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Lithologic data improve plant species distribution models based on coarse-grained ocurrence data

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Abstract

The aim of this study was to assess the improvement of plant species distribution models based on coarse-grained occurrence data when adding lithologic data to climatic models. The distributions of 40 woody plant species from continental Spain were modelled. A logistic regression model with climatic predictors was fitted for each species and compared to a second model with climatic and lithologic predictors. Improvements on model likelihood and prediction accuracy on validation subsamples were assessed, as well as the effect of calcicole–calcifuge habit on model improvement. Climatic models had reasonable mean prediction accuracy, but adding lithologic data improved model likelihood in most cases and increased mean prediction accuracy. Therefore, we recommend utilizing lithologic data for species distribution models based on coarse-grained occurrence data. Our data did not support the hypothesis that calcicole–calcifuge habit may explain model improvement when adding lithologic data to climatic models, but further research is needed.

Key words: environmental niche modelling, chorologic atlas, calcicole–calcifuge habit.

Resumen

La información litológica mejora los modelos de distribución de especies de plantas basados en datos de baja resolución espacial

El objetivo de este estudio es evaluar la mejora que supone la incorporación de la litología a modelos climáticos de distribución de especies basados en datos de baja resolución espacial. La zona de estudio es la España peninsular. Se ha ajustado un modelo de regresión logística con variables climáticas para cada una de las 40 especies vegetales consideradas y se ha comparado a un segundo modelo con variables climáticas y litológicas. Se ha evaluado la mejora en la verosimilitud y la capacidad predictiva en submuestras de validación, así como el efecto del grado de preferencia de las especies por suelos calcáreos o silíceos en dicha mejora. Los modelos climáticos ofrecen una capacidad predictiva media razonablemente buena, pero la adición de la litología aumenta la verosimilitud del modelo en la mayoría de los casos y la precisión media de las predicciones aumentan significativamente. Se recomienda utilizar información litológica para los modelos de distribución de especies de plantas basados en datos de baja resolución espacial. Con los datos usados no se puede aceptar la hipótesis de que el grado de preferencia de las especies por suelos calcáreos o silíceos explica las diferencias entre especies en la mejora de los modelos debido a la incorporación de información litológica, pero este aspecto debe ser estudiado con más profundidad en futuras investigaciones.

Palabras clave: modelización de nicho ecológico, atlas corológicos, calcífugas, calcícolas.

Introduction

Predictive modelling of species distribution is an increasingly important tool to address various issues in ecology, biogeography, evolution and, more recently, in conservation biology and climate change research (Guisan & Thuiller, 2005). Modelling species distribution is also useful for plant species selection in ecological restoration (e.g. Felicísimo, 2003; Heredia *et al.*, 2007).

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Species distribution atlases are a valuable source of data for species distribution models (e.g. Thuiller *et al*., 2004; McPherson *et al*., 2005). Species occurrence data in atlases is often coarse-grained: 10 km × 10 km grids in national atlases in the Spanish study area (e.g. Alejandre *et al*., 2006) or 50 km × 50 km grids in European atlases (e.g. Jalas & Suominen, 1972).

Climate is often assumed to be the most determinant ecological factor in plant species distribution, and it is widely accepted that its importance increases as the spatial resolution of occurrence data decreases (Thuiller *et al*., 2004), consequently spatial distribution of plant species is often studied with regard to climatic factors alone (Coudun *et al*., 2006). Simultaneous study of the response of plant species to both climatic and soil factors is rare (Coudun *et al*., 2006), moreover, when coarse-grained data are used, few modelling studies consider soil factors (e.g. Schmidtlein & Ewald, 2003; Svenning & Skov, 2005) and the majority do not (e.g. Hoffmann, 2002; Thuiller *et al*., 2003; 2004; Araújo *et al*., 2005). Assuming that climatic models can reasonably explain the distribution of most plants at coarse-grained resolutions, should it be recommended that soil-related data be considered in these models? We tried to answer this general question by adding lithologic data to climatic models and assessing the increase of model likelihood and improvement of model predictive accuracy.

A secondary objective of this study was to test the dependence of the model improvement on calcicole–calcifuge habit of species. The hypothesis was that the stronger the preference of a species for calcareous or siliceous soils, the greater the model predictive accuracy due to adding the lithologic data.

Methods

Species occurrence data

Distribution maps (10 km × 10 km grid) of 40 woody plant species in continental Spain were used in this study (Soriano, 2002). Initially, classical botanical records (herbaria and published checklists) were used to build the distribution maps. Classical botanical data are often gathered without any predefined sampling strategy and only presence is recorded, consequently the reliability of absence is unknown. As species absence input into models should be as reliable as species presence (Lobo, 2008), classical botanical records may be insufficient for accurate modelling. To avoid this problem, woody plant surveys from the Forest Map of Spain (Ruiz de la Torre, 1990–1999) were added to the distribution maps. As a result of exhaustive field work, the contribution of the Forest Map to the chorology of woody plants may double the known distribution area (Gastón & Soriano, 2006) and therefore increase the confidence in absence data.

Climatic data

Climatic data were estimated using Estclima, a multiple regression model based on meteorological station data (Sánchez-Palomares *et al*. 1999). As Estclima needs elevation data, a digital elevation model with a horizontal grid spacing of approximately 1 km (GTOPO30, U.S. Geological Survey, 1996) was used as input for Estclima, obtaining estimations for 28 climatic variables for each 1-km^2 cell. A set of 16 variables commonly used in tree species autoecology in Spain (Sánchez-Palomares, 2001) were derived from the output of Estclima (Table 1). A "direct approach" (McPherson *et al*., 2005) was used to amalgamate the climatic data within each species-occurrence cell (10 km × 10 km) by simply taking the average value. To avoid collinearity, a subset of representative variables were selected, as follows: (1) groups of similar variables were drawn according to the results of a principal components analysis; (2) one representative variable of each group was selected; and (3) the remaining variables of the group were discarded if Pearson's correlation coefficient with the representative variable was > 0.9.

Lithologic data

Data on calcicole–calcifuge habit are common in species habitat descriptions (Castroviejo *et al.*, 1986–2008; López-González, 2002; Ruiz de la Torre, 2006), but more detailed knowledge on soil species preferences is not available for many species. The response to soil carbonate content is better known for more plant species, and this soil feature was chosen as a first attempt at including soil factors in coarse-grained models. Since there was no carbonate content map for the study area, the distribution of calcareous parent material from the European Soil Database (Van Liedekerke *et al*., 2006) was used as an indicator of soil carbonate content. Original lithologic data (1 km grid) was amalgamated within each species-occurrence cell (10 km × 10 km) by simply taking the proportion of area occupied by calcareous parent material.

We assumed that any soil sample obtained inside a calcareous area according to the European Soil Database must have significant carbonate content. This assumption may not be true for various reasons: e.g. map spatial errors, incorrect inference of the parent material from soil taxonomic units (for details see Van Liedekerke *et al*., 2006) or complete leaching of soil carbonates. To check the reliability of the assumption, field measures of soil carbonate content (percent in fine earth) were compared with the distribution of calcareous parent materials. Field measures were taken from the ICP-Forests Level I network (Montoya & López-Arias, 1998): 464 forest plots on a 16 km × 16 km grid covering all of Spain.

Calcicole–calcifuge habit

Species were classified regarding to calcicole–calcifuge habit following habitat descriptions of botanical handbooks (Castroviejo *et al.*, 1986–2008; López-González, 2002; Ruiz de la Torre, 2006). As no homogeneous classification was available, habitat descriptions were adapted to an *ad hoc* classification developed for this study: (1) strict calcifuges (SCF), species that only occur in siliceous or completely decarbonated soils; (2) non-strict calcifuges (NSCF), species that clearly prefer siliceous soils, but tolerate calcareous soils; (3) indifferent (IND), species with no clear preference for siliceous or calcareous soils; (4) non-strict calcicoles (NSCC), species that clearly prefer calcareous soils, but tolerate siliceous soils; and (5) strict calcicoles (SCC), species that only occur in calcareous soils.

Another species grouping criterion that considered the strength of preference of species for either calcareous or siliceous soils was used for data analysis: intolerance (SCF + SCC), preference (NSCF + NSCC) or indifference (I).

Data analysis

Logistic regression, a particular case of generalized linear models, is often used in species distribution models (Guisan & Zimmermann, 2000). This kind of regression is appropriate for presence–absence response variables and quantitative environmental predictors (Legendre & Legendre, 1998). The present study used second-order polynomial terms in the linear predictor to model unimodal responses of species to environmental gradients (Legendre & Legendre, 1998). Once the model was fitted, it returned probability of occurrence of species.

Results of logistic regression are sensitive to prevalence (proportion of positive cases in the sample) and sampling prevalence of 50% can lead to an optimal balance between false positive (commission) and false negative (omission) errors (McPherson *et al*., 2004). A training sample prevalence of 50% appeared ideal in the present study, since there was no reason to prefer commission or omission errors. In the original dataset prevalence was always lower, and to reach exactly 50% the absences were randomly subsampled.

Model fitting used a forward stepwise procedure based on Wald's statistic with a significance threshold of 0.05 to enter and 0.10 to exit. For each species two models were fitted following the same procedure but with different sets of variables: (1) a model with only climatic predictors (those selected in the stepwise procedure); and (2) a model with climatic and lithologic predictors (a lithologic predictor was only included if it significantly increased likelihood). Half of the sample was randomly subsampled for model fitting and the other half was reserved for validation (keeping prevalence at 50% in both subsamples).

The ability to discriminate between presence and absence was used for model validation, using Area Under ROC Curve (AUC) as recommended by McPherson *et al*. (2004). AUC indicated model predictive accuracy: poor was 0.5–0.7, reasonable 0.7–0.9, and good 0.9–1 (Swets, 1988). The statistical package SPSS (ver. 11) was used for both model fitting and validation.

The effect of adding lithologic data to climatic models was assessed by comparing models for each species. First, the proportion of species for which the model likelihood increased when adding lithologic data was calculated (those cases where a lithologic predictor was retained in the final model after stepwise variable selection). Second, a t-test of paired samples compared AUC of climatic models against AUC of climatic–lithologic models. The dependence of model accuracy improvement on species calcicole–calcifuge habit and the strength of preference were tested using one-way analysis of variance (ANOVA).

Results

Variables were grouped according to the results of a principal components analysis (Fig. 1). Mean annual temperature, mean maximum temperatures of the warmest month, mean minimum temperatures of the coldest month, mean annual rainfall and mean summer rainfall were selected as representative variables of each group to avoid collinearity (Table 1). Dry season length (sensu Gaussen), was also selected due to a weaker correlation (0.8) with the representative variable of the group.

There was a high level of concordance between calcareous parent material distribution (according to the map) and soil carbonate content (field measures): soil carbonate content was > 1% in 89% of the sample plots in calcareous areas, and < 1% in 90% of those in non-calcareous areas. These results support the use of the lithologic data from the European Soil Database as a predictor for the species distribution models.

The stepwise variable selection procedure retained the lithologic predictor in the final model for 36 species (90%); therefore, in most cases the likelihood was greater for climatic–lithologic than for climatic models (table 2). A lithologic predictor was not retained (i.e. there was no significant improvement) in the final model for 10% of the species: two indifferent species (*Arbutus unedo* and *Olea europaea*) and two non-strict calcifuges (*Cistus monspeliensis* and *Ilex aquifolium*).

AUC for climatic models had a range of 0.733–0.964 with mean of 0.846; consequently, mean predictive accuracy could be considered reasonable (Swets, 1988). Mean AUC for climatic–lithologic models was greater

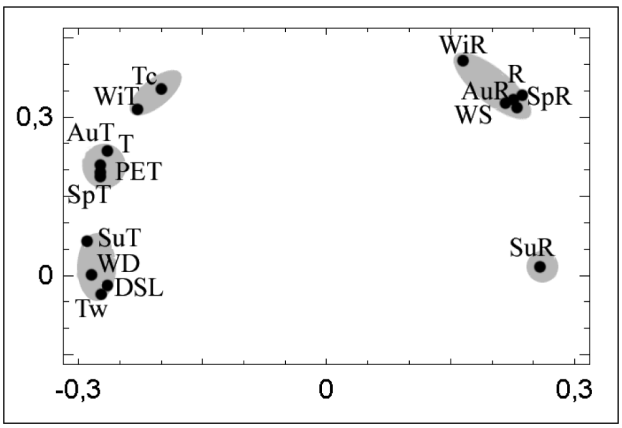

Figure 1. Principal components analysis of climatic variables in a 2D plot of component weights (first and second components account for 91.7% of the variability).

Table 1. Description and codes of original climatic variables. * indicates those variables that were selected and used in the models to avoid collinearity

Code	Description	Units
WiR	Mean winter rainfall	mm
SpR	Mean spring rainfall	mm
SuR *	Mean summer rainfall	mm
AuR	Mean autumn rainfall	mm
R *	Mean annual rainfall	mm
WiT	Mean winter temperature	ºC
SpT	Mean spring temperature	ºC
SuT	Mean summer temperature	ºC
AuT	Mean autumn temperature	ºC
T *	Mean annual temperature	ºC
Tw *	Mean of maximum temperatures of the warmest month	ºC
Tc *	Mean of minimum temperatures of the coldest month	ºC
DSL *	Dry season length (Gaussen)	months
PET	Mean annual potential evapotranspiration (Thornwaite)	mm
WS	Mean annual water surplus (Thornwaite)	mm
WD	Mean annual water deficit (Thornwaite)	mm

(0.863) and the mean difference (0.017) was significantly different from zero (P = 0.0002 for a paired t-test).

There was no significant difference between the mean difference from one class of calcicole–calcifuge habit to another (Table 3 and Fig. 2). A similar result was obtained when species were grouped according to strength of preference for either calcareous or siliceous soils (Table 4 and Fig. 3).

Discussion

Geographical distributions of the considered species can be mainly explained using climatic variables as predictors of a logistic regression and this seems to be the case in most species when coarse-grained occurrence data is used (Thuiller *et al*., 2004). Even so, other predictors may improve climatic models, as shown for land use variables (Pearson *et al*., 2004; Gastón, 2006). The mean increases in AUC from adding lithology in the present study may appear small, but were greater than those of Thuiller *et al*. (2004) for shrub species at European-level by adding land use data (i.e. 0.017 cf 0.003). Although lithology is rarely used in species distribution

Table 2. Species, calcicole–calcifuge habit and predictive accuracy of the models. SCF: strict calcifuge; NSCF: non-strict calcifuge; I: indifferent; NSCC: non-strict calcicole; and SCC: strict calcicoles

	Calcicole–calcifuge habit	**Likelihood increase after adding lithologic data**	**AUC of the models**		
			Climatic predictors (1)	**Climatic and lithologic predictors (2)**	**Difference (2)–(1)**
Adenocarpus complicatus (L.) J. Gay	SCF	Yes	0.810	0.856	0.046
Anthyllis cytisoides L.	NSCC	Yes	0.930	0.923	-0.007
Arbutus unedo L.	I	No	0.799	0.799	0.000
Bupleurum fruticosum L.	I	Yes	0.800	0.873	0.073
Buxus sempervirens L.	NSCC	Yes	0.870	0.899	0.029
Cistus albidus L.	NSCC	Yes	0.818	0.84	0.022
Cistus ladanifer L.	SCF	Yes	0.870	0.918	0.048
Cistus laurifolius L.	NSCF	Yes	0.873	0.878	0.005
Cistus monspeliensis L.	NSCF	No	0.901	0.901	0.000
Cistus populifolius L.	SCF	Yes	0.813	0.819	0.006
Cytisus multiflorus (L'Hér.) Sweet	SCF	Yes	0.934	0.962	0.028
Cytisus scoparius subsp. ***scoparius*** (L.) Link	NSCF	Yes	0.788	0.862	0.074
Cytisus striatus (Hill) Rothm.	SCF	Yes	0.887	0.910	0.023
Ephedra fragilis L.	NSCC	Yes	0.826	0.867	0.041
Erica arborea L.	NSCF	Yes	0.773	0.806	0.033
Erica australis L.	SCF	Yes	0.860	0.891	0.031
Erica multiflora L.	NSCC	Yes	0.964	0.971	0.007
Erica scoparia L.	SCF	Yes	0.733	0.704	-0.029
Genista florida L.	SCF	Yes	0.909	0.917	0.008
Ilex aquifolium L.	NSCF	No	0.895	0.895	0.000
Jasminum fruticans L.	I	Yes	0.734	0.743	0.009
Juniperus communis L. (except subsp. ***alpina***)	I	Yes	0.936	0.937	0.001
Juniperus oxycedrus L. (except subsp. ***macrocarpa***)	I	Yes	0.774	0.771	-0.003
Juniperus phoenicea L. (except subsp. ***turbinata***)	I	Yes	0.781	0.859	0.078
Juniperus thurifera L.	NSCC	Yes	0.905	0.924	0.019
Lonicera implexa Aiton	I	Yes	0.831	0.772	-0.059
Myrtus communis L.	I	Yes	0.839	0.859	0.020
Nerium oleander L.	I	Yes	0.919	0.898	-0.021
Olea europaea L.	I	No	0.825	0.825	0.000
Phillyrea angustifolia L.	I	Yes	0.766	0.809	0.043
Phillyrea latifolia L.	I	Yes	0.815	0.849	0.034
Pistacia lentiscus L.	I	Yes	0.882	0.884	0.002
Retama sphaerocarpa (L.) Boiss.	I	Yes	0.856	0.859	0.003
Rhamnus alaternus L.	I	Yes	0.791	0.816	0.025
Rosa sempervirens L.	I	Yes	0.924	0.923	-0.001
Rosmarinus officinalis L.	NSCC	Yes	0.857	0.863	0.006
Spartium junceum L.	NSCC	Yes	0.845	0.860	0.015
Taxus baccata L.	I	Yes	0.859	0.869	0.010
Teucrium fruticans L.	I	Yes	0.873	0.871	-0.002
Viburnum tinus L.	I	Yes	0.796	0.854	0.058

Table 3. ANOVA table for differences in AUC between models due to lithologic data by calcicole–calcifuge habit (indifferent, non-strict calcicole, non-strict calcifuge or strict calcifuge)

Source of variance	Sum of squares	Degrees of freedom	Mean square	F-ratio	P-value
Between groups	0.0005	3	0.0002	0.20	0.8944
Within groups	0.0286	36	0.0008		
Total	0.0290	39			

models based on coarse-grained data, our results encourage consideration of calcareous parent material distribution as a predictor in such models. The relevance of lithologic predictors in species distribution models based on data with lower spatial resolution (e.g. 50 km × 50 km grid) will presumably be lower, but may be as significant as other non-climatic factors (e.g. land use by Thuiller *et al*., 2004), therefore, further research is needed in this direction.

In regard to the secondary objective of this study, the data did not support the hypothesis that calcicole–calcifuge habit could explain model improvement when adding lithologic data to climatic models. It is possible that sample size (40 species) was too low to detect slight differences in AUC increases between groups (range 0.002–0.008). Unfortunately, there is little accurate distribution data for plant species in the study area. Moreover, the spatial resolution of data may be too low to assess this issue and fine-grained data may provide better results.

For some species, soil preferences from botanical handbooks did not match with preferences according to our data. For example, *Juniperus phoenicea* is considered indifferent to soil carbonate content (López-González, 2002; Ruiz de la Torre, 2006), but the species was clearly more prevalent in calcareous than in siliceous areas (48.2 and 2.1%, respectively). According to Castroviejo *et al.* (1986–2008), *Cistus ladanifer* does not tolerate calcareous soils and *Cytisus scoparius* subsp. *scoparius* tolerates both calcareous and siliceous soils but prefers the latter. Our dataset tells a different story: prevalence in siliceous areas was similar for both species (45.6 and 51.9%, respectively). Such mismatches occurred for around 25% of the considered species and may have disrupted any relation between improved model accuracy due to lithologic data and calcicole–calcifuge habit. A quantitative assessment of realized niche in regard to soil carbonate content is beyond the scope of this study, but further research could help clarify any contribution of calcicole–calcifuge habit to lithologic data improving the accuracy of models.

In conclusion, we recommend utilizing lithologic data as a predictor in species distribution models based on coarse-grained occurrence data, but further research is needed to better understand species soil preferences influence on model accuracy.

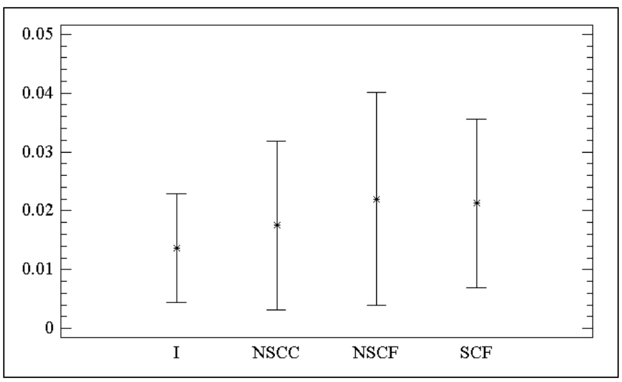

Figure 2. Mean differences in AUC between models due to lithologic data for each calcicole–calcifuge habit (indifferent, non-strict calcicole, non-strict calcifuge or strict calcifuge) and 95% confidence intervals based on Fisher's least significant difference procedure.

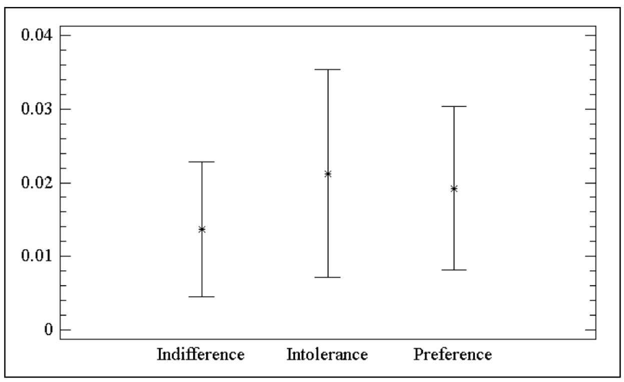

Figure 3. Mean differences in AUC between models due to lithologic data for each class of strength of preference for either calcareous or siliceous soils (indifference, intolerance or preference) and 95% confidence intervals based on Fisher's least significant difference procedure.

Table 4. ANOVA table for differences in AUC between models due to lithologic data by strength of preference for either calcareous or siliceous soils (indifference, intolerance or preference)

Source of variance	Sum of squares	Degrees of freedom	Mean square	F-ratio	P-value
Between groups	0.0004	2	0.0002	0.27	0.7647
Within groups	0.0286	37	0.0008		
Total	0.0290	39			

Aknowlegments

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