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RESEARCH PAPER

Geographical patterns in prediction errors of species distribution models

Jan Hanspach[1]*, Ingolf Kühn[1], Oliver Schweiger[1], Sven Pompe[1,2] and Stefan Klotz[1]

[1]*UFZ, Helmholtz Centre for Environmental Research – UFZ, Department of Community Ecology, Theodor-Lieser-Strasse 4, 06120 Halle, Germany,* [2]*Institute of Ecology, Friedrich-Schiller-University Jena, Dornburger Strasse 159, 07743 Jena, Germany*

ABSTRACT

Aim To describe and explain geographical patterns of false absence and false presence prediction errors that occur when describing current plant species ranges with species distribution models.

Location Europe.

Methods We calibrated species distribution models (generalized linear models) using a set of climatic variables and gridded distribution data for 1065 vascular plant species from the Atlas Florae Europaeae. We used randomly selected subsets for each species with a constant prevalence of 0.5, modelled the distribution 1000 times, calculated weighted averages of the model parameters and used these to predict the current distribution in Europe. Using a threshold of 0.5, we derived presence/absence maps. Comparing observed and modelled species distribution, we calculated the false absence rates, i.e. species wrongly modelled as absent, and the false presence rates, i.e. species wrongly modelled as present, on a 50 × 50 km grid. Subsequently, we related both error rates to species range properties, land use and topographic variability within grid cells by means of simultaneous autoregressive models to correct for spatial autocorrelation.

Results Grid-cell-specific error rates were not evenly distributed across Europe. The mean false absence rate was 0.16 ± 0.12 (standard deviation) and the mean false presence rate was 0.22 ± 0.13. False absence rates were highest in central Spain, the Alps and parts of south-eastern Europe, while false presence rates were highest in northern Spain, France, Italy and south-eastern Europe. False absence rates were high when range edges of species accumulated within a grid cell and when the intensity of human land use was high. False presence rates were positively associated with relative occurrence area and accumulation of range edges.

Main conclusions Predictions for various species are not only accompanied by species-specific but also by grid-cell-specific errors. The latter are associated with characteristics of the grid cells but also with range characteristics of occurring species. Uncertainties of predictive species distribution models are not equally distributed in space, and we would recommend accompanying maps of predicted distributions with a graphical representation of predictive performance.

Keywords

Commission, Europe, false absence rate, false presence rate, omission, species distribution models, validation.

*Correspondence: Jan Hanspach, UFZ, Helmholtz Centre for Environmental Research – UFZ, Department of Community Ecology, Theodor-Lieser-Strasse 4, 06120 Halle, Germany.
E-mail: jan.hanspach@ufz.de

INTRODUCTION

Species distribution models serve as an important tool for understanding the relationship between species ranges and environmental parameters. Species distribution models are applied in ecology and conservation biology to predict current and projected future species distributions (Huntley *et al.*, 1995; Guisan & Zimmermann, 2000). However, model uncertainty presents many challenges, and can result from: (1) the context (i.e. the boundaries of the system to be modelled), (2) model

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uncertainty (i.e. derived from the model concept, the computational implementation, or the model specification), (3) inputs (i.e. description of the reference system and the external forces that are driving changes in the reference system), (4) parameter uncertainty (associated with the data and the methods used to calibrate the model parameters), and (5) model outcome uncertainty (i.e. the accumulated uncertainty associated with the model outcomes of interest) (Walker *et al.*, 2003). Most often, data deficiencies and model specifications are seen as the main drivers of uncertainty in species distribution models (Barry & Elith, 2006; Heikkinen *et al.*, 2006; Dormann *et al.*, 2008). Uncertainties in general, and prediction errors in particular, frequently occur in species distribution models because these models necessarily simplify the real world as well as ignore important aspects of species ecology (e.g. Hampe, 2004). The number of prediction errors varies considerably among modelling techniques (Muñoz & Felicísimo, 2004; Segurado & Aráujo, 2004; Lawler *et al.*, 2006; Pearson *et al.*, 2006; Meynard & Quinn, 2007; Dormann *et al.*, 2008), as well as with the degree of equilibrium with environmental conditions (Araújo & Pearson, 2005) and species traits (Pöyry *et al.*, 2008; Hanspach *et al.*, 2010). In the majority of cases, when only species presence or absence is predicted, two different types of prediction errors can occur: false absences and false presences (see Table 1; Fielding & Bell, 1997). False absences (also called false negatives or omissions) occur when an observed presence is predicted as absent. False presences (false positives, commissions) describe a predicted presence which is unconfirmed by an observation. Both errors are frequently combined in indices like Cohen's kappa (Cohen, 1960) or the area under the curve (AUC) of a receiver operating characteristic (Hanley & McNeil, 1982; Fielding & Bell, 1997) to obtain an overall estimate of the predictive performance (Fielding & Bell, 1997). Though such measures of predictive performance have been widely used, they suffer from serious shortcomings (McPherson *et al.*, 2004; Lobo *et al.*, 2008).

Geographical patterns of prediction errors have rarely been addressed, although it has been recognized that prediction errors do not occur randomly nor are they distributed evenly (La Sorte & Hawkins, 2007). Hortal & Lobo (2006) hypothesized that prediction errors are spatially structured and accumulate across many species, and results from other authors indicate the existence of such accumulations (Thuiller *et al.*, 2004a; Araújo *et al.*, 2005). Within this study, we describe the accumulation of prediction errors, i.e. the incorrect description of the current species distribution using predictive modelling, across geographical space and hypothesize that this can be attributed to: (1) data quality and resolution, (2) species disequilibrium with climate, and (3) range characteristics (Table 2).

The importance of the quality of the mapping data on species distribution models has been highlighted by various studies (Loiselle *et al.*, 2008; Lobo *et al.*, 2010; Rocchini *et al.*, in press). Data from areas that are not sufficiently sampled are confounded by a higher proportion of species that are falsely described as absent, which in turn results in a higher false presence rate. Given that data quality is frequently environmentally biased (Bierman *et al.*, 2010), species distribution models would wrongly describe the conditions assumed to be suitable for a species, causing high rates of false absences (Hortal *et al.*, 2008). Since the distribution data used in this study are exhaustive atlas data from the Atlas Florae Europaeae (Lahti & Lampinen, 1999), we assume a minor importance of this error. Further, an overly coarse resolution of the mapping units may increase modelling error in heterogeneous areas, e.g. by averaging across the heterogeneity or recognizing the most abundant features only (Trivedi *et al.*, 2008). False absence errors might accumulate, for example, in mountainous areas where many species only occur under microclimatic conditions that are not represented in the coarse-scale environmental variables, and therefore not described by a model that is based on these data.

Areas with a large number of species that are not in equilibrium with climate should have a higher rate of false presence errors. Several factors such as anthropogenic, historic, geographic and biotic interactions could be responsible for this. A high intensity and/or a long history of human land use, as can be found in central and southern Europe, may reduce the influence of climate on species distributions and thus decrease the predictability of current species distributions. In Europe, moreover, many plant species are still experiencing post-glacial dispersal limitations (Svenning & Skov, 2004; Svenning *et al.*, 2008) which may lead to predictions of false presences in areas distant from glacial refugia.

More difficult to delineate geographically are biotic interactions which restrict ranges in some areas more strongly than climate (Gaston, 2003). Hortal & Lobo (2006) hypothesized that prediction errors are high where range margins coincide or in areas where community-level or historic processes strongly influenced species distribution. At range margins, increased climatic stress will make a species more sensitive to other environ-

Table 1 Confusion matrix and the calculation of false absence and false presence rate.

		Observed	
		1	0
Modelled	1	True presence	False presence
	0	False absence	True absence
		False absences/all observed presences = 1 − sensitivity = **false absence rate**	False presences/all observed absences = 1 − specificity = **false presence rate**

Table 2 Potential sources of prediction errors for species distribution models using generalized linear models and their hypothesized influence on predictive performance in a grid cell. An increase or decrease of the error rate (FA, false absence rate; FP, false presence rate) according to a certain hypothesis is indicated by a plus or minus sign. The rightmost column gives the variables that were used within this study to test the corresponding hypothesis.

Source of error	FA	FP	Analysed variable
Data quality and resolution			
Environmental bias and incomplete description of the environmental response of a species (Hortal *et al*., 2008)	+		
Mean climatic values do not resemble the conditions experienced, e.g. envelopes in mountainous areas are biased towards warmer conditions (Trivedi *et al*., 2008)	+		Altitudinal range
Species are not detected due to low sampling effort (Anderson, 2003; Gu & Swihart, 2004)		+	
Disequilibrium			
Lack of habitat (habitats not widely distributed, e.g. saline habitats, habitats disturbed by human land use), historical extinctions (e.g. due to recent fires, or other stochastic incidents), impeded colonization due to historical and geographical (dispersal and dispersal barriers, distance to glacial refuges; Svenning *et al*., 2008) or biotic factors (biotic interactions; Brown *et al*., 1996; Schweiger *et al*., 2008)		+	Human land-use intensity
Range characteristics			
Local adaptation in widespread species may lead to overestimation of the niche (Stockwell & Peterson, 2002)		+	Relative occurrence area
Absences close to suitable climatic conditions in the environmental space (large ranging species) reduce the predicted ranges size and increase the probability to include false absences in the data. Absences far from climatic suitable conditions (small ranging species) generate predictions close to potential distribution and increase the probability of making false presence errors (Lobo, 2008)	+	–	Relative occurrence area
Range edge: higher environmental stress makes species sensitive, e.g. biotic interactions (Brown *et al*., 1996)		+	Range edge rate
Due to the shape of the logistic regression curve and the need to set a threshold to convert probabilities into presence/absence, we expect the largest uncertainties where the modelled probability of occurrence changes from low to high, i.e. at the modelled range edges	+	+	Range edge rate

mental factors, e.g. competition (Brown *et al*., 1996), and the potential climatic niche may not be fully occupied, leading to the prediction of false presences (Araújo *et al*., 2005). Additionally, we expect a higher rate of prediction error at range margins since the applied modelling algorithm (generalized linear models, GLMs) rather smoothly describes species responses to the environment, leading to an unspecific increase of both false absence and false presence errors in areas with many range margins. Furthermore, characteristics of species ranges may influence patterns of predictive performance both as a statistical artefact (Thuiller *et al*., 2004b) and/or as an effect of species ecology (Stockwell & Peterson, 2002).

So far, a comprehensive study on the possible accumulation of prediction errors and its determinants is lacking, although an aggregation of prediction errors has important conservation implications (Hortal & Lobo, 2006). Here, we analyse the geographical patterns of false presence and false absence rates across Europe based on more than 1000 plant species distribution models. The results are used to test the hypotheses derived from previous studies (see above, summarized in Table 2). We explain such observed prediction errors by the spatial characteristics of mapping units and the respective species.

METHODS

Species distribution models

Species distribution data for vascular plants were obtained from the Atlas Florae Europaeae database (AFE), maintained by the Botanical Museum, University of Helsinki, Finland at a resolution of 50 × 50 km (Lahti & Lampinen, 1999). We used 2219 cells of the AFE grid covering Europe (Fig. 1) for species distribution modelling. Species with fewer than 50 presences were excluded to allow reliable modelling. Monthly, interpolated climate data (Mitchell *et al*., 2004) at a $10' \times 10'$ grid resolution, were averaged for the period 1961–90 and aggregated to the AFE grid resolution. We derived a set of 17 standard climatic variables which are commonly used to explain large-scale patterns of species distribution (see Appendix S1 in Supporting Information).

Species distribution models were developed for 1065 plant species using GLMs with a binomial error distribution and a logit link function (logistic regression models). To avoid collinearity among the explanatory variables, we performed a principal components analysis with all standardized climatic

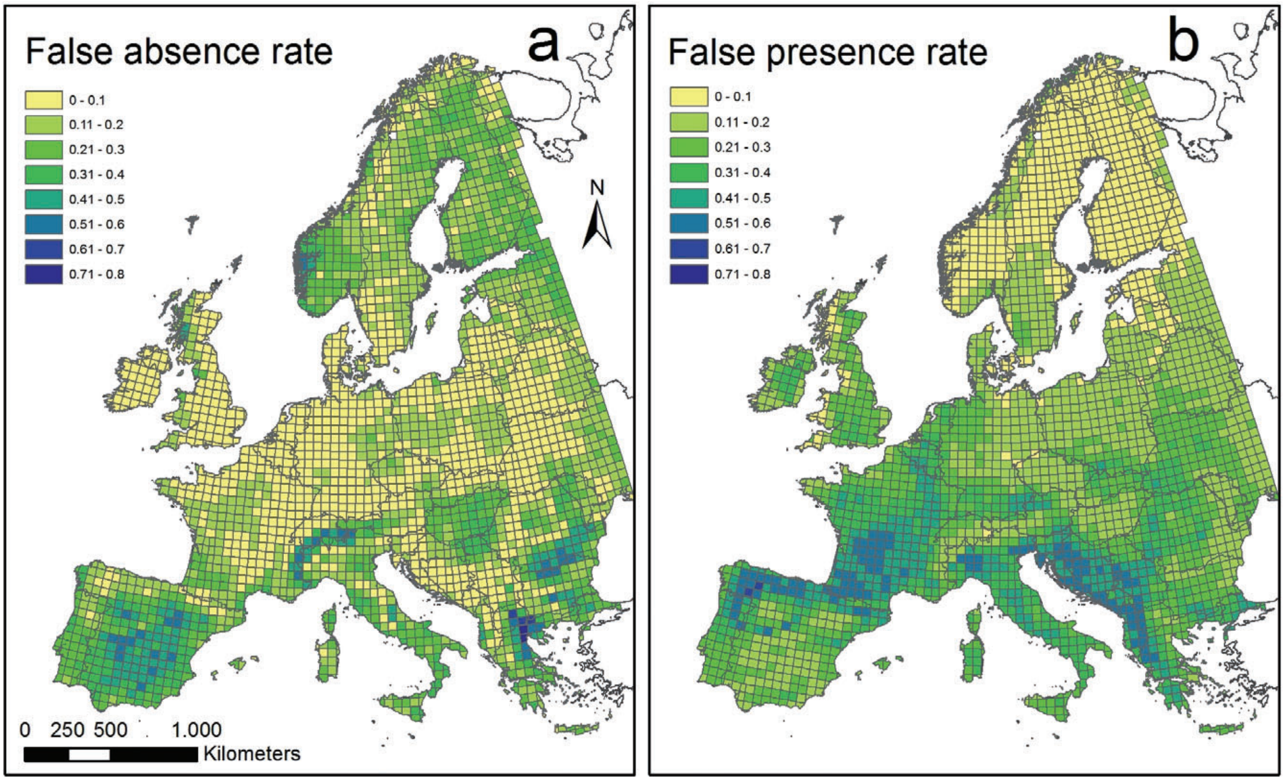

Figure 1 Spatial distribution of (a) false absence rates and (b) false presence rates in Europe (Lambert azimuthal equal area projection) based on of 1065 plant species distribution models using the grid cells of Atlas Florae Europaeae (2714 cells of nearly 50 × 50 km; see Table 1 for calculation).

variables. The first three principal components (explained variance 79.3%) were included as independent variables in the models. We included second-order polynomials to allow for curvilinear effects. We simplified the models by applying an automated model backward selection that minimized the Bayesian information criterion (BIC), to avoid overfitting.

Prevalence of the data, i.e. the proportion of the number of presences to the number of presences and absences, has been shown to have important effects on the measure of the performance of species distribution models and the selection of the threshold used to convert probability into absences and presences (Jiménez-Valverde *et al*., 2009). When comparing the performance of different models, prevalence should be kept constant at an intermediate level (McPherson *et al*., 2004; Liu *et al*., 2005). Thus, for each plant species, we randomly sampled our data points retaining a constant prevalence of 0.5. We used all presences and sampled the same number of absences if the number of presences was lower than the absences per species, and vice versa. Sampling of data points and subsequent modelling using these points was repeated 1000 times. We calculated the average of the derived model estimates and weighted them by the BIC of the model, i.e. estimates of models with a lower fit were down-weighted. Using the averaged estimates, we predicted the probabilities of occurrence for each grid cell within the study area, i.e. model validation was performed with the same grid cells that were used for model calibration. We converted the predicted probabilities into presence/absence data by using the pre-defined prevalence of 0.5 (Liu *et al*., 2005) as a threshold and obtained false absences and false presences for each grid cell and each species by comparisons with the actual observations.

Analysis of prediction errors

To quantify the rate of prediction errors, we overlaid all modelled species distribution maps and counted the number of true presences, true absences, false presences and false absences per grid cell. We calculated the false absence rate as the number of false absences over the number of all observed presences and the false presence rate as the number of false presences over the number of all observed absences per grid cell (see Table 1). We examined the relationship between error rates (log transformed to normalize data) using linear models with a set of explanatory variables, namely the intensity of human land use, altitudinal range and species range properties (Table 2; for maps of explanatory variables see Appendix S2). The intensity of human land use was measured as human appropriation of net primary productivity (%) and we calculated mean values for each grid cell (Haberl *et al*., 2007). To estimate orographical heterogeneity within a grid cell, we calculated the altitudinal range in metres from a digital elevation model with a resolution of approximately 90 m (CIAT, 2004). Mean relative occurrence area per grid cell was calculated as the mean of the relative occurrence area of all species occurring within a grid cell. Species-specific relative occurrence area was calculated as the sum of observed presences divided by the number of all grid cells within the study area (Lobo *et al.*, 2008). Large values of mean relative occurrence area indicate that most species in the gird cell have predominantly large ranges, and vice versa. We also calculated how many species have their range edge in a grid cell, which we will refer to as the 'range edge rate'. The range edge is represented by both occupied and unoccupied grid cells. Therefore, a cell was regarded to mark an edge of a species' range when at least a third of the neighbouring cells (first-order lateral and diagonal) were absences (when a species is present in the cell of interest) or presences (when a species is absent in the cell of interest).

To account for spatial autocorrelation in model residuals, we applied simultaneous autoregressive models (spatial error model using up to eight nearest neighbours if available; Bivand, 2009). We performed a hierarchical variance partitioning (Mac Nally, 1996; Walsh & Mac Nally, 2008) to obtain the independent effects of the explanatory variables. As a coefficient of determination, we calculated the squared Pearson correlation coefficient between the original and fitted values of the false absence and false presence rates separately for the non-spatial term and the spatial term (pseudo R^2; Kissling & Carl, 2008). All statistical analyses were performed in the R environment (R Development Core Team, 2008).

RESULTS

Geographical patterns of prediction errors

Modelling and validation of the 1065 species distribution models resulted in a species-specific false absence rate of 0.12 ± 0.06 (mean ± standard deviation), and a species-specific false presence rate of 0.23 ± 0.09. The aggregation of error rates across species yielded a grid-cell-specific false absence rate of 0.16 ± 0.12 and grid-cell-specific false presence rate of 0.22 ± 0.13. In 60% of the grid cells, the false presence rates exceeded the false absence rates. We found a strong geographical pattern of prediction errors. False absence rates were high in central Spain, the Alps and parts of south-eastern Europe, while they were low in western, central and eastern Europe (Fig. 1a). False presence rates were high in northern Spain, France, Italy and south-eastern Europe, while low values occurred in northern Europe (Fig. 1b).

Explanatory models of prediction errors

The false absence rates were explained by all explanatory variables (Table 3). The independent effects of range edge rate and intensity of human land use most strongly contributed to the explanation of variance (Fig. 2). False absence rates were high when range edge rate and land-use intensity were high (Table 3).

The false presence rates were also explained by all explanatory variables (Table 3), the most important variables being relative occurrence area and range edge rate (Fig. 2). Both variables were positively associated with the false presence rates.

Table 3 Result of the simultaneous autoregressive model of the false absence rate (pseudo R^2 of the non-spatial term = 0.04, pseudo R^2 of the spatial term = 0.71) and false presence rate (pseudo R^2 of the non-spatial term = 0.13, pseudo R^2 of the spatial term = 0.85) of 1065 plant species distribution models across Europe (response variables were log-transformed and explanatory variables standardized prior to analysis).

	Estimate	Standard error	*P*-value
False absence rate			
Intercept	−1.7	0.05	< 0.001
Altitudinal range	−0.053	0.01	< 0.001
Human land-use intensity	0.085	0.01	< 0.001
Range edge rate	0.046	0.01	< 0.001
Relative occurrence area	−0.081	0.02	< 0.001
False presence rate			
Intercept	−1.2	0.06	< 0.001
Altitudinal range	0.041	0.01	< 0.001
Human land-use intensity	−0.018	0.01	< 0.05
Range edge rate	0.031	0.003	< 0.001
Relative occurrence area	0.18	0.01	< 0.001

DISCUSSION

Several recent studies have provided information about uncertainties for species distribution analysis concerning methodological issues, species and species traits (see, e.g., Elith & Graham, 2009). In our study, we identified geographical patterns of grid-cell-specific prediction errors. We argue that the problems associated with the spatial pattern of prediction errors in the analysis of the current distribution of species are fundamental, and one should be cautious when potential future distributions are predicted with species distribution models. Simply calculating validation values per species (AUC, kappa) conceals the spatial variability of predictive performance and valuable information on the reliability of the model outcome is lost (Lobo *et al.*, 2008). Further, depending on the inferences made from a study, the focus may lie more strongly in reducing one or the other type of error: a low false absence rate may be more desirable for studies prioritizing areas for conservation, while studies trying to identify sites where a species may be found demand a low proportion of false presences (Fielding & Bell, 1997).

False absence rates

The most important factor influencing false absence rates was range edge rate. In grid cells where range edges accumulate, the false absence rates were high. At range margins, several factors may lead to such a type of bias. For instance, lower species abundance at the margins can lead to a lower detectability and thus to wrong absences in the observational data. Also, several

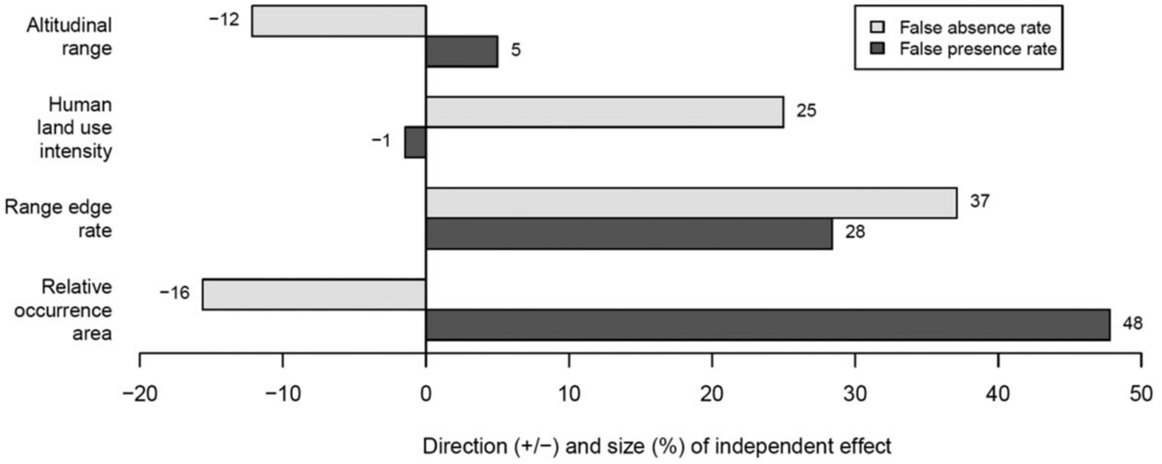

Figure 2 Hierarchical partitioning of the simultaneous autoregressive models for false absence rates and false presence rates across Europe based on 1065 plant species distribution models. The bar length and the numbers beside each bar give the independent effect in per cent. Direction of the bars (positive/negative) indicates a positive or negative association of each variable with the error rates (see estimates in Table 3).

additional factors, such as biotic interactions (Brown *et al.*, 1996; Schweiger *et al.*, in press), which may overshadow the limiting effects of climate under particular circumstances, may lead to geographically varying disequilibrium of a species with climate. This is of particular relevance for the applied modelling technique of GLMs. Within a GLM specified to model presence/absence data, a linear function is fitted that translates the presences and absences to occurrence probabilities defined by one or more environmental variables. Such a GLM equally weights the influence of presences and absences on the model parameters and the linear character of the function smoothes the response of species to the environment. Consequently, the very general description of the species response may lack precision where probabilities of occurrence change from low to high, i.e. at the range margins. How this translates to prediction errors depends on the frequency of 'wrong' observed absences (under the assumption that all observed presences are right). If they dominate at range margins, a GLM based on climate variables will underestimate the species range and the few 'true' observed presences will not be modelled as such, leading to an increased false absence rate as we have observed. However, in the opposite case, when the 'wrong' absences are in the minority, they will be modelled as presences resulting in a high false presence rate (see below).

The second grid cell characteristic connected to species range properties, the mean relative occurrence area, was also very important. Relative occurrence area has been repeatedly shown to influence prediction errors with ambiguous results (Fielding & Haworth, 1995; Araújo & Williams, 2000; Manel *et al.*, 2001; Elith *et al.*, 2002; Stockwell & Peterson, 2002). While the hypothesis that false absence rates are higher when many large-ranging species are present (Lobo, 2008) could not be confirmed, our results support opposite findings by Manel *et al.* (2001). In areas where large-ranging species dominate, i.e. in northern and eastern Europe (see also Appendix S2), their presences were modelled well. However, a high false absence rate in areas where small-ranged species dominate, i.e. in southern Europe, indicates that the presences of such species were modelled quite poorly.

The influence of the land-use intensity on the error rates did not follow our expectations. Intensive human land use is usually thought to negatively affect biodiversity, leading to a decreased false absence rate and increased false presence rate (Roy *et al.*, 1999). The positive effect of land-use intensity on false absence rates therefore seems counterintuitive. It is possible that moderate transformation of natural habitats may lead to increased heterogeneity on a landscape scale, thus harbouring more species and leading to increased false absence rates.

Furthermore, the expected influence of altitudinal range within a grid cell could not be confirmed. Although large altitudinal ranges have been shown to be an important source of uncertainty (Trivedi *et al.*, 2008; Randin *et al.*, 2009), we did not find strong support for an increase of false absences with increasing environmental heterogeneity (Luoto & Heikkinen, 2008). False absence rates were high in the Alps where altitudinal range is largest (see Appendix S3), but not in other mountainous areas of Europe (e.g. the Pyrenees, the Carpathians).

False presence rates

The most important variables describing false presence rates were the two range-specific grid cell characteristics, relative occurrence area and range edge rate, while the impact of the abiotic characteristics, altitudinal range and land-use intensity, were negligible. The strong positive effect of relative occurrence area on false presence rates follows our hypothesis that within grid cells with many large-ranging species, the probability of making false presence errors is higher (Stockwell & Peterson, 2002). Combined with the false absence errors, this means that in areas where large-ranging species dominate, too many species are predicted, thus increasing false presence rates and decreasing false absence rates. The contrary applies to areas in which small-ranged species dominate. Here, too few species are predicted, resulting in low false presence rates but high false absence rates.

Also, the positive association of range edge rate with false absence rates follows our expectations and hints at the importance of modelling technique for predictive performance. Our results show that range edge rate similarly well explains both false presence and false absence rates. This means that our models erratically over- or under-estimated the species ranges at their margins, probably depending on the species-specific data quality and (dis-)equilibrium with climate (see above). Areas in southern Europe (see Appendix S2) are particularly prone to such errors.

Alternative hypotheses

Acknowledging the large proportion of variance that was explained only by the spatial term of the simultaneous autoregressive models (Appendix S3), we present five alternative hypotheses that might be responsible for the variation of prediction errors. First, biotic interactions (e.g. competition, facilitation, herbivory/predation) restrict ranges in some areas more strongly than climate (Schweiger *et al*., in press). While the cool range margins are thought to be predominantly controlled by climate, southern and western range margins (warm margins) may be shaped by biotic interactions (Brown *et al*., 1996), potentially leading to high prediction errors in warmer areas where such margins accumulate. Though we could not directly test this hypothesis, we found some indication for it, as false presence rates increased with mean annual temperature (Pearson correlation with log-transformed false presence rate: 0.68). In addition, the high species richness in southern Europe may also lead to higher competition among species and thus to higher false presence rates in the south. Second, the abundance of vicarious species, i.e. closely related species with similar ecological requirements replacing each other in space, e.g. in the Mediterranean, may decrease predictive performance. Ranges of such species are more strongly determined by environmental barriers and dispersal limitation (Médail & Verlaque, 1997; Farnsworth, 2007; Krauss *et al*., 2010). Third, we assume that current species distributions might be influenced considerably by past land-use patterns (Motzkin *et al*., 1999; Donohue *et al*., 2000). For instance, the high false presence rate in the Mediterranean is a likely consequence of the long land-use history in this area. Fourth, another source of prediction errors may be the differing qualities of mapping in Europe (Mahecha & Schmidtlein, 2008). Lower sampling intensities in southern and eastern Europe may lead to increased error rates in these areas. The patterns of the spatial component of model residuals give an indication of this source of errors (Appendix S3). Lastly, Thuiller *et al*. (2004a) found that a truncation of species distribution data and environmental space used for model calibration leads to an overestimation of species probabilities of occurrence. We assume that cells in areas were distribution data are truncated for many species, e.g. in the Mediterranean, where many species extend to northern Africa, are characterized by higher error rates.

Though we cannot test these hypotheses, we hope that it may help to guide future research on the topic in order to gain further understanding of variation of predictive performance in space.

CONCLUSIONS

Geographical patterns in prediction errors of species distribution models exist and should be taken into account, since species ranges are shaped by a multitude of factors (Gaston, 2003) as are the prediction errors. In general, results from species distribution models may be less (or more) reliable than measures of predictive performances per species suggest. Thus, we suggest that models of actual species distributions or species numbers as well as future projections should be accompanied by a measure of uncertainty in space (Rocchini *et al*., in press).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Climatic variables that were used for species distribution models and their loadings on the first three principal components (PC).

Appendix S2 Maps of the variables used within the simultaneous autoregressive models to explain false absence rate and

false presence rate. (HANPP = Human appropriation of net primary productivity)
Appendix S3 Maps of the variables used within the simultaneous autoregressive models to explain false absence rate and false presence rate. (HANPP = Human appropriation of net primary productivity)

BIOSKETCH

Jan Hanspach is a research fellow at the Helmholtz Centre for Environmental Research – UFZ. He is trained as a plant ecologist, with primary research interests in species distribution modelling, biogeography and dryland ecology.

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