Evaluating the predictive performance of stacked species distribution models applied to plant species selection in ecological restoration

Aitor Gastón * and Juan I. García-Viñas

EGOGESFOR Research Group, Universidad Politécnica de Madrid, Escuela de Ingeniería Forestal y del Medio Natural, Ciudad Universitaria s/n, 28040, Madrid, Spain. Telephone, +34913367669. Fax, +34915446025.

* aitor.gaston@upm.es (corresponding author)

Abstract

We propose an evaluation approach to validate stacked species distribution models applied to plant species selection in ecological restoration. The evaluation method does not assess the accuracy of individual species models, but focuses on the ability of the stacked models to discriminate between present and absent species in a vegetation relevé. We measured the discriminative ability using the area under the ROC curve (AUC) to avoid the drawbacks of converting occurrence probabilities into binary predictions. Using the proposed method, we compared competing sets of predictors and validated stacked species distribution models for plant species selection in ecological restoration projects in Spain. 120,938 vegetation relevés included in the Forest Map of Spain were used to train models for 188 species and an independent set of 100 vegetation relevés was used for validation.The best performing set of predictors included climate and soil related predictors derived form coarse resolution datasets. The model performance was acceptable on average (mean AUC: 0.88, sd: 0.07) and high (AUC > 0.9) in 42% of the relevés evaluated. We recommend the proposed evaluation approach to validate stacked species distribution models used to support species selection in ecological restoration projects.

Key words: Habitat models, model validation, revegetation

1. Introduction

Ecological restoration is an intentional activity that initiates or accelerates the recovery of a degraded ecosystem with respect to its health, integrity and sustainability (SER, 2004). Restoring plant communities frequently involves planting or seeding (Clewell et al., 2005), therefore, a proper species selection is mandatory in such projects. Although many different criteria may be used in species selection, the selected species should be matched to local environmental conditions (Peman Garcia et al., 2008). Matching species to sites requires the estimation of habitat suitability for the considered species. Such estimations are part of the outputs of predictive species distribution models (SDMs), which relate field observations to environmental predictor variables (Guisan and Thuiller, 2005).

As with any predictive empirical model, SDMs should be validated through an evaluation of their predictive performance prior to use by practitioners (e.g. Fielding and Bell, 1997). Several authors have provided guidelines for model validation, although methodological decisions should be contingent on the user's intent (Araújo and Peterson, 2012). When models are used to predict areas for restoration, translocation, or reintroductions, performance evaluations should focus on the reduction of errors of omission (Araújo and Peterson, 2012). However, the goal of a restoration project is not always to predict areas for restoration of populations of given species, but to predict the most suitable species for a given site (e.g., restoring a degraded plant community). The number of suitable plant species can easily exceed the maximum number of species (*n_i*) that can be introduced for practical reasons, therefore, practitioners must identify the most suitable n_i species from among a limited number of commercially available species (*N*). This kind of decision requires one SDM for each one of the *N* species in order to predict the occurrence probability for each species in the site to be restored. The concern of the practitioner is the ability of the *N* stacked models to rank the *N* species according to habitat suitability at a particular site to be restored.

The evaluation of predictions from stacked SDMs against observed species assemblages has often been used in ecological research and environmental management. Some evaluations measure the likelihood of observing the assemblage given the predictions of the stacked SDMs using the Log-likelihood (Oberdorff et al., 2001, Clarke et al., 2003). This approach allows us to directly compare predicted probabilities of occurrence with observed occurrences, although probabilities are more often converted to occurrences using a threshold prior to measuring predictive performance, which allows the comparison of predicted and observed species assemblages. Some authors use compositional dissimilarity indices between observed and predicted assemblages, e.g., Bray-Curtis Index (Oberdorff et al., 2001, Clarke et al., 2003, Hallstan et al., 2012, Larsen et al., 2012), Simpson's index of dissimilarity (Baselga and Araújo, 2009), Jaccard's CC index (Tanaka and Koike, 2011) or Sorensen index (Pellissier et al., 2011). Other approaches focus on measures derived from the confusion matrix, e.g., false positive and false negative rates (Avery and Van Riper, 1990, Block, 1994, Feria and Peterson, 2002), true positive and true negative rates (Feria and Peterson, 2002, Kattwinkel et al., 2009), correct classification rate (Kattwinkel et al. 2009, Gabriels et al. 2007) or Cohen's Kappa (Kattwinkel et al. 2009, Gabriels et al. 2007).

We are not aware of any existing performance evaluation of stacked SDMs applied to plant species selection in ecological restoration. As mentioned above, the concern of the practitioner is the ability of the stacked models to discriminate between present and absent species at a particular site. This issue may be solved using a discrimination measure that compares predictions from stacked SDMs against observed species assemblages at the sites evaluated. The measures previously used to evaluate stacked SDMs require the adoption of a threshold to convert probabilities into predicted occurrences. One problem with the threshold dependent measures is their failure to use all of the information provided by the model (Fielding and Bell, 1997). In the case of species selection for ecological restoration, converting probabilities into predicted occurrences equates species with different suitability values for the restoration site (e.g. 0.2 and 0.9 are equal for a threshold of 0.15). One way of avoiding this problem is to use threshold-independent measures, such as the area under the receiver operating characteristic curve (AUC). The AUC measures the probability that a random selection from the positive group will have a score greater than a random selection from the negative class (Fielding and Bell, 1997). In this case, the AUC would be computed for each site and would estimate the probability that the stacked SDMs offer a higher suitability estimate for a present species than for an absent species (both of them picked at random). Here we propose the use of site AUC to evaluate the predictive performance of stacked SDMs applied to plant species selection in ecological restoration (fig 1). First we fitted SDMs for 188 plant species native to Spain (see section 2.1) using national scale datasets (see section 2.1 and 2.2) and penalized logistic regression (see section 2.3). We then applied the proposed evaluation approach to validate stacked SDMs for plant species selection in ecological restoration projects in Spain (see section 2.4) using an independent set of vegetation relevés (see section 2.1). We focused on two potential applications for the proposed evaluation approach: the estimation of the overall performance of the stacked models and the comparison of the performance of different sets of predictors.

The proposed evaluation approach allows the modeller to build SDMs better suited for plant species selection in ecological restoration. More accurate models are expected to decrease the likelihood of selecting unsuitable species and, consequently, improve the success rates of the restoration projects.

2. Material and methods

2.1. Species occurrence data

We fitted SDMs for vascular plant species native to continental Spain using data from 120,938 vegetation relevés carried out between 1986 and 1997 as part of the field survey of the Forest Map of Spain (Ruiz de la Torre, J., 1990). The vegetation relevés in the Forest Map of Spain include all the woody species as well as some large and dominant grasses. The relevés include non-forest species (e.g. shrubs like *Atriplex halimus* or grasses like *Lygeum spartum*) as the map covers not only forests, but also open woodlands, shrublands and grasslands. Species with less than 15 occurrences were excluded, resulting in 188 species to be modelled (77 trees, 104 shrubs and 7 large grasses). The number of occurrences ranged from 15 to 42,720 with 90% of the species between 28 and 8,735 occurrences.

An independent set of vegetation relevés by Prof. Ruiz de la Torre (Gastón et al., 2011) was used for model evaluation. Only relevés from locations with evidently low degrees of human perturbation were used (tree cover more than 75%, more than 3 tree species and no evidence of human perturbation). 100 relevés (see figure 2) met the requirements with an average of 8.3 tree species and a mean tree cover of 87%. The presence or absence of the 188 modelled species was extracted for the 100 relevés that met the requirements.

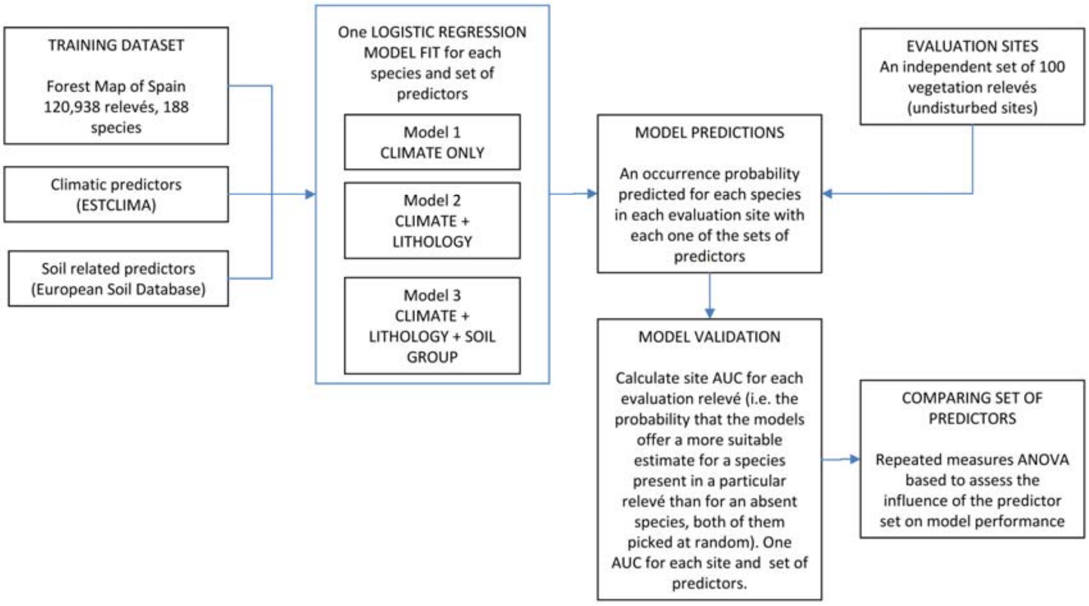

Figure 1. Conceptual diagram of the modelling approach, including model training and validation.

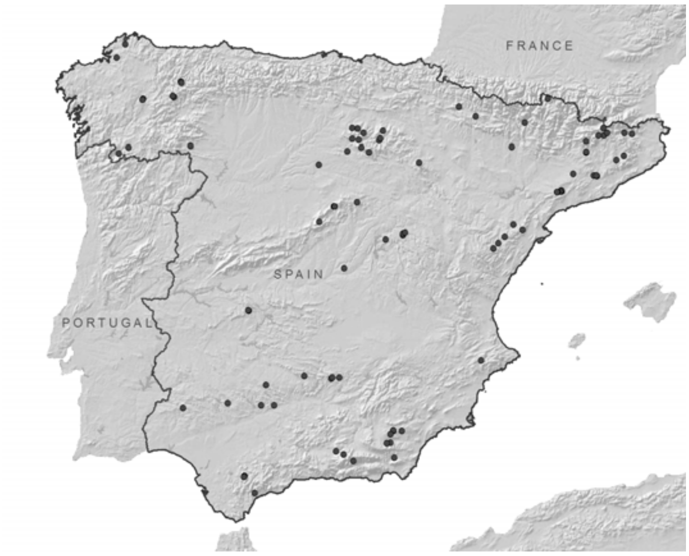

Figure 2. Limits of the study area (continental Spain) and location of the vegetation relevés by Prof. Ruiz de la Torre (Gastón et al., 2011) used for model evaluation (not used for model training). Only relevés from locations with evidently low degrees of human perturbation were used (tree cover more than 75%, more than 3 tree species and no evidence of human perturbation).

2.2 Environmental variables

Climatic data grids were derived by applying a multiple regression model based on meteorological station data (Sánchez Palomares et al., 1999) to the STRM 3-arc-second (≈ 90 m) elevation dataset (Farr et al., 2007). A set of 17 climatic variables commonly used in tree species autoecology in Spain (e.g., Gandullo and Sánchez Palomares, 1994) were initially considered as candidate predictors: mean seasonal rainfalls (4), mean annual rainfall, mean seasonal temperatures (4), mean annual temperature, mean maximum temperature of the warmest month, mean minimum temperature of the coldest month, dry season length, dry season intensity, mean annual potential evapotranspiration, mean annual water surplus, and mean annual water deficit.

A variable clustering approach was used as a variable reduction strategy (Harrell, 2001). Hierarchical clustering was conducted on a similarity matrix (squared Spearman correlation coefficients) using the complete linkage clustering method. Once the variable groups had been defined, the first principal component of each group was taken as representative of that group. The data reduction procedure resulted in five groups of variables related to various environmental conditions (Figure 3): (1) mean thermal conditions (*SpT*, *AuT*, *T*, *PET*), (2) summer thermal conditions (*SuT*, *Tw*), (3) winter thermal conditions (*WiT*, *Tc*), (4) water availability during the dry season (*DSL*, *DSI*, *SuR*, *WD*), and (5) mean water availability (WiR, AuR, WS, SpR, R).

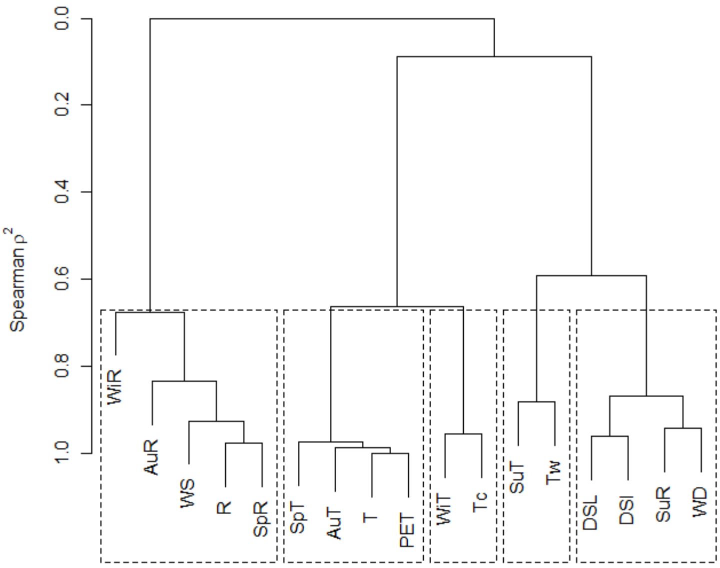

Figure 3. Variable hierarchical complete linkage clustering on a squared Spearman correlation matrix. Dashed rectangles indicate groups of variables. Abbreviated variable names: *WiR*, mean winter rainfall; *SpR*, mean spring rainfall; *SuR*, mean summer rainfall; *AuR*, mean autumn rainfall; *R*, mean annual rainfall; *WiT*, mean winter temperature; *SpT*, mean spring temperature; *SuT*, mean summer temperature; *AuT*, mean autumn temperature; *T*, mean annual temperature; *Tw*, mean maximal temperature of the warmest month; *Tc*, mean minimal temperature of the coldest month; *DSL*, dry season length; *DSI*, dry season intensity; *PET*, mean annual potential evapotranspiration; *WS*, mean annual water surplus; *WD*, mean annual water deficit.

The European Soil Database (ESDB, Van Liedekerke et al., 2006) was used as a soil data source. The ESDB comprises a coarse-scale soil map (1 km resolution grid) and an associated database with the values of several soil-related variables for each cell of the map. Three soil-related predictors were extracted from the ESDB: calcareous nature of the parent material (a binary value), presence of gypsum (a binary value), and major FAO soil group (14 classes).

Three subsets of increasing complexity predictors were tested: (1) climate only (15 parameters), (2) climate and lithology (17 parameters) and (3) climate, lithology and major soil group (30 parameters).

2.3. Modelling strategy

We used penalized logistic regression (Harrell, 2001) to fit the SDMs. The penalized regression outperformed an alternative regularization technique called *lasso* (Tibshirani, 1994) with small sample sizes in a comparison of regularisation methods applied to species distribution models (Reineking and Schröder, 2006) and performed at least as well as Maxent in a wide range of sample sizes (Gastón and García-Viñas, 2011).

In the penalized logistic regression, we maximise the penalized log likelihood (PML):

$PML = \log L - 0.5\, \lambda \sum (s_i\, \beta_i)^2$

where L is the usual likelihood function, λ is a penalty factor, β_i are the estimated regression coefficients and s_i are the scale factors to make $s_i\, \beta_i$ unitless. This estimation procedure shrinks the regression coefficients towards zero, causing biased predictions if applied to the training sample but improving the accuracy of new predictions. Although penalization does not eliminate predictors, it reduces the effective number of estimated parameters and, therefore, helps avoid performance problems caused by overfitting (Harrell, 2001).

We fitted penalized models using the standard deviation of each predictor as a scaling factor and used a modified version of AIC to select the optimal penalty factor (Harrell, 2001). We used the *lrm* and *pentrace* functions from the *rms* package (Harrell, 2011) in the R environment for statistical computing (R Development Core Team, 2011).

We expected nonlinear relationships between species occurrence and environmental predictors. Moreover, a significant proportion of responses may be skewed (Oksanen and Minchin, 2002). Therefore, we prespecified continuous predictor complexity to four-knot restricted cubic splines (Harrell, 2001). This way of adding nonlinear terms allows modelling responses from linear to skewed unimodal and requires the estimation of three parameters per continuous predictor.

2.4. Evaluation of predictive performance

We evaluated the ability of the 188 models to rank the 188 species according to habitat suitability in each one of the 100 independent relevés using the AUC, i.e. we estimated the probability that the stacked SDMs offer a more suitable estimate for a species present in a particular relevé than for an absent species (both of them picked at random).

The calculation procedure of Harrell's Concordance Index was used, as it is identical to the AUC in the case of binary outcomes (Harrell et al., 1982). For each relevé evaluated the occurrence probability of the 188 species was predicted using the stacked models. Each present species in a relevé was paired with every absent species and the proportion of pairs in which the present species had a higher probability was calculated (see box 1). The procedure was applied to the 100 evaluation relevés using three sets of predictors described above.

We used repeated measures ANOVA based on mixed effects models to assess the influence of the predictor set on model performance. The analysis was conducted using the *nlme* package (Pinheiro et al., 2011) in R.

Species	Predicted probability	Species occurrence
Quercus ilex	**0.61**	**Present**
Quercus faginea	**0.34**	**Present**
Pinus nigra	**0.28**	**Present**
Pinus pinaster	0.20	Absent
Pinus halepensis	**0.11**	**Present**
Quercus pyrenaica	0.04	Absent
Pinus sylvestris	0.01	Absent
Pinus pinea	0.01	Absent
Castanea sativa	0.00	Absent
Quercus humilis	0.00	Absent
Pinus uncinata	0.00	Absent
Quercus suber	0.00	Absent
Quercus robur	0.00	Absent
Quercus petraea	0.00	Absent
Quercus canariensis	0.00	Absent
Fagus sylvatica	0.00	Absent
Abies alba	0.00	Absent

CALCULATIONS

Number of pairs of present and absent species:
→ 17 species: 4 present, 13 absent
→ 4 x 13 = 52 pairs

Number of pairs in which the present species had a higher probability:
→ 51 pairs (all except *Pinus pinaster* – *P. halepensis*)

Proportion of pairs in which the present species had a higher probability (AUC):
→ AUC = 51/52 = 0.98

Box 1. Example of the calculation of the AUC using the procedure of Harrel's Concordance Index that is identical to the AUC for binary outcomes (Harrell et al., 1982).

3. Results and discussion

The proposed method offers a new approach to evaluate the predictive performance of stacked SDMs applied to plant species selection for ecological restoration. The method is well suited for addressing a frequent question in ecological restoration projects: which are the most appropriate plant species for the location to be restored? This question is tackled by estimating the ability of the stacked SDMs to discriminate present from absent species in selected evaluation sites. Unlike other evaluations involving the discrimination ability of stacked SDMs that use measures derived from the confusion matrix (e.g., Avery and Van Riper, 1990, Block, 1994, Feria and Peterson, 2002, Kattwinkel et al., 2009, Gabriels et al., 2007), the proposed method avoids the drawbacks of converting occurrence probabilities into binary predictions using the AUC (Fielding and Bell, 1997). Using the proposed evaluation approach we have compared competing modeling strategies and assessed the overall predictive performance of the stacked SDMs.

Model performance is a main concern for modellers and may be limited by many factors, including poor data quality, missing predictors, cross-scale issues and small datasets. Our proposal of performance evaluation approach may be used to improve the choice of predictors. Climate is often assumed to be the most determinant ecological factor in plant species distribution, and its importance increases as the spatial resolution of occurrence data decrease (Thuiller et al., 2004). Consequently, the spatial distribution of plant species is often studied with regard to climatic factors alone (Coudun et al., 2006). If available, direct measurements of the chemical properties of soil should be used in species distribution models (Austin, 2002). Unfortunately, these measurements are lacking in many species distribution datasets because of the cost of the required soil sampling in the field and further analyses in the laboratory. As an alternative to direct measurements, coarse resolution soil map data may be used to improve model performance. This kind of data is much more easily available for large areas (e.g., Eurasia, Van Liedekerke et al., 2006).

In our case study, the effect of adding the predictors related to soil condition was significant (see table 1). The average ability of the stacked models to discriminate between present and absent species improved due to the addition of soil related predictors. Adding the lithology (presence of calcareous or gypsiferous parent materials) yielded a weakly significant increase in predictive performance (p-value: 0.053). The inclusion of the major soil group as a predictor produced a slight but significant increase in the ability of the stacked SDMs to discriminate present and absent species in the relevés evaluated (see table 2).

	Numerator degrees of freedom	Denominator degrees of freedom	F-value	p-value
Intercept	1	198	17289.5	< 0.0001
Set of predictors	2	198	5.6	0.0041

Table 1. Assessment of the influence of the predictor set on model performance using repeated measures ANOVA based on mixed effects models.

	Estimate	Std. Error	z value	Pr(>|z|)
Climate & Lithology - Climate only	0.0061	0.0026	2.320	0.0532
Climate & Lithology & Soil group - Climate only	0.0086	0.0026	3.286	0.0030
Climate & Lithology & Soil group - Climate & Lithology	0.0025	0.0026	0.967	0.5981

Table 2. Multiple comparisons of mean effects of the predictor set on model performance (site AUC) using Tukey's contrasts.

Our results support the advice of previous research that recommends the inclusion of coarse resolution soil related data into SDMs (Gastón et al., 2009, Titeux et al., 2009). The inclusion of soil related data improved model performance despite the fact that the soil dataset had a 5-fold coarser spatial scale than the species distribution datasets (1:1,000,000 vs 1:200,000). However, the improvement may be larger if fine-scale direct soil variables are used (Coudun et al., 2006).

The average ability of the stacked models trained with the best set of predictors to discriminate between present and absent species in the evaluation sites was acceptable (mean AUC: 0.88, sd: 0.07). The minimum site AUC was 0.73 and AUC was lower than 0.8 only in 15% of the relevés evaluated (see figure 4). Site AUC was higher than 0.9 in a significant portion of the relevés (42%). The model performance of the best set of predictors was acceptable on average and high (> 0.9, Swets, 1988) in 42% of the relevés evaluated. The results validate the presented stacked SDMs as a decision support tool for plant species selection in ecological restoration projects in Spain.

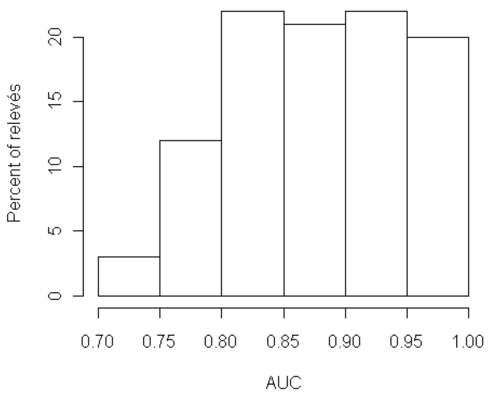

Figure 4. Relative frequency plot of the site AUC values of the best performing stacked SDMs (climate, lithology and soil group as predictors).

In this study we have used logistic regression to fit the individual SDMs, but the proposed evaluation approach may be used with any modelling method which outputs are suitability indexes that can be used to rank species (e.g., Maxent, Phillips et al., 2006, or any of the methods reviewed by Elith et al., 2006). A known limitation of the method is that the estimates may be unreliable if the number of considered species is too low. Harrell's Concordance Index is a proportion calculated among the pairs of present and absent species, if the total number of species is low the confidence interval of the proportion will be high and the estimated index will be unreliable.

We recommend the proposed evaluation approach to validate stacked species distribution models used to support species selection in ecological restoration projects. A model evaluation procedure better suited to species selection in ecological restoration projects may produce more accurate models, which are expected to decrease the risk of selecting unsuitable species and, consequently, improve the success rates of the restoration projects. Our results encourage further use of the proposed method in other cases where the predicted probabilities from stacked species distribution models have to be tested against observed species assemblages.

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