Deriving the Species Richness Distribution of Geotrupinae (Coleoptera: Scarabaeoidea) in Mexico From the Overlap of Individual Model Predictions

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ABSTRACT Predictions from individual distribution models for Mexican Geotrupinae species were overlaid to obtain a total species richness map for this group. A database (GEOMEX) that compiles available information from the literature and from several entomological collections was used. A Maximum Entropy method (MaxEnt) was applied to estimate the distribution of each species, taking into account 19 climatic variables as predictors. For each species, suitability values ranging from 0 to 100 were calculated for each grid cell on the map, and 21 different thresholds were used to convert these continuous suitability values into binary ones (presence-absence). By summing all of the individual binary maps, we generated a species richness prediction for each of the considered thresholds. The number of species and faunal composition thus predicted for each Mexican state were subsequently compared with those observed in a preselected set of well-surveyed states. Our results indicate that the sum of individual predictions tends to overestimate species richness but that the selection of an appropriate threshold can reduce this bias. Even under the most optimistic prediction threshold, the mean species richness error is 61% of the observed species richness, with commission errors being significantly more common than omission errors (71 ± 29 versus $18 \pm 10\%$). The estimated distribution of Geotrupinae species richness in Mexico in discussed, although our conclusions are preliminary and contingent on the scarce and probably biased available data.

KEY WORDS Geotrupinae, Mexico, species richness distribution, predictive distribution models

Species richness is frequently correlated with other measures of ecological, morphological, phylogenetic, and functional diversity (Gaston 1996). It provides a useful measure of biodiversity, and the study of its distribution and causes has been among the principal aims of ecology almost since the foundation of the discipline (Ricklefs 2004). Unfortunately, accurate descriptions of species richness patterns for hyperdiverse groups, such as insects, mainly depend on the sampling effort of collectors. Distributional data for such groups are often incomplete and biased (Whittaker et al. 2005).

Recently, several modeling methods have been proposed to overcome gaps in species distributional information (Guisan and Zimmermann 2000, Elith et al. 2006, Tsoar et al. 2007). However, the individual species predictions provided by such methods are difficult to validate (Lobo et al. 2008), and it is necessary to define a priori whether the distribution to be modeled represents the potential or the realized niche. Distribution models that approximate the potential distribution (all of the environmentally suitable locations in which a species could occur according to a set of environmental variables; see Soberón and Peterson 2005, Peterson 2007) can be obtained without the necessity of using absence data or of extracting pseudo-absence data from environmentally unsuitable locations (Chefaoui and Lobo 2008, Jiménez-Valverde et al. 2008). In contrast, the estimation of realized distributions requires the use of absence data from environmentally favorable locations to account for historically or geographically contingent factors (Lobo 2008). Thus, the difficulty of discriminating the causes of species absence hinders the reliability of predictions based on distribution models for obtaining accurate geographical representations of actual species distributions.

When many individual distribution models are overlaid to obtain a species richness pattern, the bias in these predictions can be inflated (Hortal and Lobo 2006). As in other studies (Cumming 2000, Ortega-Huerta and Peterson 2004, Domínguez-Domínguez et al. 2006, García 2006), we here overlay predictions derived from individual distribution models that use only presence data (a "modeling-then-classification" procedure; see Ferrier 2002 and Ferrier et al. 2002).

Because the accuracy of these individual models cannot be evaluated because of the lack of reliable

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absence data, the resulting species richness values and community compositions are validated by comparison to those obtained for Mexican states previously defined as well surveyed by using a nonparametric estimator (Colwell and Coddington 1995). To perform these comparisons, we use an exhaustive database of the distribution of Geotrupinae species in Mexico, applying a well-known presence-only modeling technique to estimate the distribution of each species. The spatial distributions of the model errors obtained for both species richness and species composition were subsequently explored, and the results were used to partially correct the overprediction of the models.

Materials and Methods

Study Area. Mexico is bordered by the United States on the north and by Guatemala and Belize on the southeast, and it has a continental area of 1,972,550 km^2. Mexico has great climatic diversity. The nation may be roughly divided into tropical and temperate areas, separated by the Tropic of Cancer. However, the uneven topography and the presence of two oceans (Atlantic and Pacific) greatly influence the climatic configuration of the country. Thus, it is possible to find high, cold mountains within a few kilometers of the warmest climates in the coastal plains. Mexico is considered to be a transitional area between the Nearctic and Neotropical regions (Williams-Linera et al. 1992). This fact, together with its high environmental diversity, makes the Mexican flora and fauna exceptionally rich and diverse in origins (Halffter 1987).

Biological Data. We developed a database compiling information available in the literature and in several unpublished studies (bachelor's, master's, and doctoral theses). The studies of Howden (1955, 1964, 1974, 2003, 2005), Halffter and Martínez (1962), and Gómez and López-Rojas (2004) were especially important. Information from the Instituto de Ecología A.C. (Xalapa, Veracruz, Mexico) and from private entomological collections (G. and V. Halffter, E. Montes de Oca, F. Vaz de Mello, M.A. Morón H.F. and A. Howden, I. Martínez, L. Arellano) was also included.

The database, named GEOMEX (Trotta-Moreu et al. 2008), currently contains 1,191 records, corresponding to the 45 Mexican Geotrupinae species (classification *sensu* Howden 2003; Table 1). Although the higher-level taxonomy and internal phylogenetic relationships of this group are not yet well established (Howden 1982; Zunino 1984; Browne and Scholtz 1995, 1999), the whole species catalog can be considered reliable. GEOMEX incorporates information in 24 data fields, which include information about the taxonomy, geographic location, date, ecological/biological characteristics, and origin of all database records. After georeferencing the localities at which each species was recorded (http://geonames.usgs.gov/gnishome.html) at a 0.08° resolution (making 25,080 grid cells across Mexico), we built distribution maps for each Geotrupinae species (Trotta-Moreu et

Table 1. Number of database records (N° DR), area (in km^2), and no. of 0.08° grid cells in which each species was observed (N° OC) for each Mexican state

State	N° DR	Area	N°OC	Data origin	Year range
Veracruz	241	71,699	79	B, C	1955–2006
México	126	21,355	51	B, C	1931–2006
Durango	122	123,451	44	B, C	1905–2006
Oaxaca	92	93,952	44	B, C	1937–2006
Jalisco	80	78,599	43	B, C	1903–2003
Michoacán de Ocampo	67	59,928	31	B, C	1947–2005
Chiapas	61	73,289	31	B, C	1939–2003
Morelos	51	4,950	19	B, C	1947–1988
Sonora	41	185,052	14	B, C	1939–1998
Guerrero	37	63,621	15	B, C	1937–1994
Sinaloa	37	58,328	13	B, C	1917–1997
Nayarit	33	27,815	17	B, C	1937–1997
Puebla	33	33,902	18	B, C	1901–2006
Distrito Federal	30	1,479	13	B, C	1939–2003
Nuevo León	27	64,924	8	B, C	1942–2006
Baja California Sur	21	73,922	19	B, C	1938–1997
Hidalgo	19	20,813	13	B, C	1960–2002
Chihuahua	18	247,938	16	B, C	1934–2005
Coahuila	10	150,615	3	B	1938–1971
Colima	9	5,191	4	B	1918–1993
San Luis Potosí	9	63,068	4	B, C	1954–1983
Baja California Norte	7	69,921	2	B, C	1938–1973
Guanajuato	6	30,491	4	B, C	1954–1962
Tamaulipas	4	79,384	3	B	1969–1983
Yucatán	3	38,402	2	B, C	1937–1995
Zacatecas	3	73,252	2	B, C	1983–1989
Campeche	2	57,924	2	B	1983
Querétaro	1	11,499	1	B	1957
Tabasco	1	25,267	1	B	1969
Aguascalientes	0	5,471	0	—	—
Quintana Roo	0	50,844	0	—	—
Tlaxcala	0	4,016	0	—	—

Data origin indicates whether the data came from the literature (B) or from natural history collections (C). The year ranges of the database records are also shown.

al. 2008) using the Idrisi Kilimanjaro program (Clark Labs 2003).

Environmental Variables. Nineteen climatic variables from the WorldClim database were used as predictors in the modeling process (Hijmans et al. 2006): mean annual temperature, mean daily temperature range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual temperature range, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter.

Model Building. A maximum entropy approach (MaxEnt) was used to estimate the potential distribution of each species in Mexico (Phillips et al. 2004, 2006). This machine-learning approach is considered to be one of the best techniques requiring presence-only data (Elith et al. 2006). MaxEnt tries to find the

closest distribution that agrees (under maximum entropy) with the available biological information and the selected environmental variables. Recommended default parameter values were used in all model runs (Phillips et al. 2006), but only linear and quadratic terms were included to obtain flexible curvilinear responses to the response variable. The MaxEnt output for each grid cell is the sum of the probability value of that cell and of all other cells with equal or lower probability. These values are multiplied by a factor of 100, producing a continuous variable that varies from 0 to 100 and that measures the relative suitability for each species. All models were run using Maximum Entropy Species Distribution Modeling v. 2.3 software (for free download, see http://www.cs.princeton.edu/~schapire/maxent/). For the six species with only one known locality [*Geotrupes* (*Onthotrupes*) *lobatus*, *Bolbocerosoma mexicanus*, *Bolborhombus nitidus*, *Bolbelasmus horni*, *Bolbelasmus bajaensis*, and *Eucanthus impressus*], the potential distribution was estimated by a 30% enlargement of the environmental values of the cell in which each species was observed. This procedure allowed us to slightly enlarge the known distribution of these rare species, encompassing other localities that are environmentally similar to those in which the species occur.

Geotrupes (*Haplogeotrupes*) *reddelli* (Howden), a narrowly distributed cave species that specializes in the consumption of bat dung, was not considered (Halffter and Deloya 2007).

Statistical Analysis. Overlaying the individual suitability values to obtain a species richness map inevitably requires transforming the continuous predicted values into presence-absence data. Therefore, we selected 21 decision thresholds, evenly spaced across the range from 0 to 100. These thresholds were used to derive presence-absence maps for each species, recognizing as a "presence" each cell with a suitability score $\geq 1, 5, \ldots, 95,$ or 100. The accuracy of the model predictions generated using each of these thresholds was determined by comparing the observed species richness in previously defined well-surveyed states against the total number of species predicted for those states when individual models were overlapped.

The number of database records was used as a surrogate for the sampling effort carried out in each Mexican state (Hortal et al. 2007), and the Chao2 nonparametric species richness estimator was calculated (Colwell 2005) for each Mexican state. Chao2 is an efficient (Walther and Moore 2005) nonparametric estimator based on incidence. In our case, it takes into consideration only the number of species with a unique database record (U_{DR}) and the number of species with two database records (T_{DR}), applying the following formula: $S_{CHAO2} = S_{obs} + (U_{DR}^2/2T_{DR})$, where S_{CHAO2} is the estimated richness and S_{obs} is the observed number of species in each state (Colwell and Coddington 1995).

The species richness values predicted by Chao2 for each state were used to estimate the survey completeness of each state ($S_{obs}/S_{CHAO2} \times 100$). Those states with completeness values > 75% ($n = 17$; Table 2)

Table 2. Area (in km^2), no. of Geotrupinae species observed (S_{OBS}), species richness errors (S_{ERROR}), and percentage of commission and omission errors over the observed no. of species (%$_{COM}$ and %$_{OMI}$, respectively) in the 17 well-surveyed states

States	Area	S_{OBS}	S_{ERROR}	%$_{COM}$	%$_{OMI}$
Baja California Sur	73,922	3	7	233.3	0.0
Chiapas	73,289	7	4	57.1	0.0
Coahuila	150,615	5	1	80.0	60.0
Durango	123,451	10	−2	10.0	30.0
Guerrero	63,621	11	8	81.8	9.1
Jalisco	78,599	11	0	27.3	27.3
México	21,355	5	8	140.0	0.0
México D.F.	1,479	4	3	75.0	0.0
Michoacan	59,928	10	4	60.0	20.0
Morelos	4,950	10	3	20.0	10.0
Nayarit	27,815	5	4	100.0	20.0
Nuevo León	64,924	9	0	22.2	22.2
Oaxaca	93,952	15	8	66.7	6.7
Puebla	33,902	10	14	140.0	0.0
Sinaloa	58,328	8	−3	25.0	62.5
Sonora	185,052	7	1	42.9	28.6
Veracruz	71,699	14	2	21.4	7.1

Errors were estimated by comparing the observed species in each state against the predicted ones generated by the application of individual distribution models in which a threshold suitability value of 75 was used to transform continuous suitability values into binary (presence/absence) predictions.

were considered to be well surveyed, and they were selected to compare their observed species richness against the species richness values derived from the overlaying of individual distribution models (S_{PDM}). The Pearson product moment correlation coefficient was used in these comparisons. To obtain the predicted species richness for each state, a species was considered to occur in a state if it was present in at least one cell within that state.

Because states with similar observed and predicted species richness can differ in their species composition, Mantel tests were also applied (Sokal 1979). These tests measure the correlation (R) between two distance or similarity matrices. Significance testing is based on the Monte Carlo permutational method to overcome the problem of lack of independence between site pairs. First, the Jaccard index was calculated among the observed assemblages in each state and the 21 predicted assemblages obtained under the various thresholds. PAST v. 1.68 software was used for these computations (Hammer et al. 2001). The threshold that generated the highest correlations in both species richness and composition values was selected as the best representation of Geotrupinae species richness distribution in Mexico. To provide an error measure for the map thus generated, we examined the errors in both species richness (differences between predicted and observed species richness values) and species composition (differences in composition between predicted and observed state inventories) for each well-surveyed state. False positives (commission errors) and false negatives (omission errors) were estimated for each state to assess the real magnitude of prediction errors according to the observed number of species.
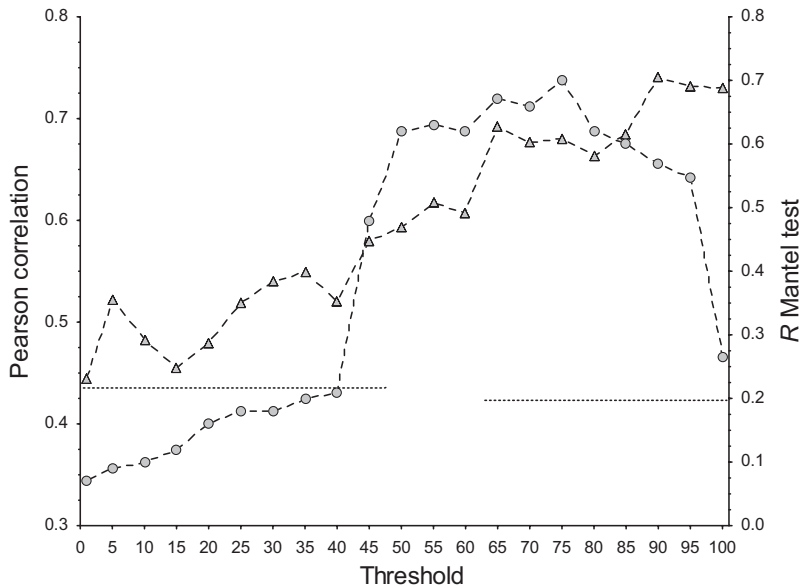
Fig. 1. Pearson correlation coefficients (triangles) and Mantel correlations (R) measuring the compositional similarity (circles) between the observed Geotrupinae species richness and composition values in the 17 well-surveyed Mexican states and those predicted by the overlaying of individual model predictions at different suitability thresholds. Dashed lines represent limits of statistically significant ($P \leq 0.05$) values for both tests.

Results

Comparison Between Observed and Predicted Values. The correlations between S_{OBS} and S_{PDM} species richness values for the 17 well-surveyed states are statistically significant for all of the thresholds used to convert the continuous suitability values for each species into presence-absence data (Fig. 1). The mean correlation is 0.60 (95% confidence interval between 0.55 and 0.64), with higher correlation values when the selected threshold is >65 (i.e., when the threshold is more restrictive). However, the results of the Mantel tests showed that all correlation values are statistically significant above a threshold of 40 (mean = 0.39; 95% confidence interval between 0.29 and 0.50). The optimum compositional correlation value was found at a threshold of 75 ($R = 0.70$; $P < 0.0001$). Because Pearson correlation values for species richness are also high at this threshold ($r = 0.68$; $P < 0.001$), it was chosen as the most appropriate to represent the variation in Geotrupinae species richness in Mexico.

Examination of Model Errors. Once this optimum threshold was selected, the errors produced by this model prediction (Table 2) were analyzed. The mean species richness error is 61% of the observed species richness in each state (95% confidence interval between 29 and 94%). Except in Durango and Sinaloa, the inventory of each state is frequently overestimated. Commission errors are significantly higher than omission errors (71 ± 29 versus 18 ± 10%; 95% confidence intervals). The states with the greatest percentage of errors are Baja California Sur, México, and Puebla, with overestimations of 233, 160, and 140% of the observed species, respectively.

Considering each species separately (Table 3), omission errors vary from 0 to 38% of cells in which the species were observed (mean = 5.8%). The lack of reliable absence information prevents us from calculating the rate of commission errors for individual species. However, for the well-surveyed states, we calculated the number of predicted presence cells in those states in which the species has not been recorded. The percentage of such cells against the total number of predicted presence cells was used as a measure of commission errors. This percentage varies from 0 to 80% depending on the species (mean = 12%; Table 3).

Discussion

In this study, the individual model predictions for each species of an insect group in a large and heterogeneous region (Mexico) were overlaid to generate a geographical representation of the distribution of species richness. This method is able to exploit the scarce and biased information available for most insect groups. The main advantage of the procedure is the ability to provide an error measure based on information from a priori well-surveyed territories. Of course, as frequently happens with insects, the available geographical data are fragmentary and probably biased (Soberón and Peterson 2004); however, this situation will not change in the near future unless a huge sampling effort is carried out. Geographical representations of species richness obtained using this procedure should be considered provisional, because they depend on the quality of the observation dataset used to

Table 3. List of Mexican Geotrupinae species, showing the no. of database records for each species (N° DR), the no. of 0.08° grid cells in which each species was observed (N° OC), the area of the predicted distribution (in km²), and the no. of cells in which the species was erroneously predicted to be absent (omission errors; OE) or present (commission errors; CE)

Species	N° DR	N°OC	Area	OE	CE
Geotrupes (Megatrupes) cavicollis	90	31	17,101	0 (0%)	0 (0%)
G. (Megatrupes) fisheri	24	14	7,275	0 (0%)	4 (6%)
G. (Onthotrupes) lobatus	1	1	247	—	—
G. (Onthotrupes) sobrinus	9	4	5,526	1 (25%)	38 (69%)
G. (Onthotrupes) herbeus	40	16	4,684	3 (19%)	0 (0%)
G. (Onthotrupes) viridiobscurus	22	7	3,352	0 (0%)	2 (6%)
G. (Onthotrupes) truncaticornis	8	2	1,388	0 (0%)	2 (14%)
G. (Onthotrupes) sallei	25	15	15,116	1 (7%)	18 (12%)
G. (Onthotrupes) nebularum	32	18	4,847	2 (11%)	0 (0%)
G. (Onthotrupes) guerreroensis	12	4	3,843	0 (0%)	4 (10%)
G. (Onthotrupes) pecki	5	4	5,254	0 (0%)	21 (40%)
G. (Onthotrupes) onitidipes	6	2	1,900	0 (0%)	0 (0%)
G. (Geohowdenius) cnephosus	8	7	10,115	0 (0%)	0 (0%)
G. (Halffterius) rufoclavatus	162	25	4,778	2 (8%)	2 (4%)
G. (Haplogeotrupes) guatemalensis	18	3	903	0 (0%)	0 (0%)
Ceratotrupes fronticornis	182	77	18,695	8 (10%)	12 (6%)
Ceratotrupes sturmi	11	5	12,278	0 (0%)	13 (11%)
Ceratotrupes bolivari	123	63	34,050	7 (11%)	9 (3%)
Bolbocerosoma ritcheri	5	3	3,161	0 (0%)	0 (0%)
Bolbocerosoma pusillum	5	3	55,916	0 (0%)	46 (8%)
Bolbocerosoma confusum	2	2	5,094	0 (0%)	0 (0%)
Bolbocerosoma mexicanus	1	1	2,871	—	—
Bolborhombus sallei	52	30	90,678	1 (3%)	14 (2%)
Bolborhombus magnus	4	3	300,228	0 (0%)	2406 (80%)
Bolborhombus parvulus	10	9	12,292	1 (11%)	9 (7%)
Bolborhombus nitidus	3	1	405	—	—
Bolbocerastes regalis	3	3	5,579	0 (0%)	0 (0%)
Bolbocerastes serratus	15	8	93,137	3 (38%)	0 (0%)
Bolbocerastes imperialis	5	4	181,998	1 (25%)	444 (24%)
Bolbocerastes peninsularis	14	10	11,905	0 (0%)	3 (3%)
Bolbelasmus arcuantus	45	28	31,473	2 (7%)	7 (2%)
Bolbelasmus horni	1	1	885	—	—
Bolbelasmus rotundipennis	7	6	229,363	1 (17%)	1489 (65%)
Bolbelasmus variabilis	86	55	37,462	3 (5%)	4 (1%)
Bolbelasmus bajaensis	2	1	1,133	—	—
Eucanthus mexicanus	17	13	61,671	0 (0%)	106 (17%)
Eucanthus impressus	1	1	6,007	—	—
Neoathyreus excavatus	17	15	68,316	0 (0%)	219 (32%)
Neoathyreus fissicornis	44	20	11,907	3 (15%)	0 (0%)
Neoathyreus granulicollis	32	20	38,477	2 (10%)	50 (13%)
Neoathyreus hamifer	5	2	815	0 (0%)	0 (0%)
Neoathyreus interruptus	18	14	47,164	0 (0%)	7 (2%)
Neoathyreus mexicanus	13	11	79,477	0 (0%)	5 (1%)
Neoathyreus mixtus	6	5	164,100	0 (0%)	149 (9%)

The percentage of omission errors (in parens) was calculated based on the total no. of cells in which the species was observed, whereas the percentage of commission errors was estimated based on the no. of erroneously included cells within the 17 well-surveyed states.

evaluate the model predictions. However, in contrast to other species richness representations generated by overlaying species distribution models (Cumming 2000, Ortega-Huerta and Peterson 2004, Domínguez-Domínguez et al. 2006, García 2006), our method provides an error measure that will decrease in future iterations as more data become available that are better distributed across the spectrum of environmental and spatial conditions present in Mexico.

Despite selecting the most appropriate threshold to convert continuous suitability values into binary presence-absence predictions, our method overestimates observed species richness values in a high percentage of well-surveyed states (61%). This overestimation is generally caused by the erroneous inclusion of species that are not currently known to inhabit the state in question. The averaged errors of individual species predictions are lower, but this should be interpreted with caution because it is almost impossible to evaluate a species model without reliable information on the locations in which the species is absent.

Despite these drawbacks, our method should be considered the first attempt to provide a species richness distribution map for an insect group over a large territory with many taxonomic and distributional deficiencies. According to the species richness map that we obtained (Fig. 2), almost 53% of the territory of Mexico is inhabited by at least one Geotrupinae species, 44% is inhabited by one or two species, and only 0.4% (~8,200 km²) is predicted to have five or more Geotrupinae species within a 0.08° cell. These species-rich areas are located in the mountain zones of the states of Guerrero, Oaxaca, and Veracruz.

Fig. 2. Estimated distribution of Geotrupinae species richness in Mexico at a 0.08° resolution, produced by overlaying all individual species models generated by MaxEnt. The representation shown used a suitability value of 75 as the threshold to convert continuous suitability values into binary ones (presence/absence). This threshold produced higher correlations of species richness and composition with the data from previously identified well-surveyed states. White areas represent absence of Geotrupinae species.

From a methodological point of view, our study highlights four important conclusions. First, this type of modeling approach generally overestimates species' distributions. Second, the overlaying of individual models does not produce an accurate picture of the distribution of species richness. Third, the selection of an appropriate suitability threshold can reduce the occurrence of species richness and compositional errors. Finally, the combined use of nonparametric estimators and individual models permits estimation of the accuracy of such predictions.

Predictive models of distribution tend to overestimate species' distributions, mainly because of their inability to incorporate absences caused by historical factors, dispersal limitation, or other biotic factors (Pulliam 1988, 2000; Ricklefs and Schluter 1993; Hanski 1998). Several authors have recognized that overprediction of species' distributions is a common shortcoming of this kind of model, particularly when limited distribution localities are used (Fielding and Haworth 1995; Araújo and Williams 2000, Stockwell and Peterson 2002, Brotons et al. 2004, Segurado and Araújo 2004, Stockman et al. 2006).

The overlaying of many individual predictions to build a representation of species richness across a territory may produce an even more unreliable representation of reality by increasing the error level in regions affected by nonenvironmental restrictions (Hortal and Lobo 2006). To partially correct these overestimations, a suitability threshold can be selected that provides higher correlations between predicted and observed species richness and compositional values for territories previously recognized as well surveyed. In this study, the most appropriate threshold is high (~75), because of the high level of overprediction in each species model. The results of similar modeling studies (Pineda and Lobo 2009) suggest different suitability threshold values depending on the taxonomic group and, probably, on the extent and characteristics of the target region.

Our method combines the use of inventory completeness measures as nonparametric estimators and distribution modeling techniques. The main advantage of this procedure is that it can provide a measure of uncertainty that can be used to show the spatial distribution of the model errors. Any model prediction must incorporate a reasonable measure of its accuracy (Fielding and Bell 1997); this is a scientific requirement to sequentially improve our knowledge of the dynamic distribution patterns of organisms.

Acknowledgments

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