

RESEARCH
PAPER



The performance of range maps and species distribution models representing the geographic variation of species richness at different resolutions

Eduardo Pineda^{1,2*} and Jorge M. Lobo²

¹Red de Biología y Conservación de Vertebrados, Instituto de Ecología, AC Apartado Postal 63, Xalapa 91000, Veracruz, Mexico, ²Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), c/José Gutiérrez Abascal 2, Madrid 28006, Spain

ABSTRACT

Aim The method used to generate hypotheses about species distributions, in addition to spatial scale, may affect the biodiversity patterns that are then observed. We compared the performance of range maps and MaxEnt species distribution models at different spatial resolutions by examining the degree of similarity between predicted species richness and composition against observed values from well-surveyed cells (WSCs).

Location Mexico.

Methods We estimated amphibian richness distributions at five spatial resolutions (from 0.083° to 2°) by overlaying 370 individual range maps or MaxEnt predictions, comparing the similarity of the spatial patterns and correlating predicted values with the observed values for WSCs. Additionally, we looked at species composition and assessed commission and omission errors associated with each method.

Results MaxEnt predictions reveal greater geographic differences in richness between species rich and species poor regions than the range maps did at the five resolutions assessed. Correlations between species richness values estimated by either of the two procedures and the observed values from the WSCs increased with decreasing resolution. The slopes of the regressions between the predicted and observed values indicate that MaxEnt overpredicts observed species richness at all of the resolutions used, while range maps underpredict them, except at the finest resolution. Prediction errors did not vary significantly between methods at any resolution and tended to decrease with decreasing resolution. The accuracy of both procedures was clearly different when commission and omission errors were examined separately.

Main conclusions Despite the congruent increase in the geographic richness patterns obtained from both procedures as resolution decreases, the maps created with these methods cannot be used interchangeably because of notable differences in the species compositions they report.

Keywords

Amphibians, MaxEnt, Mexico, range maps, spatial scale, species distribution models, species richness patterns.

*Correspondence: Eduardo Pineda, Red de Biología y Conservación de Vertebrados, Instituto de Ecología, AC Apartado Postal 63, Xalapa 91000, Veracruz, Mexico.
E-mail: eduardo.pineda@inecol.edu.mx

INTRODUCTION

Studies of the geographic distribution of species diversity on a broad scale are essential tasks in ecology, macroecology and biogeography. However, it is not easy to assess biodiversity pat-

terns in regions where collecting efforts are limited, particularly where biodiversity is high (Soberón, 1999). Given the incomplete information about species geographic distributions, two main approaches are used to generate hypotheses on the spatial distribution of species diversity: range maps and species

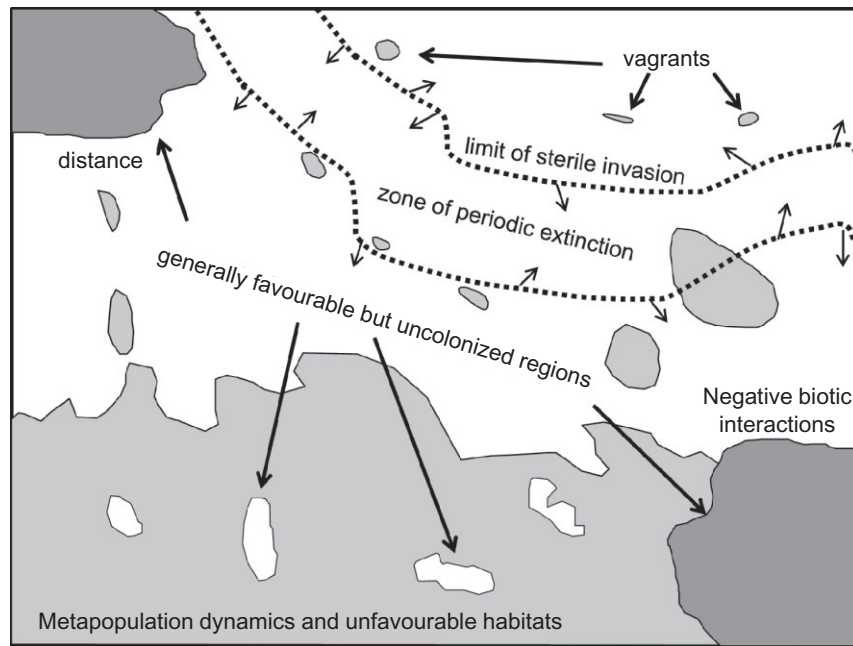


Figure 1 Schematic representation of the distribution of a species modified from Gorodkov (1986a,b) and Gaston (2003). Light grey areas represent the sites where the species is present and darker areas are regions that are environmentally favourable but uninhabited owing to dispersal limitations or biological interactions. The occupied area may include inhabited sites both under suitable and unsuitable environmental conditions, and the unoccupied area may include environmentally suitable sites. Expert maps tend to exclude these unoccupied but suitable sites as well as those beyond the line of periodic extinction. Generally, species distribution models are unable to predict the environmentally favourable but unoccupied sites because their accurate prediction requires reliable information about species absence and predictors that are able to account for the effects of these limiting factors (Lobo *et al.*, 2010). See Jiménez-Valverde *et al.* (2011) for an explanation of the relation between this distribution representation and niche concept.

distribution models (SDMs). Overlaying species range maps has been the traditional and most commonly used approach (McPherson & Jetz, 2007; Hawkins *et al.*, 2008; Hortal, 2008). A range map represents the extent of occurrence of the species, and is defined as ‘the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy’ (IUCN, 2001).

Commonly, range maps are drawn by experts who use the original records as their source of information as well as their own knowledge to establish the boundaries, shape and size of a species’ distribution (Gaston, 1996; Brown & Lomolino, 1998). Geographic representations generated by this procedure generally overestimate real occupancy (Graham & Hijmans, 2006; Jetz *et al.*, 2008) since they fill the internal unoccupied areas in the species’ distribution area that might be caused by unfavourable habitat conditions or the metapopulation dynamics of the species itself (Pulliam, 2000; see Fig. 1). At the lowest resolution, each of the individuals of a species occupies a unique site at the same time so the distributions of presence–absence or abundance are interchangeable. Tracking the location of these individuals over time would produce a geographic representation of which of the gaps within the distribution area would diminish over time. Thus, range maps can be considered spatial approximations of an unachievable reality that are highly dependent on the spatial and temporal scale being used; representations that

mainly delimit the approximate location of the known distribution without considering the habitat, demographic or the biotic factors responsible for the occurrence of a species within the area favourable for their distribution (see Fig. 1).

SDMs are being applied increasingly to generate predictions about the geographic distribution of species using the available species presence information and environmental variables as predictors (Franklin, 2009). As reliable absence information is frequently lacking, modellers primarily make use of the available easy-to-use techniques that, like MaxEnt, have been recommended in comparative studies (Elith *et al.*, 2006) and only require information on species presence. Although we recognize that without absence data it is impossible to know if the predictions represent the realized distribution area (Jiménez-Valverde *et al.*, 2008, 2011), we apply this modelling technique in order to show the reliability of the predictions obtained with it and compare them with those obtained using classical range maps. Several authors have indicated that the conclusions of studies based on species richness values, both to estimate spatial distribution and the relationship between distribution and different variables, may depend on the type of data and the resolution used for the analysis (Hurlbert & White, 2005; Graham & Hijmans, 2006; Hurlbert & Jetz, 2007; McPherson & Jetz, 2007). However, the evaluation of species richness maps generated by different methods is hindered by our lack of knowledge about the real distribution of species (Graham & Hijmans, 2006). In

order to address this, we examine the relative performance of range maps drawn by experts and SDM maps at different resolutions by assessing the concordance between predicted species richness and composition against observed real values previously obtained for each resolution.

METHODS

Range maps

We obtained digital range maps for 363 of the 370 amphibian species native to Mexico from the Global Amphibian Assessment database (IUCN *et al.*, 2006). The range maps for the other seven species (*Craugastor galacticorhinus*, *Eleutherodactylus planirostris*, *Incilius campbelli*, *Plectrohyla miahuatlanensis*, *Ptychohyla macrotympanum*, *Pseudoeurycea orchileucos* and *Pseudoeurycea orchimelas*) were digitized using information from Mendelson (1997), Duellman (2001), Brodie *et al.* (2002), Canseco-Márquez & Smith (2004), Meik *et al.* (2006) and Frost (2008). All 370 vector format maps were converted to raster format using a resolution of 0.083° (i.e. grid cells of 5' or c. 10 × 10 km) with the IDRISI Kilimanjaro GIS software (Clark Labs Idrisi Kilimanjaro, 2004), and subsequently overlapped to generate a representation of the distribution of species richness in Mexico (24,997 grid cells).

Species distribution models

We obtained georeferenced data for the 370 amphibian species from three different databases: the National Commission of Biodiversity (CONABIO, see Appendix S1 in Supporting Information for the sources of the data), HerpNet (<http://www.herpnet.org>) and GBIF (<http://www.gbif.org>). The data set was taxonomically standardized following Frost (2008) and the records for each species double-checked using spreadsheets and GIS to detect duplicates, possible errors in georeferencing and in species nomenclature. The final version of this database comprised 66,113 presence-only records.

Individual SDMs were built for each of the native amphibian species of Mexico with MaxEnt, a machine learning method that uses environmental variables to predict habitat suitability for a particular species by assessing different combinations of variables and their interactions (see Phillips *et al.*, 2006, Phillips & Dudík, 2008, and Elith *et al.*, 2011, for a detailed explanation of the method). MaxEnt was selected for its apparent comparatively high performance relative to other modelling methods (Elith *et al.*, 2006) and because this technique is now almost considered a standard procedure. SDMs for 348 of the 370 species were generated using the default options in MaxEnt software version 2.3 (Phillips *et al.*, 2006) by relating observed presence data to the 19 bioclimatic variables obtained from the WorldClim database version 1.3 (Hijmans *et al.*, 2005). The resolution of the climate layers and the species data was the same as that used for the range maps (0.083° grid cells). The remaining 22 species were not modelled using MaxEnt because, being microendemics, they occurred in only one grid cell. We assumed

that these species are only present in the cells where they were recorded and mapped them manually as such. The 370 maps were subsequently exported to obtain a matrix of suitability values for each species in every one of the 24,997 cells that cover the whole of Mexico. Cumulative output values are used to estimate the relative suitability for each species of each grid cell. As suitability values range from 0 to 100, it is necessary to set a threshold for converting each of the continuous species maps into binary ones (presence/absence) to then be able to overlap all the individual models and derive a representation of species richness. We used 21 thresholds from 1 to 100 at intervals of five to obtain the respective presence–absence maps for each species. Thus, we assumed presence in the cells with suitability scores equal to or greater than 1, 5, 10, . . . , 95, 100. After overlapping all the individual models according to the threshold used, we obtained 21 possible scenarios of modelled species richness distributions (see Pineda & Lobo, 2009, for a detailed explanation of the method). From these, we selected the one whose values were best correlated with those of the 118 well-surveyed cells (WSCs; see below) of the c. 100 km² previously identified using species accumulation curves and nonparametric estimators (Colwell & Coddington, 1994) applied to all of the occurrence data obtained from all data sources (CONABIO, HerpNet and GBIF; see below).

Data analysis

A modelling-then-aggregating procedure was applied in order to take advantage of the species data at the best available resolution. Species richness and composition data for each 0.083° grid cell were rescaled to coarser resolutions of 0.25°, 0.5°, 1° and 2° by aggregating 9, 36, 144 and 576 contiguous grid cells: 3021 cells cover the whole country at a resolution of 0.25°, 785 cells at a resolution of 0.5°, 218 grid cells at 1° and 67 cells at 2°, resulting in amphibian data for five different resolutions (from 0.083° to 2°) in grid cells of approximately 100 km² to 40,000 km². A species was considered to be present in the grid cell of a coarser resolution if it was present in any of its constituent cells.

We assessed the relative accuracy of the species richness representations obtained from range maps and SDMs by comparing their predictions with the observed values for WSCs estimated at each of the five resolutions. The WSCs were identified using three different yet complementary methods (Colwell & Coddington, 1994): (1) nonparametric estimators based on the number of rare species (Chao 2 and Jackknife 1); (2) the final slope of the accumulation function describing the cumulative rise in the number of species as the sampling effort increases (Hortal & Lobo, 2005); and (3) the number of species predicted at the 95% upper confidence interval of the accumulation curves produced with the Mao Tau analytical function (Mao *et al.*, 2005). Mao Tau, Chao 2 and Jackknife 1 species richness estimates were obtained with ESTIMATES 7.5 (Colwell, 2005). For these three estimates, the number of database records was used as a surrogate for sampling effort (Hortal & Lobo, 2005; Lobo, 2008). We considered a cell to be well surveyed if it had both a completeness value (the ratio of the observed number of species

to the 'true' number of species) higher than 75% and a final slope of less than 0.1 (see Hortal & Lobo, 2005). Completeness was calculated by relating the maximum species richness value predicted by any of the three estimators (considered the 'true' number of species) to observed richness (observed/predicted $\times 100$). These calculations indicated that 118 grid cells can be considered as well surveyed at a resolution of 0.083° , 28 cells at 0.25° , 23 at 0.5° , 23 cells at 1° and 17 grid cells at a resolution of 2° (see Appendix S2).

The species richness values obtained from range maps and SDMs were correlated (using the Spearman rank correlation coefficient) with observed richness values for the grid cells identified as well surveyed at each of the five resolutions. Additionally, the slopes and the intercepts of the regressions between the predicted and observed values were used to estimate how well each method performed. Finally, we also measured the prediction error ($|\text{observed} - \text{predicted}| / \text{observed} \times 100$), as well as the number of omission and commission errors.

RESULTS

At all five resolutions the species richness representations derived from MaxEnt have a more contrasting pattern across the country than those generated with range maps (Fig. 2). Low numbers of species characterized most of the northern region of the country and richness tended to increase in the south-east in the mountainous regions. Values of variance for species richness obtained from MaxEnt were always higher than those derived from range maps (Table 1). Furthermore, the mean species richness per cell derived from MaxEnt was significantly lower when the resolution was finest (0.083°), similar to values obtained with range maps at a resolution of 0.25° , but significantly higher at the coarsest resolutions analyzed (0.5° , 1° and 2°) (Table 1).

Correlations between the species richness values estimated with MaxEnt or range maps and the observed species richness values from WSCs increased with decreasing resolution (Fig. 3). Spearman rank correlation values between species richness derived from MaxEnt and observed species richness increased from 0.873 at a resolution of 0.083° to 0.966 at 2° . Correlation values between observed and derived species richness from range maps increased from 0.696 at a resolution of 0.083° to 0.969 at 2° (Fig. 3). From resolutions of 0.5° to 2° , correlations between estimated and observed species richness values were high and similar for both methods, while at the finest resolutions (0.083° and 0.25°) correlations were higher for species richness values derived from MaxEnt (Fig. 3).

The slopes of the linear regressions between the predicted species richness values and observed species richness in WSCs differed between the two methods (the ANCOVA results were always statistically significant; $P < 0.001$), and were constantly lower for species richness derived from MaxEnt (Fig. 3). At all resolutions the slopes of the relationship between the richness predicted by MaxEnt and the observed richness were significantly lower than unity (slope value $\pm 95\%$ confidence interval: $0.083^\circ = 0.777 \pm 0.084$; $0.25^\circ = 0.790 \pm 0.144$; $0.5^\circ = 0.632 \pm 0.137$; $1^\circ = 0.680 \pm 0.093$; $2^\circ = 0.750 \pm 0.069$) indicating that the

MaxEnt results tend to overpredict species richness in the cells that are richest in species (Fig. 3). In contrast, the slopes between estimated species richness from range maps and observed values increased with the resolution used from a value not statistically different from unity (1.015 ± 0.217) at the 0.083° resolution to values that were significantly higher than unity at the other resolutions ($0.25^\circ = 1.480 \pm 0.330$; $0.5^\circ = 1.741 \pm 0.176$; $1^\circ = 1.444 \pm 0.214$; $2^\circ = 1.278 \pm 0.103$). This shows that this method underpredicts the species richness of the richest cells at most of the resolutions. The intercepts of these linear regressions (a measure of the capacity to accurately predict species-poor cells) are only significantly different from zero for range map predictions at 0.5° and 1° (-11.833 ± 6.391 and -6.947 ± 5.751), showing that the richness of poor cells is generally underpredicted at coarse resolutions (Fig. 3).

Prediction errors did not vary significantly between MaxEnt and range map predictions at any resolution, but tended to decrease with decreasing resolution (Table 1). MaxEnt prediction errors vary from $34 \pm 6\%$ (mean $\pm 95\%$ confidence interval) at a resolution of 0.083 to $19 \pm 10\%$ at 2° , while range map prediction errors ranged from $43 \pm 8\%$ at the finest resolution to $19 \pm 10\%$ at the coarsest resolution (Table 1). However, the accuracy of the two procedures is clearly different when we consider the errors of commission and omission separately. MaxEnt predictions produce omission errors that are relatively constant and moderately low across all resolutions (between 16% and 19%) with regards to range maps, although the difference between the two methods decreases at the coarsest resolutions (Table 1). Commission errors did not differ statistically between the methods at intermediate resolutions (0.25° , 0.5° and 1°), but MaxEnt produces significantly fewer commission errors than range maps do at the finest resolution (0.083°) and significantly more at the coarsest resolution (2° ; see Table 1).

DISCUSSION

Species richness predictions derived from MaxEnt seem to provide geographic representations where the differences between species-rich and species-poor regions are better illustrated than those derived from range maps (see also McPherson & Jetz, 2007). Other studies have revealed that species richness predictions based on SDMs generally produce higher species richness values than those based on range maps (Graham & Hijmans, 2006). Our study corroborates those findings, and shows that while MaxEnt always overpredicts the species richness of rich cells, it also provides relatively accurate values for species-poor cells. In contrast, range maps provide significantly lower local species richness values than MaxEnt does at all of the resolutions used, underpredicting richness for both the richest cells and also the poor ones at coarse resolutions. Thus, the uninterrupted distribution areas derived from range maps and the concomitant increase in local species richness at finer resolutions (Hurlbert & White, 2005; Hurlbert & Jetz, 2007) may provide more accurate predictions in the richest localities than SDMs do. However, when cell size increases and resolution decreases, the species richness values derived from the overlay of

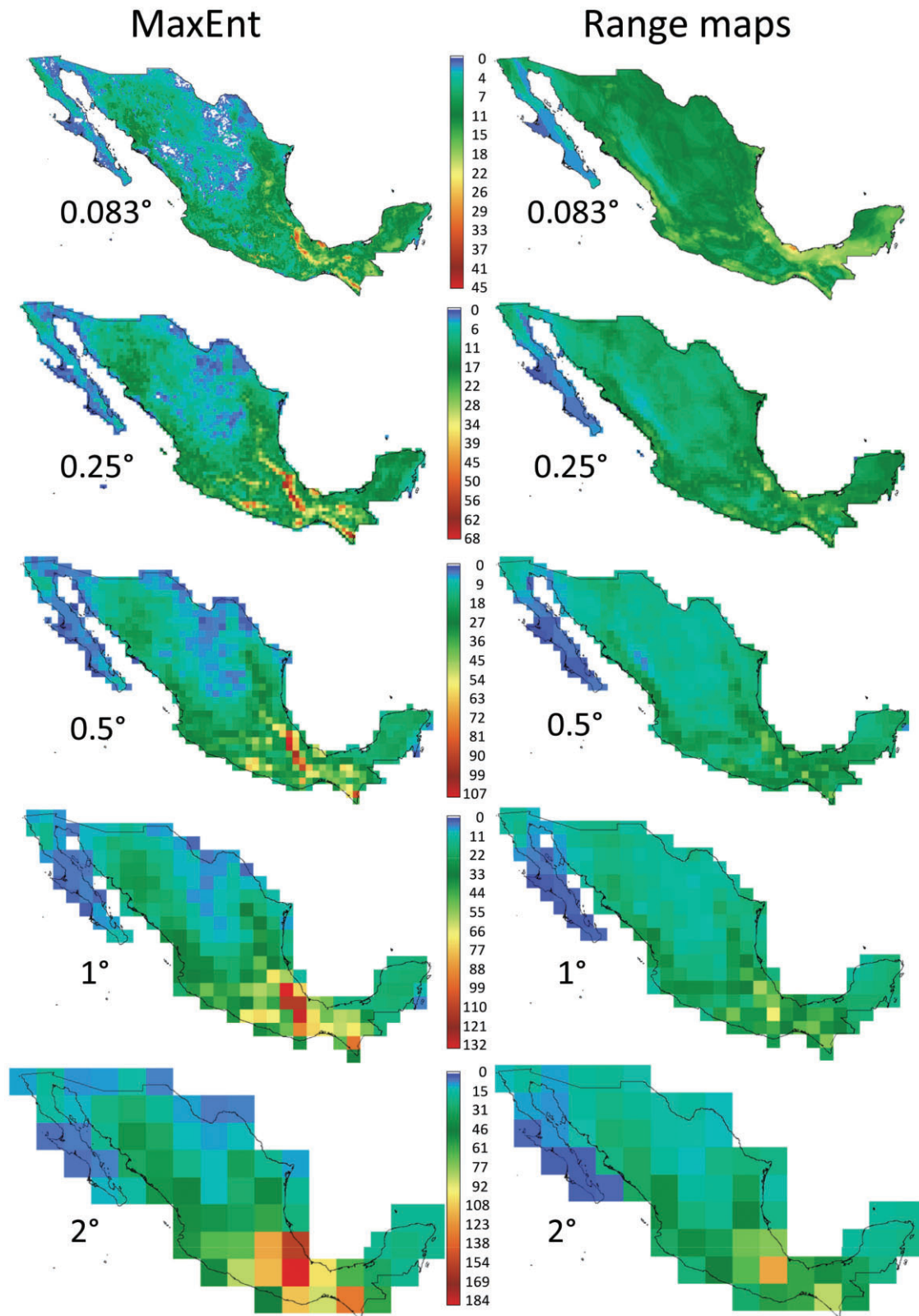


Figure 2 Spatial patterns of amphibian species richness in Mexico at five different spatial resolutions resulting from the overlay of individual MaxEnt predictions (left) or range maps drawn by experts (right).

Table 1 Mean predicted species richness, variance, mean prediction error, mean omission and commission errors ($\pm 95\%$ confidence interval) for MaxEnt (species distribution models) and range maps for amphibian species in Mexico at five different spatial resolutions. As prediction errors follow a negative exponential function, confidence intervals for mean values were calculated according to the recommendations of Zar (1999). Mean richness and variance were calculated using data from all Mexican cells. Prediction errors were calculated as $(|\text{observed} - \text{predicted}|)/\text{observed} \times 100$, with observed species richness values obtained from previously identified well-surveyed grid cells (WSCs).

Resolution	WSCs	Mean richness	Variance	Prediction error	Omission error	Commission error
MaxEnt						
0.083°	118	6.2 \pm 0.1	23.7	34.0 \pm 6.2	17.1 \pm 3.1	46.4 \pm 8.5
0.25°	28	10.8 \pm 0.3	77.2	28.6 \pm 11.3	16.6 \pm 6.6	38.0 \pm 15.0
0.5°	23	15.9 \pm 0.9	194.6	27.2 \pm 12.1	19.2 \pm 8.5	42.7 \pm 18.9
1°	23	24.1 \pm 3.0	505.8	25.5 \pm 11.3	15.7 \pm 7.0	40.1 \pm 17.8
2°	17	37.1 \pm 9.0	1398.7	18.9 \pm 10.1	18.0 \pm 9.5	34.3 \pm 18.2
Range maps						
0.083°	118	10.3 \pm 0.1	16.0	42.8 \pm 7.9	45.9 \pm 8.4	70.6 \pm 12.9
0.25°	28	11.5 \pm 0.2	25.5	28.4 \pm 11.2	37.5 \pm 14.8	40.5 \pm 16.0
0.5°	23	13.8 \pm 0.5	47.5	19.1 \pm 8.5	34.7 \pm 15.4	31.6 \pm 14.0
1°	23	18.3 \pm 1.5	125.0	19.0 \pm 8.4	27.5 \pm 12.2	24.1 \pm 10.7
2°	17	26.6 \pm 5.1	427.5	19.3 \pm 10.3	29.8 \pm 15.8	11.8 \pm 6.3

individual species distribution models are considerably greater while those derived from range maps are significantly lower: at a resolution of 2° the mean species richness in the cells is almost a 40% higher than when range maps are used. This leads us to ask, what are the real capacities of these two different methods for estimating species richness patterns at different resolutions?

The main novelty of our approach lies in our examination of the relative performance of these two methods for identifying species richness patterns against the biological information for a set of cells with reliable inventories. In the context of the species richness information for these WSCs, the accuracy of the two methods seems to change as resolution decreases. At the finer resolutions, the predictions of MaxEnt are superior, prediction errors are low in species rich cells and negligible in species poor cells. When cell size is large, the species richness predictions made by the two methods are equally correlated with the observed values, and have similar levels of prediction errors. However, MaxEnt clearly overpredicts the species richest cells at all the resolutions used in this study and the key characteristic of range map predictions at coarse resolutions is that species richness is underpredicted for both the richest and the poorest cells. Supplementary information on the relative performance of these two methods is revealed when the composition in these WSCs is taken into account (Table 1). MaxEnt incorrectly predicts 16–19% of presences of a cell as absences, regardless of the resolution, while under the best circumstances range map predictions erroneously define as absences almost 30% of cell presences. However, although MaxEnt predictions seem to be more accurate at the finest resolution, they also seem to produce an elevated rate of commission error (Table 1). The predictions of range maps are more accurate at the coarsest resolution we analysed because, on average, the rate of commission error is only 12%, while the rate of omission error is 29%. It is important to mention that our ‘observed’ values are generated from

inventories that are not necessarily 100% complete. A portion of the commission errors detected could therefore result from this, suggesting that false presences derived from both approaches could in reality be slightly lower (see Pineda & Lobo, 2009, for a description of the spatial structure of these errors).

Overpredictions and errors of commission seem to be characteristic of SDMs (Stockwell & Peterson, 2002; Brotons *et al.*, 2004; Stockman *et al.*, 2006). Previous studies indicate that MaxEnt output models clearly overpredict species richness and change species composition (Graham & Hijmans, 2006; Pineda & Lobo, 2009; Aranda & Lobo, 2011). In our opinion, this drawback may be extended to any modelling technique in which predictions are based on presence-only data and climate predictors. Both the type of distribution data used and the predictors or modelling technique have a notable effect on the capacity of representing the potential or the realized distribution of species (Soberón & Peterson, 2005; Chefaoui & Lobo, 2008; Jiménez-Valverde *et al.*, 2008; Lobo *et al.*, 2008; Lobo *et al.*, 2010). The potential distribution of a species (i.e. the places that are environmentally suitable to maintain its populations) can be considered a geographic projection of the niche conditions, but this niche cannot be derived from the occupied area because realized distributions may not be able to capture the species’ entire environmental potential (Jiménez-Valverde *et al.*, 2011) due to the role played by biotic interactions and dispersal limitations. For the realized distribution, obtaining reliable estimates requires the incorporation of explanatory variables capable of representing the factors that constrain the potential distribution of species, along with reliable absence data well distributed across the spatial and environmental gradient of the territory being studied in order to represent the effects of these non-environmental or limiting factors (see Lobo *et al.*, 2010, and references therein). In the specific case of amphibians, the prediction of the realized distributions should take into account

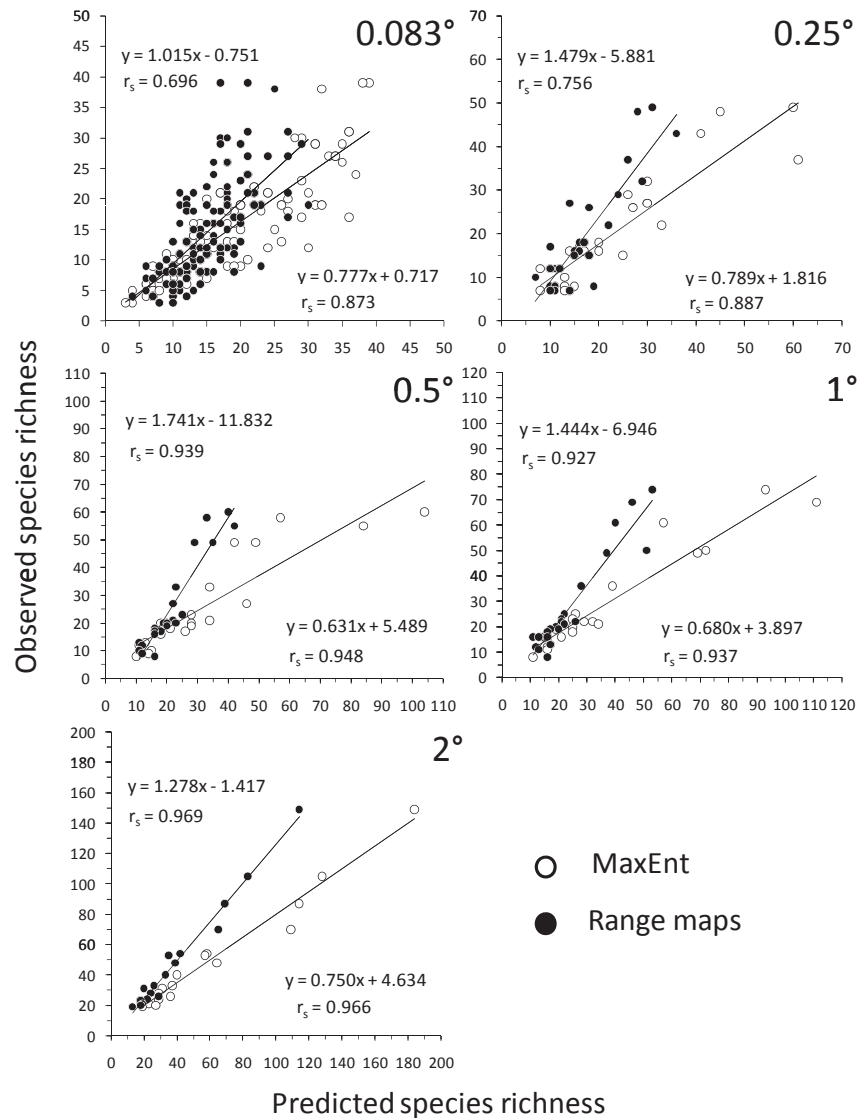


Figure 3 Relationship between observed species richness in well-surveyed cells and predicted species richness based on the overlay of individual MaxEnt species distribution models (open circles) and range maps drawn by experts (black circles) at five different spatial resolutions. Solid lines represent the linear regression; the values of the Spearman rank correlation (r_s) are given, as are the linear regression equations derived from MaxEnt (right) and range maps (left).

differences in their dispersal ability as well as historical and geographic factors – factors that could exclude a species from a climatically suitable locality, and thus minimize or even eliminate commission errors (Pulliam, 2000; Soberón & Peterson, 2005). Thus, MaxEnt predictions may not be able to provide accurate species richness maps at any resolution (Pineda & Lobo, 2009; Aranda & Lobo, 2011). Our results demonstrate that the rate of error in predicting species composition in each cell may be so great as to invalidate the usefulness of the resulting representation (see Pineda & Lobo, 2009). Confidence in these methods should be based on a careful examination – both taxonomic and spatial – of model errors. Previous results show that any particular set of species is consistently poorly predicted since around 50% of all the species seem to be erroneously included or excluded in a quarter of the cells in which they have been recorded (Pineda & Lobo, 2009; Aranda & Lobo, 2011). Furthermore, these same studies highlight the spatial and environmental structure of these prediction errors, because they are partially dependent on certain conditions and locations (see also

Hortal *et al.*, 2008). A procedure of trimming each species distribution model in consultation with experts before overlaying predicted distributions as performed by Flores-Villela and Ochoa-Ochoa in Koleff *et al.* (2008), though subjective, could reduce the occurrence of errors. Fortunately, there is a strong correlation between the observed and predicted values. Thus, although the composition of each cell is highly biased, the general picture of species richness produced seems to be relatively satisfactory. This interesting result suggests that this kind of model output should be used with caution but that, at least in this case, the picture of relative species richness provided by the sum of these individual models can be trusted.

At coarser resolutions, neither the range maps nor MaxEnt seem to offer reliable results. Although there appears to be less contrast between range map predictions, species richness maps derived from MaxEnt clearly overpredict the richest zones, while the range maps underpredict them, which coincides with findings in McPherson & Jetz (2007). MaxEnt estimated around 180 species, while range maps estimated 110 species in a cell at a 2°

resolution that is known to contain 149 amphibian species (with 87% of inventory completeness). The overprediction of the MaxEnt results seems to be related to the high commission error produced by this method; many absent species would be erroneously considered as present in the richest zones and this distorts the true species richness pattern and the relationships of species with environmental variables (see McPherson & Jetz, 2007).

Paradoxically, the overestimation of the area of occupancy by range maps (Hurlbert & White, 2005; Hurlbert & Jetz, 2007; Jetz *et al.*, 2008) is capable of providing relatively accurate predictions in our case. This overestimation may depend on the method used to delineate species range limits (Habib *et al.*, 2003), but commonly the extent of occurrence is larger than the true area of occupancy and the porosity of the ranges (areas within range not occupied by the species) is not drawn (Hurlbert & White, 2005). At coarser resolutions range map predictions always underestimate the species richness of the richest cells. For range maps this underprediction is expected to be related to the large number of omission errors generated by this procedure at coarser resolutions. Some species are erroneously considered to be absent, probably because range maps tend to not only eliminate the presence of vagrants but also to draw strict and tight distribution limits. As Graham & Hijmans (2006) state, expert maps probably do not exactly delineate historical species ranges; they exclude climatically suitable areas that are currently uninhabited owing to land use or habitat characteristics. They found a large number of distribution records outside the range maps drawn by experts for 112 of the 128 herptile species that occur in California. We detected point occurrences outside the range maps for 317 of the 370 amphibian species that occur in Mexico, a proportion similar (86%) to that reported by Graham & Hijmans (2006). Furthermore, the median proportion of occurrences outside the range maps was 38%, with a greater proportion of occurrences outside of the range maps for species with restricted ranges (frequently distributed in mountainous Neotropical environments). If range maps exclude a significant proportion of occurrences and are then overlapped, we would expect species richness to be underestimated by the models that are produced using this method. Frequently, range maps are created to provide an overview of the whole extent of species distributions, rather than accurate portraits. The problem arises when they are used for a purpose other than that for which they were created (Hortal, 2008) and without taking into account the appropriate resolution for the analysis. Additionally, in regions where sampling effort is insufficient, range maps may be less accurate because the data quality is lower than it is in better explored regions. In the latter, the cell at which the map is more accurate decreases in size, as Hurlbert & Jetz (2007) found for birds in southern Africa and Australia. These authors reported that at resolutions of less than 2° range maps overestimate the area of occupancy of individual species and mischaracterize geographic patterns of species richness. For herptiles and mammals in Europe, Hawkins *et al.* (2008) found that at a resolution of 100 km (*c.* 1°) richness estimates based on range maps seem to be robust.

The results obtained are affected by the procedure used to select the threshold to convert the continuous values of favourability variables into binary ones, but this threshold cannot be selected when the data only incorporate partial information on species presences but no information on species absences. In our approach we selected 21 uniform thresholds for all the species included, but previous results show that the selection of individual thresholds aimed at minimizing omission errors (Pineda & Lobo, 2009) or at guaranteeing that all presences are predicted as suitable (Aranda & Lobo, 2011) is not capable of providing better species richness representations. In fact, the threshold cannot be adequately selected unless there is a reliable estimate of the prevalence of the species (Jiménez-Valverde & Lobo, 2007). To be successful, any prediction requires a reliable sample capable of representing, as well as possible, the full spectrum of conditions of the variable under consideration. For species distribution, such a sample would inevitably provide information on presence and absence, and thus an estimate of species prevalence. Thus, the fact that it is impossible to select the most appropriate threshold for each species is the consequence of producing species distributions predictions without reliable information.

Our results also show that although there is increasing congruence between richness patterns created with MaxEnt and those derived from range maps with decreasing spatial resolution, the maps created with such methods cannot be used interchangeably because the production of false positives and false negatives differs notably at all the spatial resolutions we studied. Inferences based on the analysis of a richness pattern created using either method could differ, leading to confusion in ecological or biogeographical studies. Although the maps derived from both methods at the coarsest scale have the same average prediction error, one tends to overpredict richness and the other one to underpredict it. This seems to be related to the proportion of omission and commission errors generated by each method. Thus, the decision to use one approach or the other to estimate patterns of species diversity should be made based on the advantages and disadvantages of each method and the purpose of the study. A high number of commission errors in an estimated species diversity pattern leads to inflated species richness values per site or cell, and this overprediction is inevitably expected to cause an increase in the nestedness and a decrease in the turnover components (*sensu* Baselga, 2010) of compositional differences between local assemblages (see Hurlbert & White, 2005; Graham & Hijmans, 2006; Hurlbert & Jetz, 2007). On the other hand, a high number of omission errors would lead to underestimation of species richness at the site or cell level, and would increase turnover and decrease the nestedness components of beta diversity values. Further studies are needed to examine the relationships between commission and omission errors and the compositional differences that result from using SDMs and range maps.

Our results suggest that neither of the two methods provides accurate results that are free from error. The selection of one approach or the other, as well as the spatial resolution for estimating species diversity patterns, will depend on the scope of

the study, and should always take into account that species richness patterns must be evaluated before using them in order to identify the measure of error or uncertainty associated with the method.

ACKNOWLEDGEMENTS

Julián Bueno helped georeference database records, Pablo Sastre helped with GIS management and Joaquín Hortal provided valuable suggestions. B. Delfosse revised the English. CONACYT-SEMARNAT (project 23588) provided financial support. E. Pineda thanks the AECl for a post-doctoral grant. Two anonymous referees provided helpful suggestions on the manuscript.

REFERENCES

- Aranda, S.C. & Lobo, J.M. (2011) How well does presence-only-based species distribution modelling predict assemblage diversity? A case study of the Tenerife flora. *Ecography*, **34**, 31–38.
- Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.
- Brodie, E.D., Jr, Mendelson, J.R., III & Campbell, J.A. (2002) Taxonomic revision of the Mexican plethodontid salamanders of the genus *Lineatriton*, with the description of two new species. *Herpetologica*, **58**, 194–204.
- Brotons, L., Thuiller, W., Araújo, M.B. & Hirzel, A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, **27**, 437–448.
- Brown, J. & Lomolino, M.V. (1998) *Biogeography*. Sinauer Associates, Sunderland, MA.
- Canseco-Márquez, L. & Smith, E.N. (2004) A diminutive species of *Eleutherodactylus* (Anura: Leptodactylidae), of the *Alfredi* group, from the Sierra Negra of Puebla, Mexico. *Herpetologica*, **60**, 358–363.
- Chefaoui, R. & Lobo, J.M. (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling*, **210**, 478–486.
- Clark Labs Idrisi Kilimanjaro (2004) *The Idrisi Project*. Worcester, MA, USA.
- Colwell, R.K. (2005) *ESTIMATES: statistical estimation of species richness and shared species from samples*. Version 7.5. Available at: <http://viceroy.eeb.uconn.edu/estimates>.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **345**, 101–118.
- Duellman, W.E. (2001) *The hyliid frogs of Middle America*, 2 vols. Society for the Study of Amphibians and Reptiles and the Natural History Museum of the University of Kansas, Lawrence, KS.
- Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distribution from occurrence data. *Ecography*, **29**, 129–151.
- Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43–57.
- Franklin, J. (2009) *Mapping species distributions: spatial inference and prediction*. Cambridge University Press, Cambridge, UK.
- Frost, D.R. (2008) *Amphibian species of the world: an online reference*. Version 5.2. American Museum of Natural History, New York. Available at: <http://research.amnh.org/herpetology/amphibia/index.php>.
- Gaston, K.J. (1996) Species-range-size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution*, **11**, 197–201.
- Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.
- Gorodkov, K.B. (1986a) Three-dimensional climatic model of potential range and some of its characteristics I. *Entomological Review*, **65**, 1–18.
- Gorodkov, K.B. (1986b) Three-dimensional climatic model of potential range and some of its characteristics II. *Entomological Review*, **65**, 19–35.
- Graham, C.H. & Hijmans, R.J. (2006) A comparison of methods for mapping species ranges and species richness. *Global Ecology and Biogeography*, **15**, 578–587.
- Habib, L.D., Wiersma, Y.F. & Nudds, T.D. (2003) Effects or errors in range maps on estimates of historical species richness of mammals in Canadian national parks. *Journal of Biogeography*, **30**, 375–380.
- Hawkins, B., Rueda, M. & Rodríguez, M.A. (2008) What do range maps and surveys tell us about diversity patterns? *Folia Geobotanica*, **43**, 345–355.
- Hijmans, R.J., Cameron, S. & Parra, J. (2005) *WORLDCLIM version 1.3*. Available at: <http://www.worldclim.org>.
- Hortal, J. (2008) Uncertainty and the measurement of terrestrial biodiversity gradients. *Journal of Biogeography*, **35**, 1335–1336.
- Hortal, J. & Lobo, J.M. (2005) An ED-based protocol for optimal sampling of biodiversity. *Biodiversity and Conservation*, **14**, 2913–2947.
- Hortal, J., Jiménez-Valverde, A., Gómez, J.F., Lobo, J.M. & Baselga, A. (2008) Historical bias in biodiversity inventories affects the observed realized niche of the species. *Oikos*, **117**, 847–858.
- Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences USA*, **104**, 13384–13389.
- Hurlbert, A.H. & White, E.P. (2005) Disparity between range map- and survey-based analyses or species richness: patterns, processes and implications. *Ecology Letters*, **8**, 319–327.
- IUCN (2001) *IUCN Red List categories and criteria: version 3.1*. IUCN, Gland, Switzerland and Cambridge, UK.
- IUCN, Conservation International & NatureServe (2006) *Global amphibian assessment*, version 1.1. <http://www.globalamphibians.org>.
- Jetz, W., Sekercioglu, C.H. & Watson, J.E.M. (2008) Ecological correlates and conservation implications of overestimating species geographic ranges. *Conservation Biology*, **22**, 110–119.

- Jiménez-Valverde, A. & Lobo, J.M. (2007) Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica*, **31**, 361–369.
- Jiménez-Valverde, A., Lobo, J.M. & Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions*, **14**, 885–890.
- Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P. & Lobo, J. (2011) Use of niche models in invasive risk assessments. *Biological Invasions*, **13**, 2785–2795.
- Koleff, P., Soberón, J., Arita, H.T., Dávila, P., Flores-Villela, O., Golubov, J., Halffter, G., Lira-Noriega, A., Moreno, C.E., Moreno, E., Munguía, M., Munguía, M., Navarro-Sigüenza, A.G., Téllez, O., Ochoa-Ochoa, L., Townsend-Peterson, A. & Rodríguez, P. (2008) Patrones de diversidad espacial en grupos selectos de especies. *Capital natural de México, Vol. 1: Conocimiento actual de la biodiversidad* (ed. by J. Soberón, G. Halffter and J. Llorente-Bousquets), pp. 323–364. CONABIO, México.
- Lobo, J.M. (2008) More complex distribution models or more representative data? *Biodiversity Informatics*, **5**, 15–19.
- Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, **17**, 145–151.
- Lobo, J.M., Jiménez-Valverde, A. & Hortal, J. (2010) The uncertain nature of absences and their importance in species distribution modelling. *Ecography*, **33**, 103–114.
- McPherson, J.M. & Jetz, W. (2007) Type and spatial structure of distribution data and the perceived determinants of geographical gradients in ecology: the species richness of African birds. *Global Ecology and Biogeography*, **16**, 657–667.
- Mao, C.X., Colwell, R.K. & Chang, J. (2005) Estimating the species accumulation curve using mixtures. *Biometrics*, **61**, 433–441.
- Meik, M.M., Smith, E.N., Canseco-Márquez, L. & Campbell, J.A. (2006) New species of the *Plectrohyla bistincta* group (Hylidae: Hylinae: Hylini) from Oaxaca, Mexico. *Journal of Herpetology*, **40**, 304–309.
- Mendelson, J.R., III (1997) A new species of *Bufo* (Anura: Bufonidae) from the Pacific Highlands of Guatemala and southern Mexico, with comments on the status of *Bufo valli-ceps macrocristatus*. *Herpetologica*, **53**, 14–30.
- Phillips, S.J. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and comprehensive evaluation. *Ecography*, **31**, 161–175.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Pineda, E. & Lobo, J.M. (2009) Assessing the accuracy of species distribution models to predict amphibian species richness patterns. *Journal of Animal Ecology*, **78**, 182–190.
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- Soberón, J. (1999) Linking biodiversity information sources. *Trends in Ecology and Evolution*, **14**, 291.
- Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1–10.
- Stockman, A.K., Beamer, D.A. & Bond, J.E. (2006) An evaluation of a GARP model as an approach to predicting the spatial distribution of non-vagile invertebrate species. *Diversity and Distributions*, **12**, 81–89.
- Stockwell, D.R.B. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling*, **148**, 1–13.
- Zar, J.H. (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Englewood Cliffs, NJ.

SUPPORTING INFORMATION

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

Appendix S1 Original sources of the data provided by CONABIO.

Appendix S2 Location of amphibian well-surveyed cells in Mexico at five spatial resolutions.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

Eduardo Pineda is interested in the ecology and conservation of amphibians, as well as the study of spatial patterns of biodiversity at different scales.

Jorge M. Lobo is interested in the description of biogeographical patterns and the study of the probable processes that have given rise to them, as well as in the management of biodiversity information and conservation biology.

Editor: Katrin Böhning-Gaese