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ARTICLE



# Estimating patterns of reptile biodiversity in remote regions

Gentile Francesco Ficetola<sup>1\*</sup>, Anna Bonardi<sup>1</sup>, Roberto Sindaco<sup>2</sup>  
and Emilio Padoa-Schioppa<sup>1</sup>

<sup>1</sup>Dipartimento di Scienze dell'Ambiente e del Territorio, Università degli Studi di Milano-Bicocca, Piazza della Scienza 1, 20126, Milano, Italy, <sup>2</sup>Museo Civico di Storia Naturale, I-10022, Carmagnola, Italy

## ABSTRACT

**Aim** The incompleteness of information on biodiversity distribution is a major issue for ecology and conservation. Researchers have made many attempts to quantify the amount of biodiversity that still remains unknown. We evaluated whether models that integrate ecogeographical variables with measures of the effectiveness of sampling can be used to estimate biodiversity patterns (species richness) of reptiles in remote areas that have received limited surveys.

**Location** The Western Palaearctic (Europe, Northern Africa, the Middle East and Central Asia).

**Methods** We gathered data on the distribution of turtles, amphisbaenians and lizards. We used regression models integrating spatial autocorrelation (spatial eigenvector mapping and Bayesian autoregressive models) to analyse species richness, and identified relationships between species richness, ecogeographical features and large-scale measures of accessibility.

**Results** The two regression techniques were in agreement. Known species richness was dependent on ecogeographical factors, peaking in areas with high temperature and annual actual evapotranspiration, and intermediate cover of natural vegetation. However, richness declined sharply in the least accessible areas. Our models revealed regions where reptile richness is likely to be higher than currently known, particularly in the biodiversity hotspots in the south of the Arabian Peninsula, the Irano-Anatolian region, and the Central Asian mountains. An independent validation data set, with distribution data collected recently throughout the study region, confirmed that combining accessibility measures with ecogeographical variables allows a good estimate of reptile richness, even in remote areas that have received limited monitoring so far. Some remote regions that support very rich communities are covered very little by protected areas.

**Main conclusions** Integrating accessibility measures into species distribution models allows biologists to identify areas where current knowledge underestimates the actual richness of reptiles. Our study identifies regions requiring future biodiversity research, proposes a novel approach to biodiversity prediction in poorly studied areas, and identifies potential regions for conservation.

## Keywords

Amphisbaenians, biodiversity hotspots, conservation biogeography, ecogeography, lizards, predictive models, spatial autocorrelation, species richness, survey bias, turtles.

\*Correspondence: Gentile Francesco Ficetola, Dipartimento di Scienze dell'Ambiente e del Territorio, Università degli Studi di Milano-Bicocca, Piazza della Scienza 1, 20126 Milano, Italy.  
E-mail: francesco.ficetola@unimib.it

## INTRODUCTION

Our knowledge of biodiversity distribution is far from complete (Mora *et al.*, 2011). First, many species on Earth are yet

to be described (the Linnean shortfall), and second, we have a limited knowledge of the true distributions, even for the best-studied taxa (the Wallacean shortfall) (Lomolino, 2004; Cardoso *et al.*, 2011; Vale & Jenkins, 2012). This paucity of

information is a major challenge within conservation biogeography, limiting our ability to analyse biodiversity patterns and set conservation priorities (Lomolino, 2004; Cardoso *et al.*, 2011; Mora *et al.*, 2011). Unfortunately, quantifying the amount of biodiversity that remains unknown in a given area is challenging (Raxworthy *et al.*, 2003; Mora *et al.*, 2011).

Species distribution models based on relationships between biodiversity distribution and environmental features help to elucidate the factors determining biodiversity and to identify conservation targets even when information is incomplete (Raxworthy *et al.*, 2003; Qian & Ricklefs, 2008; Thuiller *et al.*, 2011). These models, being based on the available species distribution data, may be affected by poor sampling. Integrating data on the effectiveness of surveys may greatly improve the performance of models of species richness and species distribution (Kadmon *et al.*, 2004; Bini *et al.*, 2006; Phillips *et al.*, 2009; Barbosa *et al.*, 2010). Unfortunately, measures of the effectiveness of surveys are often lacking, particularly for large-scale data sets, where data are obtained from a variety of heterogeneous sources. Accessibility can be a major source of sampling bias. Monitoring in remote areas is often limited, and so biodiversity can be significantly underestimated (Nelson *et al.*, 1990; Margules & Pressey, 2000; Bini *et al.*, 2006; Sánchez-Fernández *et al.*, 2008; Barbosa *et al.*, 2010; Kent & Carmel, 2011). The accessibility of a region can thus be a useful proxy of the effectiveness of sampling in biogeographical studies. Recently, Nelson developed a global-scale measure of accessibility, quantified as the travel time from the nearest city using land-based or water-based transport (Nelson, 2008; Uchida & Nelson, 2010). However, we are not aware of studies integrating large-scale measures of accessibility into species distribution models.

The aim of this study was to analyse the richness of reptile species (considering turtles, amphisbaenians and lizards) in the Western Palaearctic, and to evaluate the importance of accessibility in determining known species richness at the biogeographical scale. The Western Palaearctic is a large biogeographical region, encompassing Europe, North Africa, the Middle East and Central Asia (Fig. 1); it contains hotspots of reptile biodiversity and endemism (Mittermeier *et al.*, 2004; Cox *et al.*, 2006; Sindaco & Jeremčenko, 2008), but is heavily threatened by growing human pressure (Brooks *et al.*, 2006; Cox *et al.*, 2006; Ficetola & Padoa-Schioppa, 2009). The area includes easily accessible, human-dominated regions (e.g. Western Europe), in which extensive inventories of reptile biodiversity have been performed, but also remote regions (Fig. 1a) where biodiversity data remain sparse (Sindaco & Jeremčenko, 2008). Furthermore, we evaluated whether integrating accessibility into species distribution models may help biologists to improve estimates of species richness, even in remote areas that have received limited surveys so far. In addition, reptiles are among the terrestrial vertebrates for which distribution data are more limited, and the only ones for which no comprehensive assessment of conservation status has been completed (Hoffmann *et al.*, 2010). The results of our study may improve knowledge of reptile biodiversity

in the study area, and provide large-scale information that can be useful for conservation planning.

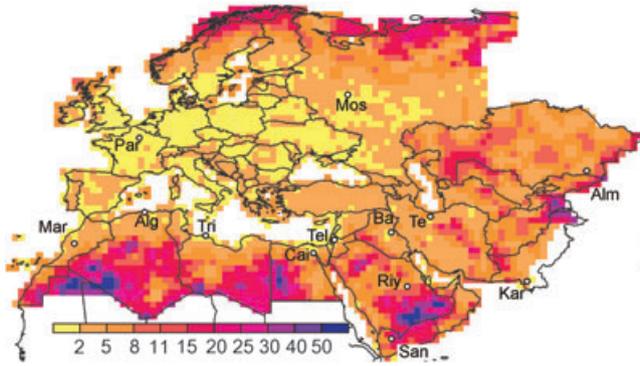
## MATERIALS AND METHODS

### Study area and data sets

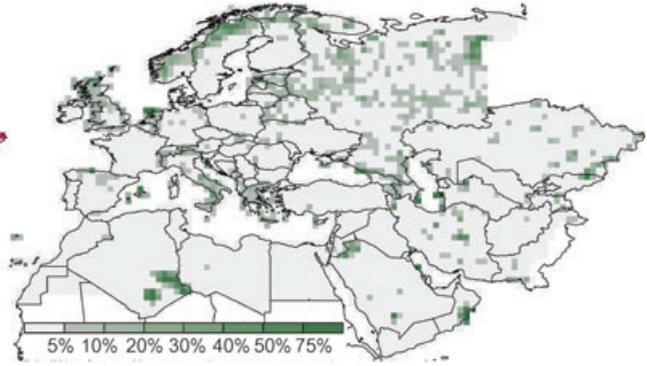
We considered the 'Western Palaearctic' according to Sindaco & Jeremčenko (2008). This region includes the western portion of the Palaearctic realm [Europe, the Arabian Peninsula, western Asia (west of the Indus Valley), the former Soviet Republics of Central Asia and Russia (west of the Ural Mountains)] and several countries of northern Africa (including the Sahara Desert north of approximately 22° N) (Fig. 1). Our data set included more than 67,000 distributional records collected before 2008, showing the known distribution of the 480 native species of terrestrial turtles, amphisbaenians and lizards occurring in the area (Sindaco & Jeremčenko, 2008). The number of records per cell cannot be considered an index of the sampling effort, because in the best-surveyed areas (e.g. Europe), data were obtained from comprehensive sources such as atlases, summarizing a much larger number of observations. Presence records of each species were mapped on a grid of 3530 cells with a resolution of 1° × 1° (the resolution of data with less accurate coordinates). Taxonomy followed the checklist of Sindaco & Jeremčenko (2008), which was based on the critical review of about 880 papers. The list includes species recognized on the basis of biological, evolutionary and morphological species concepts (Uetz, 2010). Distribution maps of each of the 480 species used for analyses are available in Sindaco & Jeremčenko (2008). Reptile richness in each cell was then calculated by overlapping the distribution maps of all the 480 species. We also considered coastal cells and islands, as they harbour multiple endemic species and can constitute important biodiversity areas, when taking into account their limited surface area (Cox *et al.*, 2006; Ficetola & Padoa-Schioppa, 2009).

As environmental variables, we considered two geographical variables – cell surface occupied by non-aquatic environments (calculated on the basis of the GlobCover land cover; Bicheron *et al.*, 2008) and elevation range (calculated on the basis of a 30-arc-second digital elevation model; Hijmans *et al.*, 2005); and three climatic variables – annual mean temperature, annual actual evapotranspiration (annual AET hereafter), and annual summed precipitation (New *et al.*, 2002), which are considered to be major drivers of reptile biodiversity (Qian & Ricklefs, 2008; Powney *et al.*, 2010). Potential evapotranspiration can also have an important role (Rodríguez *et al.*, 2005), but was not considered because it is highly collinear to the other climatic variables. Furthermore, we considered the average accessibility of each cell (Nelson, 2008) and the percentage of each cell occupied by natural vegetation, calculated on the basis of GlobCover (Bicheron *et al.*, 2008). We also calculated the percentage of each cell covered by protected areas, on the basis of the World Database on Protected Areas (<http://protectedplanet.net/>) (Fig. 1b). All variables were upscaled

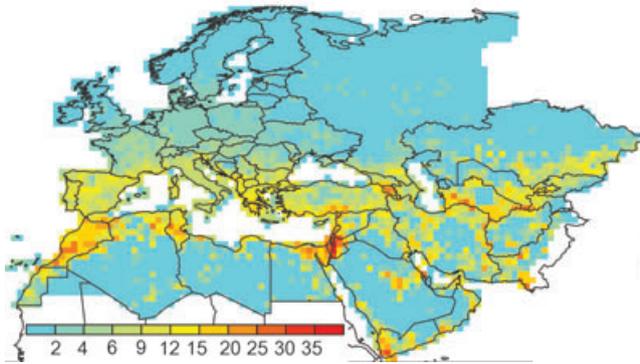
(a) Accessibility



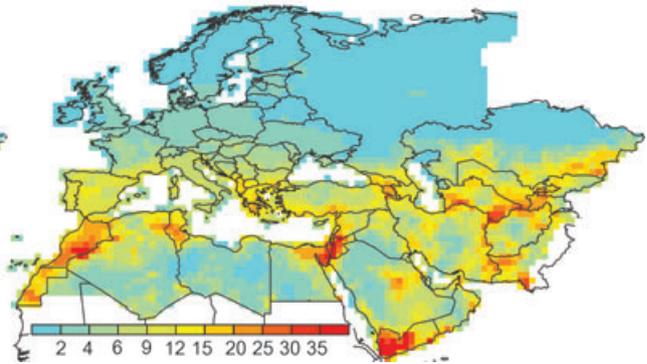
(b) Protected areas



(c) Observed species richness



(d) Predicted species richness



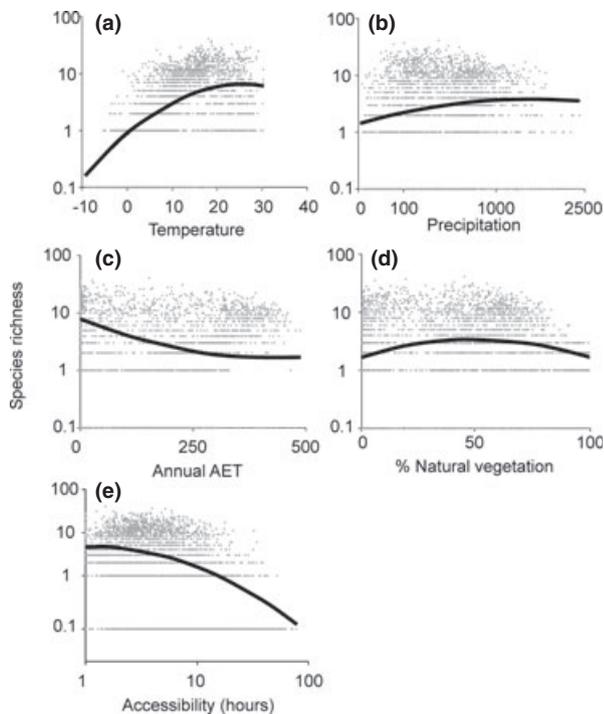
**Figure 1** Accessibility, protected areas and reptile richness within the Western Palearctic. (a) Mean accessibility of  $1^\circ \times 1^\circ$  cells within the study area (calculated following Nelson, 2008). Accessibility is measured as the travel time (in hours) from the nearest city using land-based or water-based transport. (b) Percentage of each cell occupied by protected areas (World Database on Protected Areas; <http://protectedplanet.net/>). (c) Observed species richness of reptiles across the Western Palearctic. (d) Reptile species richness predicted by models assuming that all cells are accessible in 1 h. The picture shows the average predictions of spatial eigenvector mapping and Bayesian conditional autoregressive model. Predictions of the two models are shown in Fig. S2 in Appendix S2. The locations of major cities are also shown: Alg, Algiers; Alm, Almaty; Ba, Baghdad; Cai, Cairo; Kar, Karachi; Mar, Marrakech; Mos, Moscow; Par, Paris; Riy, Riyadh; San, Sana'a; Te, Tehran; Tel, Tel Aviv; Tri, Tripoli.

(via averaging) from the original sources to match the  $1^\circ \times 1^\circ$  resolution. Accessibility represents the travel time to the nearest city (population  $\geq 50,000$  people) using land-based or water-based transport on a regular raster grid. It is based on a cost–distance algorithm computing the ‘cost’ of travelling between two locations, assuming that travelling time is affected by parameters such as road/railway network, presence of paths, navigable water bodies, slope and political boundaries. For each  $1^\circ \times 1^\circ$  cell, we obtained the average accessibility (in hours), from the  $30''$ -resolution accessibility grid layer (Nelson, 2008; Fig. 1a). A few cells (3%) had average accessibility  $\leq 1$  h. To avoid these cells acting as outliers, we assumed that all areas within 1 h of the nearest city may be surveyed with similarly high sampling effort, and were assigned an accessibility of 1 (i.e. 1 h is the minimum accessibility across the whole study area). The appropriateness of this approach is confirmed by the observation that known richness follows a nonlinear pattern, with maximum richness at accessibility  $\approx 1$  h (Fig. 2). The study area includes several remote regions in the Arabian Peninsula, the Sahara Desert, in several

areas of the Middle East and Central Asia, and in northern Russia (the latter almost devoid of reptile fauna). Although there are remote areas both in cold and warm regions (Fig. 1a), the most accessible areas tended to have higher annual AET [Dutuilleul’s (1993) correlation index:  $r = -0.69$ ,  $n = 3530$ , modified d.f. = 22.4,  $P < 0.001$ ] and more precipitation ( $r = -0.59$ ,  $n = 3530$ , modified d.f. = 24.3,  $P = 0.003$ ). The correlation with the other environmental variables was not significant [Dutuilleul’s (1993) correlation for all pairs:  $n = 3530$ ,  $P > 0.06$ ].

### Species richness models

We used regression models to evaluate the relationships between environmental features and species richness. The residuals of ordinary least squares regression were affected by significant spatial autocorrelation (Moran’s  $I = 0.40$ ,  $P < 0.001$ ,  $n = 207,214$ ), and so we integrated autocorrelation into our models. Because results may differ across statistical techniques, we used two different approaches that are



**Figure 2** Relationships between environmental variables and reptile richness for the Western Palearctic, as estimated by spatial eigenvector mapping. Predictions are shown for (a) mean annual temperature; (b) summed annual precipitation; (c) annual actual evapotranspiration (annual AET); (d) proportion of each cell occupied by natural vegetation (%); (e) mean accessibility (travel time in hours from the nearest city using land-based or water-based transport). The plots include variables for which the model takes quadratic terms into account. Grey dots represent observed species richness in cells. The predictions for each variable are made while holding the other variables fixed at their global median. Fig. S2 in Appendix S2 reports the results from the Bayesian autoregressive model and the global medians of variables.

among the best-performing techniques when using non-normal data: spatial eigenvector mapping (SEVM) and Bayesian intrinsic conditional autoregressive models (BCA) (Dormann *et al.*, 2007; Beale *et al.*, 2010). Our dependent variable was a count, and so we assumed a Poisson error distribution rather than more standard techniques such as generalized least squares, simultaneous or conditional autoregressive models, which are suitable for normally distributed data (Dormann *et al.*, 2007; Beale *et al.*, 2010). Species richness may have a maximum when certain environmental variables reach certain values; furthermore, previous studies suggested that relationships between species richness and ecogeographical variables are often nonlinear (Whittaker *et al.*, 2007; Qian, 2010). We therefore also included quadratic terms for climatic variables, vegetation and accessibility in all models, to take into account potential nonlinear relationships.

SEVM allows the translation of the spatial arrangement of data points into explanatory variables (eigenvectors) that capture spatial effects (Dormann *et al.*, 2007). Neighbouring cells were linked using a king's connection scheme and we gener-

ated eigenvectors using Moran's eigenvector maps (Dray *et al.*, 2006; Borcard *et al.*, 2011). We then selected the eigenvectors that best reduced the spatial autocorrelation of residuals, and included them as spatial predictors in generalized linear models (GLM) (Griffith & Peres-Neto, 2006; Dormann *et al.*, 2007). Comparisons among statistical methods showed that this implementation of SEVM is flexible and efficient, even when analysing non-normal data (Dormann *et al.*, 2007). To take overdispersion into account, we used a quasi-Poisson family and tested significance using an *F* test (Crawley, 2007). We used the procedure proposed by Phillips and co-workers (Phillips, 2010; Elith *et al.*, 2011) to evaluate the relative importance of predictors in SEVM. First, we built the models including each environmental variable in isolation. Subsequently, each variable (including both linear and quadratic terms) was removed in turn, and the model run with the remaining variables. The difference in explained variation between the full model and the one excluding the variable of interest provides an estimate of the independent contribution of such variable, after taking into account other parameters and spatial autocorrelation (Phillips, 2010; Elith *et al.*, 2011).

BCA is a hierarchical Bayesian technique that incorporates a spatial random effect, describing the neighbourhood of each site, into Bayesian regression models. Simulations have shown that BCA is one of the spatial techniques with the best performance under a variety of conditions (Latimer *et al.*, 2006; Beale *et al.*, 2010). We built BCA assuming a Poisson error distribution. A model assuming negative binomial error had a higher deviance information criterion, indicating that overdispersion did not affect the BCA model. To ensure convergence, we ran three different MCMC chains. For each chain, we performed a burn-in of 15,000 iterations, followed by 45,000 iterations thinned every 10 iterations. For all variables, Brooks–Gelman–Rubin diagnostics were approximately 1, indicating convergence (Kéry, 2010). We then calculated the estimates of regression coefficients and their 95% highest posterior density credible intervals (HPDI).

The results of ecogeographical studies may be affected by the scale at which analyses are performed (Hawkins, 2012). Furthermore, the large number of cells might increase the chance of finding significant results. To confirm our results, we therefore repeated our analyses using a grid with a resolution of  $2^\circ \times 2^\circ$  (975 cells).

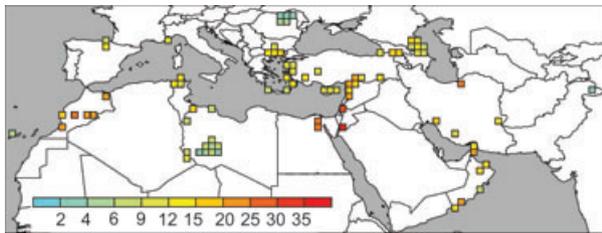
To reduce skewness and improve normality where needed, variables were transformed using logarithms (cell surface, elevational range and accessibility), square-root (summed annual precipitation) or square-root-arcsine (percentage of natural vegetation). We calculated the proportion of explained deviance ( $R^2_D$ ) as a measure of the variation explained by species richness models. For SEVM, values of  $R^2_D$  were adjusted to take into account the number of predictors in the model (Borcard *et al.*, 2011). When more than one modelling technique is used, differences among algorithms can determine differences in performance and lead to non-identical results (model-based uncertainty) (Marmion *et al.*, 2009). To reduce the model-based uncertainty for model predictions, we kept

the average consensus prediction of the two species richness models (Marmion *et al.*, 2009). Using the individual results of either model yielded nearly identical results (see Results). Subsequently, we projected models using a new data set, with identical environmental variables and spatial structure, but assuming accessibility is 1 h for all cells. This allowed us to evaluate the potential species richness of each cell, if it received a surveying effort similar to the most accessible ones ('projected richness' hereafter).

### Validation of model predictions

To test whether the projected richness is an accurate estimate of the actual species richness, we obtained recent data on reptile distributions (from recent field research or publications) in 80 grid cells that have received intense sampling (Fig. 3, and see Appendix S1 in Supporting Information). These recent data were not included in the 2008 data set used to build the species richness models. Independent validation data were obtained mostly from recent publications on reptile distributions (73 cells). In six cells, recent data were obtained both from extensive field surveys performed by the authors and from the literature. Sampling was performed from 2008 to 2010 through diurnal and nocturnal visual encounter surveys, trying to cover the widest range of environmental features (Heyer *et al.*, 1994; Ficetola *et al.*, 2010). In one additional cell, data were obtained through field surveys only (total: 80 cells with recent data) (Appendix S1). As these cells recently received an intense and focused surveying effort, they represent areas with reliable information for the validation of model predictions. We thus assumed that reptile richness recorded from recent, intensive surveys ('validation richness' hereafter) represents an improved estimate of the actual species richness in these cells. Validation cells were in multiple regions of the study area, with a wide range of accessibility (Fig. 3, Appendix S1).

In order to assess the ability of the projected richness model to correctly predict the actual species richness in the validation cells, we built three Poisson GLMs considering validation richness as the dependent variable in all cases. As potential predictors, we included (1) the projected richness (i.e. the richness predicted by the species richness model assuming accessibility is 1 h in all cells), and (2) the number of species recorded in the 2008 data set (i.e. the original data set of Sindaco & Jeremčenko, 2008). In both these models, we assumed  $B = 1$  and intercept = 0, i.e. a perfect overlap between best



**Figure 3** Distribution of the 80 validation grid cells, and observed reptile richness in the validation cells.

available value of the species richness and either (1) our projected richness or (2) the richness recorded until 2008. We considered the null model as a third GLM (3), assuming no relationships between the validation and projected species richness. We then used the Akaike information criterion (AIC) to compare the performance of the three GLMs.

Due to sampling constraints, remote cells were less frequent in our validation data. Furthermore, several validation cells were clustered, and this may affect the results of regression-based validation. As an additional metric of prediction performance, we compared the projected richness to the validation richness. For each cell, we calculated the absolute value of  $[(\text{projection} - \text{validation})/\text{validation}] \times 100\%$ . We then subtracted that value from 100%, to obtain the 'percentage accuracy' for each cell. Subsequently, we repeated the same procedure with the richness recorded until 2008.

We used Spearman's correlation to evaluate the relationship between projected reptile richness in each cell, and the cell percentage covered by protected areas. Because of spatial autocorrelation, significance was calculated using Dutilleul's (1993) degrees of freedom. We performed statistical analyses in R 2.12 (R Development Core Team, 2010) using the package *SPDEP* (Bivand *et al.*, 2010); we ran *BCA* in *WINBUGS* 1.4 (Spiegelhalter *et al.*, 2008).

### RESULTS

Average reptile richness in  $1^\circ \times 1^\circ$  cells ( $\pm$  SD) was  $4.3 \pm 5.6$  species (range: 0–41). The areas with the highest known richness were in the eastern Mediterranean and western Maghreb. Richness was irregularly distributed in wide areas of the Middle East, with species-rich cells near cells with very few known species (Fig. 1c). This pattern was most apparent in the area of Israel–Jordan–Sinai Peninsula, southwestern Yemen, and around Riyadh, Saudi Arabia (Fig. 1c). SEVM and BCA generally gave the same outcome, and their results were in strong agreement ( $R^2 = 0.82$ ; Fig. S1 in Appendix S2). Both models included 12 predictors (seven variables with five quadratic terms); SEVM also included 91 eigenvectors representing spatial autocorrelation (Table 1). Both models explained a large amount of the variation in reptile species richness (SEVM: adjusted  $R^2_{\text{ADJ}} = 0.69$ ; BCA:  $R^2_{\text{D}} = 0.63$ ). When controlling for the effect of cell surface, species richness increased with elevational range, temperature and precipitation, and decreased with annual AET. Furthermore, richness was highest in cells with intermediate values of natural vegetation cover (Table 1, Fig. 2; see also Fig. S2 in Appendix S2). Temperature, natural vegetation, elevational range and accessibility explained 20–32% of variation, when used in isolation (Table 1). After taking into account spatial autocorrelation, accessibility was the variable with the highest independent contribution to the model. The independent contribution of vegetation cover and temperature was 2–4% while, when taking the other variables into account, the independent contribution of surface, elevational range and precipitation was limited (Table 1).

**Table 1** Results of multiple regression models using spatial eigenvector mapping (SEVM) and Bayesian conditional autoregressive models (BCA), relating reptile species richness to multiple environmental variables for the Western Palaearctic.

Variable	SEVM				BCA			% Importance	
	<i>B</i>	<i>F</i>	d.f.	<i>P</i>	Median <i>B</i>	95% HPDI		with only	excluding
Surface	<b>0.128</b>	42.9	1, 3426	< 0.001	<b>0.176</b>	0.116	0.233	1.5%	0.4%
Elevational range	<b>0.133</b>	65.0	1, 3426	< 0.001	<b>0.154</b>	0.101	0.205	19.6%	0.6%
Temperature	<b>0.157</b>	210.7	1, 3426	< 0.001	<b>0.096</b>	0.058	0.138	31.9%	4.1%
(Temperature) <sup>2</sup>	<b>-0.003</b>	67.2	1, 3426	< 0.001	<b>-0.002</b>	-0.003	-0.001		
Precipitation	<b>0.051</b>	14.6	1, 3426	< 0.001	<b>0.052</b>	0.010	0.100	1.6%	0.2%
(Precipitation) <sup>2</sup>	<b>-0.001</b>	6.8	1, 3426	0.009	-0.001	-0.002	0.0002		
Annual AET	<b>-0.007</b>	84.9	1, 3426	< 0.001	<b>-0.004</b>	-0.006	-0.002	4.5%	1.1%
(AET) <sup>2</sup>	<b>0.00001</b>	42.8	1, 3426	< 0.001	0.000003	-0.000001	0.000007		
Natural vegetation	<b>1.767</b>	107.0	1, 3426	< 0.001	<b>1.516</b>	1.034	1.947	20.7%	2.1%
(Nat. vegetation) <sup>2</sup>	<b>-1.140</b>	121.4	1, 3426	< 0.001	<b>-0.952</b>	-1.219	-0.661		
Accessibility	0.083	1.3	1, 3426	0.254	0.185	-0.004	0.368	14.7%	5.3%
(Accessibility) <sup>2</sup>	<b>-0.236</b>	108.4	1, 3426	< 0.001	<b>-0.280</b>	-0.338	-0.220		
SEVM eigenv.		20.3	91, 3426	< 0.001				37.3%	17.9%

Significant coefficients (SEVM) and coefficients with 95% highest posterior density credible intervals (HPDI) not overlapping zero (BCA) are in bold. %Importance: importance of each variable estimated for SEVM. In the 'with only' column, the importance (adjusted  $R^2$ ) is assessed by building models including each variable in isolation; in the 'excluding' column, importance refers to the difference between the  $R^2_{ADJ}$  of the full model and the  $R^2_{ADJ}$  of the partial model excluding the variable of interest. Variables are: cell surface occupied by non-aquatic environments, elevational range, annual mean temperature, annual summed precipitation, annual actual evapotranspiration (annual AET), cell percentage occupied by natural vegetation, average accessibility.

When taking the other variables into account, the highest richness was observed in easily accessible cells, and gradually decreased in more remote areas, following a nonlinear pattern. For instance, if environmental features were held constant, reptile richness was 4–5 species in cells with an average accessibility of 1 h, compared with 1–2 species in cells with an accessibility of 10 h (Fig. 2e, Fig. S2e in Appendix S2). Results were extremely similar according to SEVM and BCA, although the relationship between two climatic features (annual AET and annual precipitation) were significantly nonlinear in SEVM but not in BCA (Table 1). The analysis performed at  $2^\circ \times 2^\circ$  resolution yielded very similar results (Appendix S3). For accessibility, regression coefficients were slightly different from the model at  $1^\circ \times 1^\circ$  resolution, but the negative, nonlinear relationship was confirmed (Appendix S3).

We then projected species richness models, assuming that all cells are accessible in 1 h, while keeping the original values of environmental variables. This allowed us to estimate the potential richness patterns, if remote areas received the same surveying effort as the accessible ones. In several regions, the projected consensus model predicted a higher species richness than the currently known values, particularly in the western Maghreb, in the south of the Arabian peninsula, in the Irano-Anatolian region, and in the Central Asian mountains (Fig. 1d, Fig. S3 in Appendix S2). Cells with high projected richness tended to be those with less cover of protected areas (Fig. 1; correlation between projected richness and cover of protected areas:  $r_s = -0.25$ , Dutilleul's modified d.f. = 96.9,  $P = 0.015$ ). Furthermore, in the Western Palaearctic, the cover of protected areas was highest in easily accessible cells ( $r_s = -0.24$ , d.f. = 145.3,  $P = 0.005$ ).

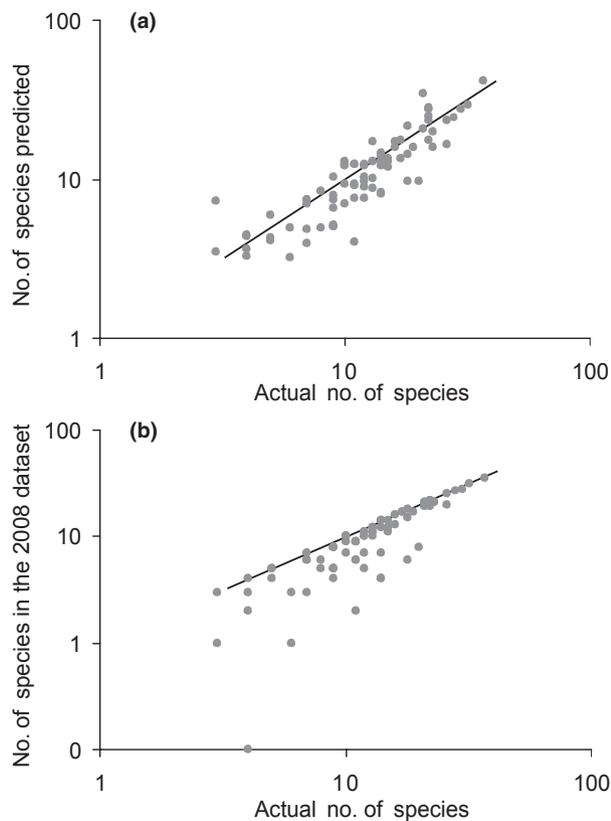
### Validation of biodiversity predictions

The recent distribution data updated the available information, and usually increased known richness in validation cells. The average number of newly recorded species per cell was 2.5 (range: 0–12; Appendix S1). The projected model predicted reptile richness in the recently surveyed cells well (GLM:  $\chi^2_1 = 195.6$ ,  $P < 0.001$ ;  $R^2_D = 0.69$ ; Fig. 4). It allowed us to estimate the validation species richness better than using the number of species reported in the 2008 data set ( $\Delta AIC = 73.0$ ) or using the null model ( $\Delta AIC = 193.6$ ) as predictors. This indicates very strong support for the predictions of the projected model. Results remain the same if SEVM or BCA are used rather than the consensus model (not shown). Nevertheless, statistical tests should be considered with caution, as validation cells were not independent and only a few of them were in remote regions, owing to the limited recent surveys in those areas.

The average accuracy of predictions in validation cells ( $n = 80$ ) was 79%, and was higher than the accuracy calculated using 2008 data (77%). The good performance of predictions was particularly evident in remote cells (cells with accessibility  $> 3$  h:  $n = 39$  accuracy of prediction = 74%, accuracy of 2008 data = 70%; cells with accessibility  $> 6$  h:  $n = 7$ , accuracy of prediction = 80%, accuracy of 2008 data = 55%).

### DISCUSSION

In remote areas, we only know part of the species richness (Nelson *et al.*, 1990), but quantifying the magnitude of richness underestimation is extremely difficult. Our analyses suggest that, after taking key ecogeographical variables into



**Figure 4** Relationship between ‘validation richness’ (species richness of reptiles of the Western Palaearctic, obtained from recently available information) and: (a) the number of species predicted in the validation cells, assuming accessibility from the nearest city by land and water transport in 1 h; (b) the number of species in the 2008 data set. Lines have an intercept of 0 and a slope of 1.

account, accessibility influences the known reptile biodiversity at the biogeographical scale. Thus, integrating accessibility into models helps to estimate reptile richness in remote, poorly studied areas (Fig. 4a). Obviously, accessibility is not a perfect proxy of sampling effort because, particularly at fine scales, other factors may influence the completeness of inventories, such as perceived attractiveness for researchers and the presence of institutions specializing in certain taxa or specific geographical areas (Nelson *et al.*, 1990; Sánchez-Fernández *et al.*, 2008; Boakes *et al.*, 2010; Vale & Jenkins, 2012). Nonetheless, broad-scale measures of accessibility can provide information on the bias of field surveys, which may be used to improve the performance of distribution models and allows first assessments of the biodiversity in remote areas where observations are sparse (Bini *et al.*, 2006).

Our analysis suggests that reptile richness in remote areas such as the Iranian Plateau (including Afghanistan and south-western Pakistan), as well as parts of Central Asia, may be higher than currently known (Fig. 1, Fig. S3 in Appendix S2). Although this region includes two of the world’s recognized biodiversity hotspots (the mountains of Central Asia and the Irano-Anatolian region), known reptile

richness is still relatively low compared with other hotspots (Mittermeier *et al.*, 2004). The remoteness of the region, the roughness of landscape and the lasting political instability may have limited systematic surveys, and the actual biodiversity is likely to be higher than currently known. Two major mechanisms may cause such underestimation of species richness (Lomolino, 2004; Mokany & Ferrier, 2011): (1) species distribution is poorly known (Wallacean shortfall), and (2) some species are yet to be described (Linnean shortfall). Recent surveys provide a measure of causes of richness underestimation: on average, surveys increased the known richness by 47% and, in 13 cells, the increase in richness was  $\geq 100\%$  (Appendix S1). Limited knowledge of species distribution was the major cause of richness underestimation, as many species are recorded for only one or very few localities, and most new records in the validation cells expanded the range of known species. The discovery of new species is much less frequent than distribution updates. Nevertheless, most of the recently described reptile species in the Western Palaearctic (see e.g. Masroor, 2008; Rösler *et al.*, 2008; Nazarov *et al.*, 2009; Torki, 2010; Busais & Joger, 2011; Torki *et al.*, 2011) have been found in areas where our model suggests a higher richness than currently reported, such as the south of the Arabian Peninsula and the Irano-Anatolian region. Finally, in recent years, molecular tools are improving our definition of species identity, with the recognition of cryptic taxa and the raising of geographically isolated ‘sub-species’ to the rank of species. These studies tend to have a geopolitical bias (Harris & Froufe, 2005), but molecular tools and integrated taxonomy are nevertheless starting to expand our knowledge of biodiversity, even for remote or understudied regions (e.g. Barata *et al.*, 2012). Overall, we conclude that both Wallacean and Linnean shortfalls affect known reptile richness and our models help to identify regions where these shortfalls are particularly strong.

Reptiles are the only terrestrial vertebrates for which, so far, no comprehensive maps of species distribution range are available at the global scale, thereby limiting large-scale analyses of biodiversity patterns. For instance, this is the first analysis of reptile richness covering the whole Western Palaearctic on the basis of a regular grid (see Rodríguez *et al.*, 2005, for an analysis of Europe). Previous large-scale studies of reptile richness highlighted that the availability of energy is the major determinant of reptile richness (Rodríguez *et al.*, 2005; Qian *et al.*, 2007; Whittaker *et al.*, 2007; Qian & Ricklefs, 2008; Powney *et al.*, 2010; Qian, 2010). Our results were in agreement with these findings, as reptile richness was highest in areas characterized by warm climate and low annual AET (Fig. 2). Integrating proxies of sampling effort, such as accessibility, may improve the performance of biodiversity models, allowing better estimates of the relationships between species richness and environmental features (Phillips *et al.*, 2009; Bonardi *et al.*, 2011; Gómez-Rodríguez *et al.*, 2012), and helping to improve our understanding of the impact of environmental changes (e.g. climate or land-use change) on species richness. This can be particularly valuable

for regions or taxa where insufficient data are available for modelling each species individually (Mokany & Ferrier, 2011). More accurate estimates of alpha diversity can also be integrated into a metacommunity framework, to estimate community composition in poorly known areas (Mokany *et al.*, 2011). Nevertheless, it should be noted that no single environmental variable explained richness well, and that spatial autocorrelation accounted for a substantial amount of the variation (Table 1), suggesting an important role of historical or other unmeasured factors.

Systematic conservation planning requires more complete knowledge of biodiversity distribution and the identification of relationships between biodiversity and environmental features (Margules & Pressey, 2000; Rondinini *et al.*, 2006; Mokany & Ferrier, 2011). Efforts to fill this gap are a priority for conservation biogeography, and must be performed in all regions and environments. Unfortunately, large areas of the globe have received limited surveys so far. Our approach allows spatially explicit estimates of unknown species richness, and can therefore guide the allocation of funding for biodiversity surveying towards specific regions, in which actual biodiversity values may be much higher than currently known.

Conservation actions are usually based on known biodiversity, with protected areas targeted to regions with high species richness, endemism and threat (Hughes *et al.*, 2002; Brooks *et al.*, 2006; Rondinini *et al.*, 2006). This may bias the allocation of conservation efforts towards the best-known areas, while regions with rich biodiversity, but that are poorly studied, may remain under-represented (Bini *et al.*, 2006). In the Western Palaearctic, remote regions can host high biodiversity, but tend to receive limited protection (Fig. 1). Our study identifies areas where the true biodiversity is probably much higher than the current known estimates. An exhaustive assessment of the network of protected areas for the conservation of reptiles is beyond the aim of this study, and should be performed at a finer spatial scale, taking into account not only species richness, but also other parameters such as the degree of endemism, the irreplaceability of areas, the presence of endangered taxa, and threatening processes (Margules & Pressey, 2000; Bini *et al.*, 2006; Brooks *et al.*, 2006). Our improved estimates of species richness can be integrated with the available information on endemism and threat, to identify regions where new protected areas may be required, despite biodiversity data remaining scarce (Hughes *et al.*, 2002; Bini *et al.*, 2006; Rondinini *et al.*, 2006). Furthermore, integrating our broad-scale analysis with high-resolution data on habitat availability and changes in land cover may allow finer-scale information to be developed (Rondinini *et al.*, 2011), which could help to refine the identification of conservation priorities. Some remote regions with high reptile richness had a very limited cover of protected areas, or no protected areas at all. There is a notable scarcity of protected areas in the south-west of the Arabian Peninsula (particularly in Yemen), in the east of the Iranian Plateau and in the western Maghreb (Fig. 1b), even though these regions are recognized as global biodiver-

sity hotspots, and have a very high proportion of endemism for both reptiles and other taxa, including several micro-endemic reptiles recorded only in one or very few localities (Mittermeier *et al.*, 2004; Sindaco & Jeremčenko, 2008).

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## SUPPORTING INFORMATION

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

**Appendix S1** Validation grid cells.

**Appendix S2** Model predictions (Figs S1–S2) and difference between projected and known richness (Fig. S3).

**Appendix S3** Results of regression models performed at the resolution of  $2^\circ \times 2^\circ$ .

## BIOSKETCHES

**G. Francesco Ficetola** is a post-doc specializing in conservation and ecology of amphibians and reptiles. He combines multiple approaches (landscape ecology, macroecology, evolutionary ecology and population genetics) to obtain information that can be used to improve conservation actions.

Author contributions: All authors jointly designed the study; R.S. gathered most of the data; G.F.F. and A.B. performed the analyses; G.F.F. wrote the first version of the paper; and all authors discussed the results and commented on the draft manuscript.

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