in a logistic regression model to determine whether MaxEnt scores were statistically relevant predictors of insect establishment rates in South Africa (with these data being entirely independent of the data used to build the MaxEnt models). A strong, positive correlation between MaxEnt scores and insect es-

establishment rates would provide support that the SDM's were useful when transferred in space (from Australia to South Africa). Moreover, we tested whether model complexity and parameter tuning could improve the accuracy and transferability of MaxEnt by comparing the predictive power of MaxEnt models calibrated with default settings and an array of optimised settings configurations.

2. Methods and Materials

2.1. Species occurrences records

A total of 103 native-range records for *D. rubiformis* were obtained from (Adair, 2004). A total of 452 invaded-range records to evaluate model transferability were taken from Impson, Kleinjan and Hoffmann (unpublished). Distribution maps for *D. rubiformis* for both native and invaded range are provided in Fig. 1.

Spatial autocorrelation is an important factor that may affect model outputs. Filtering of species occurrence data may limit the inherent biases in the data and improve model quality (Veloz, 2009). To avoid pseudo-replication, only one occurrence record per 2.5 minute grid cell was used for model calibration. Species occurrence datasets were thinned using the `spThin` package (Aiello-Lammens et al., 2015), and spatial autocorrelation analyses were performed using the `ecospat` package (Di Cola et al., 2017).

2.2. Environmental predictors

Climate data were obtained by downloading the standard set of 19 bioclimatic variables from the WorldClim ver. 1.4 database (Hijmans et al., 2005) (data available at: www.worldclim.org/download.html). This dataset is representative of annual and seasonal means and variation of temperature and precipitation metrics aver-

aged over the 1950–2000 time period (current climate) at a 5 arc minute resolution.

To reduce multicollinearity between environmental predictors and thereby decrease the risk of calibrating overfit models, Pearson's correlation coefficients were computed for all pairs of predictors, whereby predictors which were highly correlated ($|r| > 0.85$) were excluded from the final predictor set (Capinha and Anastácio, 2011). The reduced set of environmental predictors consisted of seven climatic variables, including: bio1 – annual mean temperature, bio2 – mean diurnal temperature range (mean of monthly [max temp – min temp]), bio3 – isothermality, bio9 – mean temperature of the driest quarter, bio12 – mean annual precipitation, bio14 – precipitation of the driest month and bio16 – precipitation of the wettest quarter (see Hijmans et al. (2005) for further details).

2.3. Model calibration

Maxent was implemented in the `dismo` package in R (Hijmans et al., 2017). MaxEnt was selected as it consistently outperforms other modelling algorithms (Wisz et al., 2008). Given that MaxEnt is a presence-only modelling algorithm, model calibration requires a user-defined geographic background to sample the climate of representative grid cells where the focal species is absent (i.e. background points). Background definition can have a significant effect on model output (VanDerWal et al., 2009). The background should ideally represent the geographic areas available to the focal species, omitting areas where species absence is due to historical factors, dispersal constraints and/or biotic interactions (Sanín and Anderson, 2018). Following Webber et al. (2011), we defined the model background using the Koppen-Geiger climate classification (Available at: <http://koeppen-geiger.vu-wien.ac.at>). Only Koppen-Geiger climate zones that contained at least one native-range occurrence record for *D. rubiformis* were used as the background area from which pseudo-absences were drawn for model calibration. Koppen-Geiger climate zones were intersected using the `extract` function from the R package

raster (Hijmans et al., 2017).

2.4. Optimal model settings

Model performance and optimal settings configurations were assessed using multiple metrics that reflected aspects of model (1) discriminatory ability (AUC_{test}), (2) overfitting (AUC_{diff}), (3) omission rates (OR_{10}), and (4) overall parsimony ($AICc$) (Low et al., 2021).

- (1) AUC_{test} assesses the models ability to discriminate between predicted presence/absence at withheld portions of the data used to test the model versus background points. The area under the receiver operating characteristic curve (AUC) is one of the most popular metrics used to evaluate MaxEnt models. An AUC of less than 0.8 is considered a poor model, between 0.8 and 0.9 is a fair model, between 0.9 and 0.995 a good model, and > 0.995 an excellent model (Fielding and Bell, 1997). Thus, higher AUC_{test} values indicate increased ability to discriminate between training and background points.
- (2) AUC_{diff} calculates the difference between AUC values calculated on training points only (AUC_{train}) and AUC_{test} using cross-validation (Warren and Seifert, 2011). Thus, higher AUC_{diff} values indicate whether the MaxEnt model is overfit on the training data, and thus, performs poorly when evaluated against testing points.
- (3) OR_{10} is the proportion of testing points that are not predicted to fall within the projected model surface once the model is converted into a binary prediction output (Boria et al., 2014). Overfit models have omission rates higher than the theoretical expectation for the threshold applied (Shcheglovitova and Anderson, 2013). OR_{10} sets the binary prediction threshold at a value that excludes the 10% of the calibration localities from the model with the lowest prediction values, and therefore has an expected omission rate of 0.10 (Boria et al., 2014). As such, the OR_{10} criterion

selected models calibrated with MaxEnt settings which best approximated the expected 0.10 omission rate. Models with omission rates increasingly higher than the expected value were considered as more overfit (Boria et al., 2017).

- (4) Lastly, optimal model settings were determined by selecting model configurations which produced the lowest value for the Akaike Information Criterion corrected for small sample sizes (AICc) (i.e. $AICc=0$; following Muscarella et al. (2014)). The AICc criterion simultaneously scores models according to their complexity and goodness-of-fit, whereby models with the lowest AICc are selected as the best models. AICc was used as the primary evaluation metric as it is calculated using MaxEnt models built using the entire species occurrence dataset, unlike AUC and OR_{10} (and numerous other metrics frequently used for model evaluation) which may be spatially biased due to the partitioning of the species occurrence dataset into training and evaluation sets (Sanín and Anderson, 2018).

2.5. Assessing model extrapolation

Several authors have raised concerns over the use of correlative SDM's, such as MaxEnt, when projected into new geographic regions or time periods due to issues with extrapolation into novel/non-analogous climate (Elith et al., 2011; Elith and Leathwick, 2009; Yates et al., 2018). To address these concerns, Multivariate environmental similarity surfaces (hereafter 'MESS') (Elith et al., 2010) were computed to assess whether MaxEnt models were extrapolating or interpolating. MESS analyses measure the similarity of any given point to a set of reference points (reference points were defined as only the species presence points used to calibrate models following Kriticos et al., 2014). Negative MESS values indicate geographic regions outside the range of climate variables used to calibrate the model (i.e. extrapolation space or MESS-), while MESS values between 0 and 100 indicate geographic regions inside the range of climatic variables used to calibrate

the model (i.e. interpolation space or MESS+). MESS maps are used as a measure of prediction uncertainty or caution against inferences in extrapolation space (Elith et al., 2010).

2.6. Statistical analyses

Five candidate MaxEnt models were specified using native-range (Australia) training data. The five models differed in the feature classes and regularisation multiplier settings used by MaxEnt to build the models. The five models were specified with (1) default MaxEnt settings, and four optimised settings configurations that maximised performance based on (2) AUC_{test} , (3) AUC_{diff} , (4) OR_{10} and (5) AICc.

To evaluate the predictive performance and transferability of these models, we evaluated whether MaxEnt climatic suitability scores were correlated with increased probabilities of *D. rubiformis* establishment in South Africa. To do so, MaxEnt scores were specified as a continuous fixed effect and whether *D. rubiformis* was recorded or not (present/absent) as a boolean response variable in a logistic general linear model (GLM), using a logit link function. MaxEnt scores, bounded between 0 (not climatically suitable) and 1 (highly climatically suitable) indicating climatic similarity between the native range occupied by *D. rubiformis* in Australia and sites where it was released as a biological control agent in South Africa, were derived by projecting MaxEnt suitability rasters from models calibrated using native-range GPS records only (Australian native-range records) over South Africa, and extracting the MaxEnt suitability scores for each site where *D. rubiformis* was surveyed in South Africa using the `extract` function from the R package `raster` (Hijmans et al., 2017). GLM's were specified using the `rms` package in R (Harrell, 2017). Likelihood Ratio Tests (LRT) were performed to determine whether there was a statistical correlation between MaxEnt scores and the probability of *D. rubiformis* establishment. A statistically significant, positive correlation between MaxEnt scores and insect

establishment rates would provide support that the SDM's were useful and predictive of insect establishment, even when the insect was transferred in space. Out-of-sample AUC was calculated using the `rms` package, using 500 bootstrap replicates (Harrell, 2017) to quantify the predictive performance of MaxEnt models, whereby AUC values less than 0.80 are typically considered poor fitting models (lacks predictive power) (Fielding and Bell, 1997).

A similar approach was adopted to test if each occurrence record in South Africa was classified as being in interpolation (within the climate space occupied by the insect in its native range) versus extrapolation (outside the climate space occupied by the insect in its native range) was predictive of *D. rubiformis* establishment. Interpolation/extrapolation were quantified using MESS maps using the `mess` function from the `dismo` package in R (Hijmans et al., 2017). Interpolation versus extrapolation was fit as a categorical predictor and whether *D. rubiformis* was recorded or not (present/absent) as a boolean response variable in a logistic GLM, using a logit link function.

All modelling and statistical analyses were conducted in R ver. 4.0.3 (Team, 2020).

3. Results

3.1. Native-range models (model calibration)

Five candidate MaxEnt models were developed using native-range (Australia) training data for *D. rubiformis*. The five models differed in the feature classes and regularisation multiplier settings used by MaxEnt to build the models. The five models were specified with (1) default MaxEnt settings, and four optimised settings configurations that (2) maximised model performance based on AUC_{test} , (3) AUC_{diff} , (4) OR_{10} and (5) $AICc$ (Table S1). The AUC values for these five models ranged between 0.89 - 0.92, depending on the MaxEnt settings configuration used. As such, all five candidate models were considered

useful and had high predictive accuracy in distinguishing between *D. rubiformis* recorded presences and background points in its native range. While default MaxEnt settings produced high discriminatory power when tested in the training area of Australia (AUC = 0.89), models calibrated with tuned settings configurations led to less overfitting (lower AUC_{diff}), better omission rates (best approximated the expectation for OR₁₀), and more parsimonious models (AICc) (Fig. 2).

3.2. Model performance

When evaluated on independent testing data in South Africa, the MaxEnt models showed relatively high predictive accuracy, irrespective of the MaxEnt settings used to calibrate the model. For all models, the probability that *D. rubiformis* was recorded at a field site in South Africa increased with higher MaxEnt climatic suitability scores (Fig. 3). All five MaxEnt models demonstrated a statistically significant positive relationship between MaxEnt suitability scores and the probability of *D. rubiformis* establishment in South Africa (Table. 1), and high power to discriminate between sites where *D. rubiformis* had established or not (AUC: 0.79 - 0.91) (Fig. 4). The predicted climatic suitability for *D. rubiformis* across South Africa did vary somewhat depending on the MaxEnt settings used to calibrate the model (Fig. 5). All MaxEnt models predicted relatively high climatic suitability for *D. rubiformis* in the far south-west of South Africa and in the southern Cape region. However, the four MaxEnt models calibrated with tuned model settings differed from the default settings model by predicting climatic suitability for *D. rubiformis* along the entire south and east Coast of South Africa.

Despite the high performance of the MaxEnt models when transferred in space, MESS maps indicated that the MaxEnt models were extrapolating climatic suitability scores for *D. rubiformis* over the vast majority of South Africa (Fig. 6a). Indeed, 54 of the 78 field sites surveyed for *D. rubiformis* in South Africa occur in geographic regions where the

MaxEnt models were extrapolating. *Dasineura rubiformis* established at 23 of 24 sites in interpolation (96%), while it established at 44 of 54 sites in extrapolation (82%) (Fig. 6b). We found no evidence that a site being in extrapolation/interpolation was a statistically significant predictor of *D. rubiformis* establishment in South Africa ($X_2 = 3.40$, d.f = 1, $P = 0.07$). Moreover, classifying sites as being in extrapolation/interpolation yielded lower power to discriminate between sites where *D. rubiformis* had established or not (AUC: 0.63) than all of the MaxEnt models.

4. Discussion

Species distribution models (SDM's) are becoming increasingly important tools to support and guide the development and implementation of environmental policies and management programs (Addison et al., 2013; Schuwirth et al., 2019). The usefulness of SDM's is dependent on model performance, which is typically measured by its ability to correctly predict where a species is established and its capacity to distinguish between sites where the species is established versus a site where the species is absent (or assumed to be absent) (Smith et al., 2021). However, a number of authors have called in question the usefulness of SDM's, notably when models are transferred in space or time (Blasi et al., 2021; Yates et al., 2018). Poor transferability may lead to erroneous model predictions that may have serious negative consequences for the application of the model, and resulting policies and management programmes (Soultan and Safi, 2017). Here, we report on the validation of a SDM for an insect, (*D. rubiformis*), native to Australia, that has been intentionally introduced as a biological control agent into South Africa to reduce the invasiveness of its host-plant, *A. mearnsii* (Impson et al., 2013). The the availability of independent testing data from South Africa, a separate continent to the data used to generate the models (Australia), makes this an ideal study system for assessing the transferability of SDM's. This study represents one of only a handful of studies to validate SDM's using

independent testing data (Costa et al., 2010; Rebelo and Jones, 2010; Smith et al., 2021; West et al., 2016).

Our results indicated that MaxEnt SDM's were able to provide robust estimates of climatic suitability for *D. rubiformis* in South Africa. AUC values greater than 0.75 are typically considered good fitting models (having high predictive power) (Fielding and Bell, 1997). When MaxEnt models, calibrated using native-range records for *D. rubiformis* from Australia, were projected over South Africa, they had AUC scores of 0.89 - 0.92, indicative of high power to discriminate between sites where *D. rubiformis* had established in South Africa or not. Additionally, we showed that the probability that *D. rubiformis* was recorded at a field site in South Africa increased with higher MaxEnt climatic suitability scores. This result demonstrates the usefulness of the MaxEnt SDM and that, at least for our case-study, SDM's can be transferred into novel geographic regions, and provide valuable information to guide policy making and the development of management programmes. For example, biological control programmes such as the programme in which *D. rubiformis* is used to curtail the spread of the highly invasive weed *A. mearnsii* expend many resources (time and money) to mass-rear insect populations that are then released into the field. The positive correlation between MaxEnt suitability scores and *D. rubiformis* establishment means that researchers can develop and implement mass-rearing and experimental release programmes for the insect that prioritise releasing the insect at sites that are highly climatically suitable, and thus, more likely the insect will establish viable populations. This may assist in improving the level of control over the target weed and increasing the efficiency of resources expended by increasing the chances of establishing viable insect populations.

Our study adds to a growing body of literature indicating that SDM model complexity affects model performance and transferability when being projected into novel geographic regions. While the default MaxEnt model had the high predictive power in the training area

(Australia), this model was somewhat overfit to the training data (Warren et al., 2014). This finding corroborates other studies showing that high predictive power in the model training area is not a guarantee of transferability (Duque-Lazo et al., 2016; Warren et al., 2014). We echo that recommendations of Shcheglovitova and Anderson (2013) and Muscarella et al. (2014) that model tuning should be performed to estimate optimal model complexity when transferring MaxEnt models in space and/or time in order to maximise their usefulness.

An additional concern with transferring MaxEnt models in space or time is the potential for models to significantly extrapolate predictions when the model is projected into non-analogous conditions to those under which the model was calibrated (Elith et al., 2010; Mesgaran et al., 2014). However, the applied use of SDM's in developing environmental policy, developing management programmes for invasive species and implementing conservation programmes often necessitate that models are transferred and predictions made, even when models are extrapolating (Elith et al., 2010). Here, we showed that *D. rubiformis* was able to establish at many sites (82%) in South Africa that were outside the range of climate space it occupies in its native range (i.e. extrapolation), which was not substantially different from establishment rates at sites in interpolation. While our MaxEnt models were able to make accurate predictions of *D. rubiformis* establishment in South Africa, even when models were extrapolating, this finding in no way discounts the importance of assessing model extrapolation when transferring models in space or time. A number of tools have been developed in recent years to assist SDM users with identifying model extrapolation, e.g. MESS (Elith et al., 2010) and ExDet (Mesgaran et al., 2014), and which should be an integral component of any SDM study.

Given that the *D. rubiformis* MaxEnt models showed high predictive accuracy when transferred in space over South Africa and the statistically significant positive correlation between MaxEnt scores and *D. rubiformis* establishment, we wish to highlight how these

models can be used in an applied setting. To visualise the potential geographic regions where *D. rubiformis* may establish in South Africa, we thresholded the MaxEnt map that optimised AICc where the probability of establishment was $> 50\%$ (i.e. MaxEnt score = 0.30), given in Fig. 9. The map demonstrates that the entire south and east coast regions of South Africa are climatically suitable for *D. rubiformis*. Mass-releasing and releasing weed biological control agents is a time-consuming and costly endeavor (Coetzee et al., 2021). As such, our models provide a statistically validated approach to optimising the redistribution of *D. rubiformis* in South Africa by prioritising releases at field sites where MaxEnt scores are > 0.30 , and therefore where the probability of establishment was $> 50\%$.

5. Conclusions

Species distribution models are becoming increasingly popular with researchers, stakeholders, policy makers and land managers alike, particularly for making predictions in novel geographic regions or forecasting species responses to climate change. Transferring SDM's in space and/or time, however, has been met with justifiable resilience and concerns over how well these models perform upon transfer. In this study, we presented a case-study demonstrating that MaxEnt SDM's were able to accurately predict the distribution of an Australian insect when introduced into South Africa. Our study is one of only a few studies to date validating MaxEnt models using spatially independent data. However, the accuracy of the MaxEnt models and their climatic suitability projections were dependent on the settings used to calibrate the models. Our results demonstrate that MaxEnt can be useful in predicting where a species may establish, even when projected into a novel geographic area, but that users need to be aware of how model settings and model extrapolation can influence model outputs and usefulness. Demonstrating how SDM's can be useful, while communicating uncertainty in their predictions and outputs, is

essential for building confidence in the use of SDM's (Blasi et al. 2020). We showed how validating predictive models can be used to guide the implementation of a biological control programme by optimising the redistribution and release of *D. rubiformis* in geographic areas that are climatically suitable and where the probability of the insect establishing is greater than 50%.

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Figure and table legend

Figure 1

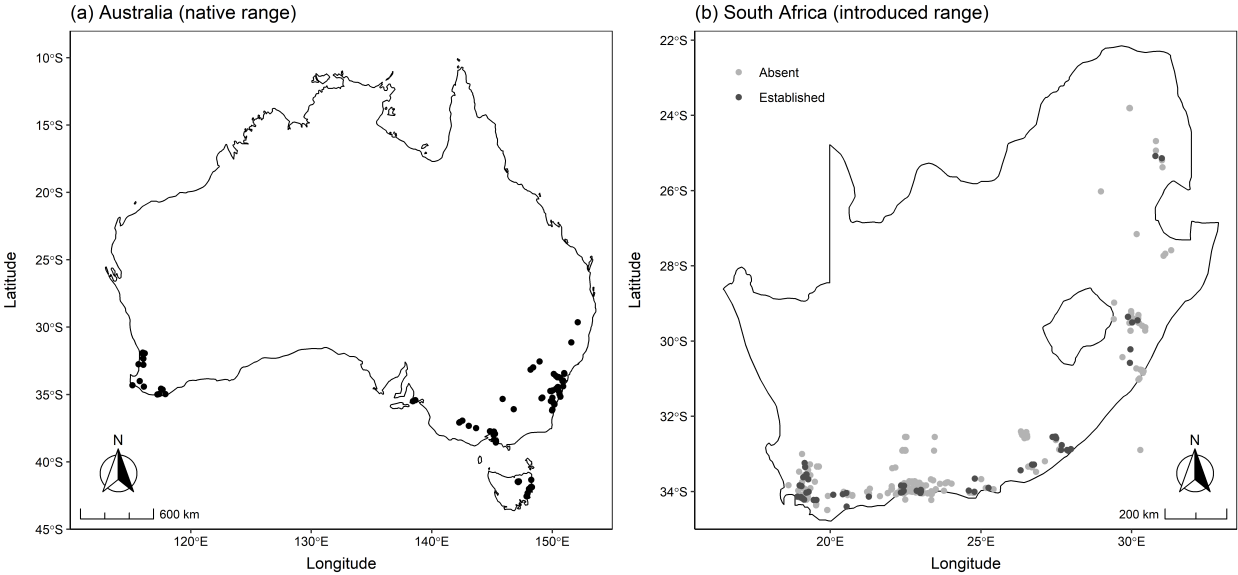


Figure 2

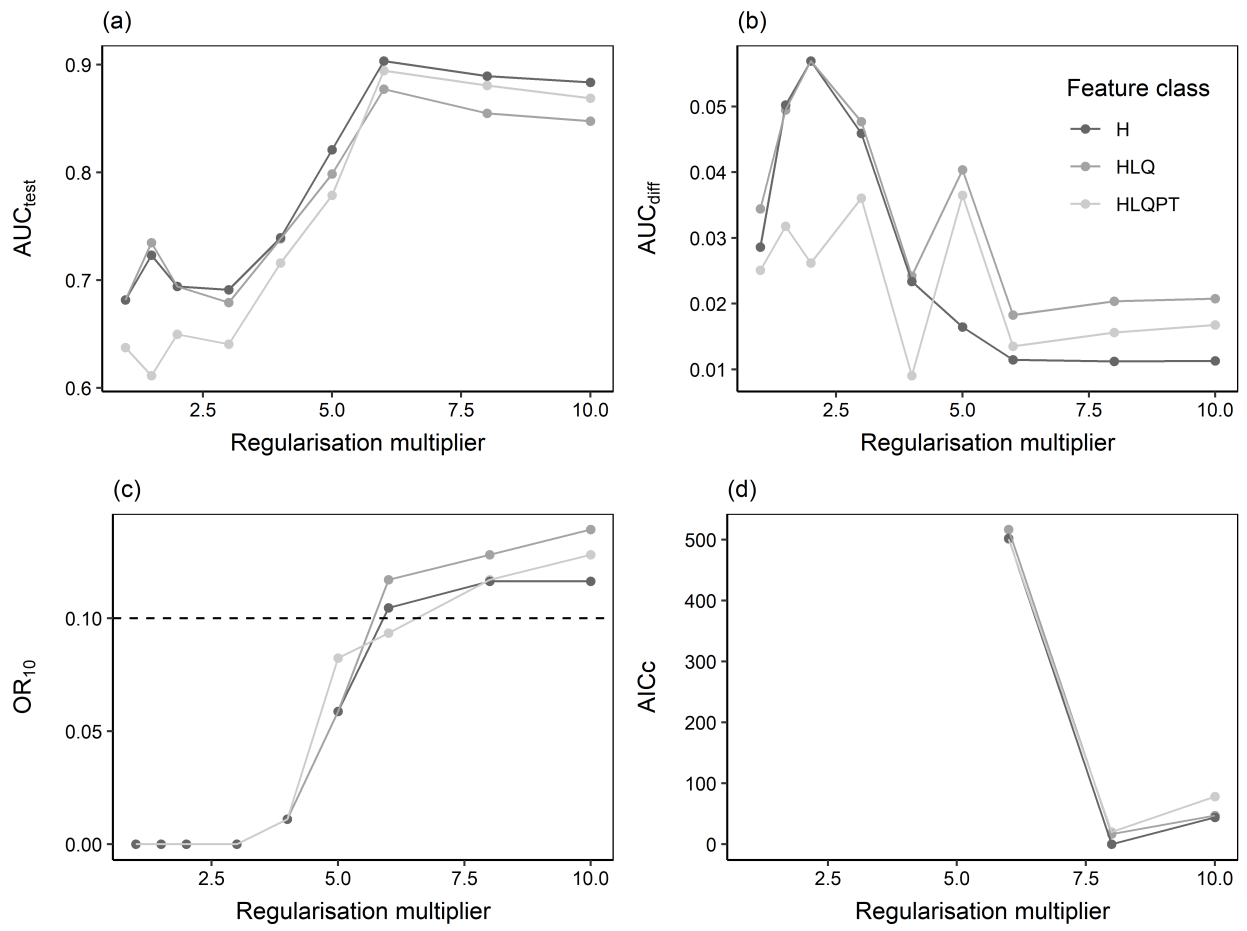


Figure 3

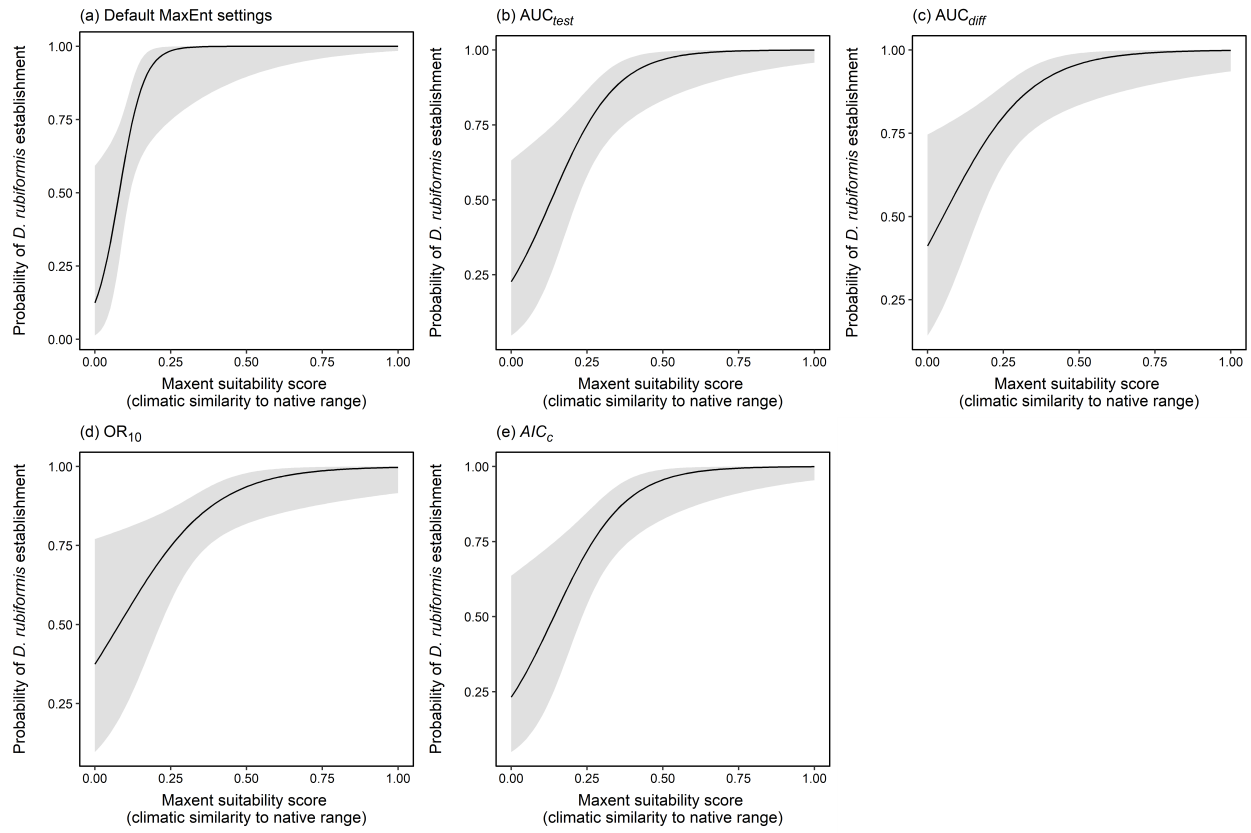


Figure 4

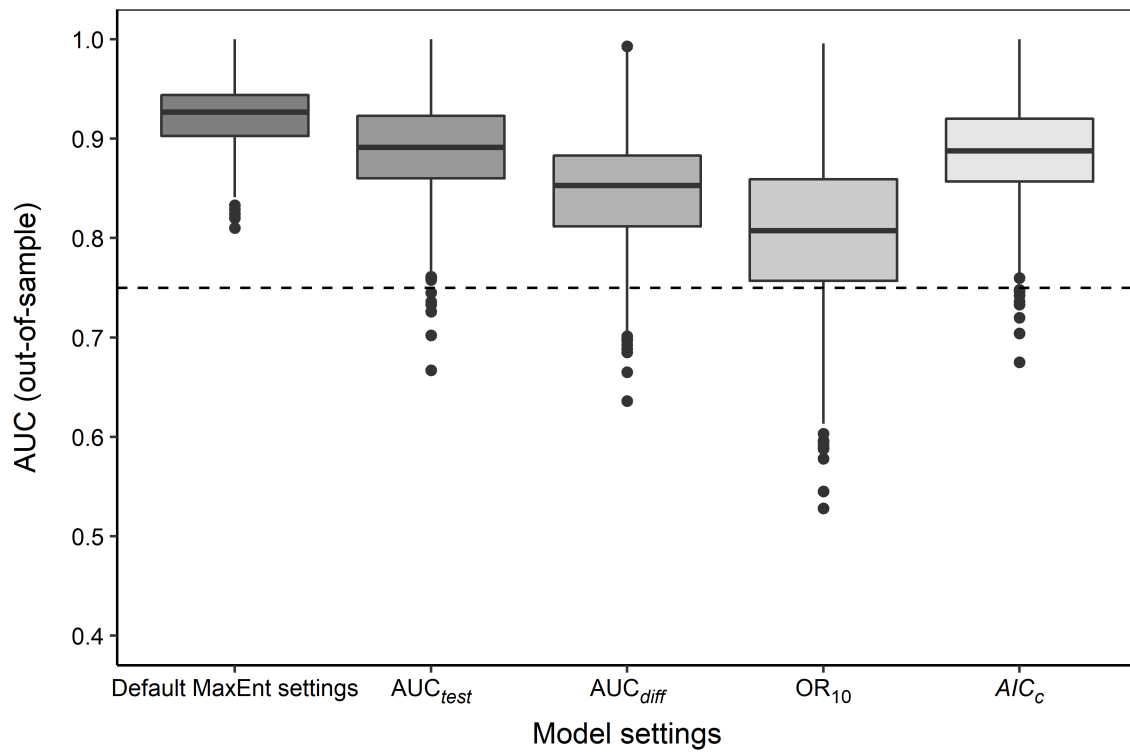


Figure 5

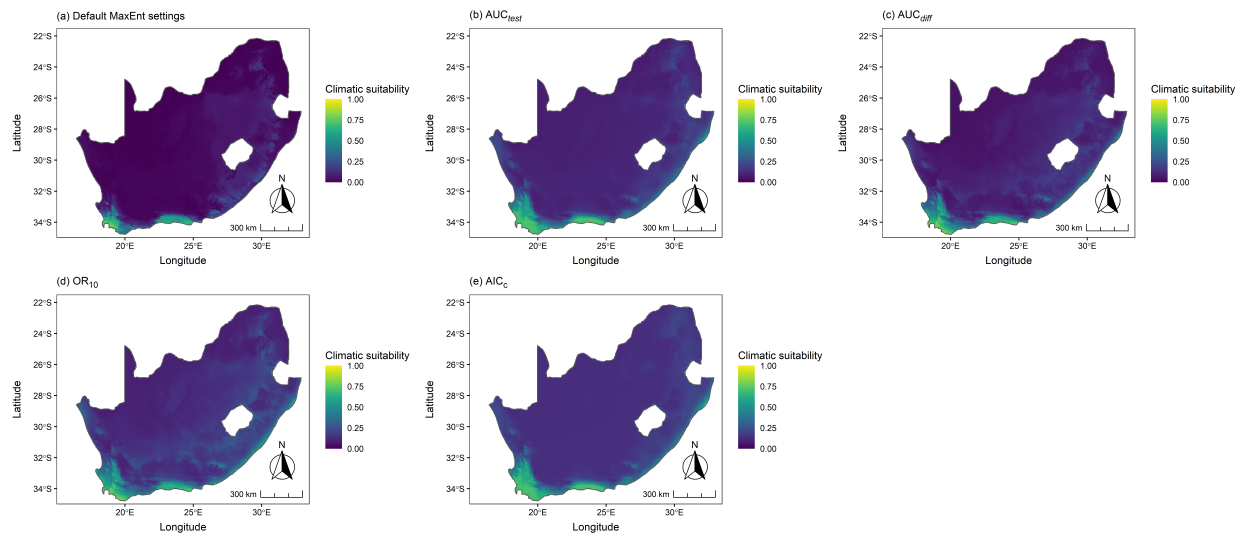


Figure 6

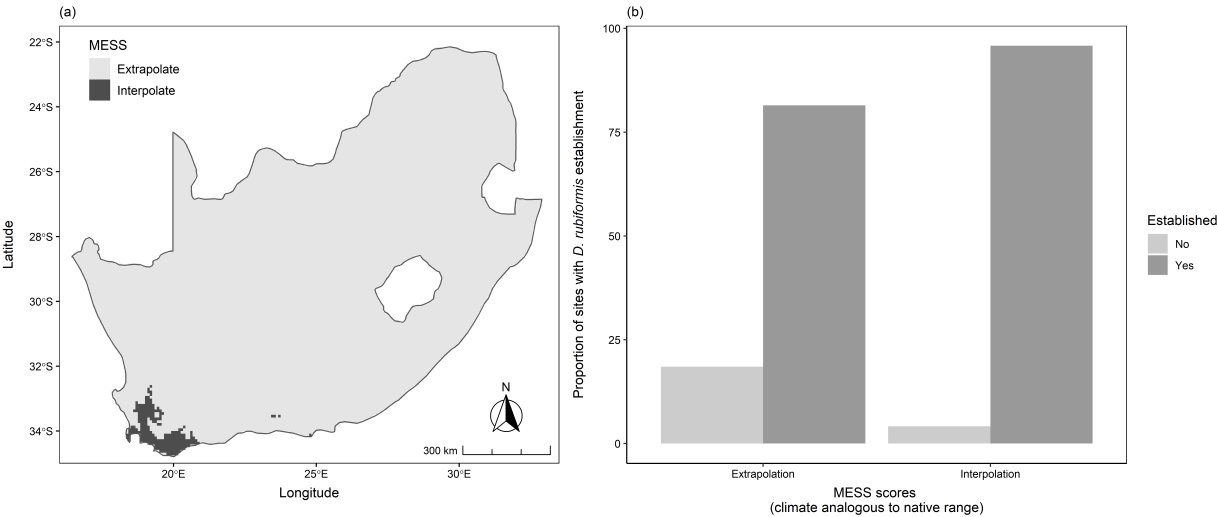


Table 1

Model	β^a	χ^2	d.f.	P
Default settings	1.11	26.21	1	< 0.001
AUCtest	1.04	17.50	1	< 0.001
AUCdiff	1.03	12.29	1	< 0.001
OR10	1.02	9.01	1	0.003
AICc	1.04	16.21	1	< 0.001

^a Adjusted to indicate change in Y for each 1% unit increase in climatic similarity

Table S1

Model	RM	FC	AUC _{test}	AUC _{diff}	OR ₁₀	AIC _c
Default	1	HLQPT	0.89	0.04	0.18	564.46
AUCtest	6	H	0.89	0.02	0.09	15.56
AUCdiff	4	HLQPT	0.89	0.02	0.13	485.91
OR10	6	HLQPT	0.92	0.02	0.12	144.39
AICc	5	H	0.90	0.02	0.09	0.00